BEHAVIOUR AND ECOLOGY OF TWO NEOTROPICAL PRESOCIAL SAWFLIES, *DIELOCERUS DIASI* SMITH AND *THEMOS OLFERSII* (KLUG) (HYMENOPTERA, SYMPHYTA, ARGIDAE)

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In accordance with the regulations of the University of Edinburgh, I hereby declare that this thesis has been composed entirely by myself and that all the work described herein was carried out by myself alone, except where stated in the Acknowledgements.

This thesis is dedicated to
my father, Dr. Domiciano P.S. Dias,
for introducing me to the study of
nature's most important and fascinating
living beings - the insects, and for his
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ABSTRACT

Both sawflies were studied in natural Cerrado communities around Brasília, Central Brazil. Both are apparently monophagous, D. diasi on Sclerolobium aureum (Leguminosae) and T. olfersii on Eriotheca pubescens (Bombacaceae). T. olfersii has 2 generations per year. Its active adults, eggs and feeding larvae are confined to the rainy season. Its prepupae enter in diapause in the dry season, probably as an adaptation against fire, apparently induced by decreasing daylength and terminated by increase in soil moisture. D. diasi has 4 generations per year, all life stages being present throughout the year. In the laboratory, half of its larvae spinning their cocoons during the early dry season entered in prolonged diapause. Both species have female-biased secondary (and apparently also primary) sex ratio. Male D. diasi wait for their sisters to emerge and attempt to copulate with them. W. D. Hamilton's models of Local Mate Competition and Outbreeding Viscous Population are used to explain their sex ratios. Females are choosy in selecting the oviposition site. Their egg clusters are aggregated into a few of the available hosts, but spaced inside each host. It is argued that the presence of one or more females in a host attracts others to the same plant. They apparently utilize visual and sonorous stimuli to locate their hosts. D. diasi females spend about 24 hours on their chosen leaflet before laying their eggs, displaying with wing-buzzing and walking in circles and zigzags. This is interpreted as a type of egg-site territorial behaviour. Both species are semelparous, laying their eggs in just one leaflet. D. diasi lays about 76 eggs spread throughout the leaflet in individual pockets, but T. olfersii lays only about 27 upright eggs tightly clustered into a small circle on the leaflet's surface. It is suggested that this difference in fertility is due to T. olfersii's commitment to produce a larger first instar larva in response to the greater thickness and toughness of its host's leaflets. Eggs and young larvae are guarded by their non-feeding long-lived mothers. T. olfersii sits astride over her egg cluster and newly-born larvae, while D. diasi stays at the leaflet's base facing the petiole and occasionally walks and sits over her eggs. As the larvae start to feed, T. olfersii females move to the base of the leaflet and D. diasi females move to the middle of the rachis and then to the base of the compound leaf. Both females react to several visual, tactile and sonorous stimuli with varied defensive and threatening behaviours: 18 different displays are described for *T. olfersii* and 11 for *D. diasi*, involving changes in body position, orientation and posture, and much use of wings and mandibles. The females, however, are unable to protect the eggs against the parasitoid wasp *Chrysocharis* sp (Eulophidae). It is argued that maternal care in these and other sawflies evolved as a protection to the eggs and young larvae against predators. So far, 18 species of sawflies in 10 genera are known in which the post-reproductive female remains beside her brood apparently to protect it. *D. diasi* females are brightly coloured, distasteful or repellent to predators and remain attached to their host after death. It is suggested that prereproductive females are better protected against some predators when selecting hosts which already have other females. The larvae of both are highly gregarious throughout the feeding stage and exhibit some coordination for feeding, moving and defence, and in *D. diasi* also for spinning their cocoons. Larvae feed in queues, one or two per leaflet along its edges, having cyclic alternation of positions in the feeding edge and waiting queue at the rear of the feeding queue. *T. olfersii* cocoons are spun singly in the top soil, while *D. diasi* cocoons are grouped into honeycomb-shaped masses covered by a thick communal envelope of silk and spun against the host's bark. Single and male *D. diasi* larvae fail to spin the complete outer envelope around their cocoons. Larval morphology, growth and sex ratio and cocoon spatial distribution are described. Heaviest mortality is in the larval stage, caused in *D. diasi* mainly by *Spathimeigenia dieloceri* (Tachinidae), *Lymeon dieloceri* (Ichneumonidae), desiccation and fungus; and in *T. olfersii* by lacewing larva (Chrysopidae) and fungus. Egg mortality is much lower averaging 25% in both species and is unevenly distributed among the clusters, and is caused mainly by *Chrysocharis* sp (in both), lacewing larva (in *T. olfersii*) and leaflet fall (in *D. diasi*). Conspecific larvae cause minor egg mortality in both species. A summary of the hostplants of Argid sawflies is given with several new additions. Several topics of sawfly biology are reviewed, specially for tropical and sub-tropical sawflies.

CHAPTER 1. INTRODUCTION

1.1 PRESOCIAL BEHAVIOUR IN INSECTS

Given the present widespread interest (both of field workers and theoreticians) on the evolution, ecology and behaviour of social animals, specially on vertebrates and the so called eusocial insects (ants, termites, social bees and social wasps) (e.g. Alexander, 1974; Crook, 1970; Eisenberg & Dillon, 1971; Herman, 1979; West-Eberhard, 1975; E.O. Wilson, 1971 & 1975), it is surprising to realize how little we know about social traits, as parental care and larval gregariousness, in non-eusocial insects, despite the commonness of these phenomena. Eickwort (in press) will be the only modern review available on the scattered literature for the whole class of insects, although a number of more restricted reviews exist: e.g. Iwata (1972) on parental care in Hymenoptera; Lengerken (1954) on parental care in Coleoptera; Lamb (1976) on parental care in Dermaptera; Bequaert (1935), Hussey (1934) and Odhiambo (1960) on parental care in Hemiptera; Allee (1931) on gregariousness; O'Byrne (1937) and Iwao (1968) on gregariousness in Lepidoptera; Uvarov (1966 and 1977) on gregariousness in grasshoppers; Chauvin & Noirot (1968) on group effect; and Peters & Barbosa (1977) on crowding effects.

What are the ecological factors which are responsible for the evolution of behaviours such as parental care and larval gregariousness? How important is kin selection in the establishing of gregariousness among cohorts of insects derived from the same egg cluster? Why is the occurrence of these social traits so common and at the same time so inconstant among the species of so many families of insects? What are the advantages of being social as against solitary, and how do insects establish a compromise between these advantages and the obvious disadvantages of decreased fertility, higher intraspecific competition, greater conspicuousness favoring predator search for prey, facilitation of disease spread, and danger of inbreeding?

Parental care has been shown to increase survival of eggs and larvae by protecting them against generalized predators and parasites, fungi and desiccation and by avoiding the dispersal of larvae and directly or indirectly providing food for the young larvae (see Bequaert, 1935; Bongers, 1968; Chondhuri & Bagh, 1974; Eberhard, 1975; Faure, 1940; Frost & Haber, 1944; Hallfter, Hallfter &

Lopez, 1974; Hinton, 1944 & 1977; Hussey, 1934; Iwata, 1972; Lamb, 1976; Lengerken, 1954; Liechti & Bell, 1975; Melber & Schmidt, 1975a & b; Milne & Milne, 1976; Mockford, 1957; Odhiambo, 1959 & 1960; Scott, 1929; R.L. Smith, 1976a & b; Sturm, 1960; Tachikawa, 1971; West & Alexander, 1963; Wood, 1974, 1975, 1976a & b). But in some cases specialized parasitoids have evolved to bypass the parental defences (Eberhard, 1975). Unfortunately we know little of the reproductive costs and benefits of such behaviour in different environmental situations. Just how effective is such behaviour? Is the evolution of parental care reversible?

It has been asked repeatedly why some of these presocial insects have not taken the final step to eusociality (E.O. Wilson, 1971). Perhaps the answer lies in the absence of nest and of parental control of food supply (see Knerer & Atwood, 1973 and Knerer, 1974) and/or male haploidy (see E.O. Wilson, 1971 and Crozier, 1979). However other factors might have an important role too. Probably most presocial insects will never evolve toward eusociality because they lack important preadaptations, and should therefore not be viewed as "primitive" or intermediate social insects, but rather as equally specialized and adapted as the eusocial species, in a different way.

We still know very little about just how common parental care is among non eusocial insects and there is certainly a need for more data. It looks, though, that parental care is more frequent among tropical insects than in temperate ones, which agrees with theoretical expectations as most tropical species are K-strategists: species living in stable (constant and/or predictable) environments (e.g. tropics) where population size is nearly constant in time, at or near the carrying capacity of the environment (K), are subject to selective pressures that lead to slower development, longer life, larger body size, delayed and repeated reproduction, increased parental care, greater competitive ability and higher efficiency of utilization of environmental resources (Pianka, 1970).

Allee (1931) reviewed the different kinds of aggregations and classified them in seven types: (1) hibernating or aestivating groups, (2) overnight aggregations, (3) aggregations on food sources,

(4) aggregations on suitable but limited substrate, (5) aggregations in shelter places, (6) breeding aggregations, and (7) partial or complete family groups. I am only concerned here with the last type. Lindauer (1965) proposed another, more functional, classification of aggregations: (1) Uncoordinated grouping (uncoordinated activities; gathering determined by external factors and/or mutual attraction; the groups are temporal, facultative and open), (2) Simple coordinated grouping (as above but the group moves together), (3) Primitive communities (more extensive coordination of moving, building and defending; gathering determined by mutual attraction and reciprocal sensorial stimulation; the groups are frequently temporary, largely facultative and open), and (4) Communities of higher social order (most activities are collective, there is division of labor; gathering determined by strong mutual attraction and social attraction; the groups are facultatively permanent, obligatory and closed). Lindauer gave the following examples of the above categories: (1) Uncoordinated groupings: sleeping aggregations of bees, wasps, butterflies, etc.; hibernating aggregations of Coccinela and Ceratina; and feeding aggregations of bugs, aphids and cockroaches, and Neodiprion sawfly larvae; (2) Simple coordinated groupings: mating swarms of mosquitoes and mayflies, and army-like aggregations of armyworms (Sciara); and migrating swarms of Odonata, Orthoptera and Lepidoptera; (3) Primitive communities: larval groupings of sawflies and Lepidoptera; defensive aggregations of aposematically coloured and distasteful beetles and bugs; and communal nesting in wasps and bees; and (4) Communities of higher social order: ants, termites, social bees and social wasps. I shall only deal with the third type of grouping, the primitive communities.

Gregariousness is a common phenomenon among free living larvae of holometabolous insects feeding on leaves: most Lepidoptera, Tenthredinoid Sawflies and Chrysomeloid Beetles. These aggregations originate from larvae hatching from one single egg cluster laid by just one female in most cases, but in cases where several females lay their egg clusters simultaneously on the same host plant the different aggregations of sibs readily merge together when they meet by chance, producing large mixed aggregations. They are clearly open groups, whose members are evidently unable to recognize their sibs from other larvae of the same species. In some cases it has been shown that the larvae are even unable to distinguish their own species from closely related species with similar behaviour: mixed aggregations of larvae from two or three different species of different genera have been found among Australian Pergid sawflies of the genera Perga and Pergagrapta (Leask, 1944b; Carne, 1962). Individuals reared in aggregations exhibit more synchronized moulting, faster development and less laboratory mortality than do isolated individuals (Eickwort, in press; Lyons, 1962; Kalin & Knerer, 1977).

It has been shown for some Diprionid sawflies that gregariousness enhances the defensive displays and release of defensive liquids efficiency against predators and parasites (Prop, 1960; Tostowaryk, 1972). Tostowaryk found that in Neodiprion larval groups with more than 10 larvae, the advantages of gregariousness due to an increase in defensive behaviour through "group effort" more than compensated for the disadvantages of gregariousness due to the increase in their conspicuousness and thus decrease in the predators searching time. Prop also observed that gregariousness enhances vigilance against potential predators and parasites.

Gregariousness has also been shown to enable larvae to feed on leaves with thick epidermis, which most larvae in the group are unable to break through alone and join those few larvae which manage to do it, either to enable the larva to emerge from its egg inside the parenchyma as in Perga (Carne, 1962) or to enable the larva to start feeding as in Neodiprion (Ghent, 1960). Carne found the same phenomenon in mature larvae of Perga when trying to dig through the hard soil crust to pupate: only a few larvae managed to break through and all the other larvae followed them.

According to Eickwort (in press) at least two instances are known of cooperative construction of shelters that would be impossible for solitary individuals to build. One of them is the construction of the elaborate communal cover on top of the cocoon masses of Dielocerus which is described in this and in the following chapters.

Seymour (1974) also found that in Perga the gregariousness diminishes the loss of heat by convection, thus increasing the larval temperature in the sun and consequently increasing the digestive rhythm.

In some instances individual differences within the group in terms of moving and building leadership have been found (Wellington, 1957, on tent caterpillers; and Carne, 1962, on Perga). Differences in the proportions of leader larvae among larval groups is probably responsible for the great differences observed in building, moving, feeding, and survival rates between the groups (Wellington, 1957; Carne, 1962).

Isolated larvae become very restless until they rejoin the group, which is done utilizing either chemical, visual or sound cues (see for example, Meyer-Rochow, 1972; Fitzgerald, 1976). In many species the gregarious behaviour becomes non-adaptive in the later instars when the larvae are larger, require more food and space, and are better able to defend themselves (Eickwort, in press; Iwao, 1968).

Gregariousness also is usually associated with distastefulness and aposematic colouration (Fisher, 1930; Hamilton, 1964; Prop, 1960).

However, we still know very little about the group feeding behaviour of gregarious larvae apart from the work of Ghent (1960) on Neodiprion. Since most of the available accounts on gregarious behaviour of insect larvae are very short and superficial, and in view of the great variety and number of holometabolous insects with gregarious larvae, it is evident that there is still much to be done in order to better appreciate the function and evolution of larval gregariousness in insects.

Most researchers interested in insect sociality have focused their attention on the Aculeate Hymenoptera because this group has evolved eusociality several times independently, whereas eusociality has evolved only once (termites) among all the other insects. Also significant is that numerous species with intermediate forms of sociality are known in this group, which have provided important clues on how eusociality evolved by means of comparative studies (E.O. Wilson, 1971; Michener, 1974; Evans & Eberhard, 1970; Iwata, 1972). One of the preadaptations thought to be partially responsible for this is the haplo-diploid mechanism of reproduction, which is characteristic to this group of insects (Crozier, 1975, 1977 and 1979). Hamilton (1964 and 1972) was the first to point out that due to this reproductive system female wasps, bees and ants, in species where females are fertilized only once and have a female biased sex ratio, share 3/4 of their genes with their sisters but only 1/4 with their brothers and only 1/2 with their sons. These females would gain in inclusive fitness if they helped their mothers to produce more sisters rather than producing their own offsprings. This theory, Kin Selection, has opened a new era of research on animal sociality, and its literature has been increasing at a very high rate (see Clutton-Brock & Harvey, 1978; Williams, 1971; E.O. Wilson, 1975).

It would seem, therefore, highly profitable to have more information on social behaviour and ecology and reproductive strategy of insects belonging to the other two large divisions of the Hymenoptera: Parasitica and Symphyta. Hamilton (1967 and 1979) has in fact shown some very interesting phenomena (female biased sex ratio, inbreeding and male fighting and winglessness) in several groups of wasps of the Parasitica division (Chalcidoids, Scelionids and Bethylids).

Kin selection theory would predict larval gregariousness to be more common and more cooperative among sawflies than Lepidoptera and Coleoptera due to the asymmetry in female-male relationship produced by haplo-diploidy. Hamilton (1964) also predicted that the habit of laying eggs in batches should be correlated with monandrous insemination of females and larval gregariousness.

All these considerations were in mind when I chose two tropical presocial sawflies as the subjects of this study.

Following is a brief introduction to the biology of Tenthredinoid sawflies, a short review of the taxonomy of Argid sawflies and a detailed review of the few published information on the distribution and biology of _Themos olfersii_ and _Dielocerus diasi_ and closely related species.

1.2 THE BIOLOGY OF TENTHREDINOID SAWFLIES

Tenthredinoid sawflies form a relatively uniform, monophyletic, successful group of insects, with more than 5,000 species described from all over the world (Rasnitsyn, 1969; Koenigsmann, 1977). All share a basic life history: males emerge earlier than females; females emerge with all or most of their eggs mature; pairs copulate soon afterwards in a back to back fashion (because the male has his genitals twisted through 180 degrees - strophandry); females have toothed saw-like ovipositors with which they cut a slit in the host plant tissue, in which they lay an egg; eggs absorb water from the plant tissue and increase several times in volume; incubation takes about two weeks; larvae are eruciform having well developed biting mouthparts and thoracic legs, having a general caterpillar-like appearance, but differing from true caterpillars in having small antennae, a single lateral eye and weak abdominal prolegs. They have a narrower range of foodplants than most Lepidoptera - most sawflies are oligophagous or monophagous. Most sawflies are external leaf feeders of Angiosperm, Gymnosperm and Pteridophyte plants. The larvae spin silk cocoons in which they pupate and the adults usually do not feed.

But there has been considerable radiation around this theme in terms of length of life cycle, number of generations per year, egg placement and saw structure, length of incubation, maternal care, host plant, larval feeding mechanism, defensive behaviour and colouration, and gregariousness, cocoon placement and structure, adult feeding, inbreeding, sex ratio, parthenogenesis, sexual dimorphism, female fertility and size, egg clustering, adult longevity and colour pattern, seasonal distribution, diapause and survival pattern.

Why is there so much variation in egg and larval clustering? What are the selective pressures related to this, and which morphological, behavioural and ecological characters are correlated with this variation in group size?

Very little is known about the ecology and behaviour of tropical sawflies. On the other hand, some temperate sawfly species are among the best ecologically studied insects due to their great economical importance as forest and crop pests. Considerable information is available today on the population dynamics, life table, biological control, spatial distribution, gregariousness, diapause, hostplant relationship, fertility, etc., for the Holoarctic Conifer forest pests of the genera Diprion, Neodiprion, Microdiprion, Macrodiprion and Gilpinia (Diprionidae) and Pristiphora, Pikonema and Pachynematus (Tenthredinidae), and to a lesser extent for the Holoarctic Broadleaf forest, orchard and crop pests of the genera Caliroa, Fenusa, Croesus, Pontania, Euura, Hoplocampa, Athalia, and a few others (Tenthredinidae), Cimbex and Trichiosoma (Cimbicidae) and Arge (Argidae). However, only two Southern Temperate species (from Australia) of Zenarge (Argidae) and Perga (Pergidae) have had their ecology reasonably well studied.

There is no comprehensive review of the extensive literature on sawfly ecology and behaviour available. Only some rather narrowly based reviews exist for particular regions. The most useful of these are those of Coppel and Benjamin (1965) on Nearctic Pine feeding Diprionids, Lyons (1964) on Nearctic Neodiprion sertifer, Pschorn-Walcher (1965) on European Neodiprion sertifer, Coppel, Mertins and Harris (1974) on Nearctic Diprion similis, Baker (1972) on Eastern Nearctic Forest sawflies, Furniss and Carolin (1977) on Western Nearctic Forest sawflies, Benson (1950) on British sawflies, Ermolenko (1972 & 1975) on Ukranian sawflies, Kontuniemi (1951 and 1960) on Finnish sawflies, and Okutani (1957) on Japanese sawflies.

The Diprionidae and Tenthredinidae are by far the best studied families, while the Argidae, Pergidae and Cimbicidae are poorly known. There is no review available of the very scattered literature on these last three families. Perhaps the best regional review on Argidae is that of Ermolenko (1975) on Ukranian species. No Argid species has been comprehensively studied from an ecological and behavioural point of view, reflecting the fact that Argids are only minor crop and forest pests, with only local economic interest. The species which have caused more economic damage and have thus received more attention are the rose pests Arge ochropus (Gmelin) and Arge pagana (Panzer), which are important pests of oil producing roses in South-eastern Europe and Turkey, and which have been periodically studied all over the

Palaerctic Region since the Seventeenth Century (see, for example, Goedart, 1662-67; Vallisnieri, 1713, Reaumur, 1740; DeGeer, 1771; Vollenhoven, 1857-61; Brischke & Zaddach, 1863; Stein, 1881; Guercio, 1893; Guilland, 1913; Fintescu, 1914, 1915, 1927 & 1938; Servadei, 1934; Tuatay, 1963; Tsalbukov, 1964; Pankevich, 1969; Mefrleire, 1969; Sharonova, 1971; Nikolova, 1972; Scheibelreiter, 1973 and Ermolenko, 1975). More than 100 papers have been written about the biology of these two Argids, but there is no review available which summarizes all this vast and scattered literature (but Ermolenko, 1975, reviews part of it). See Appendix I for further references on the biology of Argid and tropical sawflies.

1.3 TAXONOMY OF ARGID SAWFLIES

The Argid sawflies have been regarded as a distinct family since the early XIX Century (Westwood, 1840), and they are easily distinguished from all the other sawflies by having only three segments in their antennae, the third being longest and frequently furcate in the males. They are closely related to the Pergidae, both families being regarded by modern authors as recent specialized offshoots of the Tenthredinoidea (Benson, 1938a; Maxwell, 1955; Okutani, 1957; Rasnitsyn, 1969; E.L. Smith, 1970a; Togashi, 1970; Koenigsmann, 1977).

The Argidae is a cosmopolitan family with more than 500 species described already (Benson, 1951), but is richest in the tropics. The great majority of the genera described are from the Neotropical Region.

The first attempt to subdivide the family into homogeneous groups was made by Thompson (1871) who created two divisions: Hylotomides (equivalent to the present Arginae) and Schizocerides (equivalent to the present Sterictiphorinae). Benson (1938a) proposed the first comprehensive classification of the family, dividing it into 10 subfamilies: Zenarginae, Arginae, Trichorhachinae, Atomacerinae, Athermantinae, Erigleninae, Dielocerinae, Pachylotinae, Theminae and Sterictiphorinae. He regarded his Sterictiphorinae as an unnatural miscellaneous assemblage which would have to be further divided in the future. Later Benson (1962) proposed a new, more compact, classification for this family, recognizing only three subfamilies: Zenarginae (with just one genus, Zenarge, restricted to Australia), Arginae (with half the number of species in the family, divided into three tribes: Argini, the biggest, restricted to the Holoarctic and Ethiopian Regions, with only three genera; Athermantini, a small group restricted to the Eastern Palaearctic, Oriental and Ethiopian Regions, with eight small genera; and Scobini, with one genus restricted to the Australian Region and two genera restricted to the Neotropical Region), and Sterictiphorinae (with half the number of species in the family and most of the genera, divided into four tribes; Atomacerini, with only one genus, Atomacera, restricted to the Neotropical and Nearctic Regions; Trichorhachini, with only two small Australian genera; Dielocerini, restricted to the Neotropical Region, including the earlier groupings "Theminae", "Pachylotinae", Dielocerinae" and "Topotritini", contains six small genera; and Sterictiphorini, the biggest group which is cosmopolitan but richest in the Neotropics, contains some 20 genera and includes the earlier grouping "Erigleninae"). The genus Arge Schrank (Arginae, Argini) alone contains almost half of the described species of the family (over 190 species).

Keys for the genera of the world were given by Konow (1907) and Malaise (1941), who recognized 52 genera by that time in the family. The Australian Argids have been reviewed by Benson (1934, 1938b and 1962), the Ethiopian species by Pasteels (1953, 1955 and 1963), the Palaearctic species by Enslin (1917), Gussakowskii (1935), Takeuchi (1932), Togashi (1968), Berland (1947), Benson (1951 and 1968), Muche (1972 and 1977) and Ermolenko (1975), the Nearctic by Ross (1937 and 1951) and D.R. Smith (1969, 1970 and 1971). There is no comprehensive work on the Oriental species (but see Togashi, 1975). The Neotropical Argids have been worked out mainly by Malaise (1937, 1942, 1949 and 1955). D.R. Smith is working on a complete revision of the Neotropical sawflies (D.R. Smith, in preparation). There has been no recent catalogue for the world species of Argidae, the last available was made by Konow (1894), but again there is a new one in preparation by D.R. Smith.

Figure 1.1 gives an idea of the phylogenetic relationship of the different groups of Argidae based on recent authors. There are several reasons to regard the Zenarginae as the most primitive and the Sterictiphorinae as the most recent and diversified group (Benson, 1962 and 1965).

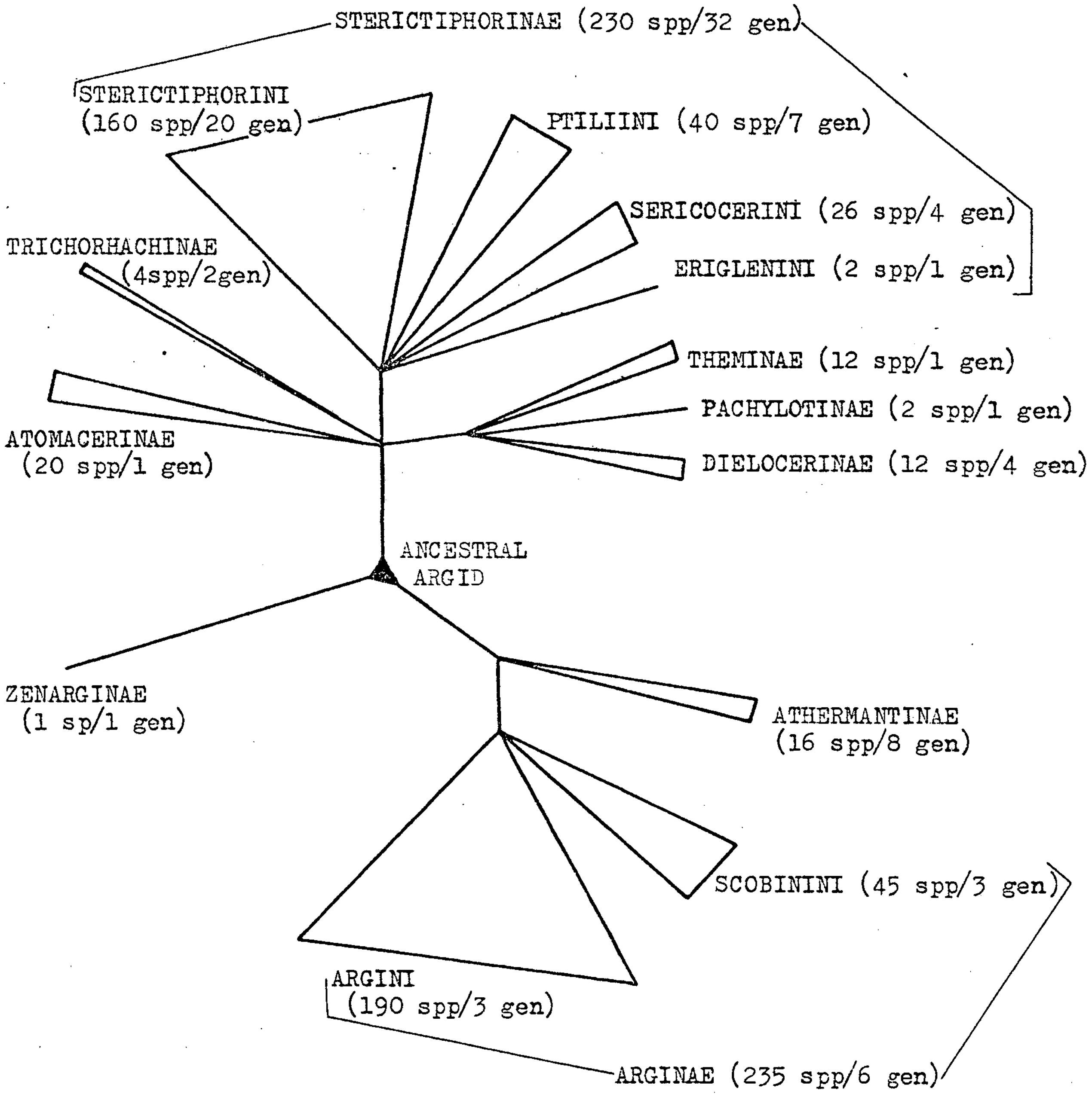


FIGURE 1.1. Approximate relationship between the different groups of Argidae based on Benson (1938a & 1962) and approximate numbers of known species and genera in the world based on the works of Benson, Ermolenko, Malaise, Muche, Pasteels, Ross, D.R.Smith, Takeuchi, Togashi and Verzhutskii.

1.4 TAXONOMY, DISTRIBUTION AND BIOLOGY OF THE DIELOCERINI

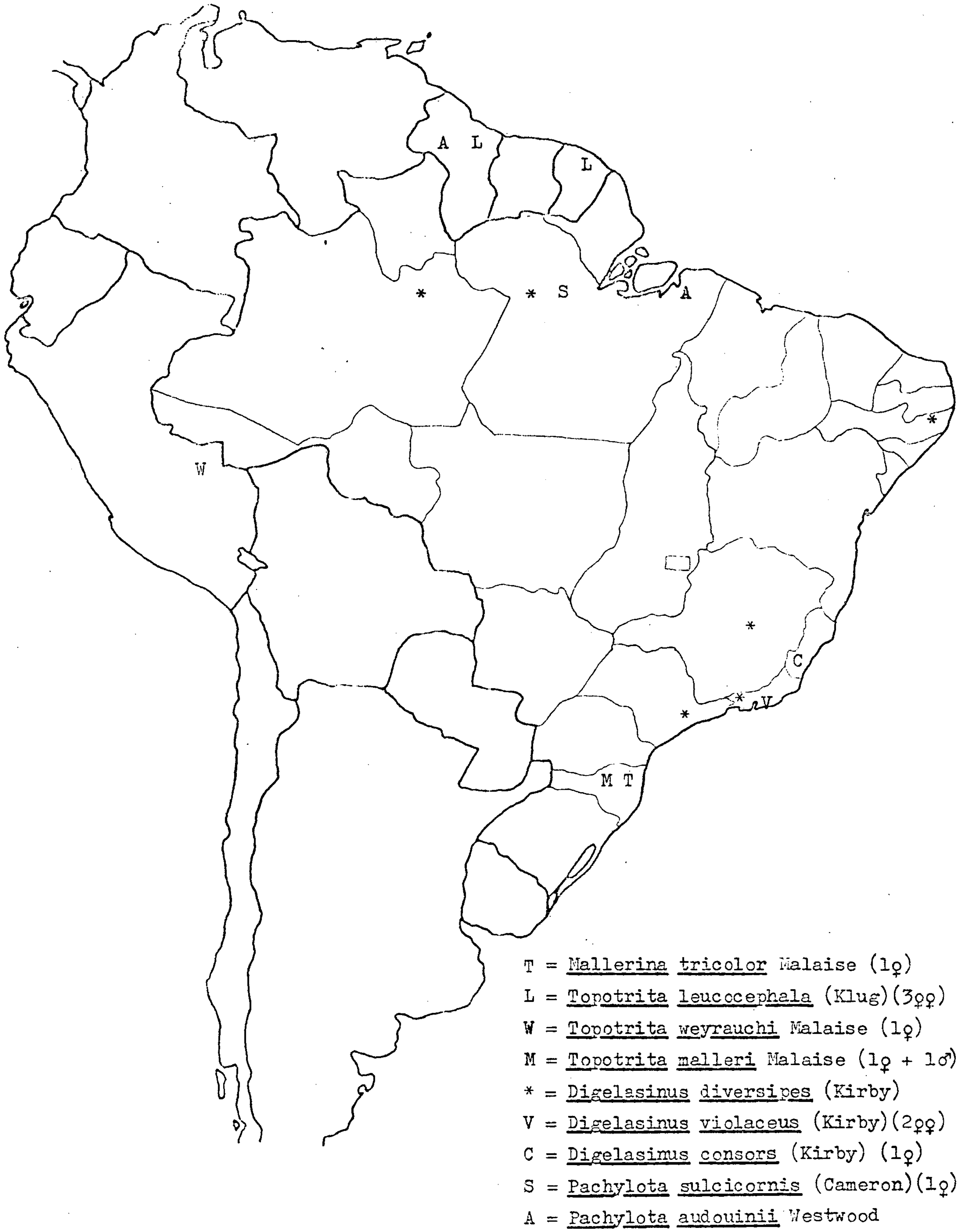
The Dielocerini (Sense Benson, 1962), to which the two species studied here belong, is a small group with some 26 described species of large and colourful sawflies restricted to South America east of the Andes (Guianas, all Brazil, and the amazonian parts of Venezuela, Peru, Ecuador and Bolivia). It contains six genera, two of which are very distinctive and have large heads and mandibles: *Pachylota* Westwood (2 species) and *Themos* Norton (12 species). *Pachylota* females have specially large mandibles and thick legs (see Benson, 1938a). The other four genera make a compact group: *Dielocerus* Curtis (5 species), *Digelasinus* Malaise (3 species), *Mallerina* Malaise (1 species) and *Topotrita* Kirby (3 species)(see D.R. Smith, in preparation). Most species in this tribe are brightly coloured black and orange being very conspicuous, and have strong sexual dimorphism, the strongest among all the sawflies.

D.R. Smith (1975) prefers Benson's earlier arrangement for dividing the Argidae into subfamilies. He prefers to maintain *Pachylota* and *Themos* in their own separate subfamilies Pachylotinae and Theminae, leaving only *Dielocerus*, *Digelasinus*, *Topotrita* and *Mallerina* in the subfamily Dielocerinae.

Nothing is known about the biology of the rare species of *Mallerina* and *Topotrita*. *Mallerina tricolor* Malaise, 1942 the single species of the genus, is known from a single female specimen from Santa Catarina state in southern Brazil. *Topotrita malleri* Malaise, 1955 is known from a single male and a single female specimen from Santa Catarina too. *Topotrita weyrauchi* Malaise, 1955 is known from a single female from amazonian Peru, and *Topotrita leucocephala* (Klug, 1834) is known from only 3 female specimens from the French Guiana and Guiana (ex-British Guiana)(Malaise, 1937 and 1955).

Digelasinus and *Pachylota* are also small genera but are better known. *Digelasinus violaceus* (Kirby, 1882) and *D. consors* (Kirby, 1882) are known from only one or two female specimens each from south-eastern Brazil (Rio de Janeiro state and an unspecified locality in eastern Brazil respectively), and nothing is known about their biology (Kirby, 1882). *Digelasinus diversipes* (Kirby, 1882), however, is known from both sexes and from several Brazilian states: Amazonas, Pará, Pernambuco, Minas Gerais, Rio de Janeiro and São Paulo (Malaise, 1937 and D.R. Smith, in prep.). Costa Lima (1937) described an Ichneumonid parasitoid, Lymeon (=Diapetimorpha) dieloceri, which was found by Oscar Monte attacking D. diversipes larvae inside their cocoons in Minas Gerais. He also gave its host plant, Pau Pombo (Erythroxylon sp, Erythroxylaceae). Benson (1938a) said that Digelasinus, most probably referring to D. diversipes, exhibits maternal care behaviour and that its larvae build cocoon masses with a communal covering. He did not give his source of information however. It is possible that he obtained the information on the gregarious behaviour of the larvae which spin cocoon masses by correspondence with Costa Lima, or he might himself have seen a cocoon mass in a museum. The British Museum (Natural History), where he worked, has a small cocoon mass of this species with no label which might have been there by the time he wrote his paper. Monte (1946) reported that D. diversipes larvae in Minas Gerais build cocoon masses attached to the bark of trees. Further information on the cocoon masses of this species will be given by Dias (in prep. b).

Pachylota sulcicornis (Cameron, 1878) is only known from a single female specimen from Pará state in Brazil and nothing is known about its biology. Pachylota audouinii Westwood, 1846, however, is known from both sexes from Pará in Brazil and Guiana. Benson (1938a) said that Pachylota, most certainly P. audouinii, also exhibits maternal care behaviour and have gregarious larvae which build their cocoons together under a communal envelope. However, he did not give his source for this information either. The British Museum (Natural History) has one cocoon mass of this species collected in Pará in 1932 by the Rev. A. Miles Moss. This cocoon mass is probably his source of information on the social habits of Pachylota larvae. However, the source for his report on the maternal care behaviour in this genus remains obscure. Further information on the cocoon masses and host plant of this species will be given by Dias (in prep.b). Figure 1.2 summarizes the known distribution of Mallerina, Topotrita, Digelasinus and Pachylota. The actual distribution of these sawflies, however, is presently grossly underestimated.



T = *Mallerina tricolor* Malaise (1♀)
L = *Topotrita leucocephala* (Klug)(3♀♀)
W = *Topotrita weyrauchi* Malaise (1♀)
M = *Topotrita malleri* Malaise (1♀ + 1♂)
* = *Digelasinus diversipes* (Kirby)
V = *Digelasinus violaceus* (Kirby)(2♀♀)
C = *Digelasinus consors* (Kirby) (1♀)
S = *Pachylota sulcicornis* (Cameron)(1♀)
A = *Pachylota audouinii* Westwood

FIGURE 1.2.Summary of the known distribution of the species of *Mallerina*,*Topotrita*, *Digelasinus* and *Pachylota* (Malaise,1937,1942,1955; Kirby,1882; Dias,in prep.b).

There are only five species of Dielocerus known: D. diasi Smith, 1975, D. fasciatus (Enderlein, 1919); D. formosus (Klug, 1834); D. hyaloptera (Perty, 1833); and a new species which is being described by D.R. Smith (manuscript name is D. ocreatus)(Dias and Smith, in prep., and D.R. Smith, in prep.). Dielocerus hyaloptera is only known from a single male collected somewhere along the Amazon River in Brazil. Nothing is known about its biology. Dielocerus fasciatus is known only from two female specimens from amazonian Ecuador and amazonian Peru. Nothing is known about its biology either. According to D.R. Smith (in prep.) D. fasciatus and D. hyaloptera could represent the different sexes of the same species. Biological evidence is needed here.

Both sexes of the other three species of Dielocerus are known, and some information is available on their biology. The species most frequently referred to in the literature is D. formosus which is known from several coastal Brazilian states: Pernambuco, Espírito Santo, Minas Gerais, Rio de Janeiro and possibly São Paulo. Curtis (1844) was the first to report on the biology of this sawfly. He received two cocoon masses and 20 adults emerged from them which were collected somewhere in Brazil by Henry Ellis (possibly in Rio de Janeiro). He was the first to correctly associate the two very distinct sexes, described in detail the cocoon mass built by the larvae in a very regular arrangement against the bark of a branch of the host tree, pointing out the complexity of the outer communal cover which envelopes all the cocoons and consists of two distinct layers of silk. He also presented good drawings of the cocoon mass, described briefly the prepupa, and how the adult escape from the cocoon mass to emerge, reported a marked female biased sex ratio (3 males and 17 females emerged from the described cocoon masses) and speculated that the function of the complex outer envelope is probably to protect the cocoons against heavy rains and the attack of Ichneumonid parasitoids. He called attention to the uniqueness of this type of larval cooperative behaviour, to build complex regular cocoon masses, among the sawflies as compared to the known gregarious larvae of several species of Diprion and Nematus which build their cocoons either singly or in small irregular groupings showing no cooperation between them. He compared this cooperative group spinning of cocoons by D. formosus larvae with that exhibited by larvae of a species of Microgaster (Braconidae). This paper had a profound impact on the literature of presocial insects, being repeatedly cited in most books dealing with insect gregarious behaviour since then.

Sichel (1862) also described briefly a cocoon mass of D. formosus and reported the emergence of some adult females after two and three years of dormancy in a cocoon mass taken to France in 1859 from somewhere in Brazil. F. Smith (1866) reported that Theodor Peckolt found D. formosus in Cantagalo, Rio de Janeiro, and was familiar with the cocoon masses built by its larvae on trees. He said T. Peckolt called this sawfly the "Marumbouda seda", the silk wasp, in allusion to its spinning behaviour. Peckolt himself wrote a paper on some Brazilian wasps in 1894 and probably included some comments on this sawfly, but unfortunately it has been impossible up to now to locate this paper. Costa Lima (1927) reported yet another cocoon mass collected in Tapera, Pernambuco, Brazil, by Rev. Bento Pickel in June of 1926 attached to a tree in the bush. He received the cocoon mass in June of 1927 together with 19 adult sawflies which had emerged from these cocoons, with a female biased sex ratio (5 males and 14 females). He opened the cocoons which were still closed and found dormant prepupae inside. He also gave a succint description of the cocoon mass and prepupae and presented some photographs of both. Bischoff (1927) also described and illustrated a cocoon mass of D. formosus. Benson (1938a) mentioned that female Dielocerus, certainly referring to this species, protect their brood, but he did not give the source of this information. He also said that its larvae are gregarious and build communal cocoon masses, giving Bischoff (1927) as reference. Monte (1941) described briefly the larva and adult of D. formosus from Minas Gerais and gave the host plant, Ingá (Inga sp, Leguminosae). Townsend (1942) described a Tachinid fly, Spathimeigenia dieloceri, found by Oscar Monte in Minas Gerais parasitizing the larvae of D. formosus. Parker et al. (1953) also recorded this fly parasitising a species of Dielocerus, probably D. formosus, from São Paulo. Further records and descriptions of cocoon masses of this sawfly will be given by Dias (in prep. b).

Dielocerus ocreatus is only known from the type locality in northeastern Mato Grosso near São Felix. Dias and Smith (in prep.) will give some notes on the biology of this species: host plant (Styrax, Styracaceae), cocoon mass, sex ratio, prolonged diapause and parasitoids.

Dielocerus diasi, one of the two species studied here, is known only from the Brazilian states of Mato Crosso, Goiás and Federal District (D.R. Smith, in prep.) and was described by D.R. Smith (1975) based on the abundant material collected by the author at the beginning of this study. Ducke's (1916) report on cocoon masses of a species of Dielocerus collected by Alípio Miranda Ribeiro attached to branches of trees in central and northeastern Mato Grosso probably refers to this species. He said that these cocoon masses were collected in the land of the Nhambiquara amerindians who eat the prepupae of this sawfly found inside the cocoon masses. He presented a photograph of one cocoon mass. Nothing else has been published on the biology of D. diasi except for a preliminary paper (Dias, 1976) on the initial results of the present study. Outside the Federal District the only records of this sawfly besides that of Ducke are: one female from Vianópolis, Goiás, and another from Chapada (?Chapada dos Guimarães), Mato Grosso (Dias, 1976). Figure 1.3 summarizes the known distribution of Dielocerus species. The actual distribution of these sawflies, however, is presently grossly underestimated.

The genus Themos has 12 known species: T. boliviensis Smith, 1975; T. concinnus Mocsary, 1909; T. laqueatus (Enderlein, 1919); T. hyaline Norton, 1867; T. nigronotum Malaise, 1955; T. olfersii (Klug, 1834); T. semiadusta (Enderlein, 1919); T. similis Mocsary, 1909; T. surinamensis (Klug, 1814); T. vigilax (Malaise, 1949); and two new species being described by D.R. Smith (manuscript names = T. malaisei and T. ochreus) (D.R. Smith, in prep.). Two species are known from single male specimens: T. hyaline (unknown locality) and T. nigronotum (Minas Gerais, Brazil). Nothing is known about their biology. Eight species are known only from 1 or 2 female specimens: T. boliviensis (northern amazonian Bolivia), T. concinnus (amazonian Peru), T. laqueatus (amazonian Ecuador), T. ochreus (amazonian Peru),

FIGURE 1.3. Summary of the known distribution of the species of Dielocerus (D.R.Smith, in prep.; Dias, 1976, in prep.b).

T. semiadusta (amazonian Ecuador), and T. similis (amazonian Peru and Amazonas, Brazil). Nothing is known about their biology.

Themos vigilax is known from only 2 females from a single locality in southeastern Brazil (Nova Friburgo, Rio de Janeiro) but Malaise (1949) reported that both females were collected by Petr Wygodzinski sitting astride over their compact eggclusters(one with 68 and the other with 87 reddish yellow eggs) on the underside of the host leaf and protected their eggs with their bodies even after dying. Unfortunately the host plant was not recorded. It seems possible to me that T. nigronotum and T. vigilax represent the different sexes of a same species due to their geographical proximity. Further biological data is necessary.

Themos surinamensis is also only known from female specimens, but it has been recorded from many specimens from a widespread area: amazonian Ecuador, Venezuela, Guiana, Surinam and Brazil (Pará, southern Goiás and Federal District)(D.R. Smith, in prep.). Nothing is known about the biology of this species except for the host plant: Ceiba pentandra (L.)(Bombacaceae)(D.R. Smith, in prep.).

Themos malaisei and T. olfersii are the only two species of the genus for which the two sexes have been associated. Themos malaisei is known from 23 females and 3 males, mainly from São Paulo state, but also from southern Goiás and northwestern Mato Grosso in Brazil and eastern Bolivia (Santa Cruz)(D.R. Smith, in prep.). One female from Barueri, São Paulo, was collected sitting on top of a compact eggcluster with about 80 eggs, an evident case of maternal care. The host plant is Luehea sp (Tiliaceae)(Dias, in prep. a).

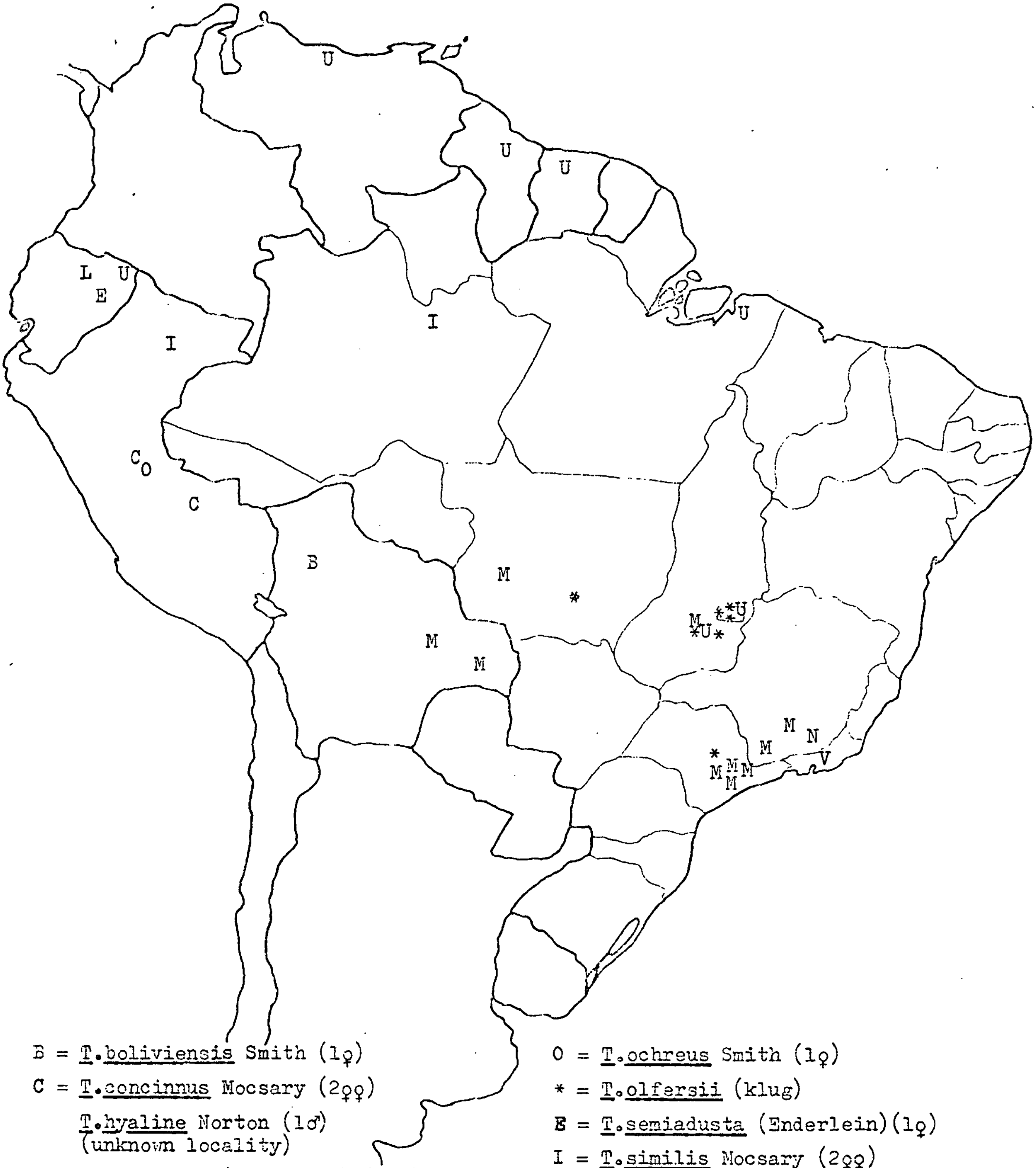
Themos olfersii, the other one of the two species studied here, is known from the Brazilian states of São Paulo, southern Goiás, Federal District and northwestern Mato Grosso (D.R. Smith, in prep.). Only about half a dozen female specimens of this species were known before the present study was started. Except for a preliminary paper (Dias, 1975) on the host plant, maternal care and larval gregariousness (initial results of the present study), the only published note on the biology of T. olfersii is a curious report by Klug (1850) of cocoon masses spun by its larvae. This behaviour of mass-cocooning has not been confirmed in the present study. Figure 14 summarizes the known distribution of Themos species. The actual distribution of these sawflies, however, is presently grossly underestimated.

1.5 OBJECTIVES

The objective of this study is to present an overall picture on the life cycle, ecology and behaviour of two presocial Argid sawflies from Central Brazil, *Dielocerus diasi* Smith, 1975, and *Themos olfersii* (Klug, 1834), which are typical representatives of the group of sawflies which exhibits the most complex social behaviour among all sawflies - the Dielocerini (sense Benson, 1962). Attention is given to several behavioural and ecological topics which might help us to understand the social life system of these two sawflies. This is a mainly descriptive work which aims at documenting the complexity, frequency and importance for survival of the social behaviours of these two sawflies in the following interactions: (1) among sib larvae; (2) between unrelated larvae; (3) between mother and offspring; and (4) between unrelated adult females. The importance of kinship is evaluated.

This work is also intended to contribute to a better understanding of the ecology and behaviour of the insect fauna of the Cerrado biome of Central Brazil. Despite the great progresses made toward a better knowledge of the ecology of the Cerrado in the last 30 years (see Ferri, 1963, 1971 and 1977, and Labouriau, 1966), the fauna, of which the insects constitute the most important group, is still very poorly known. Given the recent governmental projects to introduce modern agriculture and forestry into these vast areas (see Ferri, 1977), I believe studies on the biology and ecology of the Cerrado fauna should be intensified while the biome is still natural and little touched by man.

Finally, and more generally, this thesis aims to fill part of the enormous existing gap in our knowledge about the biology of tropical sawflies. In the course of the various discussion sections which follow I shall try to bring together some of the large, scattered and still mostly undigested sawfly literature relevant to all the topics treated in this study.



B = T.boliviensis Smith (1♀)

C = T.concinnus Mocsary (2♀♀)

T.hyaline Norton (1♂)
(unknown locality)

L = T.laqueatus (Enderlein) (2♀♀)

M = T.malaisei Smith

N = T.nigronotum Malaise (1♂)

O = T.ochreus Smith (1♀)

* = T.olfersii (klug)

E = T.semiadusta (Enderlein)(1♀)

I = T.similis Mocsary (2♀♀)

U = T.surinamensis (Klug) (♀♀)

V = T.vigilax (Malaise) (2♀♀)

FIGURE 1.4.Summary of the known distribution of the species of Themos (D.R.Smith,in prep; Malaise,1949,1955; Dias,1975)

CHAPTER 2. MATERIALS AND METHODS

Only general methods which pertain to all or several chapters are given here. For specific methods on each topic consult the different chapters.

2.1 LITERATURE REVIEW

An attempt was made to make a survey as complete as possible of the available literature on the biology of Argidae sawflies and related pertinent subjects. The main body of this survey was obtained through the following bibliographies: Bibliotheca Entomologica (from early beginnings until 1862)(Hagen, 1862-3), Zoological Record (1863-1912 and 1947-1972), Review of Applied Entomology (A)(1940-1979), Biological Abstracts (1971-1980), Bibliografia Entomológica Brasileira (1880-1962)(Araujo e Silva _et al._, 1968), Bibliografia Brasileira de Zoologia (1950-1977), Insetos do Brasil, Bibliography (Costa Lima, 1960), Bibliografia Entomológica Argentina (1874-1952)(Piran, 1954-7), Bibliography of New Zealand Entomology (1775-1952)(Miller, 1956), Bibliography of Australian Entomology (1775-1930)(Musgrave, 1932), Catalog of Hymenoptera of America North of Mexico (Muesebeck _et al._, 1951; Krombein, 1958, 1967 and 1979), Catalogue of Parasites and Predators of Insect Pests (Thompson, 1950), and a few minor ones.

This was complemented by valuable references obtained from the major taxonomic monographs on sawflies by all the main authors such as Benson, Malaise, Cameron, Enslin, Gussakovskii, Verzhutskii, Ermolenko, Tacheuchi, Togashi, Okutani, Froggatt, Riek, Muche, Zombori, Pasteels, Berland, Rohwer, Ross, Conde, Forsius, Konow and D.R. Smith. Further information was obtained from the more recent literature and review papers on the biology of sawflies, mainly those on pests of forests, crops and ornamentals .(see references cited in the Introduction and Appendix I). Several persons were also very helpful, in special D. R. Smith from Washington (see acknowledgements). The staff of several libraries in Brazil, Argentina, United States and Great Britain were also instrumental in the accomplishment of this survey (see acknowledgements).

2.2 IDENTIFICATION OF INSECTS AND OTHER ANIMALS AND PLANTS STUDIED

The host plants were identified by João Murça Pires, Ezechias P. Heringer and James Ratter; the sawflies by D.R. Smith; the Eulophids by Carl M. Yoshimoto; the Chalcidids by Gordon Gordh; the Ichneumonid by R.W. Carlson (genus only) and myself (species compared with type at the Oswaldo Cruz Institute, Rio de Janeiro); the Tachinids by Curt W. Sabrosky and José Henrique Guimarães; the Pyralid by Victor O. Becker; the ant by Walter W. Kempf; and the Arachnids by Wilson R. Lourenço (see acknowledgements). Other identifications, down to family or genus only, are my own responsibility.

2.3 VOUCHER SPECIMENS DEPOSIT

Voucher specimens of the adult sawflies, parasites, predators, commensals and host plants are kept in the Insection Collection of the Departamento Regional de Pesquisas Ecológicas, IBGE at the Reserva Ecológica do IBGE in Brasília, DF, Brasil and also in the collections of the experts who made the determinations. Voucher specimens of all immature stages of the sawflies and incomplete immature stages of parasites are also kept at IBGE.

2.4 STUDY SITES IN THE FIELD

All field studies described here were conducted in several sites around Brasília, within the Brazilian Federal District in Central Brazil (see Chapter 3).

2.5 PERIODS OF STUDY

Field and laboratory observations on Dielocerus diasi were carried out since September of 1970, sporadically at first but intensive from January of 1976 until July of 1979 (except for the period between September of 1976 and July of 1977). Observations on Themos olfersii were done intensively between October of 1973 and July of 1979 (except the same period as above). The period from September of 1976 until July of 1977 was spent in Edinburgh with literature review, planning of field studies and contacts with different specialists. Two weeks in August of 1976 and another two in October of 1979 were spent in eastern United States to contact specialists and study Museum collections (Washington, New York, Chicago, Ann Arbor and Madison, Wisconsin). From October of 1979 onwards, back in Edinburgh, the analysis of data, literature review and thesis writing were completed.

2.6 NUMBER OF INDIVIDUALS STUDIED

Over 300 egg clusters (about 22,000 eggs), 200 larval sib-groups (about 10,000 larvae), 3,000 cocoon masses (about 100,000 cocoons), 300 adult females and 50 adults males of *Dielocerus diasi* were observed in the field. Over 10,000 host trees (*Sclerolobium aureum*) were inspected in the field, over 1,000 of these periodically. Over 3,000 adult *D. diasi* and over 1,000 adult parasites and commensals were reared in the laboratory from about 100 cocoon masses. Over 100 adult parasites were reared from *D. diasi* eggs sleeved in the field.

Over 300 eggclusters (about 8,000 eggs), 200 larval sib-groups (about 4,000 larvae), less than 20 cocoons, over 200 adult females and less than 20 adult males of *Themos olfersii* were observed in the field. Over 5,000 host shrubs (*Eriotheca pubescens*) were inspected in the field, over 500 of these periodically. Only about 10 adult *T. olfersii* and 1 adult parasite were reared in the laboratory from about 100 mature larvae. Over 100 adult parasites were reared from *T. olfersii* eggs sleeved in the field.

2.7 TRANSFERENCE OF SAWFLIES TO INCREASE POPULATIONS AT RECOR

During 1977 and 1978 larval groups of both species and cocoon masses of *D. diasi* collected at several localities were transferred to study sites 13, 14 and 15 at the Reserva Ecológica do IBGE (RECOR) beside the Zoology Field Laboratory in order to increase the existing populations to provide more abundant material for observation.

2.8 PHOTOGRAPHY AND CINEMATOGRAPHY

Photographs were taken with a SLR camera with close-up lens and extension tubes, and if needed, with flash or mirror to give fill-in light.

Coloured super-8 cinefilms were taken with a Nizo 801 Macro cine camera with supplementary lenses. Best documented is the larval group feeding behaviour of D. diesi in time-lapse with intervals between 2 and 6 seconds (10 to 30 frames per minute). In all cases the camera was set on a firm tripod, the insects were given a half hour period to return to their normal behaviour and then the camera was triggered with a long cable releaser. In most instances wind brakes and strings had to be used to minimize the wind, but total elimination of wind was not done as it causes the larvae to become restless. The camera was always set on automatic exposure so that it automatically adjusted changes in light intensities caused by clouds, but in some situations mirrors had to be used to give fill-in light. The camera was always protected against direct sun and rain by an umbrella. All filming was done in the field under natural conditions, except for the fact that in several instances the larval groups had anteriorly been taken from the tall canopies and re-established on low saplings to facilitate observation.

The best sequences were analysed frame by frame either with an editor machine or by projecting on a vertical screen from which drawings were made, each one always associated with fixed reference points to allow comparisons.

CHAPTER 3. STUDY AREAS AND HOST PLANTS

3.1 STUDY AREAS

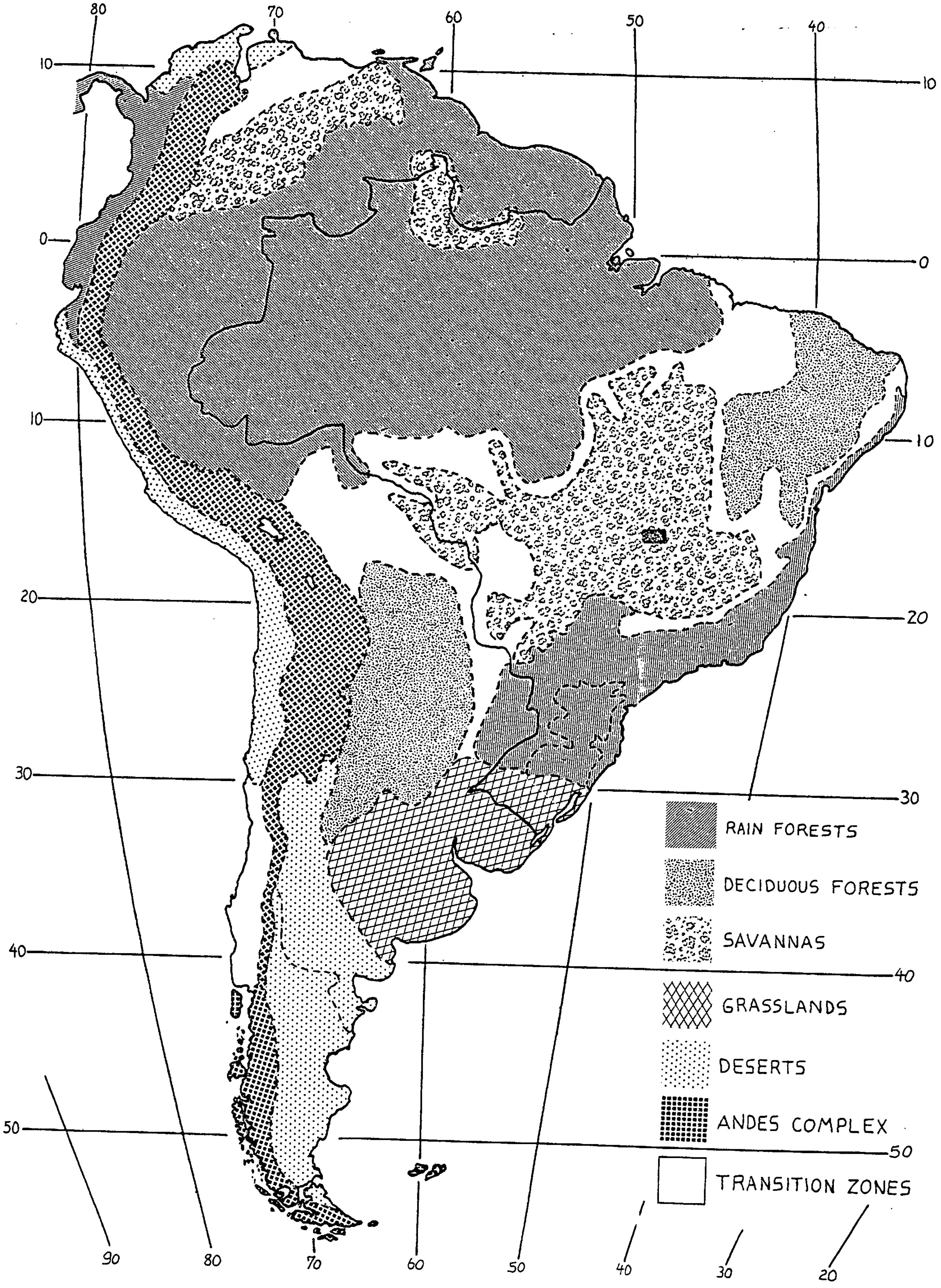
This study was carried out within the limits of the Federal District in Central Brazil in the middle of the Cerrado biome.

South America is a vast continent which exhibits great latitudinal and altitudinal diversity. Some 13 major biomes are recognized in South America east of the Andes: 2 Rainforests (Amazon and Atlantic), 2 deciduous forests (Caatinga and Chaco), 1 Conifer forest (Paraná Araucaria), 3 Savannas (Cerrado, Roraima/Guiana and Llanos), 3 Grasslands (Coxilhas, wet Pampas and dry Pampas) and 2 Deserts (Monte and Patagonia)(Ab'Saber, 1977; Cabrera and Willink, 1973; Hueck, 1966) (Figure 3.1). The term Savanna is used here in its widest sense. The Cerrado is the second largest biome in South America and covers an area of over 2 million km^2 in Central Brazil, which corresponds to about 25% of the total area of Brazil. The only other biome larger than it is the Amazon Rainforest which is more than twice as big. The Cerrado occupies most of Mato Grosso, Mato Grosso do Sul, Goiás and Minas Gerais states and occurs less frequently over parts of several other brazilian states.

The Cerrado biome is a mosaic of several different communities: Gallery rainforest and Veredas (<u>Mauritia</u> palms) along the rivers, swamp grassland with termite mounds further away from the river, dry grasslands on the valley slopes, different types of Cerrado on the slope and top of the hills and plateaux, different types of deciduous forests on patches of better soil and outcrops of limestones, and rocky grasslands on hilltops with surfacing rocks. There are complex interactions between these different communities. The different Cerrado-type communities are the dominant communities in the Cerrado biome, covering more than 70 - 80% of the area (Eiten, 1972, 1975, 1978; Goodland, 1971; Ratter <u>et al.</u>, 1973).

This biome is characterized by the very typical,rich and endemic Cerrado community flora which occurs in several transitional growth forms from open grassland Cerrado (Campo Sujo de Cerrado) to closed woodland Cerrado, according mainly to the soil type. More than 700 species of trees are known from the Cerrado flora (Rizzini, 1963). Most trees have thick bark (cork), erratic branching pattern, tough leaves, small height and very deep roots going up to 10 - 15 meters down reaching the ground water. Subterranean trunks and tuberous roots are common features of these plants.

FIGURE 3.1. The major biomes of South America. The Cerrado biome occupies most of Central Brazil. The black rectangle in the middle of the Cerrado biome is the Brazilian Federal District. The different biomes of the Andes are not differentiated here(based on Ab'Saber,1977 and Cabrera and Willink,1973).


RAIN FORESTS
DECIDUOUS FORESTS
SAVANNAS
GRASSLANDS
DESERTS
ANDES COMPLEX
TRANSITION ZONES
80
70
60
50
40
10
0
10
20
30
40
50
90
80
70
60
50
40
30
20

Most soil in this biome is poor, acid, deep and has toxic concentrations of aluminium and iron (lateritic) to plants. The climate is markedly seasonal with two distinct seasons: a rainy season between October and April and a dry season between May and September. The topsoil dries during the dry season and the grasses and herbs die or loose their aerial parts. However the ground water never dries and so the trees and shrubs with deep roots have no shortage of water, even after several months virtually without rain, and do not limit their loss of water through their stomata (Ferri, 1944 and 1955). Fire is a common phenomenon during the dry season and many herbaceous plants only flower after the Cerrado is burnt. Several Cerrado plants are resistant to fire (Coutinho, 1978; Ferri, 1973; Heringer and Graziela, 1968; Rizzini, 1976).

The fauna of the Cerrado biome as a whole is less typical and less endemic than its flora, having many elements in common with other biomes of South America, in particular with the Amazon rain forest, the Atlantic rain forest, the Caatinga and Chaco deciduous forests, the Pampas and Coxilhas grasslands and the Llanos and Roraima/Guiana Savannas. Nevertheless, there are several endemic species and several others which although present in other biomes are best represented and more abundant in the Cerrado (Sick, 1965). With regard to insects, our present knowledge is still very limited. However it is evident that most monophagous and oligophagous herbivorous insects (including the sawflies) adapted to endemic Cerrado plants must themselves be endemic to this biome.

At present most of the Cerrado is still little disturbed by man. The only economic activities in most places are extensive cattle raising and wood felling for fuel. Apparently the only elements in this biome which have already been seriously affected by man are the larger mammals (tapir, maned wolf, crab-eating fox, bush dog, jaguar, puma, coati, peccary, brocket deer, giant armadillo, giant anteater, and a few other species) and some large birds (rhea, macaws, and a few other species). However this situation is changing very fast as the Government and private companies open up large areas of Cerrado land for great agriculture and forestry projects (Ferri, 1977; Goodland and Irwin, 1977; SEPLAN, 1975).

The Federal District (Figure 3.1) has an area of 5,748 km^2 and is situated between 15°31' and 16°03' latitude South of the Equator and between 47°21' and 48°15' longitude West of Greenwich in the middle of the Central Brazil Plateau at altitudes between 950 and 1200 m above sea level. Streams originating in the Federal District flow to the three major drainage basins in South America: Amazon, Paraná and São Francisco (CODEPLAN, 1971).

The average annual rainfall in the Federal District is 1,575 mm. Maximum precipitation is between November and February. The maximum average monthly rainfall is around 300 mm, in November (Figure 4.13). In most years there is a short dry period in January lasting 1 to 4 weeks. The relative air humidity during the dry season drops below 70%, with an average of only 47% in August. It is not rare to have days with less than 20% or even 10% relative humidity during the dry season (IBDF/FBCN, 1979; Senra, 1980; Wolf, 1977).

The average temperature is 20.4°C with the monthly average ranging from 17.8°C in June to 22.2°C in September. The lowest absolute temperature registered was 3°C in May and the highest 35°C in October. Insolation is always above 130 hours per month and above 200 hours per month between May and September. Wind blows constantly from east in the dry season and from south and west in the rainy season. An important characteristic of the climate of the Federal District is its continentality: it is situated about 1000 km from the Atlantic Ocean (IBDF/FBCN, 1979; Senra, 1980; Wolf, 1977).

Roughly about 36% of the Federal District area is presently utilized by man in economic activities which resulted in the elimination of the natural communities: 10% by urban areas, 20% by agriculture, 5% by commercial forestry (Eucalyptus and Pinus) and 1% by water reservoirs. The other 64% still occupied by natural communities are distributed as follows: 25% with woody Cerrado, 32% with grassland/shrubby Cerrado, 6% with gallery rain forest, 1% with swampy grassland and 0.5% with deciduous forests (Péllico Netto, 1972).

There is one major protected area in the Federal District - the Brasília National Park with 40,000 hectares - and five secondary ones: Aguas Emendadas Biological Reserve (10,000 ha), Cabeça do Veado Biological Reserve (1,000 ha), Gama Biological Park (1,000 ha), Agua Limpa

Ecological Reserve (University of Brasília)(2,000 ha) and IBGE Ecological Reserve - RECOR (2,000 ha). Therefore about 10% of the Federal District total area is presently protected. The remaining areas of the Federal District still occupied by natural communities but not protected are subject to frequent fires, intensive hunting and damping of solid wastes.

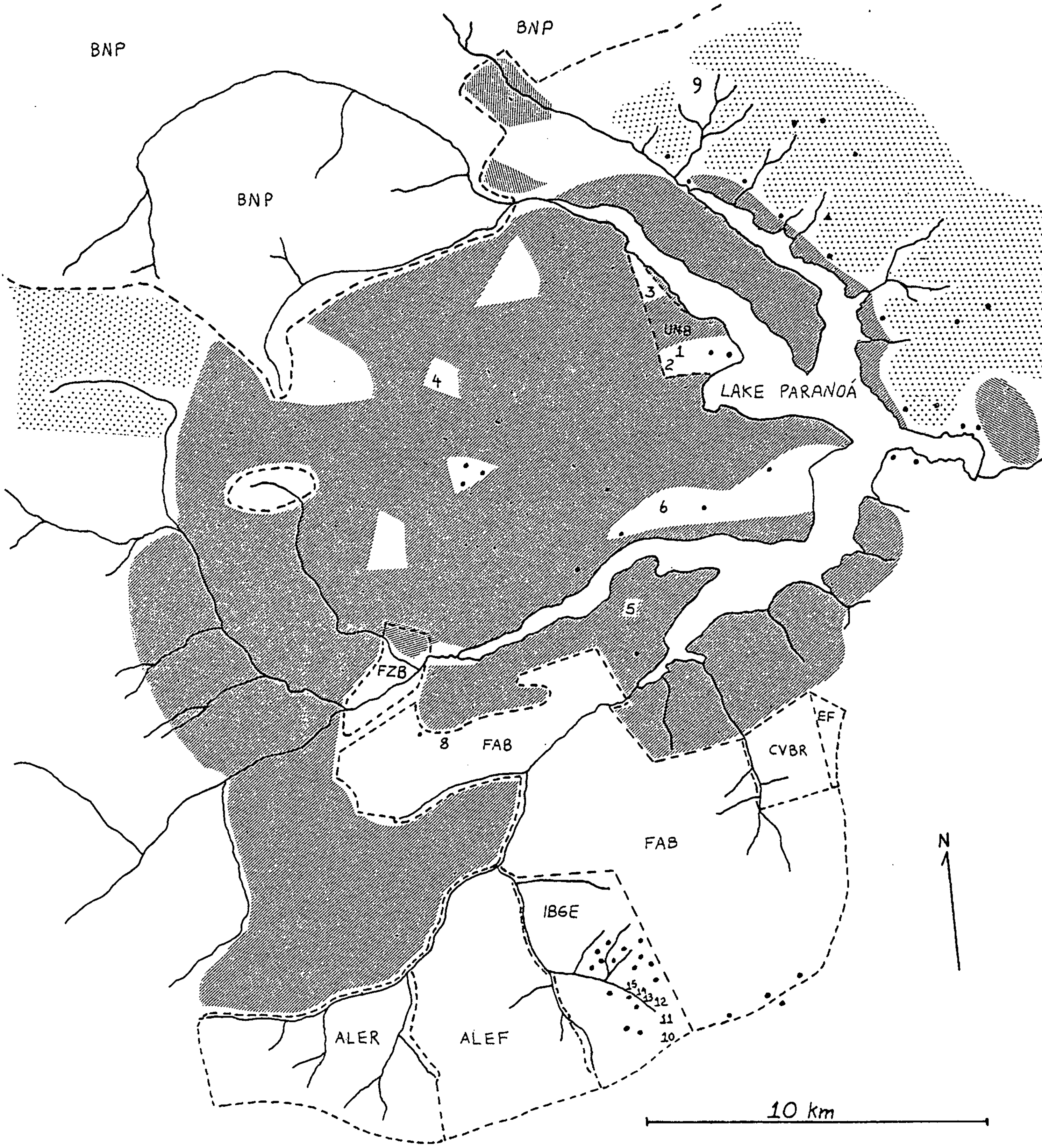
Until about 1955 the area which in 1960 became the Federal District remained very little disturbed, having only one small old village (Planaltina) and scattered cattle farms. This situation changed abruptly in 1956 with the start of the construction of Brasília.

Themos olfersii and Dielocerus diasi were observed in a large number of sites within the Federal District, mainly in the central (around Brasília), southern (within and around the IBGE Ecological Reserve), northern (around Sobradinho and Fercal) and north-eastern (around Planaltina and the Aguas Emendadas Biological Reserve) sectors of the District. The observations were concentrated on 15 of these sites - these are described below. Themos olfersii was mainly studied at sites 1 and 13 and to a lesser extent at sites 2, 5, 10, 11 and 12, while Dielocerus diasi was mainly studied at sites 3, 5, 6, 7, 8 and 15, and to a lesser extent at sites 4, 9, 12 and 14.

Sites 1 to 6 were located within the city of Brasília limits, sites 8 and 9 were located just outside the periphery of Brasília, site 7 was near Planaltina village and sites 10 to 15 were located inside the IBGE Ecological Reserve (Figure 3.2).

The six urban sites (1 - 6) were located in small relic patches of Cerrado or Campo Cerrado which had survived the impact of urban development with relatively little change in their flora and insect fauna (Figure 3.2). Three of these (sites 1 to 3) were located inside the large campus of the University of Brasília in the north-eastern sector of the city by the lake (Figure 3.3). The University campus has an area of 371 ha which until 20 years ago was totally covered by natural Cerrado and Campo Cerrado communities. By 1970, when the first observations on D. diasi were made in the campus, about two-thirds of the campus were still covered by natural communities, but

FIGURE 3.2. The city of Brasília and periphery. Urban areas are shown stripped and areas with commercial forests are shown stippled. The major protected areas around the city are indicated by the traced lines and code letters: BNP=Brasília National Park (only its southern part is shown); UNB=University of Brasília campus; FZB=Zoobotanic Foundation Zoo Park; IBGE=IBGE Ecological Reserve; ALEF=Agua Limpa Experimental Farm; ALER=Agua Limpa Ecological Reserve; CVBR=Cabeça do Veado Biological Reserve; EF=Escola Fazendaria Estate; FAB= Brazilian Air Forces Estate. The major study sites are indicated by their code numbers, and other study sites are indicated by black dots.



BNP
BNP
BNP
9
3
UnB
1
2
4
LAKE PARANOÁ
6
5
FZB
8
FAB
EF
CVBR
FAB
N
IBGE
15
14
13
12
11
10
ALER
ALEF
10 km

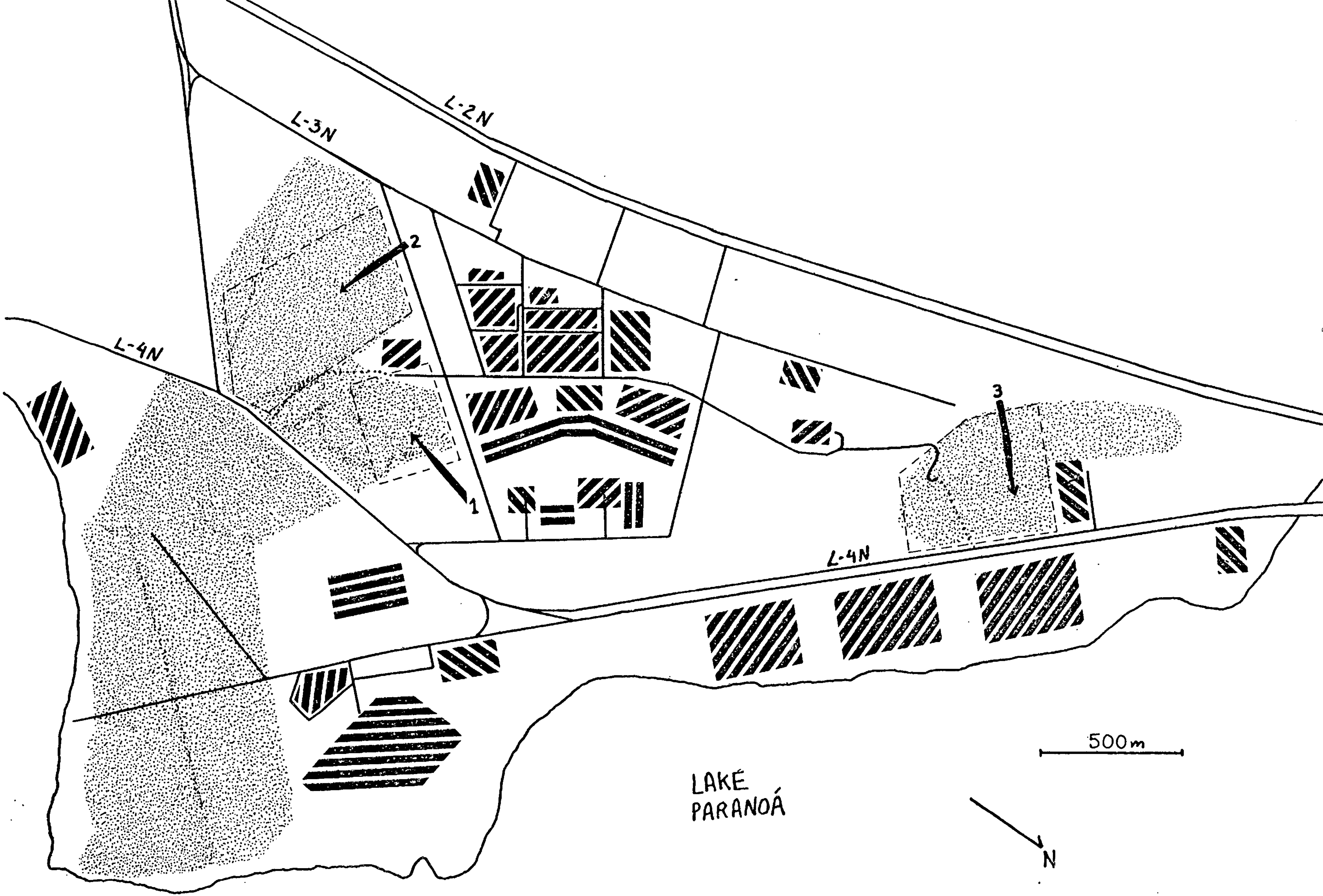
by 1975 all the natural communities in the central portion of the campus had been destroyed and substituted by buildings, car parks, roads and parks. A large block of Cerrado and Campo Cerrado remained in the southern/southeastern sector (between the lake margin and L-3N avenue) as well as an isolated smaller block of woody Cerrado in the north-western sector (around the Animal Breeding Unit). By 1978 these relic areas had been further reduced, including the area of site 1. By the time the last observations were made in the campus for this study in 1979, the area still covered by relic natural communities represented less than 15% of the total campus area.

The most common shrubs and trees in the Cerrado and Campo Cerrado in the southern sector of the campus during the period of study were: *Bauhinia* spp, *Anacardium* sp, *Zeyera montana* Mart., *Smilax* sp, *Connarus fulvus* Planch., *Erythroxylum suberosum* St.Hil., *E. tortuosum* Mart., *Psidium* sp, *Anona* spp, *Palicourea rigida* H.B.K., *Tocoyena* sp, *Styrax ferrugineum* Nees & Mart., *Stryphnodendron adstringens* (Mart.), *Pouteria* sp, *Kielmeyera coriacea* Mart., *Dimorphandra mollis* Benth., *Didymopanax* sp, *Cayaponia spelina* (Manso), *Byrsonima* spp and *Eriotheca pubescens* (Mart. & Zucc.).

SITE 1 - A small area (about 6 ha) of low Campo Cerrado at the south end of the ICC Building and east of the Tropical Medicine Institute, in the southern sector of the campus (Figures 3.2, 5.5). A fairly natural patch of Campo Cerrado with a predominance of grasses and low shrubs and with only a few dwarf trees. Fire damage frequent. 34 shrubs of *Eriotheca pubescens* (the host of *Themos olfersii*) were found in the centre of the patch within an area of 6500 m^2. These shrubs ranged from only 20 cm tall to 1.5 m high, but most were only 20 to 50cm high. Intensive studies on the *T. olfersii* population were conducted in this site. The site was destroyed in May of 1978 to make space available for the new Faculty of Medicine Building.

SITE 2 - A larger area with about 40 ha of typical Cerrado south of the Tropical Medicine Institute, east of L-3N avenue and west of L-4N avenue in the south-western corner of the campus (Figures 3.3). A natural patch of Cerrado with predominance of shrubs and dwarf trees and with a few tall trees. There was a far greater population of

FIGURE 3.3. Campus of the University of Brasília. The built-up areas are shown stripped and the areas covered by natural Cerrado vegetation, during the study period, are shown stippled. The three study sites are indicated by the traced lines and their code numbers.


L-2N
L-3N
L-4N
2
1
3
L-4N
500m
LAKE PARANOÁ
N

Eriotheca pubescens with more than 1,000 individuals of all sizes from low shrubs to tall trees 10 - 15 m high and trunk girths of up to 200 cm. The T. olfersii population was small though. Supplementary studies on T. olfersii were conducted here. Fire damage frequent.

SITE 3 - A patch of about 25 ha of woody Cerrado beside the Animal Breeding Unit in the north-western sector of the campus (Figure 3.3). A natural patch with predominance of medium and tall trees. A few dozen trees of Sclerolobium aureum (Tul.)(the host of Dielocerus diasi) were found in this site. They maintained a good population of D. diasi. One of these trees (no. 3/2) has been chronically infested by this sawfly since before 1970. Intensive studies were made in this tree. Fire damage frequent.

Sites 4 - 6 were located in other sectors within the city of Brasília. The floristic composition for all these sites is similar to that given for the University campus (see also Péllico Netto, 1972).

SITE 4 - A small patch of woody Cerrado in the western sector of the city near the Cruzeiro District, with some 10 ha (Figure 3.2). More disturbed by man than the earlier 3 sites. Had a small population of Sclerolobium aureum trees and a small population of D. diasi. Supplementary observations on D. diasi were made here. Fire damage frequent.

SITE 5 - A very small patch of woody Cerrado (c. 2 ha) in the South Lake residential District, between Conjuntos 9/13 and 9/15 (Figure 3.2). A relic of a much larger woody Cerrado patch mostly destroyed only a few years earlier. Contained several S. aureum trees of all sizes with a good D. diasi population (one of the trees was chronically infested), and several E. pubescens small trees and shrubs with a small T. olfersii population. Intensive studies on D. diasi and supplementary observations on T. olfersii were made at this site. Fire damage frequent.

SITE 6 - A large patch of woody Cerrado of about 50 ha in the South Embassies Sector of the City, along the Avenida das Nações (Figure 3.2). The understory vegetation was disturbed by repeated cutting. Trees were untouched. A large population of S. aureum trees of all sizes (some with more than 10 m high and with a trunk girth of more than 250 cm) occurred here, as well as a small number of E. pubescens shrubs.

A large population of *D. diasi* frequented this site since before 1970. Some *S. aureum* trees were chronically infested. Intensive studies on *D. diasi* were made here. Fire damage frequent.

The other sites were located outside the City in larger patches of natural communities of Cerrado.

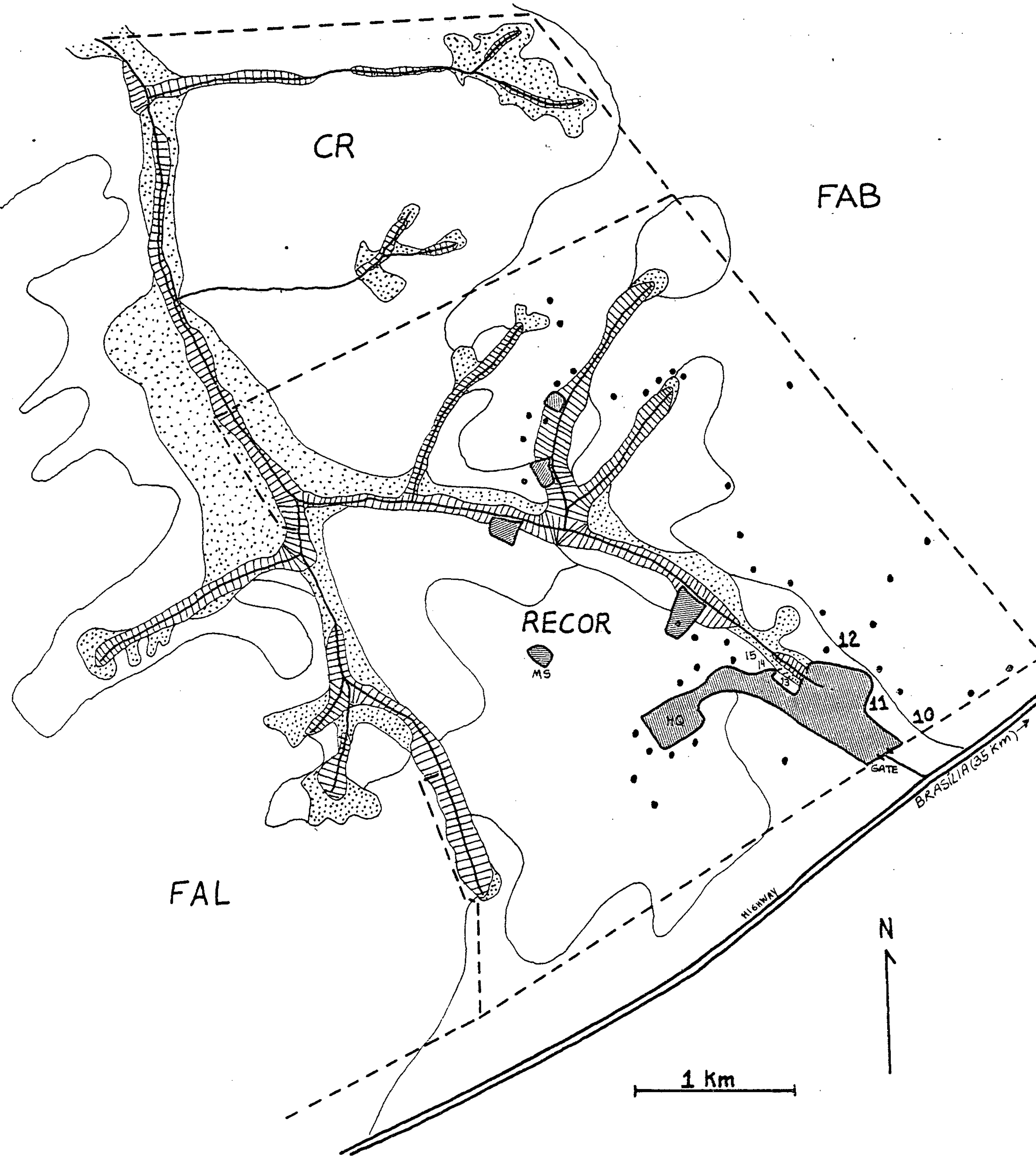
SITE 7 - A very large area of woody Cerrado with several hundred hectares along the Brasília-Formosa highway (BR 020) between the town of Planaltina and the Aguas Emendadas Biological Reserve in the north-eastern sector of the Federal District. Harboured a very large population of *S. aureum* trees with a small population of *D. diasi*. Several major observations on *D. diasi* were made in this site. Fire damage frequent.

SITE 8 - A large area of woody Cerrado with over a hundred hectares near the Brasília International Airport and along the Airport access road, just outside the city of Brasília to the south (Figure 3.2). The understory vegetation of part of the area was disturbed by repeated cutting. Trees were untouched. Had a large population of *S. aureum* trees and saplings with a large population of *D. diasi*, under observation since 1970. Some trees were chronically infested. Intensive studies on *D. diasi* were carried out here. Fire damage frequent.

SITE 9 - A large area of Cerrado and Campo Cerrado on a rocky hillside near the Sobradinho roundabout (BR 020) with about one hundred hectares just outside the City of Brasília to the north (Figure 3.2). Had a large population of *S. aureum* trees and saplings and a few *E. pubescens* shrubs, and a small population of *D. diasi*. Only supplementary observations on *D. diasi* were made here. Fire damage frequent. The natural communities were destroyed in 1978 and substituted by *Eucalyptus* forest.

Sites 10 - 15 were located inside the IBGE Ecological Reserve situated 10 km south of Brasília (Figures 3.2 and 3.4). This reserve has about 2,000 ha, of which about 90% is covered by protected natural communities. Most of the reserve is covered by Cerrado and Campo

FIGURE 3.4. IBGE Ecological Reserve in Brasília. Gallery rain forests are shown stripped, swamp grasslands are shown stippled, areas with cerrado are left in blank, built-up areas and areas with altered vegetation are shown shaded. The boundaries of the IBGE Ecological Reserve (RECOR) are indicated by traced lines. HQ=headquarters, MS=metereological station, FAB=Brazilian Air Forces Estate, CR=Cristo Redentor Estate, FAL=Agua Limpa Experimental Farm (University of Brasília). The major study sites are indicated by their code number and other sites by dots.


CR
FAB
RECOR
MS
FAL
15
14
13
12
11
10
MQ
GATE
BRASILIA (35 Km)→
HIGHWAY
N
1 Km

Cerrado communities, but swampy grasslands, Veredas, Gallery rain forests and woody Cerrado are also common. The reserve is well protected against fire and hunting and is surrounded by other protected areas: Agua Limpa Ecological Reserve and Experimental Farm, Cabeça do Veado Biological Reserve, and the large protected estates owned by FAB-Brasilian Air Forces and Escola Fazendária (Figure 3.2). Since 1973 no major fire has been recorded inside the reserve. The reserve has several facilities: laboratories, library, metal and wood workshops, cafeteria, gas station, vehicles and sleeping accommodation.

SITE 10 - A small patch of low Campo Cerrado (Campo Sujo) in the southern sector of the Reserve near the entrance gate (Figure 3.4). Has a small population of E. pubescens shrubs and small trees, with a small population of T. olfersii. Only supplementary observations were made here.

SITE 11 - A small patch of low Campo Cerrado in the southern sector of the Reserve near Orchard I (south)(Figure 3.4). Has a small population of E. pubescens shrubs and small trees with a small population of T. olfersii. Only supplementary observations on T. olfersii were made here.

SITE 12 - A small patch of Cerrado in the southern sector of the Reserve near Orchard I (north)(Figure 3.4). Has a good population of E. pubescens and S. aureum with a small population of T. olfersii and D. diasi. Only supplementary observations on both species were made here.

SITE 13 - A small patch of Campo Cerrado (Campo Sujo) behind and to the sides of the Field Zoology Laboratory at the Roncador stream (Figure 3.4). The area was seriously disturbed in the past, but several Cerrado shrubs have produced healthy regrowths including E. pubescens which has a large population here now. There are also some large E. pubescens trees in this area. Several weedy grasses and shrubs have invaded this area though. Intensive studies were made on the small T. olfersii population of this site. Several T. olfersii larval groups collected in other places were introduced in this site to increase the original population and to make observations easier.

SITE 14 - A small patch of Cerrado beside the Field Zoology Laboratory at the Roncador stream (Figure 3.4). Has a good population of *S. aureum* trees and saplings with a small population of *D. diasi*. This population was increased by repeated introductions of larval groups and cocoon masses collected in other places. Supplementary studies on *D. diasi* were made here.

SITE 15 - A large patch of Cerrado beside the Field Zoology Laboratory at the Roncador stream, opposite site 14 (Figure 3.4). Has a large population of *S. aureum* trees and saplings with a good population of *D. diasi*. This population was also increased by repeated introductions of larval groups and cocoon masses collected in other places. Intensive studies on *D. diasi* were conducted here.

3.2 THE HOST PLANTS OF *THEMOS OLFERSII* AND *DIELOCERUS DIASI*

The host plant of *T. olfersii* in the Federal District is *Eriotheca pubescens* (Mart. & Zucc.)(Bombacaceae)(Figure 3.5). *Eriotheca* was until recently treated as a subgenus of *Bombax* sensu lato. As in a few other related genera, all species of *Eriotheca* produce good fibers and abundant kapok, but remain at the moment underexploited economically. *Eriotheca* is a small genus with some 19 species restricted to South America above latitude 20° South, mainly east of the Andes (Robyns, 1963).

Only three species of this genus occur in the Central Brazil biome: *E. candolleana* (K. Schum.) which is restricted to gallery rain forest communities (recorded from Goiás, Minas Gerais, Espírito Santo, Rio de Janeiro and São Paulo states); and two species restricted to Cerrado communities, *E. gracilipes* (K. Schum.)(recorded from Mato Grosso, Goiás, Minas Gerais and São Paulo states and Paraguay), and *E. pubescens* (recorded from Goiás, Minas Gerais and Federal District states)(Robyns, 1963). *E. pubescens* is the only *Eriotheca* found in the Federal District.

E. gracilipes is very close to *E. pubescens* morphologically and could be used as an alternative host by *T. olfersii* in places where *E.*

FIGURE 3.5. Low shrub of *Eriotheca pubescens* (Mart. & Zucc.) (Bombacaceae), the host plant of *Themos olfersii*. This shrub is about 30 cm high. Picture taken at the begining of the rainy season at site 1.

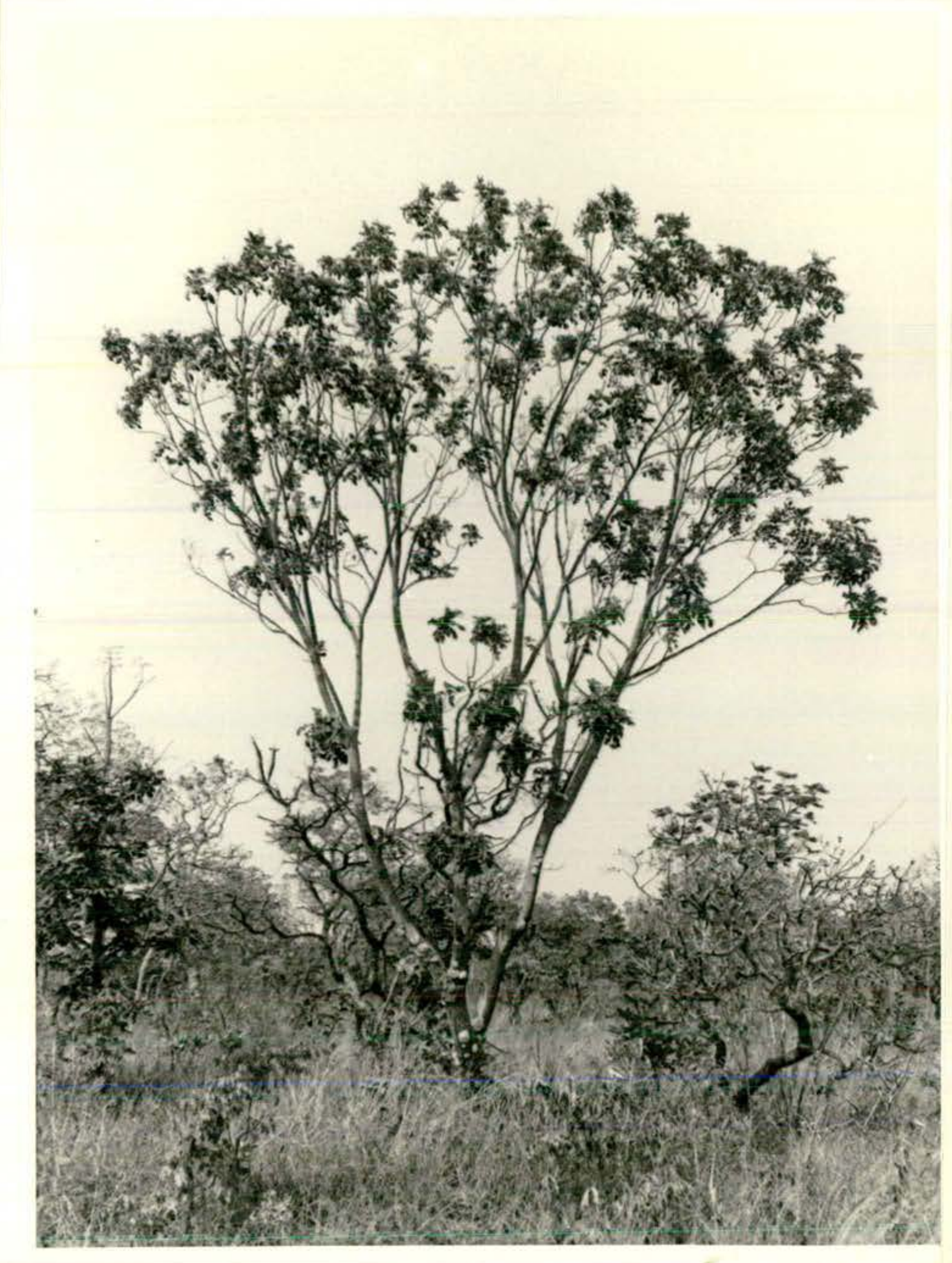
pubescens does not occur. I have seen in Museums female T. olfersii specimens with egg clusters attached to Eriotheca leaves which were collected in southern Goiás (Leopoldo Bulhões and Vianópolis) near the Federal District and in central São Paulo state (São Carlos).

E. pubescens and E. gracilipes are among the tallest trees in the Cerrado community reaching 15 m high. As all Eriotheca, both have palmate leaves with 5 to 7 large thick and hard leaflets, which are pubescent initially but glabrous and wax-covered afterwards. They grow slowly and have tuberous roots. They flower during the dry season, May to September. Some trees loose all their leaves when in flower.

E. pubescens, locally called "paineira do campo", is one of the commonest tree species in the Cerrado of the Federal District, but individuals in the shrub-state far outnumber those in the tree-state. Even so, taking only the specimens with tree habit in consideration, E. pubescens is the 17th most abundant tree in woody Cerrado and the 11th most common in Campo Cerrado communities of the Federal District, with an average of 2.5 trees per hectare (Péllico Netto, 1972). It is unevenly distributed in the Cerrado of the Federal District: it exhibits a highly aggregated patchy distribution. The number of saplings is always high around the large mature trees. It is specially common on open Cerrado and Campo Cerrado communities. It is very resistant to fire due to its large tuberous root. When the Cerrado is burnt in the dry season, the aerial parts of E. pubescens shrubs are totally destroyed, but they produce a fresh and abundant regrowth shortly afterwards, while still in the middle of the dry season.

The host plant of D. diasi in the Federal District is Sclerolobium aureum (Tulasne)(Leguminosae, Caesalpinoidea)(Figure 3.6). The genus Sclerolobium is restricted to tropical South America and has about 34 species (Dwyer, 1957). Only 3 species of Sclerolobium occur in the Central Brazil biome: S. rugosum Martius which is restricted to the gallery rain forest communities (also in the Atlantic rain forest in southeastern Brazil), S. paniculatum Vogel in the Deciduous forests communities (Mata Seca and Cerradão) and along the edge of gallery rain forest, and S. aureum which is restricted to the Cerrado communities (Dwyer, 1957). Of these, only S. aureum and S. paniculatum occur in the Federal District. However, there is a third apparently undescribed

FIGURE 3.6. Medium-sized tree of Sclerolobium aureum (Tulasne) (Leguminosae), the host plant of Dielocerus diasi. This tree is about 8-10 metres high. Picture taken at the begining of the rainy season at site 3. Cocoon masses of D.diasi are visible on its trunk and lower branches.



species of Sclerolobium with thick bark (cork) in the woody Cerrado of the Federal District.

A few cocoon masses of D. diasi were found on the trunk and branches of S. paniculatum trees in the IBGE Ecological Reserve, indicating that this species is also acceptable as host.

S. paniculatum has a wide distribution, from the amazonian Peru to the Brazilian Amazon and south to Rio de Janeiro and São Paulo states. S. aureum also has a wide distribution, including Venezuela, central and southeastern Brazil (Mato Grosso, Goiás, Minas Gerais, Bahia, Rio de Janeiro and São Paulo states) and Paraguay.

Both species are used to make charcoal, and accordingly their local name is "carvoeiro". Both are relatively tall trees reaching more than 10 m high and a girth of about 250 cm. They have paripinnate leaves with large thin leaflets, which are covered by dense golden pubescence of short hairs on the lower (abaxial) surface.

S. aureum is the 4th most abundant tree species in the Cerrado of the Federal District, with an average of 7.25 trees per hectare (Péllico Netto, 1972). It is unevenly distributed though, exhibiting a highly aggregated patchy distribution. It is specially common on the top of plateaux, on hillsides and rocky grounds. It is usually the dominant tree where it occurs. It is not found in Campo Cerrado communities. Numerous saplings are always found near large mature trees. It is not much resistant to fire.

See summary of the host plant associations of Argid sawflies in Appendix II.

CHAPTER 4. TEMPORAL DISTRIBUTION

MATERIALS AND METHODS

Host plants were inspected at all times of the year for the presence of active stages of the sawflies. Leaflets with adult females, egg clusters and larval groups were numbered at the apex with a pointed pencil, and the host shrubs or trees were numbered with china ink on hard paper labels covered with wax. Detailed maps were prepared for each study site indicating the exact position of each host plant. These maps were up-dated at the start of each new season. Most observations on *T. olfersii* were done at site 1 and on *D. diasi* at sites 5 and 15, at daily or three times a week intervals. The dates of egg laying, egg hatching, spinning of communal cover of cocoon mass (in *D. diasi*) or digging in the soil (in *T. olfersii*), adult emergence from cocoon and adult female death were recorded to the nearest day.

No attempt was made to measure the duration of each larval instar individually, nor the durations of the larval, prepupal, pupal and adult stages inside the cocoon before emergence.

Cocoons were kept in the laboratory to complement field observations on the duration of the cocoon stage (= period from the time the larvae dig under the soil (in *T. olfersii*) or spin the communal cover of the cocoon mass (in *D. diasi*) until the time when the adults emerge) in the different generations along the year, with or without dormancy or prolonged dormancy. These cocoons were kept at room temperature and humidity similar to those in the natural environment, each cocoon mass (*D. diasi*) or group of cocoons derived from one larval sib-group (*T. olfersii*) was kept in a separate container with perforated top. *T. olfersii* cocoons were kept buried in the soil inside the containers.

A record was kept, for some large cocoon masses of *D. diasi*, of the time of each adult's emergence and its position within the cocoon mass.

The number of *T. olfersii* sib-groups at the egg, larval (= from hatching until digging into the soil) and cocoon stages per week was recorded for 3 spring generations (1973, 1974 and 1977) and for 1 summer generation (1978) at site 1.

4.A THEMOS OLFERSII

There are two distinct synchronous generations of *Themos* per year in the Federal District (bi-voltinism): a spring generation (named after the season when the eggs are found) from October until March, or in some years until May, and a summer generation from January until December.

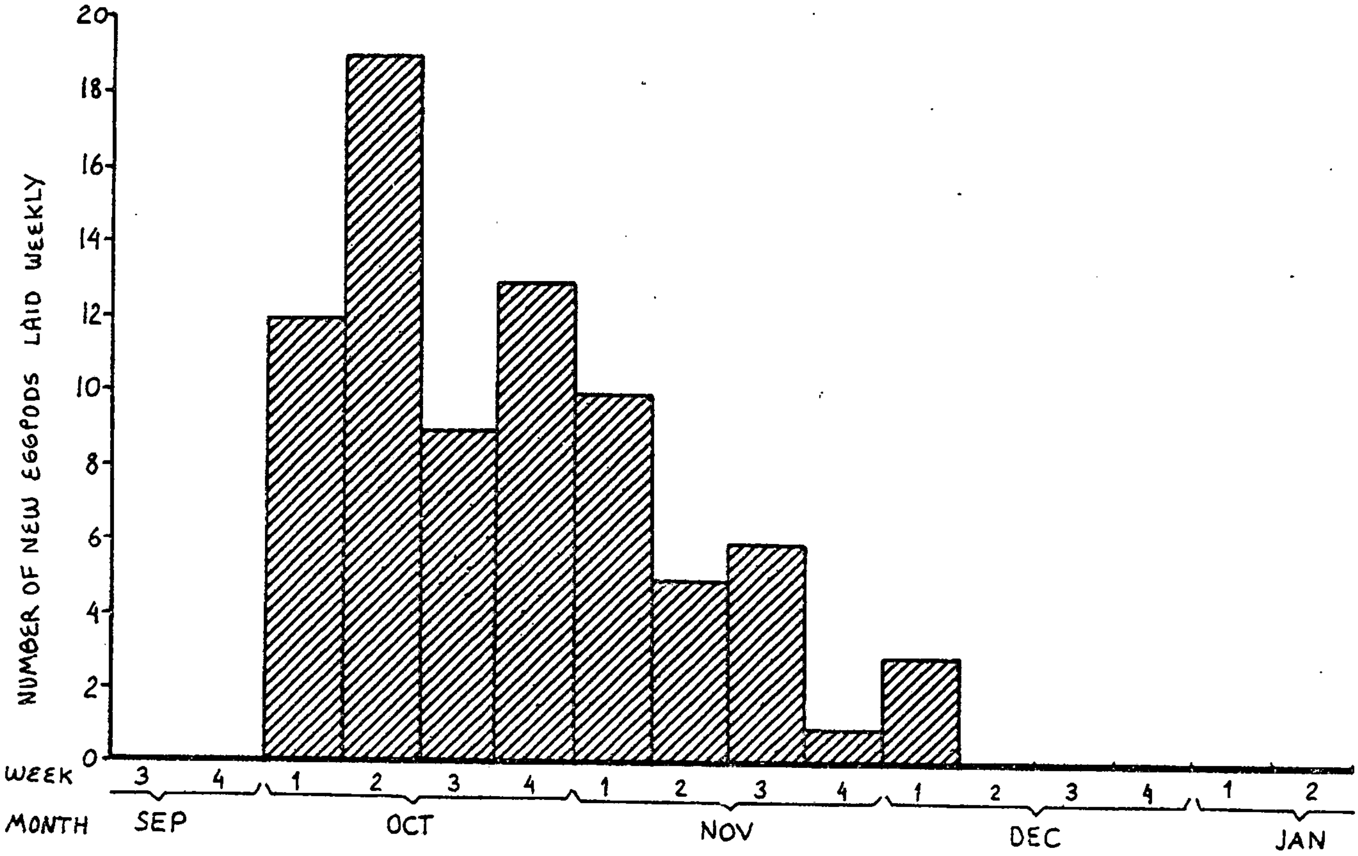
4.A.1 EGGS

The incubation period for *Themos* eggs is in average three weeks ($\bar{x}$ = 21.4 days; N = 9 egg clusters; range = 19-23 days). Approximate values for 25 other egg clusters confirm this. The length of the incubation period was the same during the four generations studied (spring and summer) and also constant within any one generation. All or most of the eggs in a cluster hatch on the same day, within a few hours.

After the dry season (May to September), the first egg clusters of *Themos* are laid at the beginning of October (early spring). Many (40%) egg clusters are laid during the first two weeks of October. The number of clusters laid weekly then reduces gradually until the first week of December when the last clusters of the spring generation are laid (Figure 4.1). The egg laying curve for the spring generation is very asymmetric thus, with a sharp rise and a slow and tailed decrease. The egg laying period therefore lasts 9 weeks. The eggs start to hatch during the fourth week of October. Many (50%) eggs hatch between the end of October and the middle of November. The hatching continues, but in smaller numbers, until the end of December (Figure 4.2). The hatching period thus lasts also 9 weeks from the end of October to the end of December. The cumulative frequency distribution of egg clusters of all ages present per week (Figure 4.3) is more normal-shaped and has the modal class at the fourth week of October.

By the third or fourth week of December the first egg clusters of the second (summer) generation of *Themos* are laid.

The number of clusters laid weekly increases gradually until the first week of February. Thereafter the rate of egg laying decreases



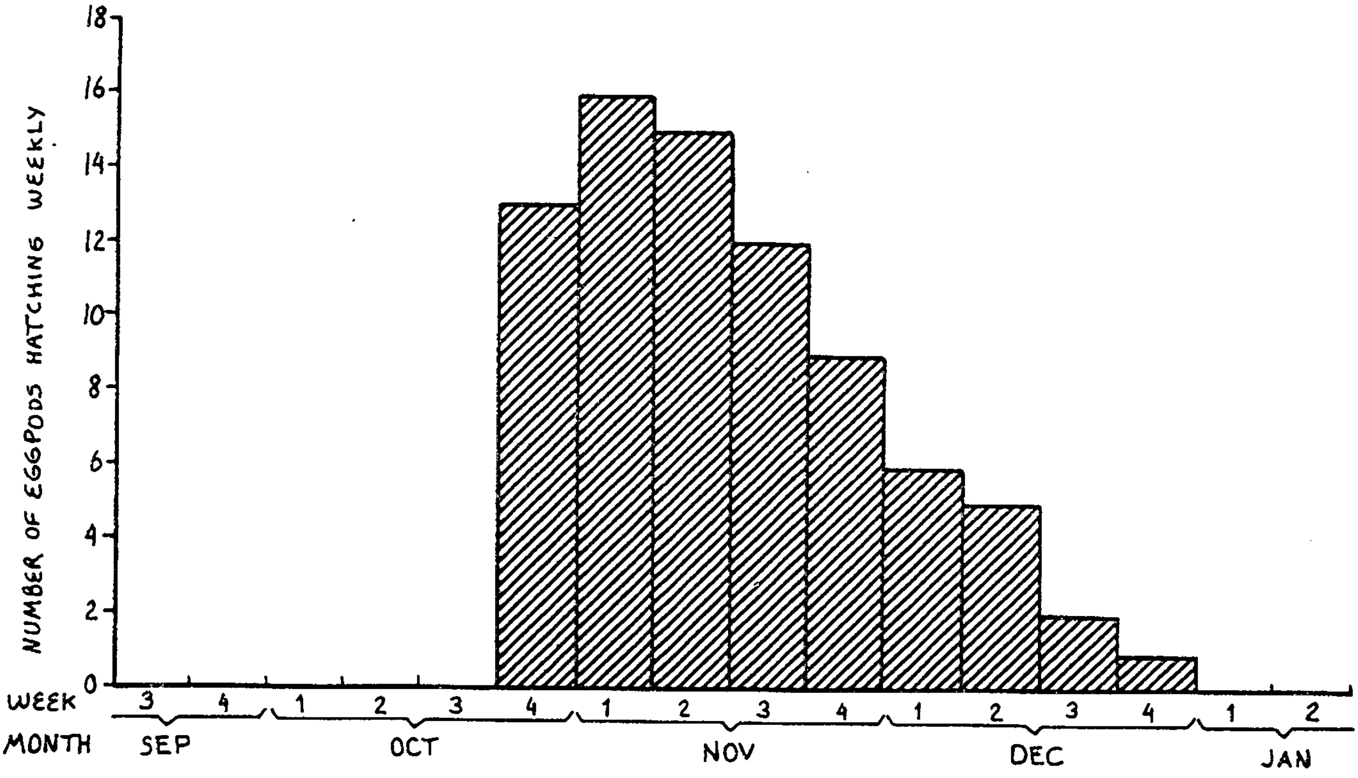


FIGURE 4.1 (top). Frequency distribution of new egg clusters of Themos olfersii laid weekly in the spring generation at study site One. Sum of the three years: 1973, 1974 and 1977. N=78 egg clusters.

FIGURE 4.2 (bottom). Frequency distribution of Themos olfersii egg clusters hatching weekly in the spring generation at study site One. Sum of the three years: 1973, 1974 and 1977. N=78 egg clusters.

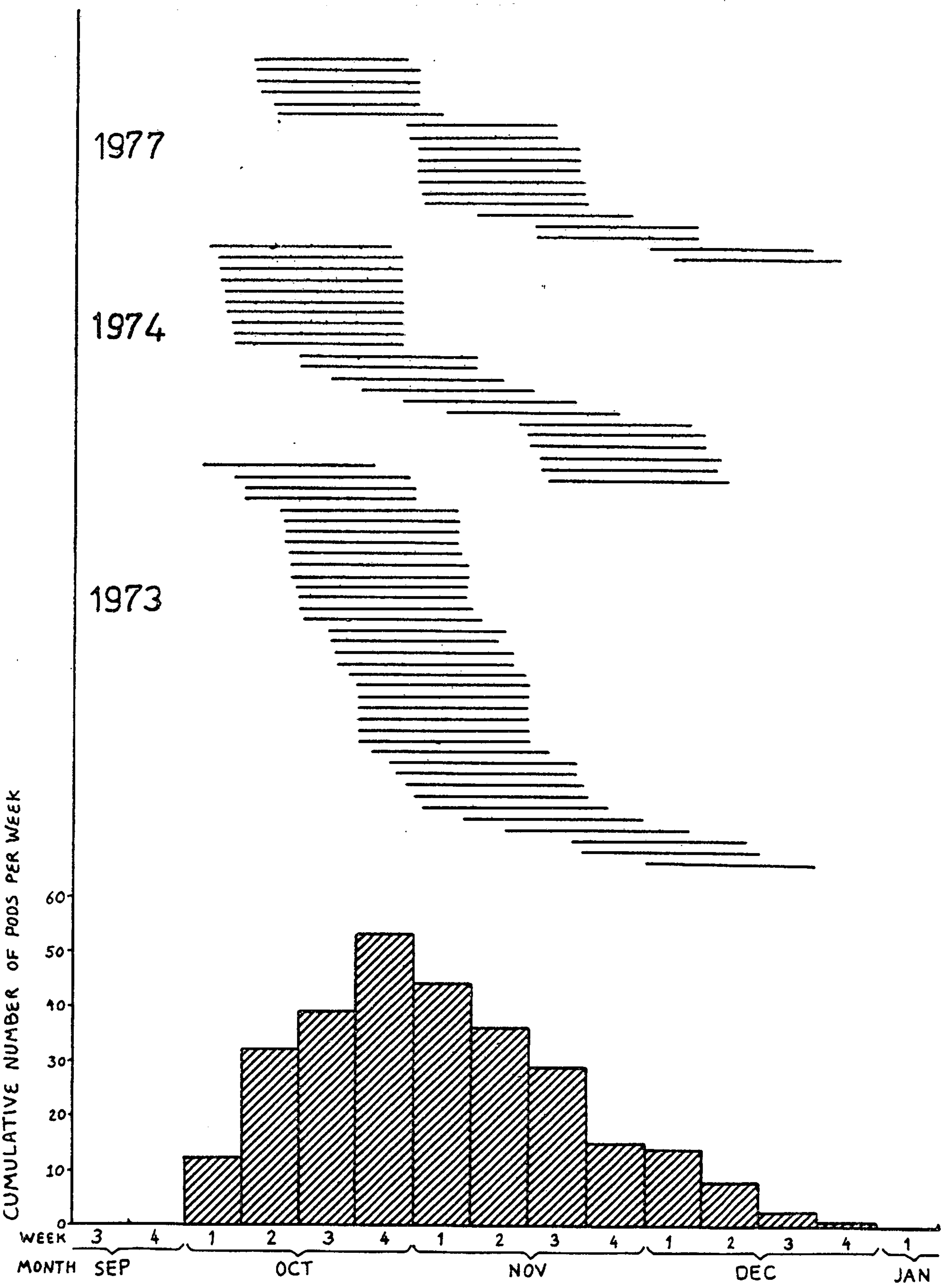


FIGURE 4.3. Temporal distribution of Themos olfersii egg clusters in the spring generation at study site One. Each horizontal bar represents one egg cluster in time, from laying until hatching. The last three weeks of December of 1974 were not documented. The bottom histogram gives the cumulative frequency distribution of egg clusters of all ages present per week, for the three years studied. N=78 egg clusters.

gradually until the third week of March when the last clusters of this generation are laid (Figure 4.4). The egg laying curve for the summer generation is much less asymmetric than that for the spring generation. The egg laying period therefore lasts 12 weeks. The first eggs hatch during the third week of January and the last ones hatch during the second week of April. The peak of egg hatching occurred at the last week of February (Figure 4.5). The egg hatching period thus lasts for 12 weeks. The maximum number of egg clusters of all ages occurs at the middle of February (Figure 4.6).

No more eggs of Themos were laid in the study site One after March and until October in most years. The same was found in the several other sites studied. But in early May of 1975 at site One several egg clusters halfway through their incubation were found. These were laid at about the middle of April and probably represented the last clusters laid during the summer generation in that year. In the summer of 1979 at study site 13 the last clusters were laid as late as the last week of March. There is no evidence of a third generation occuring in Brasília during the dry season (winter).

4.A.2 LARVAE

The first larvae of Themos of the spring generation emerge by the end of October. Most larval emergence takes place between the end of October and the middle of November. The last larvae emerge by the end of December. The emergence period lasts 9 weeks (Figure 4.2).

The larval feeding period, from emergence until burrowing in the soil for cocooning, takes 24 to 36 days, 30 days in average (N = 11 larval groups) in the spring. The spring generation larvae start to burrow in the ground at the end of November, and the last larvae burrow by mid-January. The peak of the burrowing occurs at the end of December (Figure 4.7). The burrowing period lasts 8 weeks. The maximum number of larval groups of all ages occurs at the end of November and beginning of December (Figure 4.8).

The first larvae of the summer generation emerge by the third week of January and the last ones at the second week of April. The peak

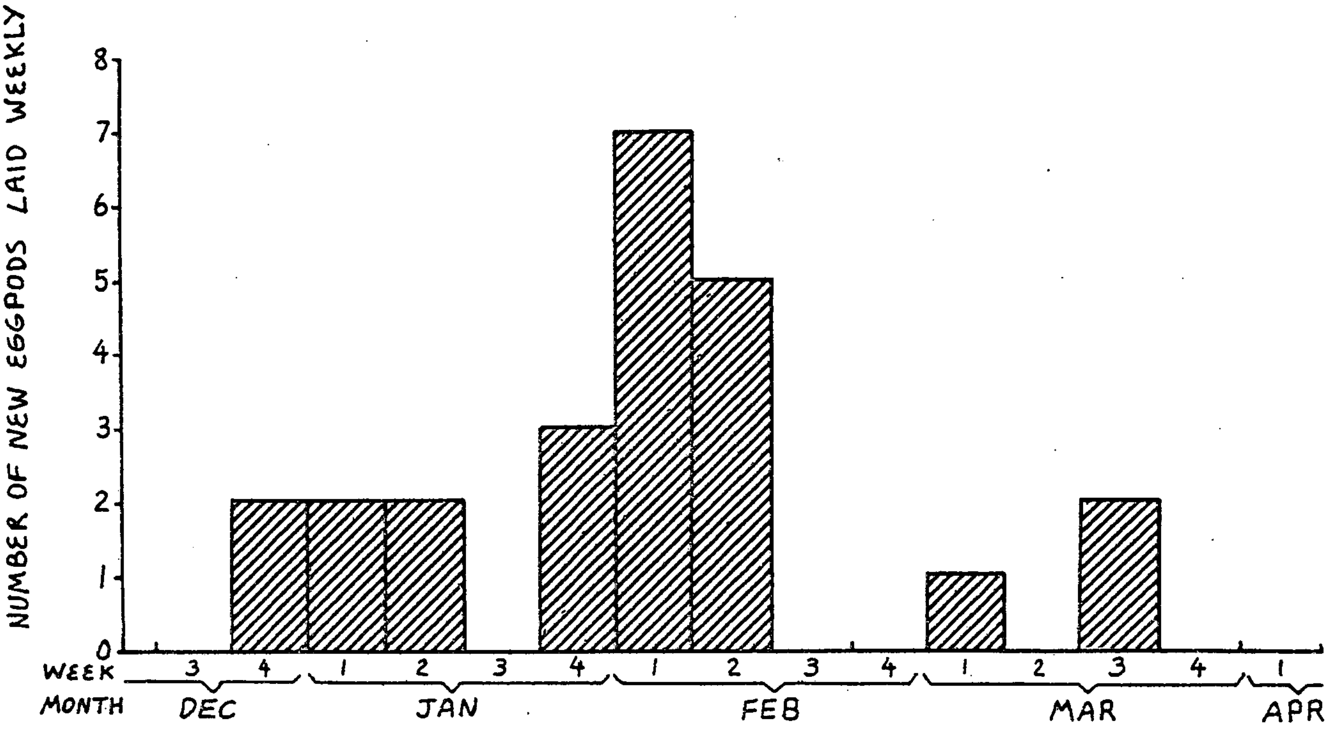


FIGURE 4.4 (top). Frequency distribution of new egg clusters of <u>Themos olfersii</u> laid weekly in the summer generation at study site One in 1978. N=24 egg clusters.

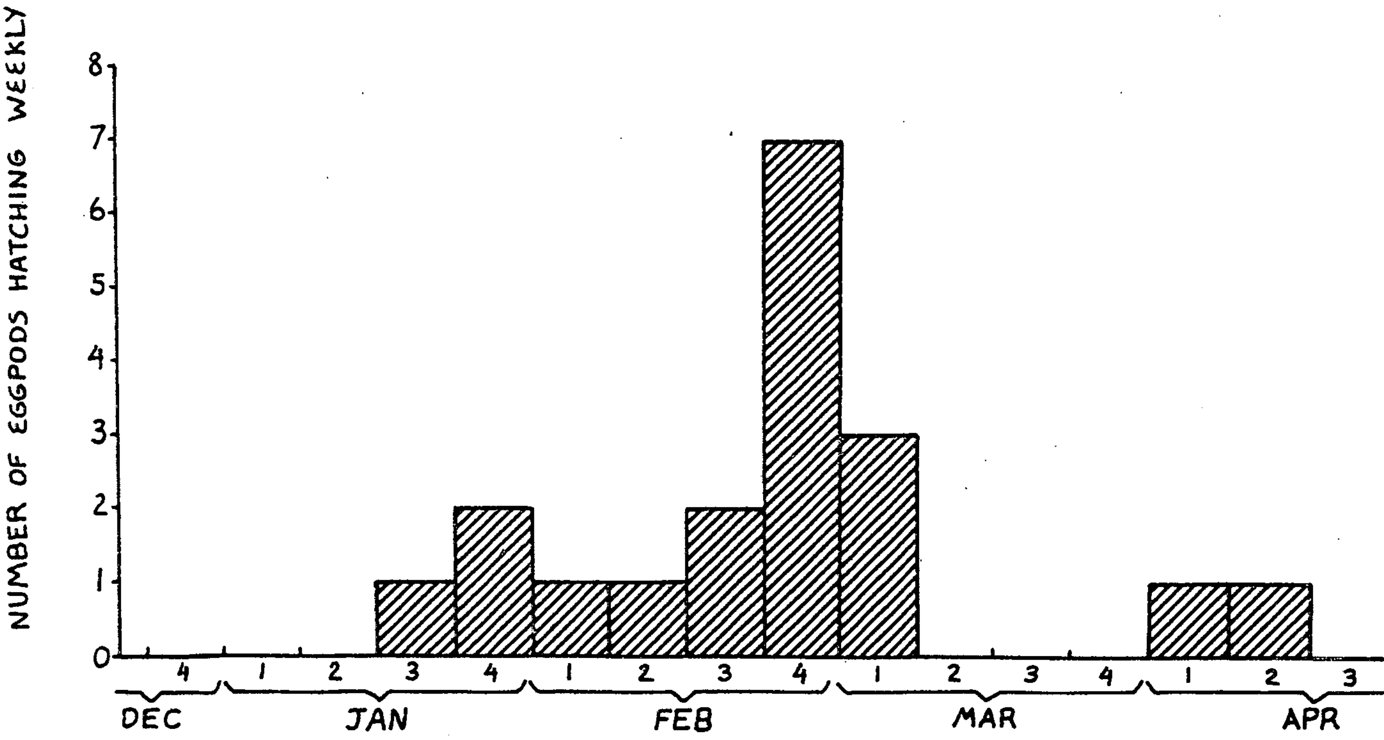


FIGURE 4.5 (bottom). Frequency distribution of <u>Themos olfersii</u> egg clusters hatching weekly in the summer generation at study site One in 1978. N=24 egg clusters.

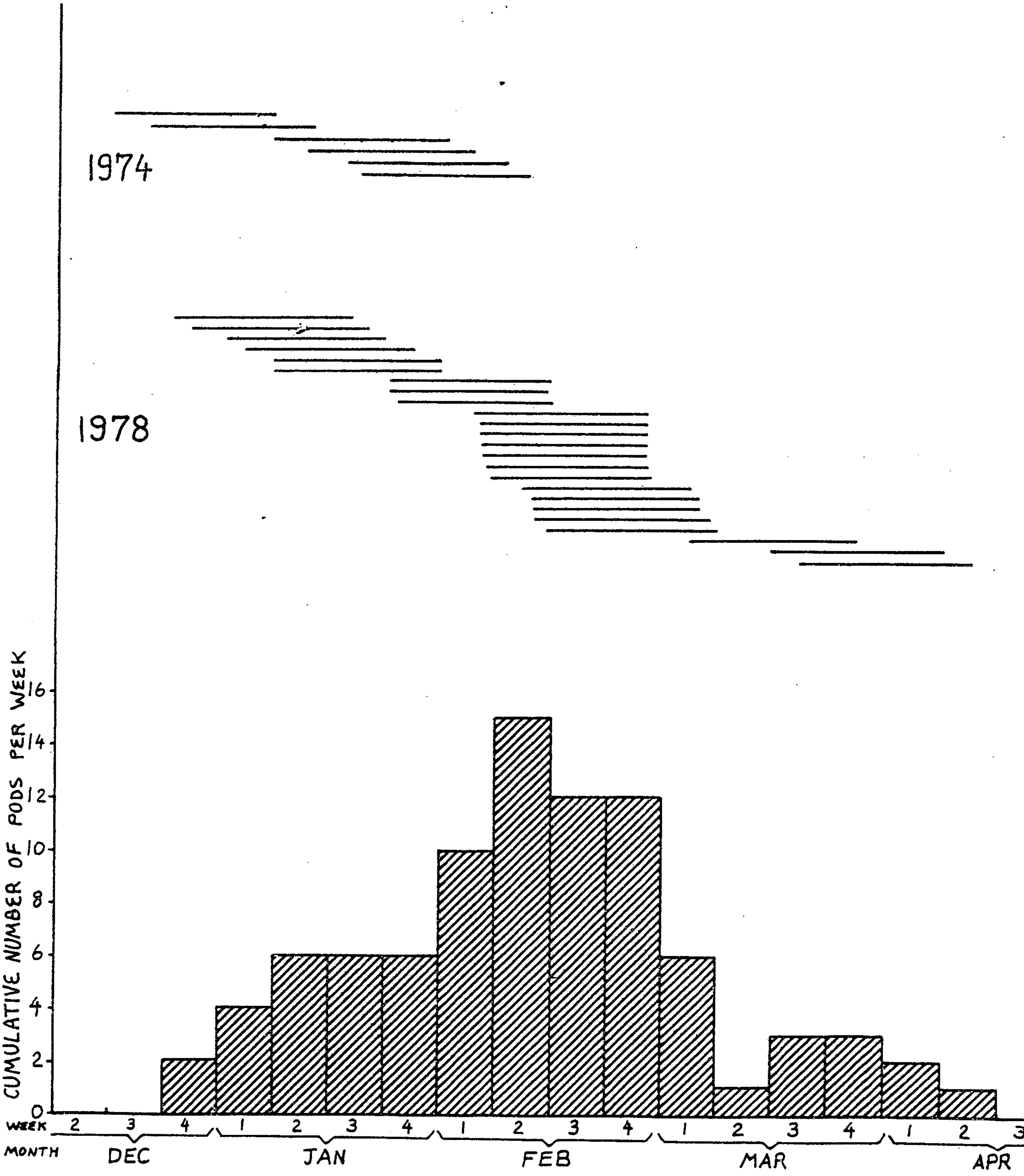
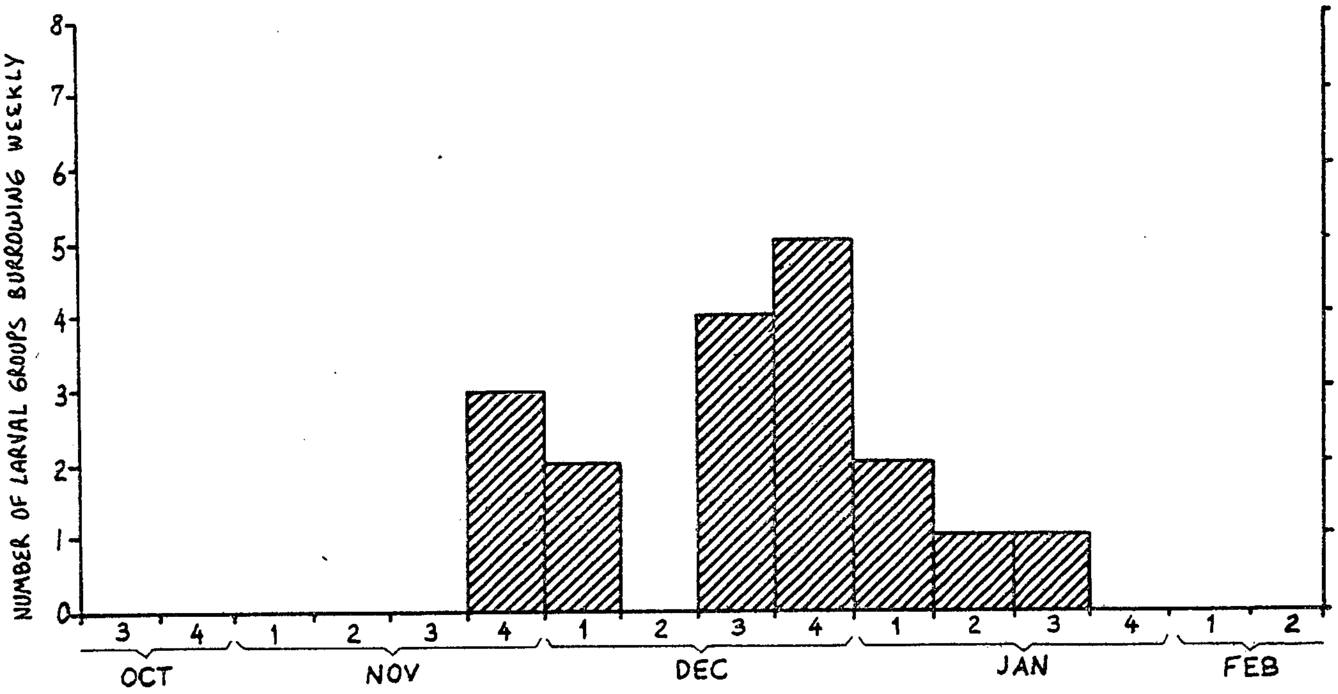


FIGURE 4.6. Temporal distribution of *Themos olfersii* egg clusters in the summer generation at study site One. Each horizontal bar represents one egg cluster in time, from laying until hatching. Only the first six egg clusters of the 1974 summer generation are shown. The bottom histogram gives the cumulative frequency distribution of egg clusters of all ages present per week for the 1978 summer generation. N=24 egg clusters.



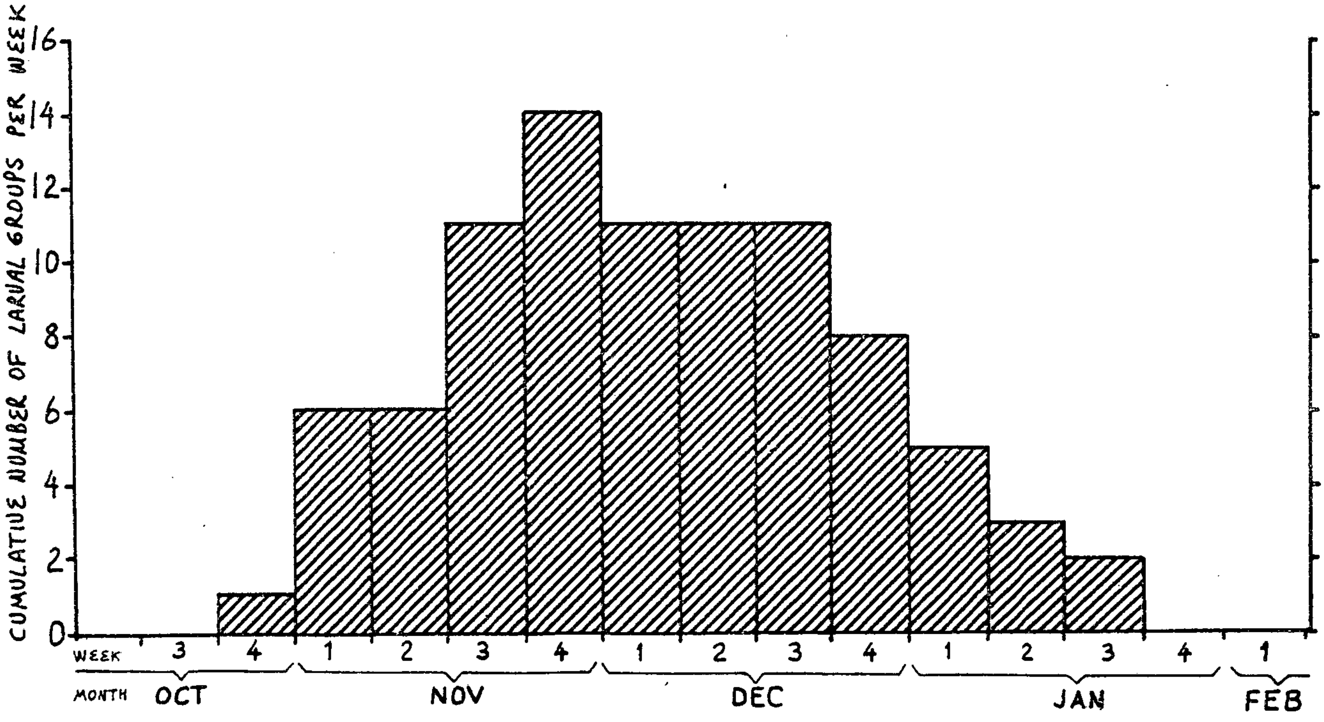


FIGURE 4.7 (top). Frequency distribution of <u>Themos olfersii</u> larval groups burrowing weekly in the soil to cocoon during the spring generation at site 1 in 1977/1978. N = 18 larval groups.

FIGURE 4.8 (bottom). Cumulative frequency distribution of <u>Themos olfersii</u> larval groups of all ages present per week in the spring generation at site 1 i 1977/1978. N = 18 larval groups.

of emergence is at the end of February and beginning of March. The emergence period lasts 12 weeks (Figure 4.5).

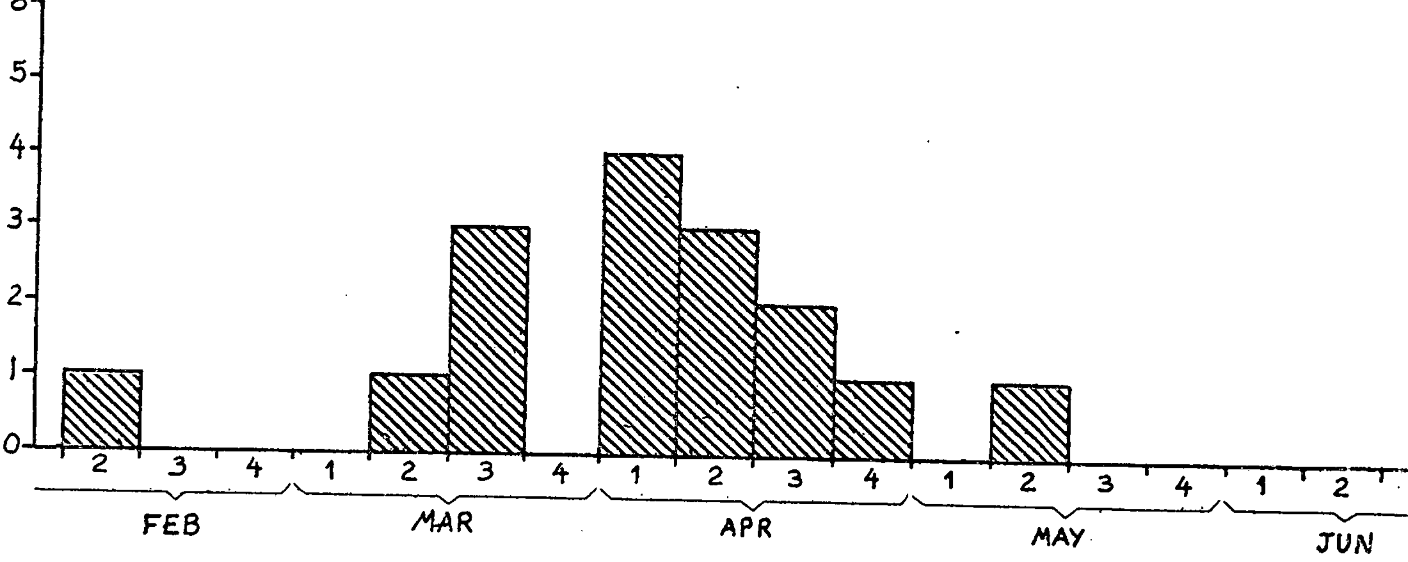
The larval feeding period takes 34 to 47 days, 40 days in average (N = 4 larval groups) in the summer. The larvae of the summer generation start to burrow in the ground at the second week of February and the last ones burrow by the second week of May. The peak of burrowing occurs during the first two weeks of April (Figure 4.9). The maximum number of larval groups of all ages occurs at the first two weeks of March (Figure 4.10). The late broods found in May of 1975 at site 1 hatched during the second week of May and their larvae completed their development and burrowed in the soil at the end of June.

4.A.3 COCOONS AND DORMANCY

The spinning of the cocoon in Themos starts almost immediately after burrowing and takes a couple of days. The frequency distribution of new cocoons spun per week thus virtually coincides with the burrowing distribution. The cocoon spinning period in the spring generation, thus, lasts 9 weeks from the end of November to the end of January, with a peak at the end of December (Figure 4.7). In the summer generation the cocoon spinning period lasts 12 weeks from the second week of February to the second week of May (occasionally until the end of June) with a peak at the first week of April (Figure 4.9).

The temporal distance between the larval burrowing curve of the spring generation of Themos and the egg laying curve of the summer generation indicates that the duration of the cocoon stage of the spring generation is about 30 days. This was confirmed twice in the laboratory in 1973 and 1974 with two groups of larvae taken from the field at the end of November in both years. The adults emerged on average 30 days after their cocoons were spun. Based on these informations, an estimated cumulative frequency distribution of cocoon groups of all ages present per week was calculated (Figure 4.11). The estimated peak of cocoon groups of all ages is between the end of December and the third week of January.

The prepupae of the summer generation enter in aestival dormancy at the onset of the dry season. The temporal distance between the



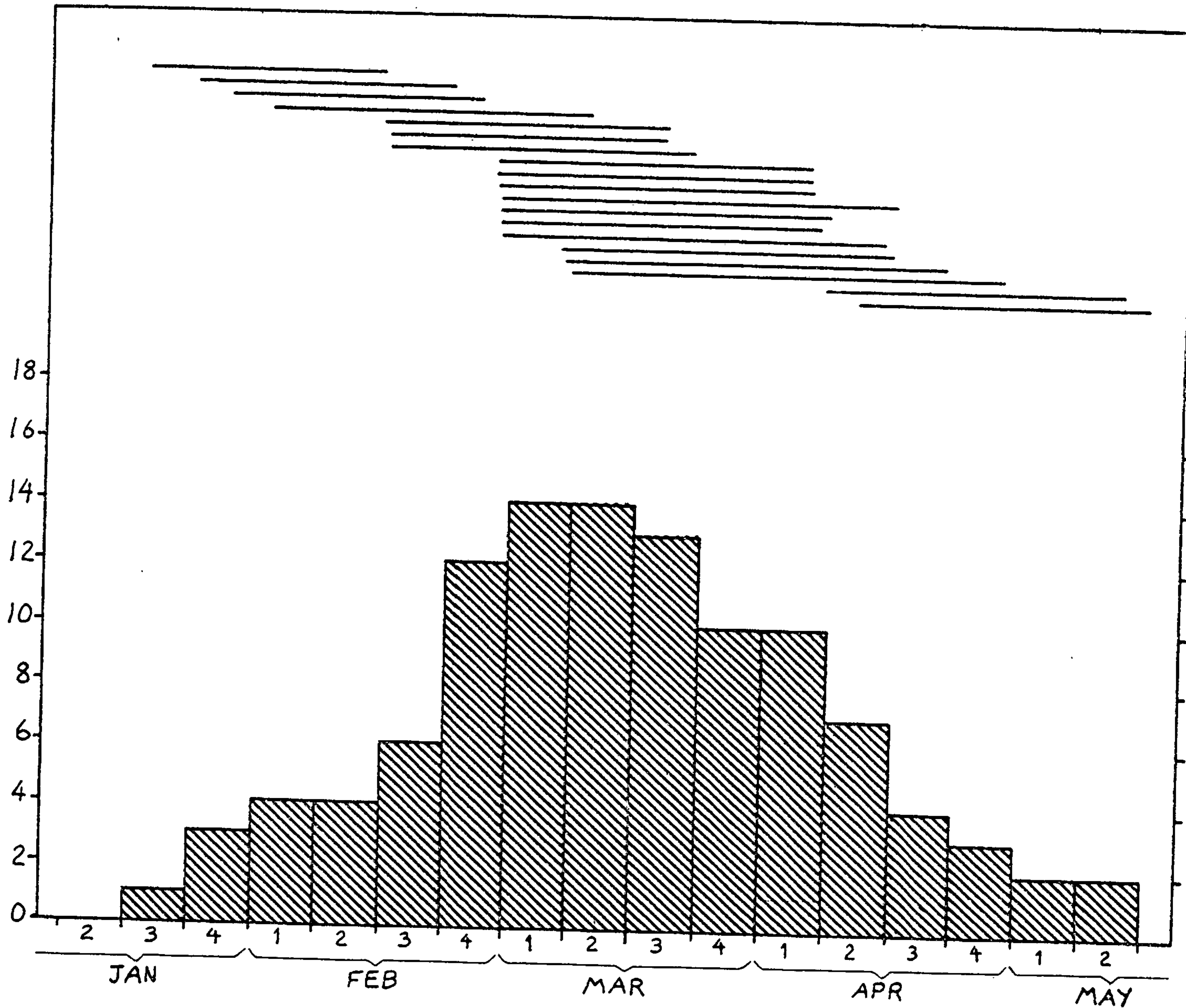
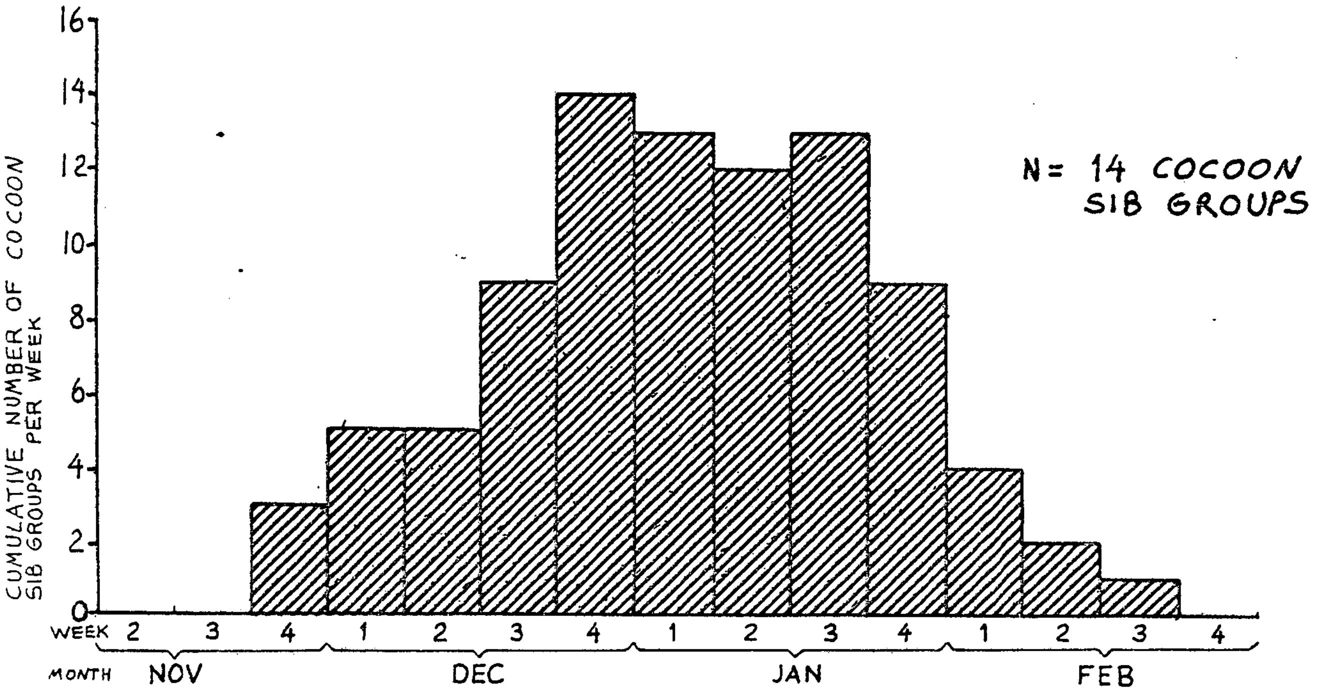


FIGURE 4.9 (top). Frequency distribution of Themos olfersii larval groups burrowing weekly in the soil to cocoon during the summer generation at site 1 in 1978. N = 16 larval groups.

FIGURE 4.10 (bottom). Temporal distribution of Themos olfersii larval groups in the summer generation at site 1 in 1978. Each horizontal bar represents one larval group in time, from hatching until burrowing. The bottom histogram gives the cumulative frequency distribution of larval groups of all ages present per week. N = 19 larval groups.



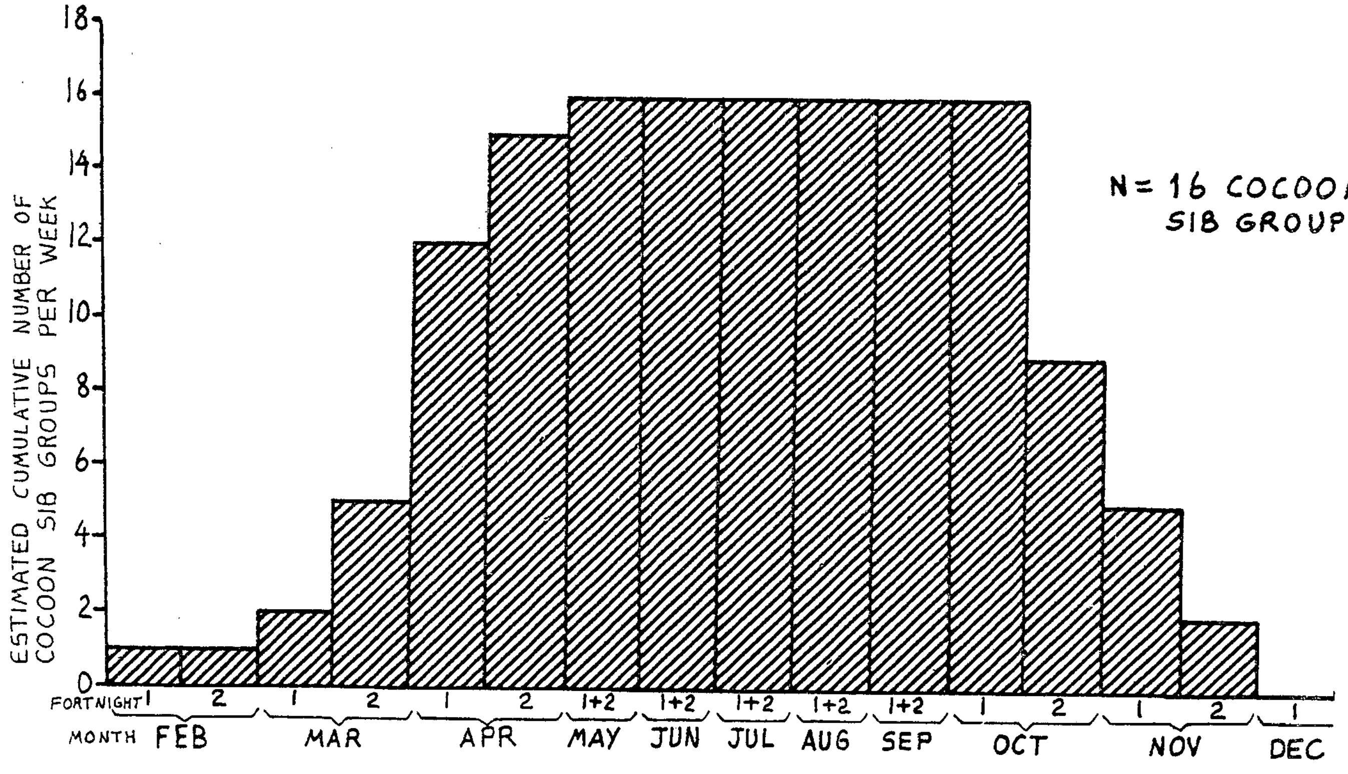


FIGURE 4.11 (top). Estimated cummulative frequency distribution of cocoon groups of Themos olfersii present per week in the spring generation at site 1 in 1977/1978.

FIGURE 4.12 (bottom). Estimated cummulative frequency distribution of cocoon groups of Themos olfersii present per fortnight in the summer generation at site 1 in 1978.

larval burrowing curve of the summer generation and the egg laying curve of the next spring generation indicates that the duration of the cocoon stage of the summer generation is about 210 days (seven and a half months). The dormancy is spent as prepupa, and lasts thus approximately 180 days. Based on these informations an estimated cumulative frequency distribution of cocoon groups of all ages present per fortnight was calculated (Figure 4.12). I do not know if the cocoons of Themos can stay in prolonged dormancy for more than one year. Larvae of the summer generation develop at the time of the year when the daylength decreases steadily whereas the larvae of the spring generation develop at a time when the daylength is maximum and virtually constant (Figure 4.13).

4.A.4 ADULTS

The pre-reproductive period is very short for adult female Themos, lasting apparently only one day for most females after emergence from the cocoon. Post-reproductive females have a relatively long life span of up to 5 weeks.

The temporal distribution of Themos adult females agrees closely with that of the distribution of the eggs (see Figures 4.1 - 4.6), except that females appear at least one day before the eggs are laid and die either before or up to 2 weeks after the eggs hatch. The adult female flying period for Themos is from early October to early December (spring generation) and from late December to late March, or occasionally until late May (summer generation).

Males were rarely found. The dates when these rare males were found are: 6 November 1973 (two), 14 February 1978, 11 April 1978 and 17 October 1978. Two other males emerged in the laboratory on 31 December 1973 and 10 January 1975 from cocoons spun in early December. Finally, 8 males were caught in February of 1979 in two Malaise traps. I have no information on their longevity.

The life cycle of Themos olfersii in Brasília is summarized in Figure 4.14.

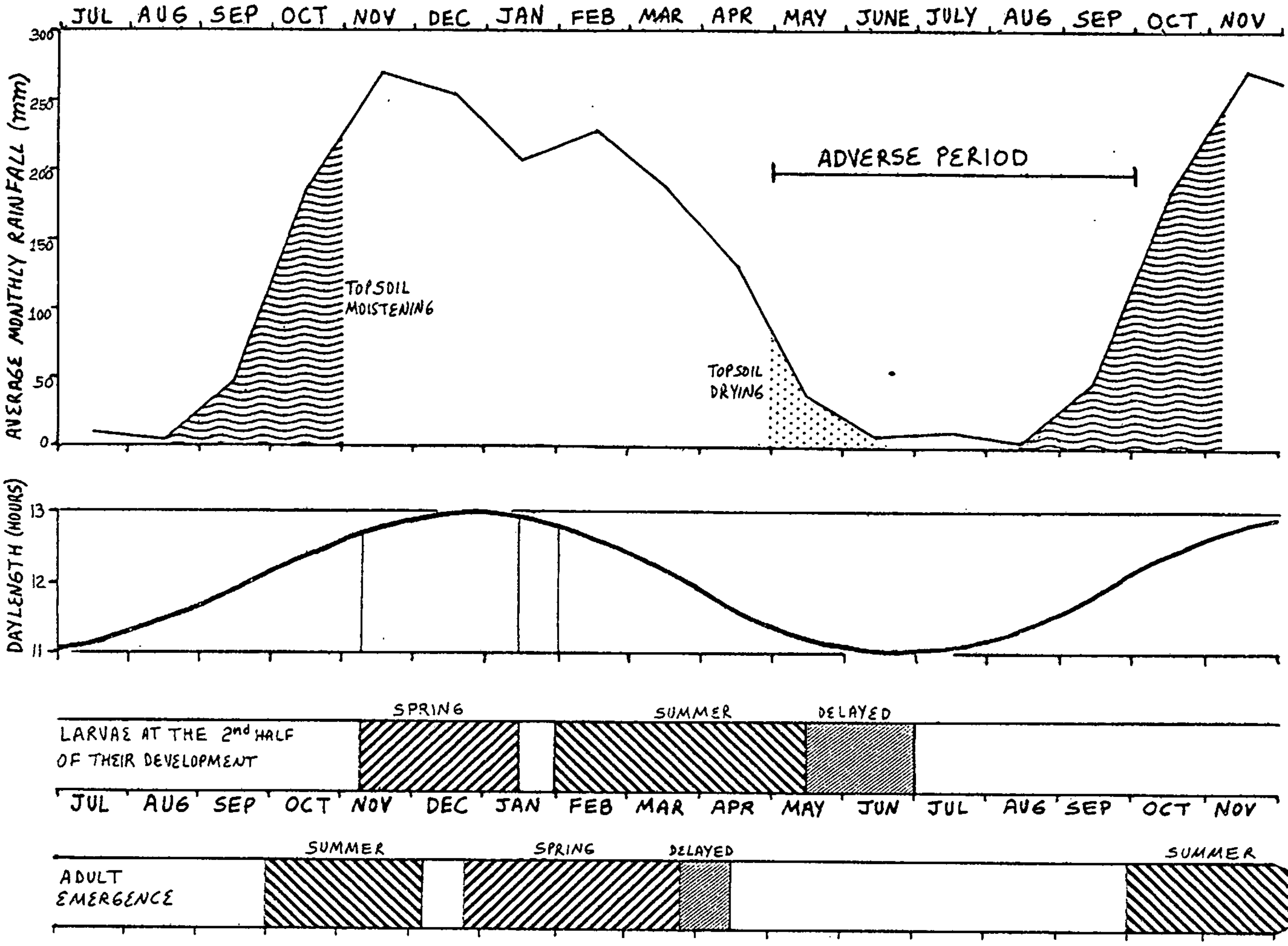


FIGURE 4.13.Correlation between the life cycle of Themos olfersii and the rainfall (average of 9 years,1961-1969) and daylength seasonal fluctuation patterns in Brasília (source: Departamento Nacional de Metereologia, Ministerio da Agricultura, Brasília,DF). The periods when larvae at the second half of their development occur are indicated for each generation. A few late adults of the spring generation emerge only in April and their brood only complete their feeding period by the end of June. See discussion text for interpretation of this figure.

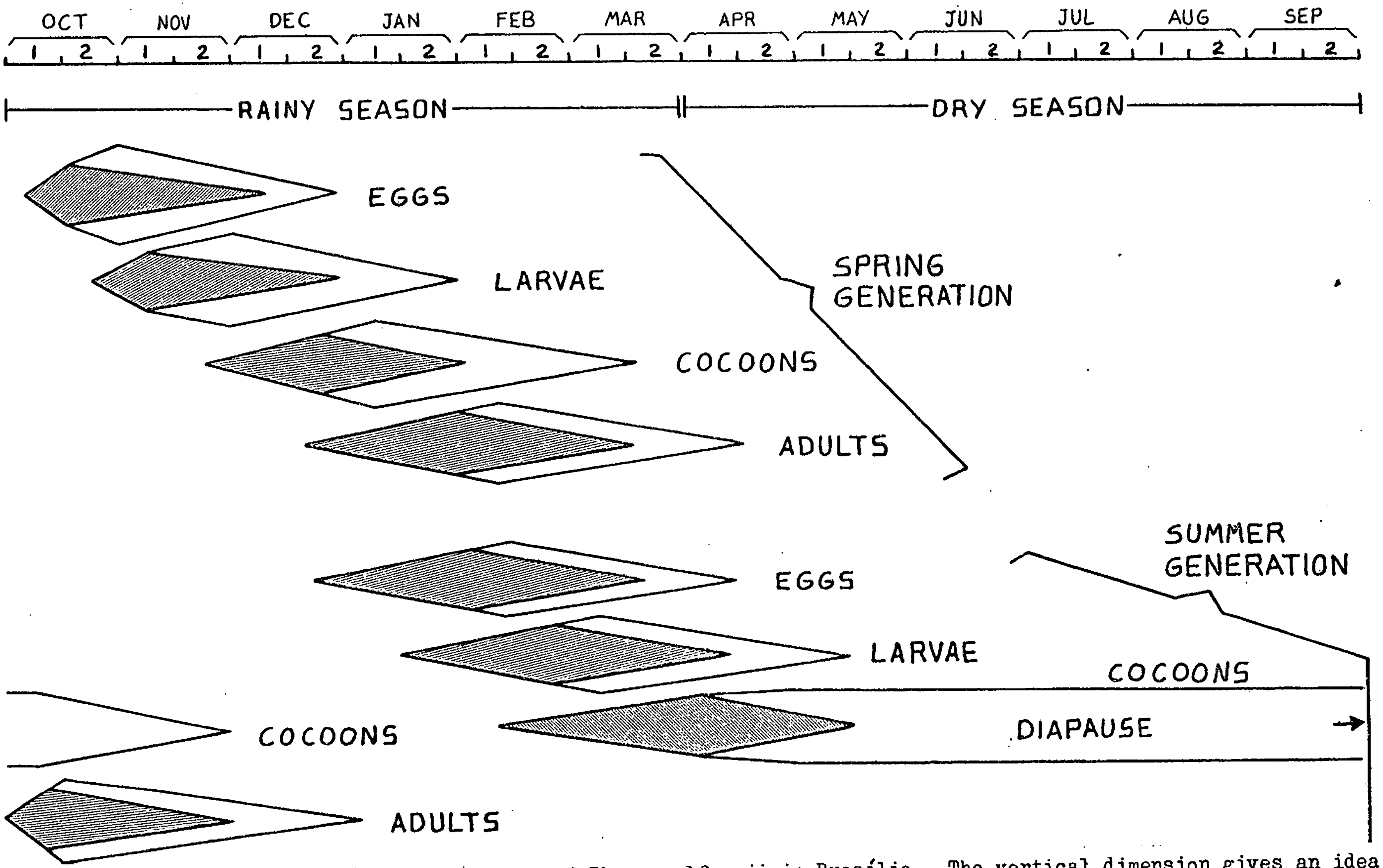


FIGURE 4.14. Summary of the annual life cycle of *Themos olfersii* in Brasília. The vertical dimension gives an idea of the relative abundance of each life stage through time. The shaded areas represent the number of new sawflies entering in each life stage, while the total areas (shaded plus non-shaded) represent the cumulative frequencies of sawflies of all ages in each stage. Obs.: In some years the emergence of adults of the spring generation prolongs until mid-April, and in consequence the period of occurrence of eggs and feeding larvae of the summer generation also prolongs for about a month such that the last larvae of this generation will only spin their cocoons in late June.

4.B DIELOCERUS DIASI

There are four partly-overlapping generations of *Dielocerus* per year in the Federal District (tetra-voltinism): an early spring generation (named after the season when the eggs are found) from early August until late January, a late spring generation from early November until late April, a summer generation from late January until late July and an autumn generation from mid-April until mid-November. As the start of each generation is not synchronic and extends through 3 months, and as the development between the time the egg is laid until the adult emerges from the cocoon takes only 3 months in the first 3 generations, all four generations intergrade into an almost continuous flow of development which is only interrupted for one or two months during the dry season at the prepupal stage of the fourth generation.

Therefore, all life stages can be found simultaneously at any time of the year. Nevertheless, there is some fluctuation in the abundance of each life stage at different times of the year. Adults and egg clusters arefound more commonly during the late dry season and early rainy season (August to October) and during the late rainy season and early dry season (February to May), and are specially rare during the early-mid dry season (June and July). Larval numbers fluctuate less as larvae can be easily found at any time of the year. Cocoon numbers fluctuate even less because some prepupae stay in prolonged dormancy for one or two years before resuming their development.

There is, however, a tendency for synchrony of life stages within individual host trees (see Figure 4.15) and even within one patch of host trees. It is not rare, for example, to find one or two dozens of adult females laying their eggs simultaneously on the same day on the same host, while sawflies in other nearby trees are at different stages of development. But when analysing sawfly populations across different patches of host trees this synchrony disappears.

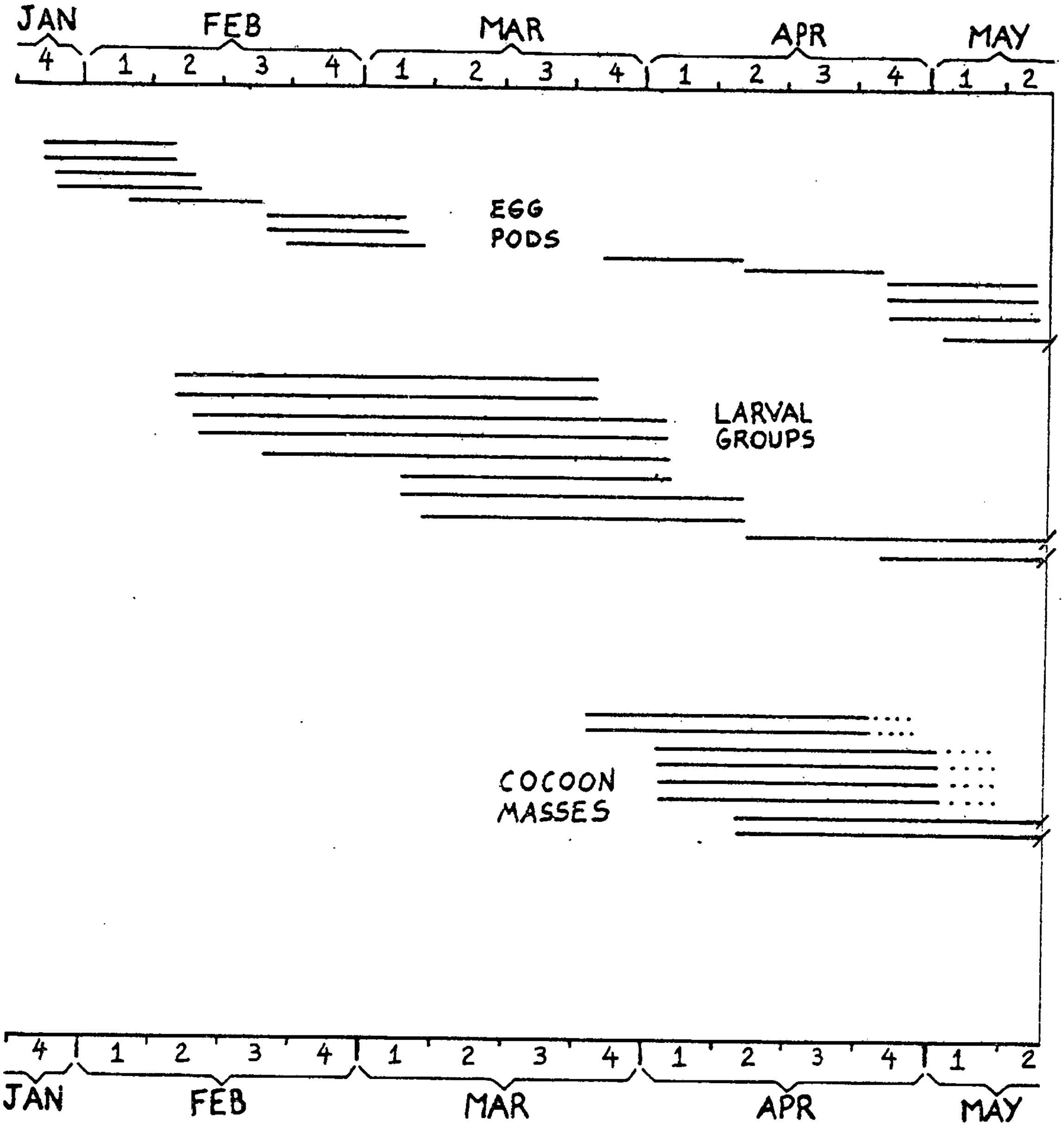


FIGURE 4.15. Temporal distribution of Dielocerus diasi in one host tree at site 5 from late January to early May of 1976. Each horizontal bar represents one sib-group in one particular life stage, from the start to the end of the stage. N = 14 broods.

4.B.1 EGGS AND LARVAE

The incubation period for Dielocerus eggs is on average 14 days. Its duration was the same during all generations in all years studied. All, or most, of the eggs in a cluster hatch on the same day within a few hours.

The larval feeding period, from hatching until spinning of cocoon, lasts about 45 days, ranging from 30 to 50 days (N = 6 larval groups). Its duration was roughly the same during all the generations. All larvae in one sib-group spin their cocoons together on the same day. All larvae in mixed groups resulting from the fusion of two or more sib-groups also spin their cocoons together on the same day even if the sib-groups are of different ages. In this case the oldest group determines the time to cocoon. In some cases larvae which had joined older larvae spun their cocoons only 30 days after hatching (Figure 4.15).

4.B.2 COCOONS AND DORMANCY

The duration of the cocoon stage (period from the time the cocoon mass cover is spun until the adult emerges) varies for the different generations and is apparently dependent upon the weather (humidity) and daylength during the active larval stage. During the rainy season, the adults emerge only 19 to 30 days after the cocoons were spun (Figures 4.15, 4.16 and 4.18). This short cocoon stage is typical of the two spring generations and occurs in the earlier part of the summer generation. Those cocoons spun in the later part of the summer generation (beginning of the dry season) last 20 to 70 days with an average of 30 to 40 days.

On the other hand the cocoons of the autumn generation (spun during mid-dry season) last 50 to 110 days, with an average around 70 days (Figure 4.18). The emergence period of adults from the same cocoon mass, thus, spreads through 1 or 2 months from the first to the last adult to emerge (field and laboratory observations). It is not clear yet whether this longer cocoon stage of the fourth generation is due to a slower rate of development or to the existence of a short dormant period.

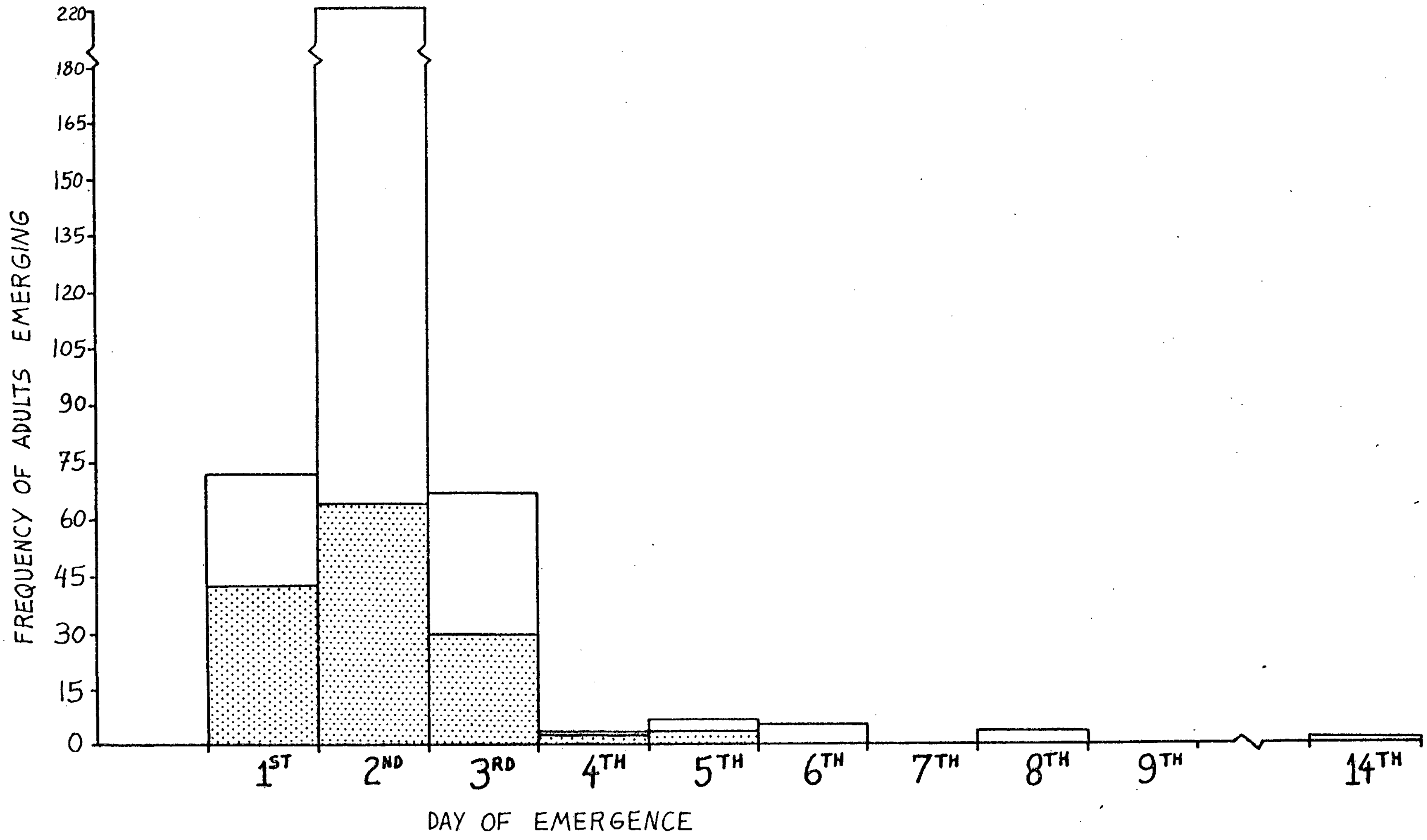


FIGURE 4.16. Frequency of adult Dielocerus diasi emerging from one large cocoon mass, with 500 cocoons, spun at the end of February of 1975. All adults emerged within a period of 8 days between 18 and 31 of March of 1975. Male frequencies are stippled.

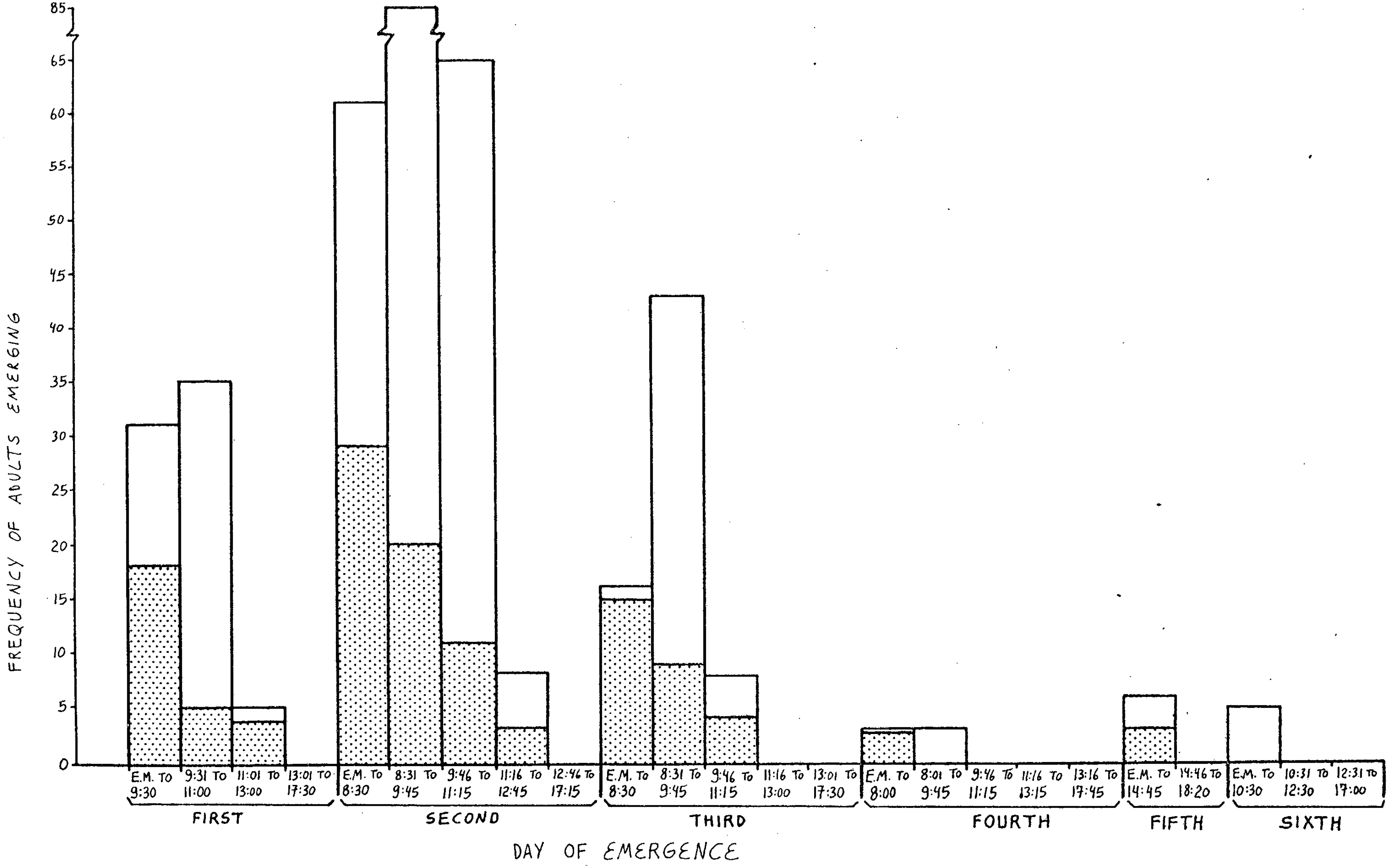


FIGURE 4.17. Frequency of adult Dielocerus diasi emerging from a large cocoon mass (same of FIGURE 4.16.) between the first and the sixth day of emergence at different intervals of time of the day. Male frequencies are presented stippled and female frequencies blank. E.M.= early morning.

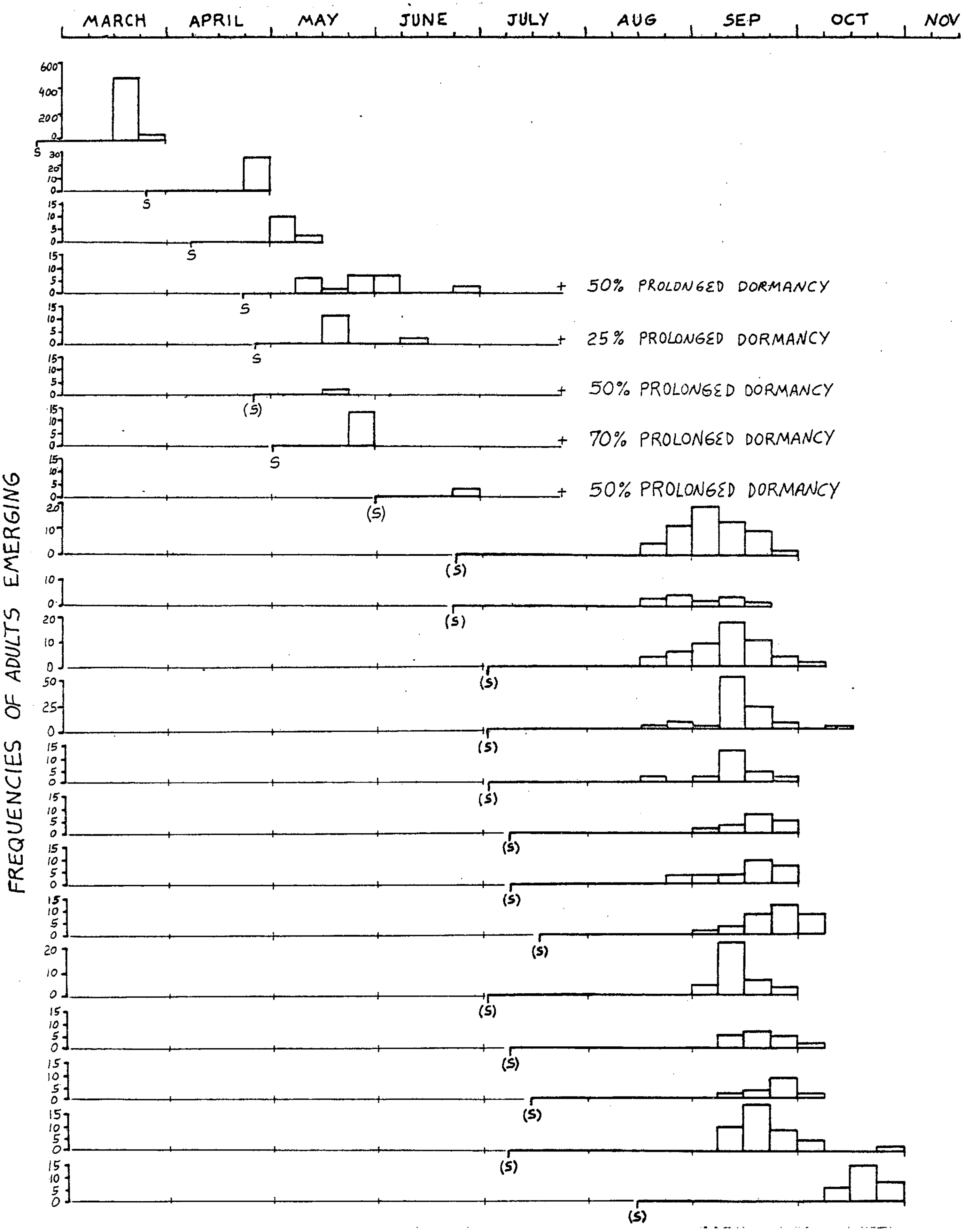


FIGURE 4.18. Weekly frequency distribution of adult Dielocerus diasi emerging from their cocoons per cocoon mass at different times of the year. The exact, s, or approximate, (s), time when the cocoon masses were spun are given. Only in cocoon masses spun between the end of April and the end of June did some of the prepupae enter in prolonged dormancy for one or two years.

About half of the prepupae of the third generation taken to the laboratory entered in prolonged dormancy for one or two years (Figures 4.18 and 4.19). I do not know if this also happens in the field. For example, from 9 cocoon masses of the third generation taken to the laboratory, 93 adults emerged 20 to 30 days after the cocoons were spun, 62 emerged after one year of dormancy and 20 emerged after two years of dormancy. No prepupae from the other generations ever entered in prolonged dormancy in the laboratory. Larvae of the third generation develop at the time of the year when the daylength decreases steadily (February to May)(Figure 4.21).

In cocoon masses of the third generation, most sawflies emerging without dormancy come out of peripheric cocoons whereas most sawflies emerging after a period of prolonged dormancy come out of internal cocoons within the mass. In one cocoon mass for example (Figure 4.20) where half of the 44 cocoons are peripheric and half are internal, 77% of the sawflies in the peripheric cocoons emerged within 19 to 64 days after they were spun and 23% emerged after one year of prolonged dormancy, while only 23% of the sawflies in internal cocoons emerged within 19 to 64 days after they were spun and 77% emerged only after one year of prolonged dormancy.

4.B.3 ADULTS

Adults always emerge during the morning, from around 7 to 11 a.m. (occasionally until 12 a.m.), with a peak between 8.30 and 9.30 a.m. (field and laboratory observations). Males tend to emerge earlier than females with a peak of emergence before 8.30 a.m. whereas the females have a peak between 8.30 and 9.30 a.m. (Figure 4.17).

The pre-reproductive period is very short, lasting apparently only one day for most females after emergence from the cocoon. Post-reproductive Dielocerus adult females have a long life span of up to 4 weeks. Males lived for up to 2 weeks in the laboratory without food or water.

The life cycle of Dielocerus diasi in Brasília is summarized in Figure 4.22.

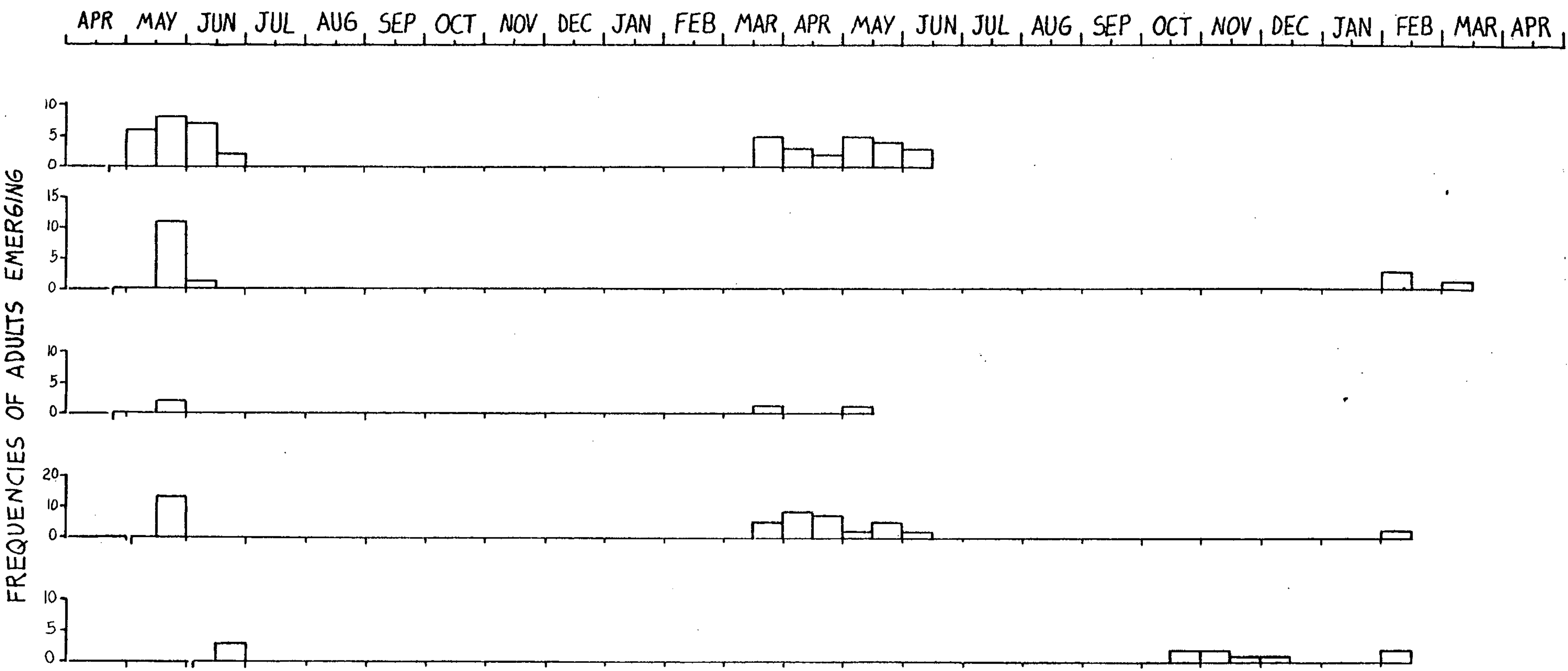


FIGURE 4.19. Adult emergence frequency per fortnight for 5 cocoon masses of Dielocerus diasi spun between late April and early June, in which several prepupae entered in prolonged dormancy for one or two years.

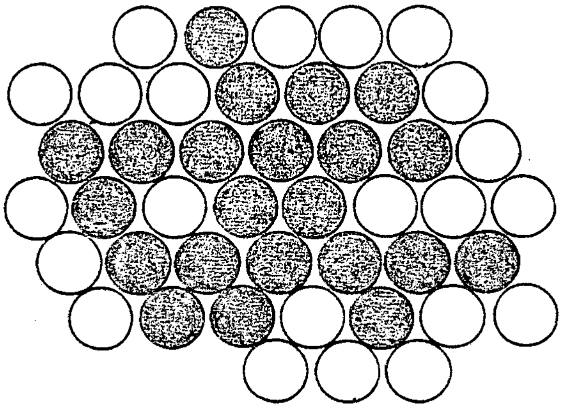


FIGURE 4.20. Diagrammatic top view of a cocoon mass of Dielocerus diasi with the outer cap removed showing the emergence pattern of adults. Those cocoons from which the sawflies emerged within 19 to 64 days after they were spun are indicated as open circles, and those cocoons from which the sawflies only emerged one year later due to a prolonged dormancy of the prepupae are shown as dark circles. N = 44 cocoons.

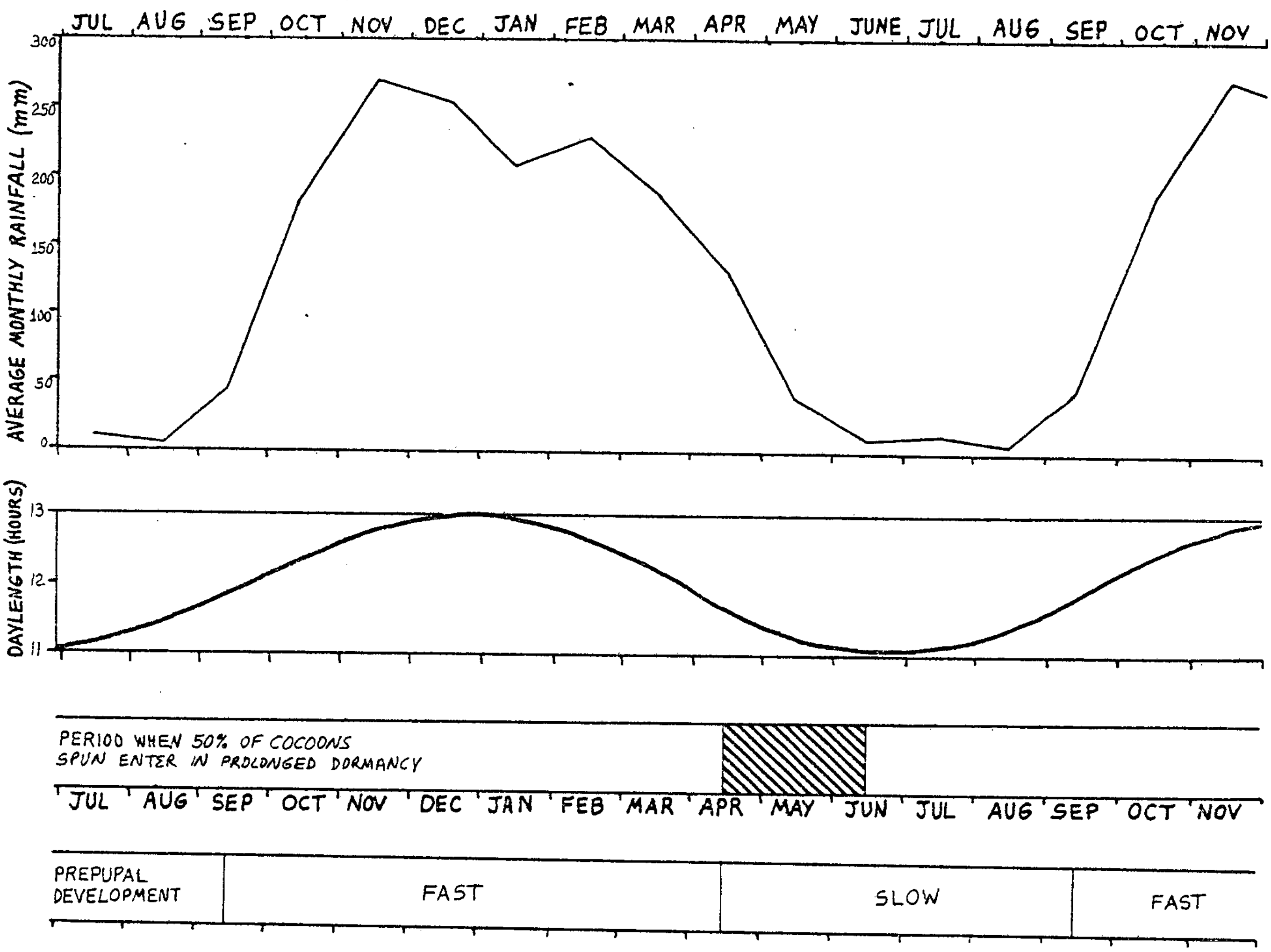


FIGURE 4.21. Correlation between the rate of prepupal development and the occurence of prolonged dormancy in Dielocerus diasi and the rainfall (average of 9 years, 1961-1969) and daylength seasonal fluctuation patterns in Brasília (source: Departamento Nacional de Meteorologia, Ministerio da Agricultura, Brasília, DF). The periods of fast and slow prepupal development are indicated in the bottom as well as the period when half the cocoons spun enter in prolonged dormancy (mid-April to mid-June). See discussion text for interpretation of this figure.

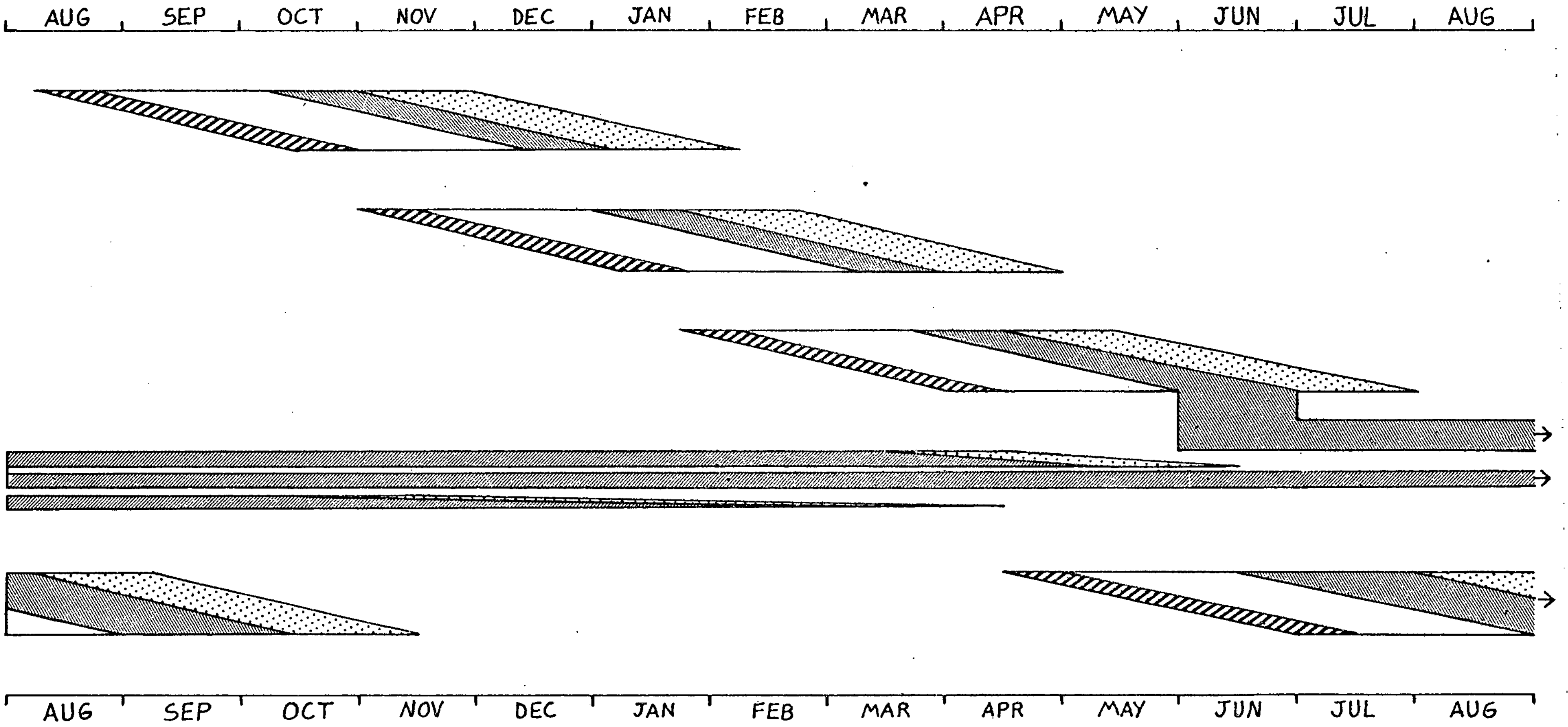


FIGURE 4.22. Summary of the annual life cycle of Dielocerus diasi in Brasília. There are 4 generations per year. The egg stage is shown stripped, the larval stage blank, the cocoon stage shaded, and the adult stage stippled. Approximately half of the prepupae of the third generation enter in prolonged dormancy for one or two years. This is indicated in the diagram.

4.C DISCUSSION

Most sawflies require high relative humidity levels for survival and are only found in places with humid climate or during humid seasons, such as periods during or just after rains, in marshes, woods, mountain slopes and along rivers (Benson, 1950). Adult sawflies are usually found on wing only during the early morning or late afternoon in non-windy days. They have evolved several adaptations to provide high humidity micro-habitats for their immature stages: eggs embedded in plant tissues; larvae feeding within plant tissues, on the underside of leaves, in rolled leaves or feeding only at night and hiding away in the daytime (Benson, 1950). In unfavourable situations desiccation can become a major mortality factor during the egg, larval and cocoon stages (Bodeheimer, 1932; Carne, 1969; Benson, 1950; Thielmann, 1938).

It would be expected then that tropical sawflies should be mostly restricted to permanently moist rain forests, gallery forests along watercourses, cloud forests on high mountains and swamps. In fact they are very numerous in such places. Malaise (1945) found sawflies to be very common in the cloud forests of Burma above 2500 metres above the sea, but below this level they were restricted to places near watercourses. He never found sawflies more than 50 metres away from water. Outside the cloud forests sawflies were seen on wing only between 5 and 6 p.m. and occasionally in the early morning, and only during the rainy season (Malaise, 1945).

Thus, sawflies were thought to be absent or rare in the drier Savanna-type biomes which exhibit a marked seasonal climate with well defined rainy and dry seasons, the last one prolonging for several months. The discovery by the author of a rich sawfly fauna in the Cerrado biome in Central Brazil (Dias, in prep. c; D.R. Smith, in press), of which _T. olfersii_ and _D. diasi_ are members, disproves this idea.

Nevertheless, most Cerrado sawflies found so far have a marked seasonal life cycle with the active adult, egg and active larval stages restricted to the rainy season (October to March)(Dias, in prep.c). This is the case of _Themos olfersii_ which exhibits a multivoltine life cycle with two synchronous and distinct generations during the rainy season: a spring generation from October to March and a summer generation from January to December. The individuals of the spring generation complete their development from the time the egg is laid until adult emergence from cocoon in 80 days on average. But the individuals of the summer generation stop their development at the end of the larval stage as prepupae inside the cocoon and pass through the dry season in a dormant state until the first rains of the next spring come. Their total development takes about 270 days, 180 of which is spent in the dormant state. Pyenson (1940) also found that the dry season is spent in a dormant state as prepupae by three sawflies which feed on guava in the Brazilian semi-arid Northeast: Haplostegus epimelas Konow, Acordulecera megacephala (Benson) and Metapedias pyensoni Benson.

The fact that the earliest cocoons of the summer generation of T. olfersii are spun in the second week of February, and half of all cocoons are spun by the first week of April while water deficiency in the top soil only starts in May, indicates that top soil water deficiency is not the proximal factor causing or inducing the prepupae to enter a dormant state. Otherwise we would have a partial third generation starting in mid-March when there is still plenty of rain, but this does not happen.

Neither is temperature likely to be involved in this dormancy as it changes very little throughout the year and daily fluctuation of temperature is much larger than seasonal fluctuation. In addition the temperature in the soil where the cocoons are spun is much more stable than that of the air. The relative air humidity remains very high (always above 75%) from October until the end of April, and so cannot also be responsible for the initiation of the dormancy of the prepupae (CODEPLAN, 1971).

I conclude that there is no evident climatic factor which could be directly responsible for the initiation of dormancy in the prepupal stage of the second (summer) generation of T. olfersii. I believe, therefore, that the observed dormancy in T. olfersii is not a case of quiescence, but rather a genuine case of diapause. If, as in other studied sawflies, the sensitive period for diapause induction is in the larval stage, specially the late larval stage before the spinning of the cocoon, the sensitive period for the summer generation T. olfersii would be between early February until mid-May. The environmental factor most probably responsible for inducing diapause at this time is the shortening of the daylength, for other major climatic parameters do not change markedly in this period as discussed above. Rainfall, however, does fall continuously during this period, but remains fairly high throughout (above 130mm monthly until the end of April).

Although daylength changes very little throughout the year in Brasília (15° 47' latitude South of the equator), there is a difference of 2 hours between the longest day (21st December = 13 hours) and the shortest day (21st June = 11 hours) of the year. And it is exactly within this period between early February and mid-May that the largest decrease in day length occurs, from approximately 12h 40' to 11h 10'. On the other hand, the presumed sensitive period of the first (spring) generation occurs between early November and early January when the daylength is at its maximum and changes very little from approximately 12h 40' to 13h.

Themos olfersii, then, is a longday species exhibiting a facultative prepupal diapause probably induced by decreasing daylength (Eudiapause). Whether or not the larvae could detect such a small change in daylength compared with the very large changes found in temperate regions, is perhaps open to question and would certainly need to be tested, but studies on northern temperate insects indicate that several species are very sensitive to small changes of less than one hour in daylength (Saunders, 1976). I suggest that the termination of the prepupal diapause in the summer generation of this sawfly is probably triggered by the sudden increase in moisture of the top soil promoted by the first heavy rains of early spring at mid-September. Temperature and photoperiod probably do not play any role here as the cocoons are buried in the soil. Differences of up to one week in the first appearance of flying adults in the spring of one year to another are probably due to differences in the timing of the first heavy rains in September.

Facultative prepupal diapause during the winter induced by short or shortening daylength and terminated by chilling have been demonstrated for several sawfly species of northern regions of two families: Diprionidae (Neodiprion spp, Diprion spp and Gilpinia spp) and Tenthredinidae (Pristiphora spp, Lygaeonematus sp and Athalia spp) (Bombosch and Ramakers, 1976; Eichhorn, 1976-79; Knerer, 1977; Philogène, 1971; Philogène and Benjamin, 1971; Saunders, 1976). This type of diapause is probably the most common among holoarctic sawflies, including several genera of Argidae. However I do not know of any study for Argid sawflies on the factors which induce and terminate their prepupal diapause.

There are, however, a few species of northern temperate sawflies (Neodiprion spp and Apethymus spp) which spend the winter in diapause in the egg stage and exhibit yet another diapause during the summer in the prepupal stage (Benson, 1950; Brygider, 1952; Philogène, 1971). It has been demonstrated that the prepupal summer diapause in several Neodiprion spp is induced by long or increasing daylength and the duration is proportional to the temperature (Philogène, 1971; Sullivan and Wallace, 1965, 1967, 1968; Wallace and Sullivan, 1963, 1966).

Diapause during the dry season is a very common phenomenon in the tropical regions with marked rain seasonality (Owen, 1976). The ultimate cause for the evolution of this diapause may be different for different species of animals and plants: lack of appropriate food in the dry season, danger of excessive desiccation, dryout of pools and other temporary habitats, fire, hardening of top soil, etc. In the case of T. olfersii good candidates for the ultimate cause of diapause during the dry season are: low relative humidity of air and top soil and increased insolation (danger of desiccation), absence of fresh new leaves (oviposition sites and larval food shortage), decrease in leaf turgescence (danger of egg desiccation), hardening of top soil (impair larval digging to spin cocoon), and fire (direct killing of active stages or of food plants).

Due to the high incidence of fire during the dry season in the Cerrado vegetation when the aerial parts of all grasses and low shrubs are totally burnt (including those shrubs of Eriotheca pubescens prefered by T. olfersii), I suggest that fire is probably a major ultimate factor responsible for evolution of aestivating prepupal diapause in this sawfly. However, fire does not occur every year in every patch of Cerrado. Those E. pubescens shrubs which escape burning remain green throughout the dry season for they have very deep roots which are able to collect water from ground water which never dries up in this region, even though the surface soil remains very dry until September. New leaves, however, are not produced during early and mid-dry season unless the shrubs are burnt, and could be a limiting factor too. There is considerable controversy as to how common natural fire was in the Cerrado before man arrived some 10,000 years ago (Ferri, 1973; Coutinho, 1978; Rizzini, 1976; Sternberg, 1968; Martin, 1973). The existence of this aestivating diapause in all populations of T. olfersii in the Federal District promotes the synchrony of its generations throughout this area. I do not know if prolonged diapause occurs in this sawfly.

The situation of D. diasi is somewhat different. All life stages are found throughout the year, but adults and eggs are rather rare during the middle of the dry season (June and July). But these stages are common in August and September at the peak of the dry season. Feeding larvae and prepupae inside their cocoons, however, are commonly found during all the dry season. This sawfly is multivoltine, having four partly-overlapping generations per year. Development from the time the egg is laid until the adult emerges from the cocoon takes only about 85 days during the rainy season. Also during the rainy season (October to March) all sawflies in the same cocoon mass emerge as adults within a period of only one or two weeks, but during the dry season (April to September) the emergence period of sawflies from the same cocoon mass usually spreads through one or two months. This slower development inside the cocoon might be provoked by the low air moisture vigent during this period. The average relative humidity of the air in Brasília in August is only 47% compared with values above 75% during the rainy season. It is not rare to have some days in the dry season with less than 20% or even 10% relative humidity in Brasília.

However, nearly half of the larvae which spin their cocoons between mid-April and early June enter in a state of prolonged dormancy for 10 to 21 months. As these larvae were exposed to the period of greatest decrease in daylength, it seems possible that this prolonged dormancy is a case of prolonged diapause induced by decreasing daylength. This will have to be tested.

Prolonged prepupal diapause is not a rare phenomenon among sawflies. Species of *Gilpinia* (Prebble, 1941), *Diprion* (Eichhorn, 1976-79), *Neodiprion* (Philogène, 1971), *Pristiphora* (Drooz, 1960), *Perga* (Carne, 1962), *Pergagrapta* (Raff, 1934), *Pseudoperga* (Raff, 1934) and *Zenarge* (Moore, 1962) have been found to stay up to 2 to 6 years in prolonged diapause. Another species of *Dielocerus*, *D. formosus* (Klug), is known to enter prolonged diapause for a few years (Costa Lima, 1927; Sichel, 1862). In all these cases it is always only a certain percentage of contemporaneous individuals which enter prolonged diapause. Eichhorn (1976-79) found that the percentage of prolonged diapause in Central European populations of *Diprion pini* (L.) varies between 0 and over 90%, but is remarkably constant from year to year for each locality. He presented evidences to show that these geographic differences are genetically controlled. Pschorn-Walcher (1970) found that the percentage of larvae entering in prolonged diapause in European *Neodiprion sertifer* (Geoff.) is a function of the date when the cocoon is spun - the earlier the date of spinning, the higher the percentage of prolonged diapause in the brood. Sullivan and Wallace (1967) established that in this species the rate of prolonged diapause is a function of photoperiod and temperature. However, according to Philogène and Benjamin (1971), prolonged diapause in *Neodiprion swainei* Midd. does not seem to be related to photoperiod, temperature or both. Carne (1962 and 1969) found that the rate of prolonged diapause in *Perga affinis affinis* Kirby varies both in time and space. He also found that the incidence of prolonged diapause is higher in populations with higher densities and smaller prepupae, and increases with exposure of prepupae to high temperature in the laboratory which,correlates with field data showing that prolonged diapause was high following hot and dry summers. Both Pschorn-Walcher (1970) and Carne (1969) showed that most prolonged diapause lasted only one year, being insignificant the number of individuals successfully passing through prolonged diapause of more than 18 months.

The function of prolonged diapause in these sawflies is believed to be an insurance mechanism against unpredictably harsh unfavourable seasons, as the diapausing prepupae is more protected against environmental hazards than the active stages.

Compared to the sawflies studied so far, thus, D. diasi is very resistant at all life stages to hot and dry weather. The studied species which approach D. diasi in this resistance are Zenarge turneri (Moore, 1962), Schizocerella pilicornis (Force, 1965) and Athalia spp (Benson, 1950).

A very significant difference between D. diasi and T. olfersii related to their seasonality is the height of canopy where the active stages of these two sawflies live. As D. diasi only attacks tree canopies above 1.5 metres, and usually above 4 metres above the ground, its active stages escape the fire during the dry season, which however hits badly the low canopies of hosts of T. olfersii. This very important difference in habitat selection might be the main cause of the observed differences in temporal pattern of distribution between the two species.

CHAPTER 5. PRE-REPRODUCTIVE ADULT BEHAVIOUR AND SPATIAL DISTRIBUTION

METHODS

Emergence of D. diasi adults was observed in the laboratory and in the field, starting at 0600 h (dawn) several times.

Adults in the field were observed at frequent short intervals, each observation lasting from just a few seconds to several minutes usually, but sometimes up to 3 hours, depending on the activity of the insect. Adult behaviour was recorded mainly in field notebooks, but also in drawings, time tables, photographs (black and white, and coloured) and coloured super-8 film.

Virgin D. diasi females at RECOR were put into cages, with perforated metal screens, attached to branches of host trees to test if they would attract males.

Males of T. olfersii were also collected with Malaise traps (BMNH model) at RECOR.

Secondary sex ratio in D. diasi was obtained by examining the proportion of males and females emerging from 10 large cocoon masses (about 1,000 adults emerged from these) taken to the laboratory. But in T. olfersii it was obtained by examining the proportion of males and females in 11 larval sib-groups (with about 190 larvae) in the field, as very few adults could be reared in the laboratory.

Detailed surveys on the spatial distribution of T. olfersii egg clusters on each host plant throughout each generation were conducted at sites 1, 2 and 13. The position of the egg clusters in relation to the host characteristics such as leaf age, health, size and height above the ground, and in relation to the position of other egg clusters was recorded. The distribution of egg clusters among the different host shrubs within a patch at site 1 is compared with Poisson and Binomial distributions in four generations of T. olfersii.

The spatial distribution of D. diasi between trees and patches was studied by surveying the distribution of cocoon masses on the tree's trunk and branches, because these are more accessible to the observer than the eggs and larvae high up on the tree's canopy. The frequency distribution of cocoon masses of D. diasi of different sizes (number of cocoons per mass) in one heavily infested host tree (no. 3/2) was used to give an estimate of the average frequency of occurrence of contemporaneous egg clusters on the same tree.

5.A. Themos olfersii

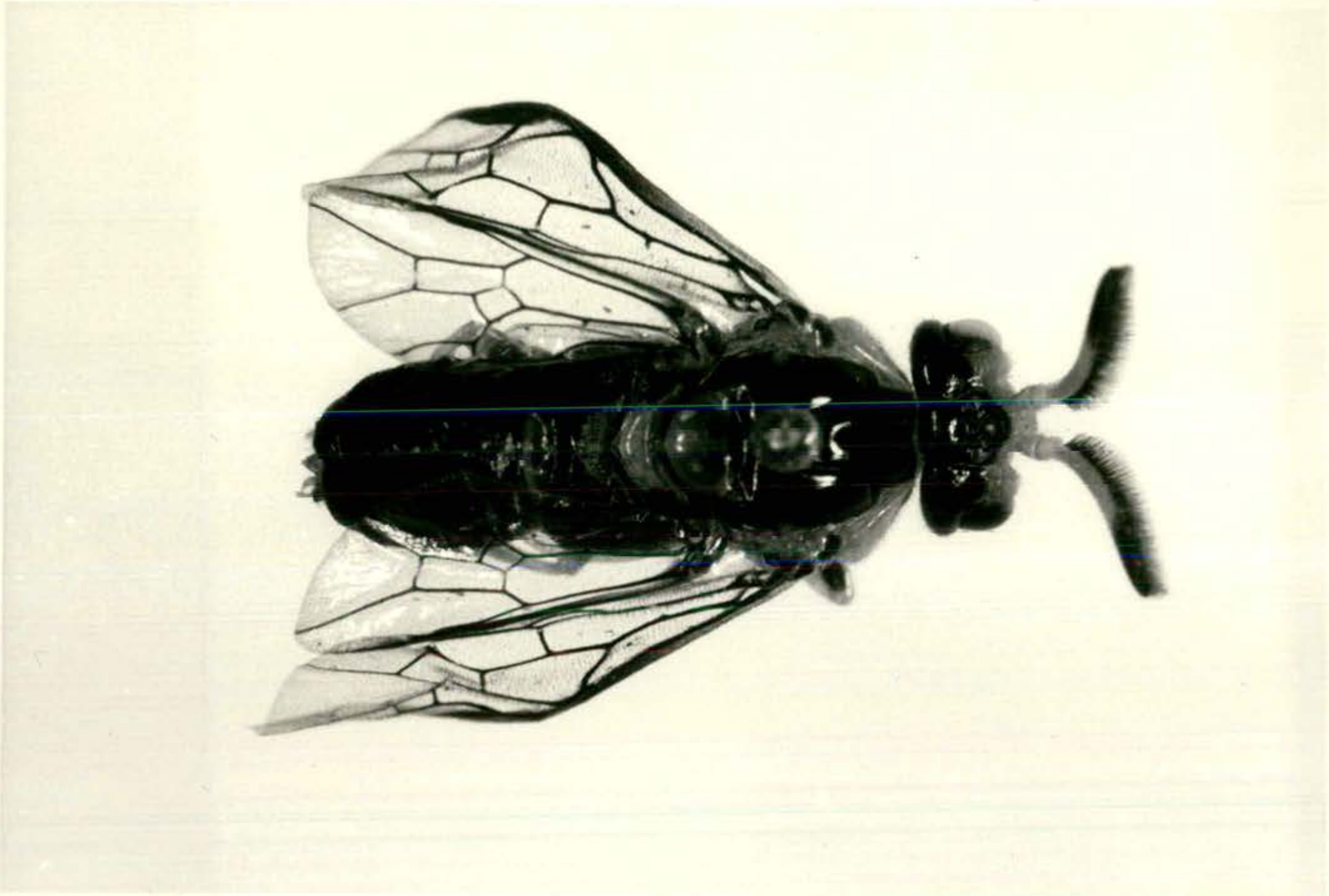
5.A.1 ADULT DESCRIPTION

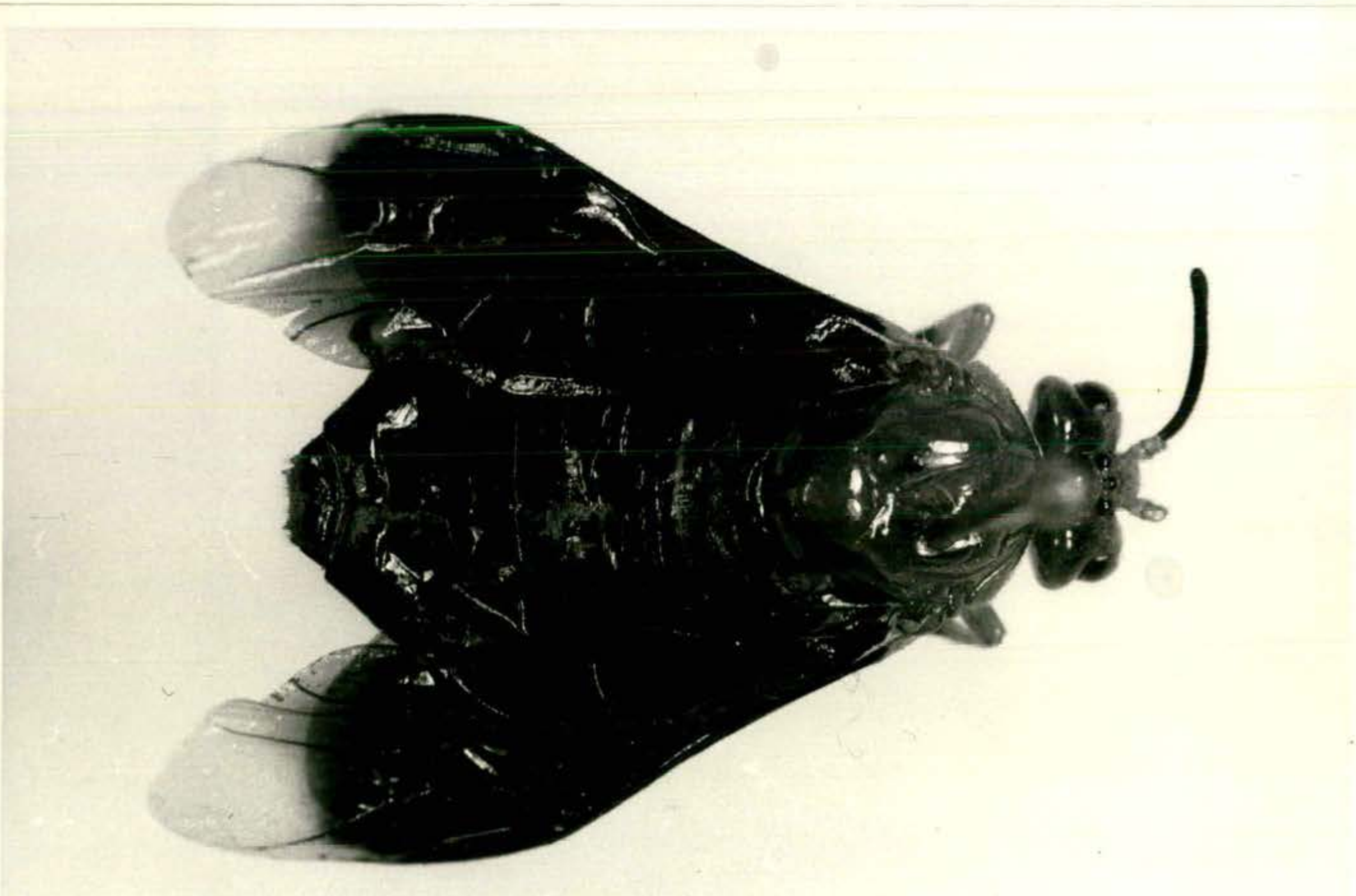
This species has a very strong sexual dimorphism in terms of size, colouring and structure - one of the strongest among all Tenthredinoidea - and far more pronounced than that exhibited by D. diasi. Females are much larger than males, weighing 2 to 3 times as much and have a length of 12-17mm compared with 10-11mm for males. The two sexes also have completely different colour patterns. Females have the head, thorax and legs (except for tarsal segments and distal apex of tibiae) bright orange, and abdomen, tarsal segments, distal part of tibiae and third antennal segment black. Their wings are darkly infuscated all over except for the apex of the front wing beyond the stigma which is hyaline, and they have simple antennae with minute dark hairs.

Males, on the other hand, have parts of head, thorax, abdomen and legs light yellow and bluish-black. Wings are uniformly hyaline with veins and stigma black. The third antennal segment is yellow, furcate and bears abundant long hairs all facing forward. Females have extremely robust mandibles. A more detailed description of this species together with illustrations of mandible, tarsal claw, sheat, lancet and male genitalia was given by D.R. Smith (1975)(in his description of the male, the colours "light yellow" and "bluish-black" should be used where he gives "pale orange" and "black" respectively). See also Benson (1938a) for additional illustrations (Figure 5.1).

Female Themos sp.n. (D.R. Smith, in prep.) is very similar to that of T. olfersii and difficult to tell apart, but differences in leg coloration and in the genitalia separate the two. Male Themos sp.n., however, are easily separated from those of T. olfersii as they have the same colour pattern as the female (D.R. Smith, in prep.).

FIGURE 5.1. Adults of <u>Themos</u> <u>olfersii</u> (Klug). The male (left) is magnified 11X, and the female (right) is magnified 7.5X. Note the female's infuscated wings and the males's bristly antennae.





5.A.2 SEX RATIO

As very few adults were obtained in the laboratory by rearing larvae, and as very few males were seen in the field, no reliable information is available on the secondary sex ratio of T. olfersii in the adult stage. The apparent rarity of males in the field could indicate a female biased sex ratio, but when Malaise traps were set in the Reserva Ecológica do IBGE in the summer of 1978, several males, but no female, were caught in a short time.

As the sexes can be easily differentiated during all larval stages due to the strong size dimorphism, the secondary sex ratio can be calculated for larval sib-groups. This was in average 0.45 males : female (N = 51 larvae of 3 sib-groups) during the spring generation of 1977 and 0.59 males : female (N = 136 larvae of 8 sib-groups) during the summer generation of 1978, approaching an overall average of 2 females for each male. No significant difference in sex ratio was detected between young (including the first instar) and old larval groups. Therefore, unless there is differential mortality between the two sexes during the cocoon stage, the secondary sex ratio during the adult stage should approach 0.5 males : female.

5.A.3 ADULT EMERGENCE FROM COCOON

I have no observation of the actual act of emergence of adult T. olfersii. But to emerge, adults have to cut an opening through their individual cocoons buried in the soil and then dig a passage through the soil towards the surface. The adults cut an irregular sub-circular lid on the top or slightly away from the top of the cocoon. This opening varies between 3 to 7mm in diameter (see Figure 7.28). Adults emerge dirty with earth particles but soon clean themselves.

5.A.4 MALE BEHAVIOUR

Males of T. olfersii were seen in the field either flying and landing on host plant bushes, or resting alone on a leaflet of a host plant, or courting females which had mated already and were either in the process of laying their eggs or taking care of already laid eggs or young larvae. The mated females did not react to or alternatively avoided the courting males, who approached with curved abdomen and tried to mount them. The males were seen active between 1100h and 1600h.

5.A.5 FEMALE SELECTION OF EGG-LAYING SITE

A few females were seen in flight visiting host plants before establishing on the egg-laying site. These flights took place between 1100h and 1500h. They fly between 0.5 and 1.5 metres above the ground in a steady noisy flight. Females fly in almost straight lines from one low shrub to another, 1 to 20 metres apart from each other. When approaching a shrub, the female hovers a few centimetres above the bush for a few seconds and then flies off to another shrub, or lands slowly on a leaflet of that shrub, walks over its surface and to neighbouring leaflets and flies to other leaflets further away in the same shrub and then takes off to another shrub.

When exploring a shrub she alternates between walking with her wings spread open and flying in order to visit other leaflets within one shrub. Visits to shrubs other than E. pubescens are very brief (a few seconds only), but visits to E. pubescens shrubs can take a much longer time, with the female visiting repeatedly certain leaflets where she curves her abdomen and presses it against the leaflet's upper (adaxial) surface while walking. Sometimes she remains motionless for several minutes on a leaflet of a shrub, E. pubescens or other.

The females visit only low shrubs with foliage similar (large glabrous leaflets) to that of E. pubescens as Zeyhera sp, Erythroxylum spp, Anona spp, Pouteria sp, Didymopanax sp, Byrsonima spp, Cayaponia sp, and Anacardium spp. Females visit dozens of bushes in less than one hour. The overall flight pattern is that of subcircles, with females exploring several host plants within a patch, and returning to shrubs which they had visited already (Figure 5.2).

Eventually the female establishes herself on a chosen leaflet, to which she had returned repeatedly, and from then onwards she never flies again. I do not know how long females take to select an egg-laying leaflet after flying off from their natal shrub. Once established on the selected leaflet, the female stays quiet, mostly on the

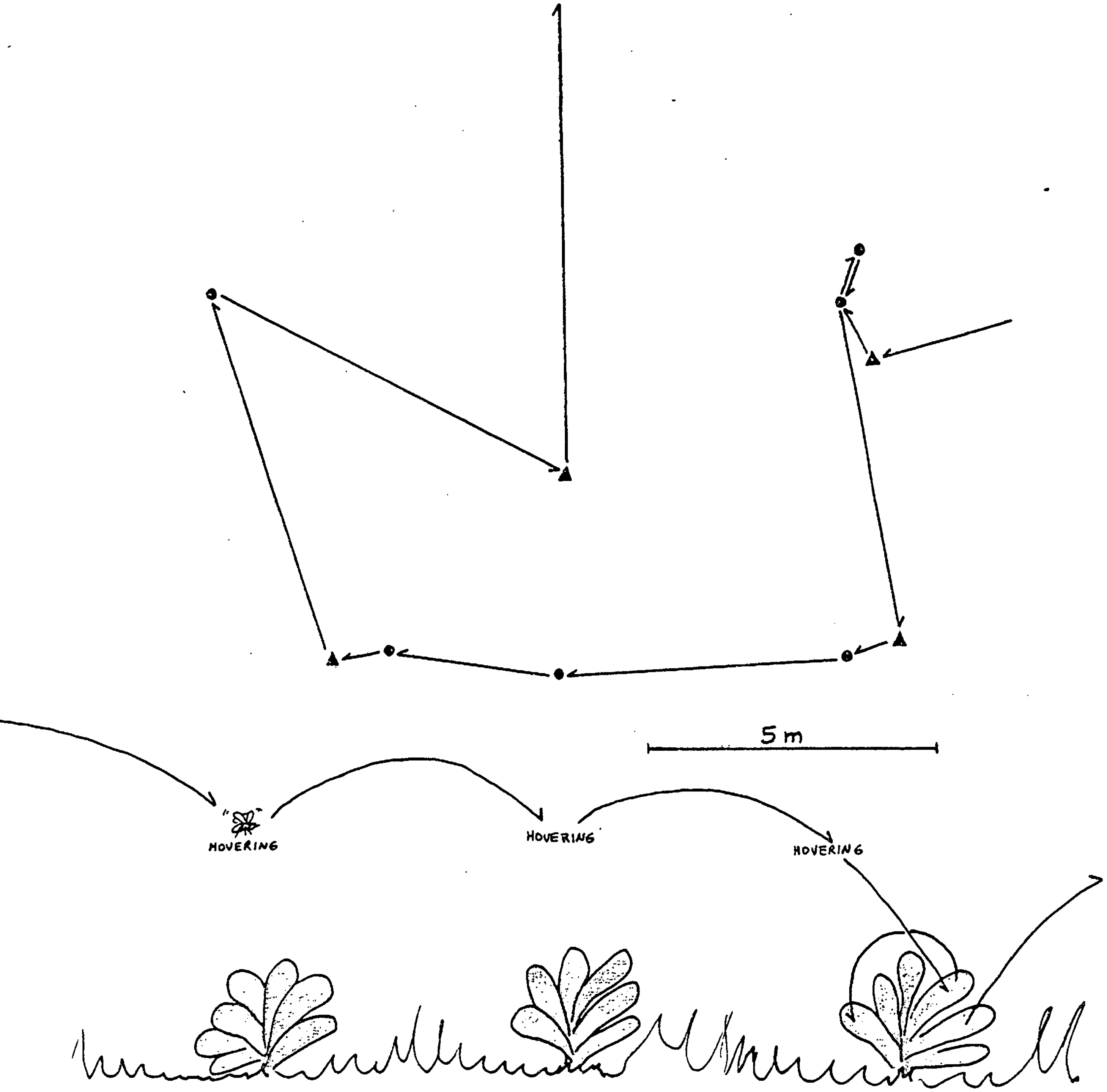


FIGURE 5.2. Typical host-visiting flight pattern of a *Themos olfersii* female. The circles represent shrubs over which she hovered, and the triangles represent shrubs over which she hovered and landed on for brief walking exploratory visits. Only some of the approached shrubs were of *Eriotheca pubescens*, her host, while the others were shrubs with foliage similar to its hosts but belonging to several different species.

dorsal surface of the leaflet, with no buzzing of wings, for a certain period before starting to lay her eggs. It is uncertain how long females stay on the selected leaflet before starting to oviposit, but incomplete observations indicate that it is more than 2 hours and could possibly be as long as one whole day.

The females were seen to start laying their eggs between 1030h and 1700h.

5.A.6 SPATIAL DISTRIBUTION OF EGG CLUSTERS WITHIN A HOST

Egg clusters are apparently laid with equal probability on any one of the leaflets of the palmate leaf of the host plant. There is a strong selectivity, however, for the height of the oviposition site. Among 150 egg clusters studied, 97% were laid on leaflets situated 10 to 40cm above the ground. Only four egg clusters were found above this height. They were found between 135 and 170cm above the ground, and curiously two were found together at the same time on the same shrub and the same happened with the other two. All four were laid during the summer generation. Only once were two egg clusters found on the same leaflet, and then the older cluster had most of its eggs parasitized by the time the second cluster was laid. It was also very rare to find more than one egg cluster on neighbouring leaflets belonging to the same leaf. Usually only hard, dark green, mature leaflets not damaged by earlier attack of insects or disease were utilized as oviposition sites. Oviposition sites are either exposed on top leaves or covered by other leaves.

5.A.7 SPATIAL DISTRIBUTION OF EGG CLUSTERS BETWEEN PLANTS AND PATCHES

Populations of _T. olfersii_ in the Federal District are very patchy. Several places with a good supply of host plants were inspected carefully and repeatedly for some years with no sign of the sawflies. Nevertheless, the species is widely distributed in the District. Most places where _Themos_ was found had low density populations. So far the greatest density for a _Themos_ population was found at the study site 1 where a third of the available shrubs received egg clusters each generation for several years continuously, a density of 20-40 egg clusters per hectare per generation.

Themos egg clusters are not randomly distributed among the available shrubs in a given patch of Eriotheca bushes in each generation. The distribution is very clumped: a few shrubs receive most of the egg clusters and several shrubs do not receive any. The observed frequency distributions of shrubs with none, one, two, three, four, five, six, seven and eight egg clusters per generation at site 1 differ significantly from the expected Poisson distribution (Table 5.I). A very strong departure from the expected random distribution is the occurrence of shrubs with 7 and 8 egg clusters, at frequencies much larger than expected. Three of the four studied seasons had one shrub each which alone received a fifth to a third of all the egg clusters laid in the season. On the other hand, more shrubs than expected received no egg clusters in each generation. Some shrubs are avoided in all seasons whereas some others always receive at least one egg cluster in every season (Table 5.II). But the number of egg clusters received in each season varies greatly for each shrub (Table 5.II). Shrubs which received a large number of egg clusters in one season usually received very few in the other seasons just before or after that.

When comparing the distribution of egg clusters in the spring generations of the years of 1973, 1974 and 1977, the observed number of shrubs which received egg clusters in all three seasons, in just two, in just one or in none is not significantly different from the expected ones if the distribution in one season is not affected or correlated with that observed in the other seasons, i.e. they are independent events (Binomial distribution)(See Table 5.III).

Therefore the preferred shrubs (those which received large number of egg clusters) changed in each season. This is not surprising for each year during the dry season all the aerial parts of most shrubs are totally burnt, and so, most shrubs produce a totally new aerial part each spring. But when comparing the distribution of egg clusters in the spring and summer generations within a single rainy

TABLE 5.I

Distribution of *Eriotheca pubescens* shrubs according to the number of *Themos olfersii* egg clusters received in each studied generation at study site 1 compared with the expected Poisson distribution

No. Egg Clusters per Shrub(X)	NUMBER OF SHRUBS WITH X *T.OLFERSII* EGG CLUSTERS PER SEASON							
	SPRING, 1973		SPRING, 1974		SPRING, 1977		SUMMER, 1978	
	O	E	O	E	O	E	O	E
0	5	2.9	5	3.4	21	16.8	19	15.1
1	7	5.6	4	4.8	7	10.3	6	11.3
2	2	5.4	3	3.4	2	3.2	4	4.3
3	1	3.5	1	1.6	0	0.6	2	1.1
4	3	1.7	0	0.6	0	0.1	1*	0.2
5	1	0.7	0	0.2	0	0.01	0	0.03
6	0	0.2	0	0.04	0	0.001	0	0.004
7	0	0.06	1*	0.01	0	0.000	0	0.000
8	1*	0.01	0	0.002	1*	0.000	0	0.000
No.Shrubs Studied	20		14		31		32	
No.Shrubs with eggs	15		10		10		13	
Total no. of egg clusters	39		20		19		24	
Average no. egg cluster per shrub	1.95		1.43		0.61		0.75	

O = Observed frequencies

E = Expected frequencies (Poisson distribution with same mean)

* = Observed frequency is much larger than expected.

TABLE 5.II

Number of egg clusters of *Themos olfersii* laid in each marked *Eriotheca pubescens* shrub at study site 1 in four generations

	NUMBER OF EGG CLUSTERS PER SHRUB						
Shrub No.	SPRING 1973	SPRING 1974	SPRING 1977	SUMMER 1978	TOTAL (a)	NO.SEASONS STUDIED(b)	PREFERENCE INDEX(a/b)
1	8	1	2	1	12	4	3.0
2	4	1	2	1	8	4	2.0
3	0	-	-	0	0	2	0
4	1	1	0	0	2	4	0.5
5	1	7	0	0	8	4	2.0
6	0	-	-	0	0	2	0
7	2	0	0	0	2	4	0.5
8	3	2	1	2	8	4	2.0
9	1	0	1	3	5	4	1.25
10	0	0	0	0	0	4	0
11	1	3	0	1	5	4	1.25
12	1	1	1	0	3	4	0.75
13	4	0	0	1	5	4	1.25
14	1	2	0	2	5	4	1.25
15	5	-	1	0	6	3	2.0
16	2	2	0	4	8	4	2.0
17	0	-	0	0	0	3	0
18	1	-	0	0	1	3	0.33
19	4	-	1	3	8	3	2.67
20	0	1	0	0	1	4	0.25
21	-	-	0	0	0	2	0
22	-	-	0	0	0	2	0
23	-	-	0	0	0	2	0
24	-	-	0	1	1	2	0.5
25	-	-	0	0	0	2	0
26	-	-	1	1	2	2	1.0
27	-	-	0	0	0	2	0
28	-	-	0	0	0	2	0
29	-	-	0	0	0	2	0
30	-	-	0	0	0	2	0
31	-	-	0	1	1	2	0.5
32	-	-	0	0	0	2	0
33	-	-	1	0	1	2	0.5
34	-	-	8	2	10	2	5.0

Obs.: the bars indicate that the shrubs were not studied in those seasons.

TABLE 5.III

Observed and expected (Binomial) frequencies of Eriotheca pubescens shrubs at site 1 which received egg clusters of Themos olfersii in the springs of 1973, 1974 and 1977 (the probability of a shrub receiving an egg cluster in any one spring is $p = 0.64$).

NUMBER OF SPRINGS RECEIVING EGG CLUSTERS	FREQUENCIES OF SHRUBS OBSERVED	FREQUENCIES OF SHRUBS EXPECTED	
none	1	0.6	$50\% < p < 100\%$
1	3	3.4	variance ratio test
2	6	6.2	$F = 1.1334$
3	4	3.7	
TOTAL	14	14	

TABLE 5.IV

Observed and expected (Binomial) frequencies of Eriotheca pubescens shrubs at site 1 which received egg clusters of Themos olfersii in the spring and summer of 1977/78 (within one rainy season)(the probability of a shrub receiving an egg cluster in any of the two generations of the sawfly is $p = 0.36$).

NUMBER OF GENERATIONS RECEIVING EGG CLUSTERS	FREQUENCIES OF SHRUBS OBSERVED	FREQUENCIES OF SHRUBS EXPECTED	
None	16	13.10	$5\% < p < 10\%$
One	9	14.75	Goodness of fit test
Both	7	4.15	$\chi^2 = 4.84$
TOTAL	32	32	

season (1977/78), the observed ratio of shrubs which received egg clusters in both generations, one generation only, or not at all is apparently significantly different from the expected ratio (Binomial distribution) (see Table 5.IV). Therefore there seems to be a correlation between the egg cluster distribution of two consecutive generations within the same rainy season. This means that some shrubs are apparently intrinsically more attractive to females than others, but this attractiveness changes from year to year when shrubs are burnt and have to produce a totally new canopy. Table 5.V and Figure 5.3 present the sequences in which the females selected the shrubs at site 1 for egg laying in four generations. In two of these, 1974 and 1977, the first bush to receive two egg clusters immediately attracted the next 5 females looking for egg laying sites. In 1973 the first two shrubs to receive two egg clusters attracted only some of the following females. In these three seasons the first bush(es) to receive two egg clusters were eventually the preferred ones in the generation. In 1978 no shrub received more than two simultaneous egg clusters. Almost half of the egg clusters were laid in bushes which already had at least one previous egg cluster, even though these bushes were always in fewer numbers than the shrubs with no egg cluster (Table 5.VI).

In _Themos_ there is a strong preference for low bushes (less than 0.5 metres high) as egg laying sites (Table 5.VII). Among the low shrubs the preference goes to those with a larger canopy. There is a good correlation between the number of leaves in a low bush and the average number of egg clusters it receives per generation (Figure 5.4). Most of the preferred shrubs at site 1 were located in the northeast sector (Figure 5.5) of this patch of _Eriotheca_. The closest other population of _Eriotheca_ and _Themos_ (site 2) is located more than 150m south of this patch.

5.B _Dielocerus diasi_

5.B.1 ADULT DESCRIPTION

This species also exhibits a strong sexual dimorphism in size, colour and structures. Females are much larger than males and weigh twice as much. They have an average length of 14-16mm compared

TABLE 5.V

Number of *Themos olfersii* egg clusters already present at chosen shrub at the time each female arrived to lay their eggs at study site 1 in four generations, given in chronological sequence of arrival of the females.

	NUMBER OF EGG CLUSTERS ALREADY PRESENT AT CHOSEN SHRUB			
FEMALE ARRIVAL SEQUENCE	SPRING 1973	SPRING 1974	SPRING 1977	SUMMER 1978
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0	0	0
5	0	1	0	0
6	0	2	1	1
7	1	3	0	1
8	2	4	2	0
9	0	5	2	1
10	1	6	3	0
11	2	0	4	1
12	0	0	5	0
13	0	0	0	0
14	3	0	0	1
15	1	1	0	0
16	1	0	0	0
17	4	1	0	0
18	2	0	0	0
19	1	1	1	0
20	1	0		0
21	1			0
22	2			1
23	0			0
24	0			0
25	0			
26	3			
27	3			
28	0			
29	2			
30	0			
31	2			
32	3			
33	0			
34	1			
35	1			
36	0			
37	2			

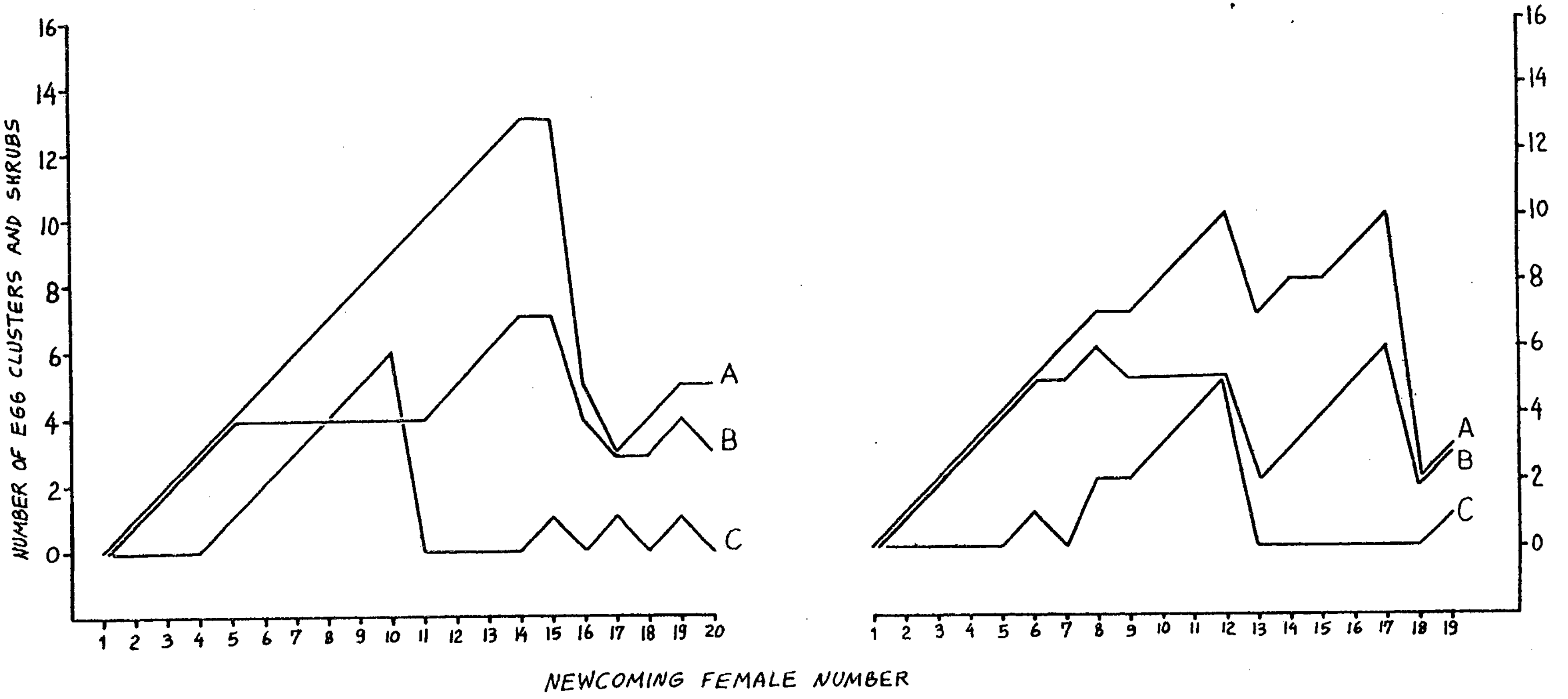


FIGURE 5.3. Sequences in which the shrubs of Eriotheca pubescens at site 1 were chosen by newcoming Themos olfersii females in the spring of 1974 (left) and spring of 1977 (right), in relation to the presence of egg clusters laid by previous females in the chosen shrubs and in the whole patch at the time of each choice. A = total number of egg clusters in the patch at the time of each choice; B = number of shrubs in the patch with egg clusters at the time of each choice; C = number of egg clusters present in the chosen shrub at the time of each choice.

TABLE 5.VI

Number of *Themos olfersii* egg clusters already present on chosen shrub at time of laying eggs at study site 1 in four generations.

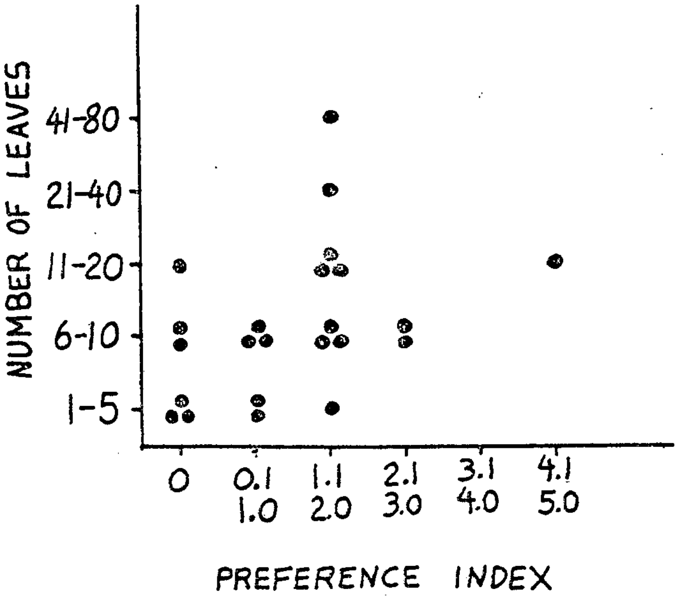
NO. EGG CLUSTERS ALREADY PRESENT	NUMBER OF EGG CLUSTERS LAID PER GENERATION									
	SPRING 1973		SPRING 1974		SPRING 1977		SUMMER 1978		TOTAL	
0	16		11		12		18		57	
1	9	21	4	9	2	7	6	6	21	43
2	7		1		2		0		10	
3	4		1		1		0		6	
4	1		1		1		0		3	
5	0		1		1		0		2	
6	0		1		0		0		1	

TABLE 5.VII

Correlation between *Eriotheca pubescens* plants height and incidence of *Themos olfersii* egg clusters at study sites 1 (sum of four generations) and 2 (one generation only).

HOST PLANT HEIGHT CLASS	HEIGHT (METERS)	NUMBER OF PLANTS OBSERVED			
		SITE ONE		SITE TWO	
		TOTAL	WITH EGGS	TOTAL	WITH EGGS
Tall tree	>5	0	0	5	0
Medium tree	3-5	0	0	8	0
Small tree	2-3	0	0	14	0
Tall shrub	1-2	9	4	19	0
Medium shrub	0.5-1	2	0	30	0
Low shrub	<0.5	23	17	134	6
TOTAL		34	21	210	6

Obs. only a sample of the host plants from site 2 is presented.



NO. OF LEAVES PER SHRUB	AVERAGE PREFERENCE INDEX
1-5	0.4
6-10	1.3
11-20	1.9
21-40	2.0
41-80	2.0

FIGURE 5.4. Correlation between the number of leaves in low bushes(less than half metre high) of *Eriotheca pubescens* and the preference index (average number of egg clusters per generation received per shrub) of *Themos olfersii*.

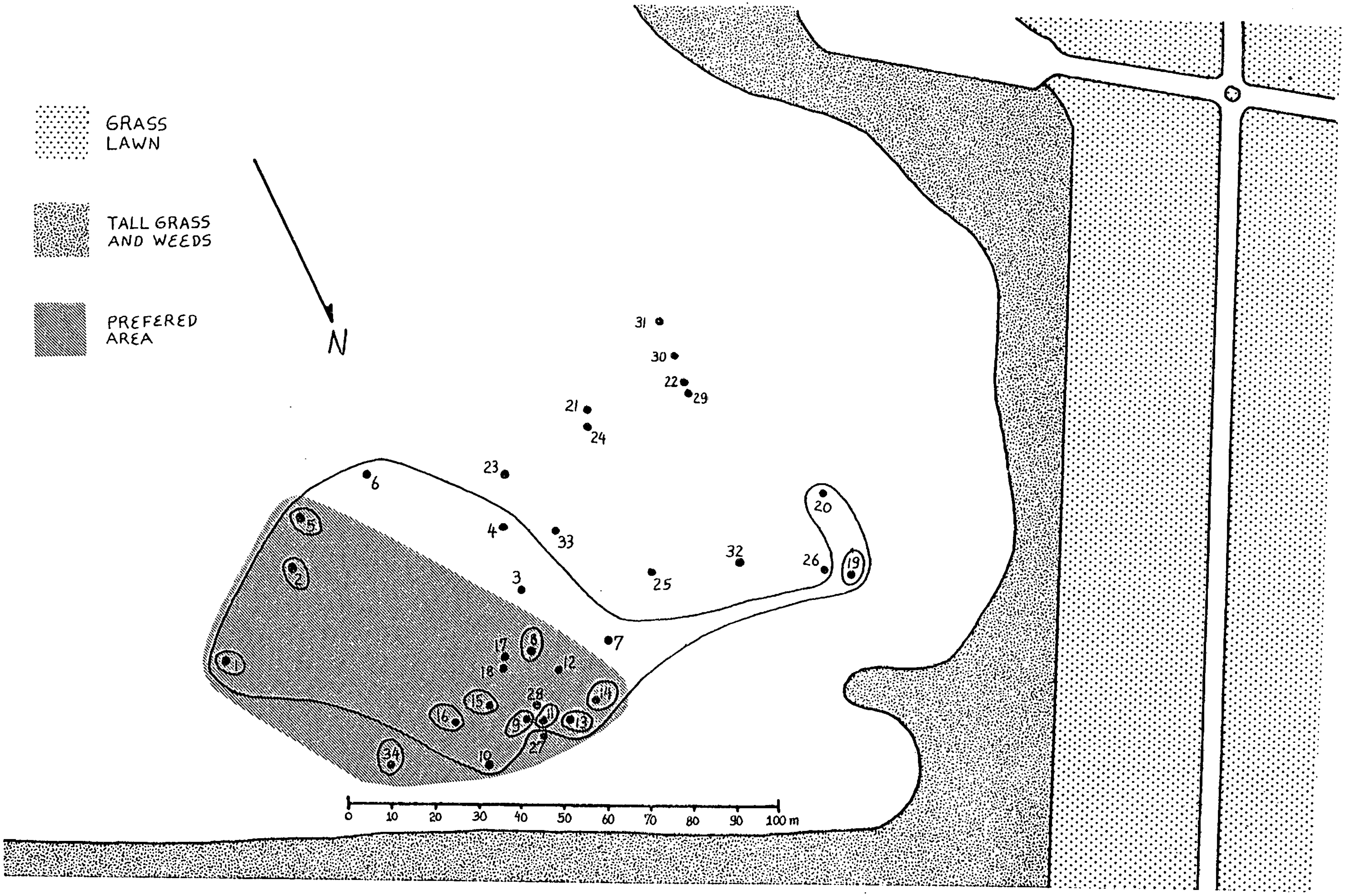


FIGURE 5.5. Spatial distribution of *Eriotheca pubescens* shrubs at study site One. Each dot represents one shrub. All shrubs present in this area are shown. The prefered shrubs (those which received most egg clusters of *Themos olfersii*) are indicated by a ring around the dot. The prefered area (shaded) is that with the highest density of *Themos olfersii*. A continuous line encloses the shrubs studied during all four years.

with 11-13mm for males. Both sexes have a similar colour pattern of bright orange head, thorax and legs, and black abdomen with basal sternites orange, but males have less orange on the thorax, and their wings are totally hialine except for the black stigma and furcate antennae with abundant long black hairs facing forward. Females have mostly hialine forewings with a dark band in the centre and a small dark dot at the extreme apex, infuscated hindwings and simple antennae with minute black hairs. Both sexes have sharp-pointed sickle-shaped mandibles. A more detailed description of this species together with some illustrations of the forewing, sheath, lancet, and male genitalia was given by D.R. Smith (1975)(see Figure 5.6).

A notch near the apex of the radial cell of the forewing of both sexes readily differentiates this species from the very similar _Dielocerus formosus_ (see D.R. Smith, 1975 and in prep. for more details on the separation of both species).

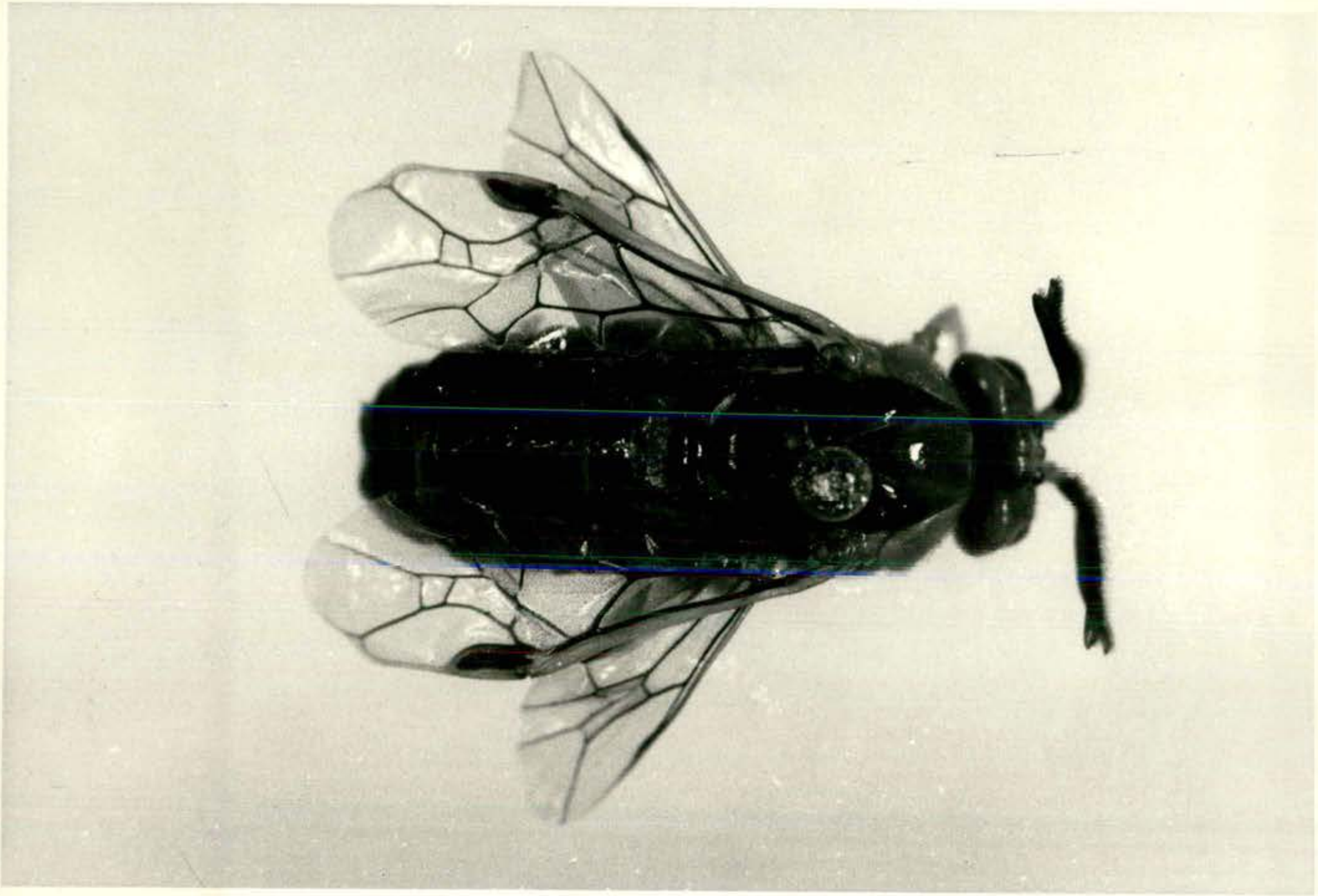
5.B.2 SEX RATIO

The secondary sex ratio in the adult stage, at the time of emergence from cocoon, was calculated from 922 adults of _D. diasi_ which emerged in the laboratory from 29 cocoon masses collected in several areas in the field. The male-to-female sex ratio ranged from 0.18 to 0.61 males:females per cocoon mass, with an average of 0.31 ± 0.19 males:female (standard deviation given after the mean). The larger cocoon masses, resultant from the fusion of several larval sib-groups, departed less from the average. Therefore, there are on average 3 females for each male _D. diasi_ in the adult stage. The sex ratio also approaches 3 or more females per male during all the larval feeding stages including the first instar (see Chapter 7).

5.B.3 ADULT EMERGENCE FROM COCOON

Adults always emerge during the morning period from about 0730h ($1\frac{1}{2}$ hours after dawn) to 1200h, both in the laboratory and in the field. Males emerge on average earlier than females. The peak of male emergence is from 0730h to 0830h, while the peak of female

FIGURE 5.6. Adults of <u>Dielocerus diasi</u> Smith. The male (left) is magnified 9X, and the female (right) is magnified 7.5X. Note the dark band on the female's forewing and the male's bristly furcate antennae.



emergence is from 0830h to 0930h (see Figure 4.17). Adults emerge with their exoskeleton and wings already hard and dry, which indicates that they must go through their last moult (from pupa to adult) a few days before the emergence day. To get out of the cocoon mass, the adults must bite open a passage through the 0.2mm thick hard wall of their own individual cocoon, then through the 5-10mm thick spongy layer of the communal covering envelope (see Chapter 7), and finally through the thin papery external cap of the covering envelope. Each adult makes its own exit tunnel in the communal cover. All these activities take more than one hour to be completed.

Using their sharp-pointed sickle-shaped mandibles and rotating their bodies, the adults open a very neat circular lid on the top of the cocoon. The lid's complete circumference is cut out and the lid is detached free from the rest of the cocoon. Males cut lids of 4mm diameter on average, and females lids of 5mm (see Figure 7.27). The exit way which they open through the spongy layer of the communal cover is very narrow and the adults have to push forward in order to pass, but this is no problem as this layer of silk is very compressible. The opening through the external papery cover is made through an irregular opening, which results from several semi-circular cuts close to each other, one beside the other parallel, or in different angles (see Figures 7.33).

5.B.4 DEFECATION AND DEFENSIVE REACTIONS

While still halfway through the spongy layer, or halfway through the external papery cap, or just after emergence before leaving the cocoon mass, the adults eject their meconia. The wastes are abundant, very liquid, olive-brown and bad smelling. The external cap of the cocoon mass becomes stained by the wastes of the many adults emerging from it.

If disturbed just after emergence, the adults eject a jet of liquid wastes. Another defensive reaction exhibited by newly-emerged adults is feigning death: they bend their legs closely to their bodies, close their wings, and stay motionless for an average of 30 seconds (N = 25 females tested in the laboratory). In one exceptional case, one female remained immobile for 16 minutes.

5.B.5 FEMALE BEHAVIOUR BEFORE FLYING

Once out of the cocoon mass the adults behave differently according to their sex. Females start moving upwards immediately at a fast pace. They walk with their wings partially open, hindwings foremost, and never stop on top of the cocoon mass unless forced to do so by males (see below). They always exhibited a very strong negative geotropism reaction when tested in the laboratory. The females move almost non-stop up the tree trunk and main branches until they reach a leaf in the lower canopy of the tree where they were born.

During occasional stops on their upward march and specially once they are established in a leaf in the lower canopy, they perform cleaning movements. They clean the head, legs, wings and abdomen with their mouth appendages and legs, specially the front and hind legs. To clean the dorsum of the abdomen, they partially open their wings, lower the abdomen tip and put both hind legs over the abdomen. Then, with alternating movements they scratch their legs over the top of the abdomen from front to back. To clean their wings, they close them laterally against the abdomen and move their hind legs from front to back over them.

Once the females reach a leaf in the lower canopy, they climb to one of its leaflets, giving preference to those exposed to direct sun. Several females emerging from the same cocoon mass were seen going to the very same leaflet in consecutive days. On their chosen leaflet, each female stays for about 10 minutes to 3 hours, most of this time motionless on the upper surface of the leaflet sun basking, but other times cleaning themselves or moving about over the leaflet and nearby ones. After some time they start to vibrate their wings producing a loud buzzing sound. The frequency and intensity of this wing buzzing increases progressively and soon they take off and fly.

5.B.6 MALE BEHAVIOUR BEFORE FLYING. MATING

Males are better fliers than females, and can fly well just after emerging, although they rarely do so. On the contrary, most males stay for several minutes, up to some 20 minutes, on top of or beside the cocoon mass from which they emerged. In this position they stay motionless for most of the time, but also spend some time with cleaning behaviour, just as the females. They remain vigilant and readily approach any adult emerging from their own or other neighbouring cocoon mass. At times several males may be found waiting on top or just around a cocoon mass, specially above the cocoons along the tree trunk or branch, but there was no evidence of animosity between them.

When a female emerges and starts moving rapidly away from the cocoon mass, the waiting male, or males, try to intercept her path. If this fails they start to chase the female, which shows no interest in and even tries to avoid them. Some females escaped to the tree canopy without being caught by males. If one male succeeds in intercepting or catching up with a female, he approaches with the tip of his abdomen extended and bent downwards and immediately tries to mount her. If successful, he connects the genitalia and then turns 180° to face away from the female in a back-to-back fashion. The male abdomen becomes much stretched during copulation. Matings lasted 4 to 9 minutes usually, occasionally more than 10 minutes. During copula the pair stay motionless, but occasionally, specially if disturbed, they move about slowly with the larger female dragging the male behind. It is the female which takes the initiative to end the mating by moving forward vigorously or kicking the male with her hind legs. After mating, both adults move about vigorously and perform much cleaning behaviour. Females then readily continue their upward march to the tree canopy.

Males are ready and willing to mate again immediately after disconnecting from the earlier female. They try to mate with as many females as they can find, even with females in coitus with other males and with females which have already mated. In circumstances when there are several males present close together, it is not rare to see one or two males mounted on top of a pair already in coitus.

Once mated, females do not mate again and actively avoid males, at least for the first hour or two after emergence from cocoon (N = 60 females tested in the laboratory). But at least one female was seen mating with a second male near the cocoon mass before flying, in the laboratory. I never saw females mating after they flew from their birth tree, but this must happen as many females observed in the field flew away without mating.

5.B.7 SEX PHEROMONE

Newly emerged females produce a smell which is highly attractive to males: any object (even the observer's fingers) which stays in contact for a few minutes with newly emerged females becomes itself very attractive to males, which then try to mate with it. Newly emerged virgin females, however, failed to attract any male in the field when put into cages with perforated screens attached to branches of potential host trees, although males were known to be common in the tested area.

5.B.8 MALE DISPERSAL FLIGHT

After spending up to 20 minutes near the cocoon mass from which they emerged, males climb the trunk or branch of the host tree a little. In this new position, still on the trunk or branch, they stay either motionless or perform cleaning activities for another period of minutes, up to one hour, and eventually take off flying. I seldom saw *D. diasi* males in the field after they had left their birth tree. Apparently they fly actively visiting several host trees looking for virgin females. No male was ever seen, however, approaching females already established in their egg-laying sites. I do not know how far the males fly.

5.B.9 FEMALE DISPERSAL FLIGHT

In the laboratory, newly emerged adults exhibit strong positive phototropism. When flying, females produce a buzzing sound just like flying stink bugs (Pentatomidae). Females can fly just a few minutes after emerging, but then the flight is short and heavy. After one or two hours they are able to make a sustained flight for long periods. Females being heavier, are worse fliers than males.

After take-off in the field some females fall to the ground just beneath their natal tree and then climb whatever grass stalk or twig they find up to the top, vibrate their wings vigorously and take to the air again. Most females, however, are successful in their first attempt to fly. They usually fly around the top of the canopy of their natal tree before taking a straight ascending flight path downwind. During the months of August and September, when most observations on departing females were made, the main wind blew from southeast to northwest and most females took that direction. It appeared they always headed toward the nearest tall host trees. Several females were observed landing on the top of the canopy of their natal tree, where they stayed from a few seconds to up to one hour before taking off again and flying downwind. I do not know if some females can establish themselves in the canopy of their own natal tree without going through a dispersal flight.

The dispersal flight is done at a height between some 5 to 10 metres above the ground, which is the height of the canopies of mature *S. aureum* trees. I do not know how much above the host trees these sawflies can fly, neither how far away from their natal tree.

Most females initiated their dispersal flight between 1000h and 1300h.

5.B.10 SELECTION OF EGG-LAYING SITE

A female arriving near a potential host tree of S. aureum flies in circles around its upper canopy and lands on a healthy young leaf on its top. She walks silently over both surfaces of several leaflets in this leaf, keeping her wings closed over her abdomen and moving in a fast pace. A few seconds later she takes off, circles around the tree canopy again and lands on another young leaf on the top of the canopy, where she repeats her exploratory movements. Again she takes off a few seconds later and repeats her flying-round-the-canopy and landing-and-exploring-young-leaves circles several times. Occasionally she stops for one minute or more on a leaflet, but then takes off to continue her circling exploratory behaviour. She also visits leaves where other females have laid their eggs, but explores only the neighbouring leaflets and does not go on to the occupied leaflet, and almost immediately withdraws from the leaf.

Eventually she starts to land again on leaves which she has visited before. After some 15 minutes from the arrival in the tree, she tends to visit more and more one particular leaflet and spend more and more time wandering over it. A few minutes later she stops flying and lands on her favourite leaflet: she has finally chosen and established herself definitively on her egg-laying site.

I saw females arriving to host trees only during the early warm hours of the day between 1100h and 1300h. It took more than one hour after arrival for some females to become definitively established on their chosen leaflet, but it took as little as 25 minutes for others. Once established on their chosen leaflet, females never fly again.

Most landing is done on leaflets of the apical or subapical pair of leaflets in a leaf. When exploring a leaf, females move in semi-circles all over a leaflet and transfer to the next leaflet in the same leaf by walking through the rachis. Females restrict their walking in each landing to leaflets in the same leaf, never passing to other nearby leaves by walking through rachis and branches. All movements between leaves are made by flight.

Only rarely were two exploring females seen to land on the same leaflet at the same time. In these occasions there was no sign of animosity, no buzzing or other display, and a few seconds later one of the females (the second to arrive) departed.

5.B.11 TERRITORIAL BEHAVIOUR

Once the female has decided on the egg-laying site, she establishes herself definitively on the leaflet and marks this by buzzing the wings loudly while moving in zigzags, circles and semicircles all over the leaflet surface, but specially on its ventral (abaxial) surface. For the next 24 hours, during day time, the female alternates active and passive periods, each lasting from a few seconds to one or two minutes.

During the passive periods, the female stays motionless, with her wings partially open and usually facing the leaflet's base, on the ventral surface of the leaflet, always on the same spot - the core area - which is always halfway between the midrib and one of the margins and about halfway between the base and apex of the leaflet. Sometimes the female buzzes with her wings while stationary.

During the active periods, the female walks in zigzags and circles over the whole leaflet but specially over and around the core area on the ventral surface of the leaflet (Figure 5. 7). While walking, the female alternates silent periods, when the wings are kept motionless partially open, with noisy periods when the wings are vigorously vibrated producing a loud buzzing sound which is clearly audible from more than 10 metres away. The buzzing periods last only a few seconds, 5 to 10 usually, but occasionally can last for almost one minute. All the buzzing is done while the female is on the ventral surface of the leaflet. While moving in zigzags, the female usually turns backwards a little before turning to the other side. While moving through the leaflet, the female approaches her mouthparts and tip of abdomen close to the leaflet's surface. As the time passes, the female spends

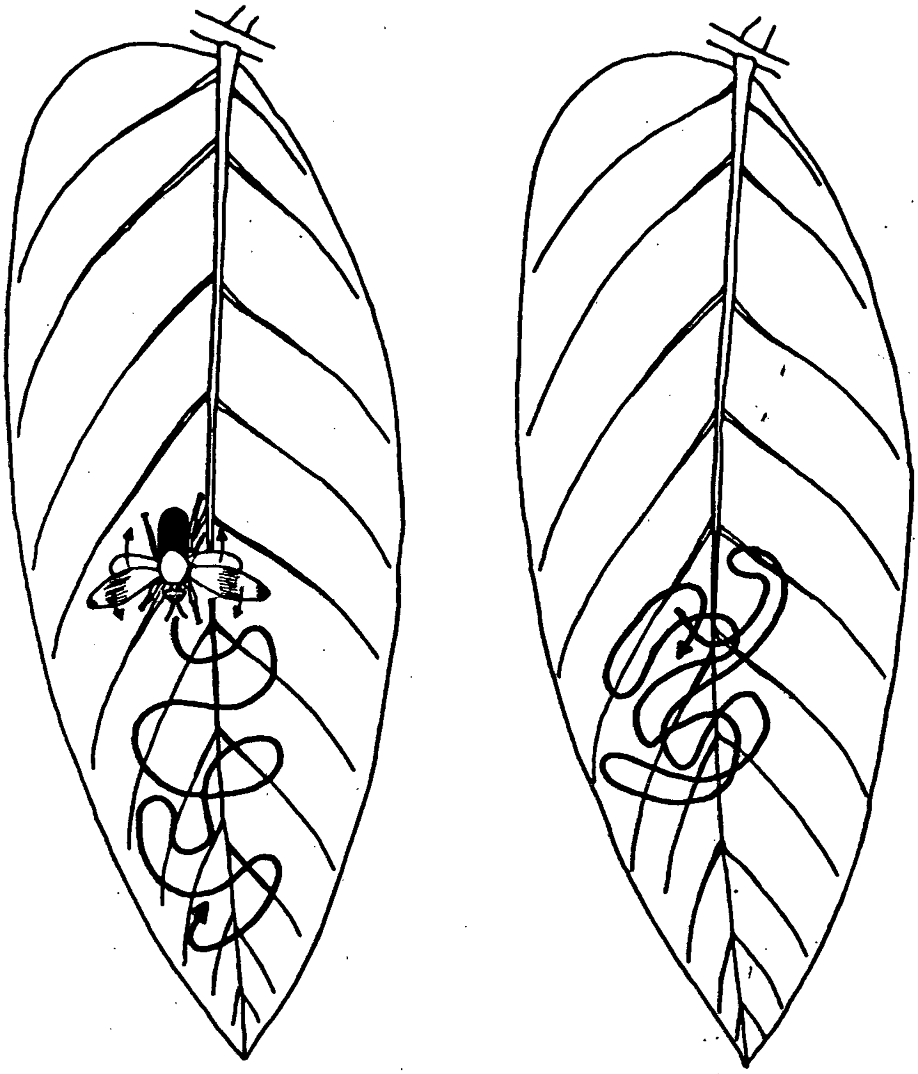


FIGURE 5.7. T.olfersii female walking in semi-circles and zigzags, while buzzing her wing, over an area on the underside of her chosen leaflet prior to laying her eggs - ?territorial display.

more and more time walking in circles just over the core area.

During the dark hours the female stays motionless, with her wings partially open, on the core area facing the leaflet base.

It is not rare to find several females in one host tree simultaneously establishing and "advertising" their territories on their chosen egg-laying leaflet. Trees in these occasions become very noisy with an almost continuous orchestration of buzzing sounds.

I did not see any sign of aggressiveness, in the few cases witnessed, when newcoming females landed on leaflets already occupied by established females. The established females remained motionless while the newcomers wandered over the leaflets and eventually departed.

Between 1100h and 1200h in the day after establishing themselves on their chosen leaflets, the females start to lay their eggs.

5.B.12 SPATIAL DISTRIBUTION OF EGG CLUSTERS WITHIN A HOST

Chosen leaflets had an average length of 11.3cm, with a range from 5 to 14cm long (N = 40 leaflets). There is a strong selectivity for the height of the oviposition site, all egg clusters being found above 1.5 metres from the ground. Most egg clusters, however, are laid much above this limit, usually between 4 and 10 metres above the ground. Only leaflets on the outer edge of the canopy, specially those on the top, are utilized for oviposition. Intact mature leaflets are preferred, but in trees heavily infested by the sawfly, and so with few intact leaves, it is not rare to find egg clusters on partially eaten leaflets. There is also a strong selectivity for the position of the leaflet inside the leaf. The oldest and youngest leaflets are rarely utilized for oviposition. Most egg clusters were found on the second or third pair of leaflets, counting from the leaf apex. In older leaves most egg clusters were on the second pair of leaflets, whereas on young leaves most egg clusters were found on the third or even fourth pair of leaflets. Never were two egg clusters found on the same leaflet, and only twice were two egg clusters found on neighbouring leaflets of the same leaf.

5.B.13 SPATIAL DISTRIBUTION BETWEEN TREES AND PATCHES

The populations of D. diasi in the Federal District are very patchy. Several places with a good supply of host plants were inspected carefully repeatedly for several years with no sign of the sawflies. Nevertheless the species is widely distributed in the District. Population densities, though, can be high locally: sites with more than 100 egg clusters per hectare per generation were common.

Egg clusters were always heavily clumped in a few host trees among the many available in a patch. Very often 10 to 20 simultaneous egg clusters could be seen on the same tree, whereas most S. aureum trees in any one patch do not receive any egg cluster at all.

Because the egg clusters are laid high up in the tree canopy and are, therefore, difficult to see from the ground, data on the spatial distribution of D. diasi egg clusters were collected in an indirect way by observing the distribution of cocoons (which are spun on the trunk and lower branches, and are thus much easier to observe) between trees and patches of trees (see Chapter 7 for more information on cocoons). This indirect method is reliable because there is no larval migration from tree to tree, but it gives an underestimate of the actual number of egg clusters laid because mortality during the egg and larval stages can cause total extinction to several sib-groups before they reach the stage to spin their cocoons. A further complication is that the larval sib-groups may split or fuse with others before spinning the cocoon masses (see Chapter 7).

Dielocerus only attack Sclerolobium aureum plants with a tree habitus, usually over 3 metres in height. Only a small percentage of S. aureum trees in the Federal District during the study period had Dielocerus of any life stage. Some of the patches of Sclerolobium harboured a larger sawfly population than others. In several patches Dielocerus seemed to be totally missing. The sawfly populations were faithful to their host plant patches. The sawfly incidence remained fairly constant from year to year in each patch.

The incidence of Dielocerus sawflies among the available host plants within a patch varies greatly: it is clearly clumped and not random (Table 5.VIII). Most patches have a few host trees which are very heavily infested, with several dozens and sometimes even several hundred cocoon masses (see Chapter 7). These masses include cocoons of several different years. A few other trees in each patch have some cocoon masses and all the other trees do not have any.

Old cocoon masses of Dielocerus remain attached to the tree trunk for several years before falling to the ground where they are finally decomposed. Some cocoon masses remained on the trunk for at least 10 years before falling. Thus, the number of cocoon masses present in each tree at any one time gives a good index of each tree's attractiveness to Dielocerus females. Surveys of cocoon masses per tree as given in Table 5.VIII actually represent a cumulative sensus of each tree's population in the last few years.

Heavily infested trees with more than 100 cocoon masses on the trunk and branches were usually found close to roads and buildings, and this was not due to the greater accessibility of such trees to the observer.

The Dielocerus population in the Federal District is much below the carrying capacity of the environment in terms of host plant availability (for egg laying, larval feeding, and cocoon spinning). Several other insects attack Sclerolobium aureum in this area but there is no indication of any significant competition with Dielocerus. Perhaps the two organisms which could sometimes be limiting the availability of fresh leaves to Dielocerus are: (i) a weevil (Coleoptera, Curculionidae) which bores in the trunk and major branches of the trees, eventually leading to the death of several lower branches; and (ii) a rust (fungus) which attacks the leaves.

TABLE 5.VIII

Three examples of the spatial distribution of *Dielocerus diasi* cocoon masses within patches of the host plant *Sclerolobium aureum* compared with the expected Poisson distribution.

NO. COCOON MASSES PER HOST TREE		FREQUENCY OF HOST PLANT TREES IN 3 SITES					
		SITE 6		SITE 16		SITE 8	
RANGE	AVERAGE	O	E	O	E	O	E
0	0	14*	0.44	24*	1.41	61	45.53
1-5	3	12	25.99	13	35.93	11	26.47
6-10	8	5	10.33	2	5.63	0	0.000
11-15	13	5*	0.22	1*	0.04	0	0.000
16-20	18	0	0.000	0	0.000	0	0.000
21-25	23	1*	0.000	1*	0.000	0	0.000
26-30	28	0	0.000	2*	0.000	0	0.000
>31	-	0	0.000	0	0.000	0	0.000
TOTAL NUMBER OF TREES		37		43		72	
AVERAGE NUMBER OF COCOON MASSES PER TREE		4.4324		3.4186		0.4583	

O = observed frequencies

E = expected frequencies (Poisson distribution with same mean).

* = observed frequency is much higher than expected.

The frequency distribution of cocoon masses of different sizes can be used to give a rough estimate of the average number of larval sib-groups which form each cocoon mass, which will indicate the average composition of the local mating population in the natal tree over the cocoon mass before dispersion. As the actual average number of larvae per sib-group reaching the end of the feeding period is not known, four estimated averages ranging from 25 to 40 larvae per sib-group (see Chapter 7 for more information) were used to calculate the most probable number of sib-groups needed to form each cocoon mass size class from 6 to 440 cocoons per mass for 283 cocoon masses of tree no. 3/2 (see Chapter 7)(Table 5.IX). In this calculation the cocoon masses with less than 6 larvae were not taken into consideration for they are regarded as stray larvae (see Chapter 7), and the cocoon masses with 6 to 16 or 6 to 20 cocoons are considered to be half-sib-groups which had split before spinning their cocoons (see also Chapter 7), and so their frequencies were divided by two.

This calculation gives an average of 1.5 to 2 sib-groups per cocoon mass according to the average size of sib-groups at the end of the feeding period (Table 5.1X). Another way to estimate this is by dividing the total number of cocoons in masses with 6 or more cocoons (N_1 = 11,207 cocoons in total) by the number of masses with more than 16 cocoons plus half the number of masses with 6 to 16 cocoons (N_2 = 180 + (103:2) = 231.5 cocoon masses). An average of 49 cocoons per mass is obtained, which means an average of 1.6 to 2 sib-groups per cocoon mass, when the estimated size of sib-groups at the end of feeding is 25 or 30 larvae per group. But when the estimated size of sib-groups is 35 or 50, cocoon masses with 16 to 20 cocoons must be counted as half-sib-groups also. Thus N_2 becomes equal to 163 + (120:2) = 223 cocoon masses, and the obtained average is 50 cocoons per mass, which means an average of 1.3 to 1.4 sib-groups per mass.

As the occurence of contemporaneous egg clusters on the same tree is usually a prerequisite for the existence of large coooon masses which result from the fusion of several larval sib-groups (each originating from one egg cluster) of about the same age, the average

TABLE 5.IX

Estimated frequency distributions of the number of larval sib-groups of *Dielocerus diasi* per cocoon mass at tree no. 3/2 based on four different estimates of the average number of larvae per sib-group surviving until the spinning of their cocoons.

No. COCOONS PER COCOON MASS (CLASSES OF 10)	ESTIMATED NUMBER OF SIB-GROUPS PER COCOON MASS*				FREQUENCY OF COCOON MASSES
	X_1 = 25	X_2 = 30	X_3 = 35	X_4 = 40	
431 - 440	17	14	12	11	1
271 - 280	11	9	8	7	1
241 - 250	10	8	7	6	1
231 - 240	9	8	7	6	1
161 - 170	7	6	5	4	2
151 - 160	6	5	4	4	4
141 - 150	6	5	4	4	2
131 - 140	5	4.5	4	3	2
121 - 130	5	4	3.5	3	3
111 - 120	5	4	3	3	4
101 - 110	4	3.5	3	3	5
91 - 100	4	3	3	2	6
81 - 90	3	3	2	2	5
71 - 80	3	2.5	2	2	8
61 - 70	3	2	2	2	6
51 - 60	2	2	2	1	16
41 - 50	2	1.5	1	1	16
31 - 40	1	1	1	1	31
21 - 30	1	1	1	1	49
16 - 20	1	1	½	½	17
11 - 15	½	½	½	½	36
6 - 10	½	½	½	½	67
1 - 5	-**	-**	-**	-**	76
AVERAGE NUMBER OF SIB GROUPS PER COCOON MASS	1.97	1.75	1.60	1.46	

* X_1, X_2, X_3 and X_4 are the four estimated average larval survival per sib-groups.

** groups with less than 6 larvae are not considered (stray larvae).

number of sib-groups per cocoon mass will give an underestimate of the actual number of contemporaneous egg clusters laid per tree, in other words, the average number of females colonizing a host tree contemporaneously at any one time.

As apparently only about ¾ of the original sib-groups survive through the egg and active larval stages to spin their cocoons (see Chapters 6 and 7), the calculated average number of sib-groups per cocoon mass would be a proportional underestimation of the original number of contemporaneous egg clusters. However, as not all contemporaneous sib-groups fuse with each other before spinning their cocoons, the obtained estimate represents an even smaller proportion of the average number of contemporaneous females colonizing the host. This indicates that the average number of contemporaneous females colonizing one preferred host is above 3 or 4.

5.C DISCUSSION

5.C.1 MATING, SEX PHEROMONE AND MALE COMPETITION

Relatively little detail is known about the mating behaviour of sawflies. Most studies have concentrated on some species of Diprionidae and Tenthredinidae only, and all the other groups are very neglected.

Females usually mate only once (Benjamin, 1955; Coppel *et al.*, 1960; Gorske *et al.*, 1977; Regas-Williams & Habeck, 1979; but see Dahlsten, 1961 and Gordh, 1975 for cases of polyandry) while males are polygynous (Benson, 1950; Coppel & Benjamin, 1965; Lyons, 1976; Regas-Williams & Habeck, 1979; Tozawa, 1940). This was also found to be true for *Dielocerus diasi* in this study. Lyons (1976) found that in the laboratory male *Neodiprion sertifer* (Geoffr.) mated on average with 4 females, sometimes with up to 11 females, but perhaps could have mated with even more females under ideal conditions of *ad libitum* supply of virgin females.

It has been frequently reported that virgin females of several sawfly species usually avoid males - "females are often without any apparent desire to copulate, and have to be captured and held by the males" (Benson, 1950) and "appear to resist the attempts to mate offered by the males" (Middleton, 1921). This resistance or avoidance of male's attempts to mate has also been observed here for D. diasi. After mating once the females cease to be attractive to males (e.g. Coppel et al., 1960).

Females of most studied species of sawfly are prone to start looking for the host-plant and start laying eggs soon after emergence without waiting to be fertilized by males (e.g. Pristiphora conjugata (Dahlbom) - Delmas, 1926; Zenarge turneri(Rohwer)- Moore, 1962; Arge humeralis (Beauvois) - Regas-Williams & Habeck, 1979). But females in several other species of sawfly definitely wait, usually on a sun-warmed leaf in the canopy of the host tree where they were born or a nearby one, for several hours or even one whole day until they are found by a male, and only after being fertilized do they fly away to look for a host plant where to lay their eggs (e.g. Neodiprion spp. - Benjamin, 1955; Bobb, 1972; Dahlsten, 1961; and Croesus septentrionalis (L.) - Caccamo, 1966). This is the case of D. diasi females. Whatever the female's strategy, most mating in sawfly species occurs on the foliage of the host-plant or on flowers (in species where adults feed)(Benson, 1950).

Males of several groups of Tenthredinoid sawflies have branched antennae with abundant long sensitive hairs: all Diprionid, some Pergid (all Pterygophorinae, some Perreyiinae and some Euryinae) and a few Tenthredinid (Cladius spp) males have pectinate highly pubescent antennae, while most Argid (all Trichorhachinae, Dielocerinae, Pachylotinae, Theminae, Erigleninae and Sterictiphorinae) males have furcate and very pubescent antennae. The males of both species studied here are an example of this phenomenon. These specialized antennae ought to be used to enable the males to find females, most probably by detecting sex pheromones released by these.

However, up to now the existence of sex pheromones in Tenthredinoid sawflies has been demonstrated only for the Diprionid genera Diprion and *Neodiprion* (Coppel *et al.*, 1960; Casida *et al.*, 1963; Jewett *et al.*, 1976; Bobb, 1972). Coppel *et al.* (1960) found that the sex pheromone in *Diprion similis* (Hartig) is produced by abdominal glands, and reported that individually caged females were able to attract more than 10,000 males each in one week. They also found that the female's attractiveness to males was greatest just after emergence from the cocoon, decreased in the following days and ceased completely after mating once. Bobb (1972) found that female *Neodiprion pratti* (Dyar) were able to attract males over 170 metres away from the nearest pine forest. Evidences of female produced sex pheromone attracting males have been reported for several other species of sawflies, including an Argid, *Schizocerella pilicornis* (Holmgren)(Webster & Mally, 1900).

Despite the failure of caged *D. diasi* females to attract males in field trials, I think there still are strong evidences to believe that females of this species do produce a sex pheromone to attract males, and probably that is just what the females do when they are sun basking on the lower canopy of their natal host tree before flying away. According to Benjamin (1955), Bobb (1972) and Dahlsten (1961) female *Neodiprion lecontei* (Fitch), *N. pratti* (Dyar) and *N. fulviceps* (Cresson), respectively, which emerge from cocoons in the forest soil or litter, fly to the crowns of pine trees (their hosts) before they start attracting males (releasing sex pheromone).

Sawflies exhibit little or no courtship - males usually dart over the female and try to hold her as soon as they come close to one, then if successful they mount over the female. But as all Tenthredinoid sawflies have the male's genitalia rotated 180 degrees on the median axis - strophandry (Crampton, 1919; Boulangé, 1924) - the males have to turn round over the female's abdomen while trying to insert the aedeagus, ending up in a back-to-back (tandem) coital position (Benson, 1950; Delmas, 1926; Ghent, 1959; Gordh, 1975; Lyons, 1976). The observations on the mating of *D. diasi* agree well with this general picture. Gordh (1975) described the use of wing vibration by *Hemitaxonous dubitatus* (Norton) males while mounted on the female and prior to the insertion of the aedeagus, and noted the conspicuous absence of intensive antennal vibrations in the male behaviour, so common in parasitic Hymenoptera. No wing or antennal vibration was observed in the behaviour of D. diasi males. The evolutionary significance of the genital rotation is still unclear (Gordh, 1975).

The duration of coitus is highly variable among the sawflies: ½ to 2 minutes in average for the Tenthredinidae (Benson, 1950; Gordh, 1975); 2 to 100 minutes for the Diprionidae (Coppel & Benjamin, 1965; Dahlsten, 1961; Lyons, 1976; Rohwer, 1915); 8 to 30 minutes for the Cimbicidae (Bodenheimer, 1932; Enslin, 1917); 1½ to 25 minutes for the Argidae - Arge spp (Regas-Williams & Habeck, 1979; Tozawa, 1940) and Schizocerella pilicornis (Gorske et al., 1977) - but Guercio (1893) reported 5 to 6 hours (!) for Arge pagana (Panzer). No information is available for the Pergidae. The values obtained here for D. diasi fit well within these limits.

This is apparently the first time that sib-mating is reported as a common event in the field for a sawfly species: D. diasi (see discussion below).

Although most Tenthredinoid sawflies have polygamous males there is little evidence of aggressive, territorial or swarming behaviour among the males. I found no evidence of aggressiveness between D. diasi males waiting for females on top or near the cocoon mass. However, male swarming and clustering have been reported for Dolerus niger (L.)(Benson, 1950), Trichiosoma lucorum (L.)(Cameron, 1882), Trichiocampus viminalis (Fallén)(Downes, 1925), Arge gracilicornis (Klug)(Loiselle, 1907), and Sericoceros krugii (Cresson) (Martorell, 1941). Cameron (1882) wrote that males of T. lucorum flew around the tops of birch trees (their host-plant) on hot days producing a loud buzzing, just as bumblebees, and reported seeing fighting between these males: "I was once the witness of a battle between two males of T. lucorum, which lasted for nearly ten minutes, or perhaps longer, for they flew away, and may have continued the fight after I lost sight of them. Their mode of fighting was simply to fly at each other in the air, a concussion (violent collision) of the two bodies being the result; and they must have come together with some force for the noise made thereby could be distinctly heard. I did not observe whether they tried to use their mandibles or not, but Westwood (1839-40) mentions having caught two males with their mandibles interlocked" (Cameron, 1882). This behaviour should be better studied as it seems to be a case of male territorial behaviour parallel to those evolved by several aculeate wasps and bees to gain control over an area from which virgin females are emerging, in the sawfly's case this territory is the host tree (see e.g. Alcock et al., 1978 and Bibolini, 1967).

5.C.2 SEX RATIO, PARTHENOGENESIS AND INBREEDING

There is no satisfactory overall account of the sex ratio of Tenthredinoid sawflies. In fact there is even some disagreement as to its general trend in this group. Coppel and Benjamin (1965) for example, say the secondary sex ratio of nearctic Diprionids at adult stage approaches 1:1 for most species but may vary considerably from locality to locality for the same species. Verzhutskii (1966), on the other hand, found a general predominance of females over males at the adult stage in sawflies of eastern Central Siberia (Baikal region), and pointed out that in the warmer Baltic region the female-bias was smaller, according to Tsinovskii (1953). Verzhutskii gave the following species as good examples of this general trend: Arge ustulata (L.), A. gracilicornis (Klug), Cimbex femorata (L.), Tenthredo mesomelas L. and Pachyprotasis rapae (L.).

Several species of sawfly, however, specially in the Tenthredinidae but also in a smaller scale in the Cimbicidae, Pergidae and Diprionidae (but not in the Argidae), are known to exhibit thelytokous parthenogenesis (where unfertilized eggs produce only females)(Benson, 1950; Cameron, 1882-85; Carne, 1962). These species have unknown or very rare functionless males. Benson (1950) called attention to the existence of thelytoky and arrhenotoky (where fertilized eggs produce only females and unfertilized eggs produce males only) in closely related species or races within several genera of sawflies: e.g. Dolerus, Eriocampa, Fenella, Pristiphora and Nematus (Tenthredinidae), Cimbex and Abia (Cimbicidae) and Gilpinia (Diprionidae). The type of parthenogenesis and the sex ratio vary geographically for many sawflies, and are apparently fixed genetically for each local population and correlated with the climate so that the warmer the temperature, the higher the proportion of males in the population (Benson, 1950; Carl, 1972; S.G. Smith, 1940). I have not seen, however, any functional explanation as to why this should be so.

Most Tenthredinoid sawflies, like the majority of the Hymenoptera, exhibit arrhenotokous parthenogenesis only (Benson, 1950). The secondary sex ratio of arrhenotokous sawflies at the time of adult emergence from cocoon rarely approaches the 1:1 ratio: e.g. Gilpinia frutetorum (F.)(Raizenne, 1957), G. coreana (Takagi) (Verzhutskii, 1966) and Nesodiprion biremis (Konow)(Beaver & Laosunthorn, 1975)(all Diprionidae) and Athalia rosae (L.)(Verzhutskii, 1966) and Pontania crassipes (Thompson)(Verzhutskii, 1966)(Tenthredinidae). The great majority of arrhenotokous species have female-biased secondary sex ratios (at the time of adult emergence) between 1.5 to 5.4 females per male, most commonly around 2 or 3 females per male (Benjamin, 1955; Bodenheimer, 1932; Caccamo, 1966; Kurir, 1977; Raizenne, 1957; Scheibelreiter, 1973; Tsinovskii, 1953; Verzhutskii, 1966). The best studied species so far in this respect are seven Nearctic species of Neodiprion of which over 27,000 adults were reared in the laboratory from larvae collected in the field in southern Ontario over a period of 16 years - they exhibited secondary sex ratios averages ranging between 1.6 to 2.5 females per male (Raizenne, 1957). All the few Argids studied up to now proved to be arrhenotokous (Benson, 1950; Gorske et al., 1977; Moore, 1962; Siebold, 1884; Tozawa, 1940), and exhibited female-biased secondary sex ratios between 1.5 to 5.3 females per male: Arge pectoralis (Leach)(Raizenne, 1957), A. ustulata (L.)(Tsinovskii, 1953 and Verzhutskii, 1966), A. dimidiata (Fallén)(Verzhutskii, 1966), Schizocerella pilicornis (Holmgren)(Gorske et al., 1977), Zenarge turneri (Rohwer)(Moore, 1962).

Therefore, the secondary sex ratios found in this study for Dielocerus diasi (around 3 females per male) and Themos olfersii (around 2 females per male) are in agreement with the results obtained so far for most arrhenotokous sawflies. This fact together with the frequent observation of matings supports the idea that D. diasi, and perhaps T. olfersii also, reproduce by arrhenotokous parthenogenesis. This will have to be finally verified by breeding the eggs of unfertilized females.

Unequal secondary sex ratios, such as these reported for most arrhenotokous Tenthredinoid sawflies, can result either from strong differential mortality between the sexes during the egg, larval and pupal stages favouring female survival, or result from unequal primary sex ratios. Although differential mortality between the sexes is known to occur during the developmental stages of sawflies (Carne, 1969; Hard, 1971; Lyons, 1964; Lyons and Sullivan, 1974), females experience a greater mortality than males in the latter part of the larval and in the cocoon stages owing to disease, starvation, parasitism and predation, because of their longer feeding period and larger size. If the primary sex ratio were 1:1, this greater female mortality would produce a male-biased secondary sex ratio, which is not the case. Lyons and Sullivan (1974), however, found a higher male mortality during the egg and early larval stage of Neodiprion sertifer, which would tend to counterbalance the higher female mortality in the later developmental stages. Therefore, an unequal female-biased primary sex ratio must be the major factor contributing to the observed female-biased secondary sex ratios at the adult and larval stages of most sawflies.

An important question remains though: why do most arrhenotokous sawflies have female-biased primary sex ratio? Hamilton (1964) initially proposed that since haploid males contribute only half as much as diploid females to the gene pool of future generations, it is more profitable in arrhenotokous species to produce more females than males. Later on, however, Hamilton (1967, 1971) realized that "gametes from sons carry the mother's genotype in full concentration whereas gametes from daughters carry it diluted by half and this exactly offsets the difference in number of progeny. Thus a 1:1 population sex ratio is as basic to male haploidy (arrhenotoky) as to normal reproduction" (see also Charnov, 1978 and Trivers & Hare, 1976).

As Fisher (1930) pointed out in his sex ratio theory, the primary sex ratio will depend on the relative expensiveness of producing the two sexes, including expenses with parental care. Thus if both sexes cost the same to be produced (for the parents), the optimal sex ratio is 1:1, but if one of the sexes is more expensive to produce then the ratio will be biased to the cheaper sex proportionally to the difference in cost to produce the two sexes, so as to equalize the parents' total investment on both sexes. Such difference in cost to produce each sex is most usually brought about by the existence of size dimorphism and/or differential mortality between the sexes at early development before the end of the period of parental care (Fisher, 1930; Bodmer & Edwards, 1960; Leigh, 1970; Spieth, 1974; Willson & Pianka, 1963).

Even though several arrhenotokous sawflies exhibit size dimorphism between the two sexes, with males usually smaller than the females (as in the case of the two species studied here where females are about twice as heavy as the males), this difference is mostly due to differential feeding during the larval stage. As the parent sawflies to not control the supply of food for the larvae, this can not affect the primary sex ratio. Maternal care when present (see Chapter 6) involves equal expenditure for both sexes as it does not involve feeding of the offspring. The small, but significant, difference in size found between newly-hatched first instar larvae of the two sexes in T. olfersii and D. diasi implies, however, that there is some difference in maternal expenditure to produce eggs of different sexes. However this difference is only in the order of 10 to 30% and would, in fact, work in the opposite way to induce a slightly male-biased primary sex ratio.

Differential mortality between the two sexes during the early developmental period has been reported for some sawflies (Carne, 1969; Hard, 1971; Lyons & Sullivan, 1974), but as most sawflies have no parental care after egg-laying this would not have any effect on their primary sex ratio. But early differential mortality occuring in species with maternal care, as the two species studied here (see Chapter 6), as long as it occurs before the end of the period of maternal care, would be expected to impose selection for the establishment of unequal primary sex ratio. However, as the overall mortality during the incubation period of both D. diasi and T. olfersii is low, in the order of only 10% for egg clusters escaping from total loss (see Chapter 6), any existing differential mortality during the egg stage (not detected) would have a very small effect on the primary sex ratio.

Apparently, then, the only major factor which is correlated with the observed departure from the 1:1 sex ratio in the arrhenotokous sawflies is inbreeding. Hamilton has proposed two different models for the effect of inbreeding on the sex ratio: the "Local Mate Competition" (LMC) model (Hamilton, 1967) and the "Outbreeding Viscous Population" (OVP) model (Hamilton, 1972). The first assumes that males and females always, and only, mate at the site where they are reared (host), and the composition of the local mating group is entirely determined by the number of females which colonize the host contemporaneously within a certain time interval such that the offspring of these females emerge at the same period of time. Only after mating will the females disperse to choose a host in which to lay their eggs. Therefore, the amount of inbreeding is inversely correlated with the number of females colonizing the host contemporaneously. In the case where the local mating group is derived from only one female all the matings will be between sibs, and to minimize competition between brothers to mate, the mothers are expected to strongly bias the sex ratio of their progeny towards females and produce only enough males to ensure the fertilization of all the daughters. This is exactly what is found among several species of parasitic wasps where sex ratios up to 46 females per male may be found (Hamilton, 1967, 1979).

This model (LMC) also predicts that females which are able to change the sex ratio of their progeny according to their perception of the host's quality, will tend to produce less female-biased primary sex ratios in their progeny when they detect that other conspecific females have already laid eggs in their chosen host, so as to adjust the proportion of sons to the relative level of local mate competition (Hamilton, 1967). This has been confirmed experimentally for the parasitic wasp, Nasonia vitripennis (Walker) (Pteromalidae)(Werren, 1980). Alexander and Sherman (1977) collected evidence which indicate that at least some amount of LMC is rather common among the species of Hymenoptera, "whose haplodiploid system of sex determination makes them capable of reducing deleterious consequences by sex ratio adjustments" (Alexander & Sherman, 1977), and also because male haploidy works as a powerful filter against unfavourable mutations and the deleterious effects of inbreeding (Rasnitsyn, 1969).

The second model, OVP, assumes that the population is inbred but that males and females are, nevertheless, equally dispersive, i.e. it supposes a "viscous" population in which males and females can and do fly equally far (mostly within a patch of the environment), and females always do so before mating. Sib mating can occur but is relatively rare (Hamilton, 1972). In this model a female is more related to a daughter than to a son by a factor of (1+3F)/(1+F) (F being the Inbreeding coefficient), so that she is selected to bias her ratio of investment towards females proportionately. The maximum bias in sex ratio obtainable in this model is 2 females per male when the Inbreeding coefficient is F = 1 (Hamilton, 1972).

The fact that most studied arrhenotokous sawflies have a secondary sex ratio around 2 to 3 females per male, that both sexes have functional wings and are about equally able to disperse (there is only one known case of winglessness among sawflies - female Cacosyndia dimorpha Freymouth are apterous whereas the male has normal wings - Benson, 1950), and that females of most species probably release sex pheromones to attract males, all indicate that viscous outbreeding must predominate. However varying amounts of local mating before dispersal must also be present in most species - i.e. a mixed OVP-LMC mating strategy (with predominance of OVP) must be the rule for most arrhenotokous sawflies. The present study indicates that D. diasi exhibits such mixed mating strategy, but the proportion of females following each strategy is unknown. I do not know if LMC occurs in T. olfersii, but if it does it must be less frequent than in D. diasi as indicated by the sex ratio and cocoon spinning behaviour (see Chapter 7).

5.C.3 HOST-PLANT FINDING AND SELECTION OF EGG-LAYING SITE

Apparently all Tenthredinoid sawflies behave similarly in their selection of the egg-laying site(s): the females fly actively from host-plant to host-plant landing on attractive foliage and walk over several leaves exploring them before flying off again and landing on other branches where they repeat their exploratory behaviour. Females usually visit a great number of leaves before selecting one for laying their eggs - they are very choosy! There is no evidence that sawflies have any dispersal phase before starting to look for host-plants (see discussions below).

Virtually nothing is known about which stimuli orientate female sawflies to find their host-plants from a distance. It is known for other insect groups, however, that chemical and/or visual stimuli are important for host finding at long distances (see e.g. references in Jermy, 1976). Field observations of _T. olfersii_ reported in this study indicate that females use mainly visual stimuli to locate their host-plants: they always orientate their short flights toward low shrubs with foliage similar to that of their host, so that females were often seen landing on or hovering over shrubs which were not of the host species but had a similar habitus. However, the egg-laying site is only selected in _T. olfersii_ and _D. diasi_ after the female has visited numerous specimens of the host-plant.

Once the female has landed on the foliage of a plant, however, chemical stimuli are apparently important in the recognition of the host species and in selecting the egg-laying site. The exploratory behaviour of female sawflies on plant foliage has unfortunately been little studied so far, the best studies available being those of Delmas (1926) on _Pristiphora conjugata_ (Dahlbom) and Ghent (1959) on _Neodiprion sertifer_ (Geoffr.). During this exploration phase, females walk in a fast pace over both surfaces of the leaves in a sinuous path, stopping occasionally. There is some evidence available to show that females probe the leaf surface with various sensory organs to detect the presence of eggs already laid and obtain other information on the quality of the leaf (chemical stimuli). Some species use their antennae for this purpose, striking them at a fast rhythm against the leaf surface: *Neodiprion sertifer* (Ghent, 1959), *Pristiphora conjugata* (Martelli, 1954), *Croesus septentrionalis* (L.)(Caccamo, 1966). Others use their mouthparts (? palps): *Eriocampa ovata* (L.)(Mackay & Wellington, 1977), *Perga affinis* Kirby (Carne, 1959). Yet others press the tip of their abdomen (? sheath and cerci) against the leaf surface, a behaviour coined "réflexe de flexion" by Delmas (1926): *Pristiphora conjugata*, *Athalia rosae* (L.), *Macrophya albicincta* (Schrank)(Delmas, 1926), *Tenthredo mesomelas* L. (Boulangé, 1924), *Perga affinis* (Carne, 1962), *Arge humeralis* (Beauvois)(Regas-Williams & Habeck, 1979), *Themos olfersii* (this study). Delmas (1926) described in detail this behaviour and said it is widespread among the sawflies. In the case of *Athalia rosae* and *Arge humeralis* the leaf epidermis is actually cut by the female's lancet during this "flexion reflex". Regas-Williams and Habeck (1979) have suggested that this scratching of the selected leaf's surface is possibly a display of territorial marking behaviour (see below).

The process of selecting a leaflet as egg-laying site described in this study for *T. olfersii* and *D. diasi* - repeated visits to the preferred leaflet(s) within one host while still visiting other leaflets, with a gradual increase in the time spent on the preferred leaflet until the female's definitive establishment is made there - is very interesting and is apparently described here for the first time for a sawfly. The female sawfly seems then to be actively comparing certain qualities of the leaflets she visits. One such quality appears to be the presence of other conspecific females nearby.

In all sawflies studied so far, once the egg-laying site has been selected the female immediately starts to lay her eggs. The only known exception is *Perga affinis* which first works for 2-4 hours scraping away the waxy layers from both surfaces of the chosen leaf of *Eucalyptus* with the distal portion of the ovipositor valves (the "saw-bench" ridges). Only after finishing this does the female start to lay her eggs (Carne, 1962).

Therefore, the observation that D. diasi females spend around 24 hours on the chosen leaflet before starting to lay the eggs has no parallel among studied sawflies. The production of a buzzing sound by vibrating the wings during this stage is also unique. The function of this very elaborate behaviour is puzzling. Why should D. diasi females delay their oviposition for such a long time (see also Tripp, 1965), when it is known that they have all their eggs already mature and ready to lay at the time they emerge from the cocoon (see Chapter 6) and mating occurs shortly after emergence? In so doing they certainly increase the risk of being preyed upon before laying their eggs.

One hypothesis is that females which had failed to mate at or near their natal tree just after emerging from the cocoon would behave in such a manner to attract males. The fact that all females observed in the field exhibited this behaviour and that no male was ever seen near females during such periods refutes this idea.

A more plausible hypothesis is that during this period females are advertising their territories against newcoming conspecific females which are still looking for an egg-laying site. Each territory would occupy one whole compound leaf. The spaced distribution of egg clusters with virtual absence of more than one egg cluster in any one compound leaf (see discussion below) supports this idea, but the lack of aggressiveness of established (territorial) females against invading newcoming females goes against it (but see Chapter 6 for territorial behaviour of postreproductive females). However as only a few actual encounters between prereproductive established females and newcoming females were witnessed in the field, it will be necessary to have more observations to test this hypothesis.

In fact, aggressiveness between females choosing their egg-laying site has only been reported twice in the sawfly literature so far as I am aware. Mackay and Wellington (1977) reported aggressiveness between caged Eriocampa ovata females, with females interfering with each other at the egg-laying site resulting in reduced egg-laying and shortened life span. The most striking case, however, was described by Dhillon (1966) who reported fighting between females of Athalia proxima (Klug) in the field over egg-laying sites: "Usually the males are with peaceful disposition. This is not true for the females who struggle, sometimes grimly, to eliminate the rivals while selecting egg-laying sites. The two such rival females, prior to fighting, face one another with their antennae wavering up and down. The clash is initiated by the collision of the heads and it is followed by an entanglement of the forelegs. During the clash, while their wings are fluttering, they try hard to dislodge one another. Finally, the weaker of the two gives away and flies off" (Dhillon, 1966). He does not mention if the females get damaged during these fights. I suspect that this type of aggressiveness between females for egg-laying sites probably occurs in several other species of sawflies but remains unknown due to our general lack of information on the prereproductive behaviour of most sawflies. It is probably symptomatic that Benson (1950) advised collectors to keep live sawflies in individual containers otherwise they are "likely to bite off each other's legs and antennae".

Yet another hypothesis is that D. diasi females, during their 24-hour buzzing period on the selected egg-laying site before oviposition, are trying to attract other females to join them at the host tree which they selected. The common occurence of numerous females simultaneously establishing their egg-laying site on a same tree supports this idea. Female D. diasi were found to be very sensitive to the buzzing sound produced by conspecific females (see Chapter 6). The function of such female-attraction strategy would be to increase the size of the local population to enhance the effectiveness of their aposematic colouration (see Chapter 6) and decrease the inbreeding caused by their mating strategies. This would also explain the observed clumped distribution of D. diasi egg clusters. Most probably the same applies to T. olfersii, although more data is needed on the prereproductive behaviour of adult females of this species before any conclusion can be reached.

The only dispersal stage in *D. diasi* and *T. olfersii*, as for most sawflies, is as adults. Eggs and cocoons are firmly attached to a substrate (host plant or soil beneath the host) and are thus immobile, and larval movements are confined to the individual host plant selected by the mother and the ground immediately surrounding it. However, larval dispersal from one host plant to another does occur in heavily infested sites in species of *Perga* (Carne, 1962 and 1965), *Pergagrapta* (Meyer-Rochow, 1972), *Perreyia* (Wheeler and Mann, 1923; Camargo, 1956; Costa Lima, 1941), and *Neodiprion* (Benjamin, 1955; Smirnoff, 1960). But even here the main dispersal still happens in the adult stage.

In species with no interhost larval dispersion, as in both species studied here, the spatial distribution of eggs, larvae and cocoons between individual hosts and between patches of the environment are totally determined by the adult females. Therefore, a description of egg cluster spatial distribution between hosts also applies to larvae and cocoons. However, when looking at the spatial distribution of eggs, larvae and cocoons within one host this is not true. Although the egg distribution is totally controlled by the adult female, the distribution of larvae and cocoons within a host is mainly determined by larval movements. Larval distribution and movements within a host will be described and discussed in Chapter 7.

Sawflies are highly selective in their choice of oviposition sites. First of all, they are very specialized in their larval food plant requirements, being usually monophagous or oligophagous (see Appendix II). Both species studied here are apparently monophagous, at least in the study region.

The best studied sawflies, so far, in terms of spatial distribution are *Perga affinis affinis* Kirby (Carne, 1965) and several *Neodiprion*, specially *N. sertifer* (Geoff.)(Ghent, 1955, 1959; Hardy & Allen, 1975; Lyons, 1964; L.F. Wilson, 1975). Female *Perga* and *Neodiprion* do not lay all their eggs in just one leaflet as do those of *Themos* and *Dielocerus*, for they need several leaves (or needles) to accommodate all their egg complement, but they always select neighbouring leaves from the same shoot. There are a few odd species of Neodiprion which do not cluster their eggs, but wherever the genus Neodiprion is cited in this discussion it will only refer to the egg clustering species.

Therefore, females of these four genera are similar in that they lay all their egg complement in just one large egg cluster, a case of extreme semelparity. They concentrate all their reproductive investment in just one place and time. We should, therefore, naturally expect them to be highly selective and demanding in their requirements for oviposition sites, for any hazard affecting their egg cluster may completely destroy their fitness. Probably a larger proportion of females fail to leave any descendant due to egg mortality in species which cluster all their eggs when compared with species which disperse their eggs through several hosts and sites (see Discussion in Chapter 6). Most probably the selective pressures for the evolution and maintenance of egg clustering in several groups of sawflies are acting on the advantages of group living during the larval stage (Lyons, 1962; see also Discussion in Chapter 7). Selective pressures, then, must be very strong for the females to select the best oviposition sites available and to provide further protection to the egg cluster through maternal care (see Chapter 6).

5.C.4 SPATIAL DISTRIBUTION OF EGG CLUSTERS WITHIN A HOST

Themos olfersii and Dielocerus diasi females are very selective with respect to the height, age, health state and position (within the leaf) of the leaflet chosen as oviposition site, and also with respect to the presence of other egg clusters in neighbouring leaves and leaflets. They differ markedly in their selection for height: while D. diasi prefers the upper crown (4 to 10 metres high), T. olfersii prefers the lower crown (10 to 40 cm above the ground only). Preference for lower crown in T. olfersii might be a reflex of wind avoidance as in Perga, or a preference for epicormic foliage resultant from burning during the dry season. Preference for upper crown in D. diasi, in contrast, might be an avoidance of the dry season fire, or a preference for young shoots which are located in the upper crown in larger numbers. *Neodiprion* sawflies also prefer the upper crown, but apparently because they avoid shade (Borodin, 1973; L.F. Wilson, 1975). In fact both *Perga* and *Neodiprion* sawflies have been shown to exhibit strong preference for well illuminated shoots exposed to the afternoon sun (but see Benjamin, 1955). Shade avoidance is seemingly unimportant in both *T. olfersii* and *D. diasi* as they attack plants which are well spaced one from the other and thus receive direct sunshine in the whole canopy all day long. *Dielocerus diasi* egg clusters and larvae are well exposed to strong winds.

Both *T. olfersii* and *D. diasi* prefer young mature leaflets, avoiding very young (still growing) and old ones. The same happens with *Perga affinis*, but most *Neodiprion* species avoid young needles prefering the old ones. The leaves of *T. olfersii*'s host are compound palmate, all leaflets being of about the same age and size, and each leaflet apparently has the same chance of being selected. But the compound leaves of *D. diasi*'s host are pinnate, having a clear age and size gradient from the small young leaflets at the distal end to the large old leaflets at the basal end. Female *D. diasi* avoid the distal and basal leaflets, their egg clusters being laid in leaflets of the second, third or fourth (counting from the distal end) pair of leaflets.

Females of both *T. olfersii* and *D. diasi* avoid leaflets which had been damaged by other biting, mining or gall forming insect, or by rust fungi. The same avoidance is found in *Perga*. But in trees with high infestation and a shortage of undamaged leaflets, female *D. diasi* accept partially eaten leaflets. Both *T. olfersii* and *Perga affinis* exhibit strong preference for epicormic foliage (regrowth from fire damage). *Perga affinis* has also strong preference for narrow elongated leaves and for less waxy leaves as well. *Neodiprion* sawflies, in addition, prefer needles at the upper side of the shoot, close to the apical end of the shoot, having a large angle in relation to the shoot axis, without teeth, with large resin canals, with a width larger than 2mm and with a low water content.

Most interesting of all is how the egg clusters are distributed in relation to the presence of other egg clusters laid by other females of the same species. Three types of distribution are possible:

1) random - the females ignore the presence of other egg clusters;
2) spaced - the females are aware of the presence of other egg clusters and strongly avoid selecting the same leaflets, leaves or shoots which already bear egg clusters;
3) contagious - two completely different phenomena can bring about this type of distribution:
    - A) the females are aware of the presence of other egg clusters and strongly select shoots, leaves of leaflets which already bear egg clusters; or
    - B) the females ignore the presence of other egg clusters but aggregate in the same shoot, leaf or leaflet because of its intrinsic higher attractiveness.

Female T. olfersii and D. diasi strongly avoid compound leaves which already have egg clusters. So not only do they avoid the leaflets which bear egg clusters but they also avoid all the other neighbouring leaflets of the same compound leaf. This leads to a spaced distribution within a host, which prevents too much overcrowding on a single host. Possibly the main function of this spacing behaviour is to prevent early egg mortality due to the invasion of the egg-bearing leaflet by conspecific larvae. Although the larvae do not eat the eggs, their damage to the leaflet makes it dry out and kills the egg cluster. As the young larvae of both species start by eating the leaflets of the leaf where they hatched (see Chapter 7), before proceeding to another compound leaf, it is obvious females face a serious risk if they select to oviposit in a compound leaf which already has an egg cluster. The second egg cluster to be laid will always be the loser unless it is laid almost simultaneously with the first, for then both have the same chances, or both might be lucky to hatch at about the same time and avoid destruction. Even then it might not be profitable for the two females as their young larvae will have a smaller initial food supply in the first compound leaf (where they were born) and will be forced to migrate earlier than usual to another compound leaf (see Chapter 6 for evidence that early migration is not desirable). It is not surprising, therefore, to find spacing and the conspicuous displays exhibited by females on the egg laying site before ovipositing most certainly plays an important role in bringing this about.

This spacing of egg clusters has apparently not been observed before among sawflies. On the other hand, contagious distribution of egg clusters within a host has been reported several times. Martorell (1940), for example, reported up to 17 egg clusters of Sericoceros krugii on a single leaf of its host. The question in such cases is whether the aggregation of egg clusters is due to a mutual attraction between egg-laying females or because there is a higher intrinsic attractiveness of a particular leaf or shoot to egg-laying females regardless of the presence of other egg clusters. Carne (1965) has shown that in the case of Perga affinis the contagious distribution of egg clusters is due not to the presence of other clusters but to the intrinsic quality of given shoots which makes them more attractive to females. Perga affinis females, thus, ignore the presence of other egg clusters in the shoot when selecting their own ovipositing site, although they do avoid the leaves which already have egg clusters.

It could be, however, that in the above mentioned case of Sericoceros krugii there is definitely a gregarious nature among adult females laying their eggs, for this would probably be valuable in enhancing the efficiency of the aposematic display of the bright orange-coloured females which sit astride over their egg clusters (see Discussion in Chapter 6).

5.C.5 SPATIAL DISTRIBUTION OF EGG CLUSTERS BETWEEN INDIVIDUAL HOSTS IN A PATCH

Both T. olfersii and D. diasi egg clusters are overdispersed among the available suitable host plants within a patch of the environment. They have a contagious distribution which differs significantly from Poisson. This means that in any patch of host plants there are more individual hosts which receive no egg cluster than would be expected if the distribution was random, and there are a few hosts which receive many more egg clusters than expected too. It was found that individual hosts do differ markedly in their attractiveness to the female sawflies. Such contagious distribution has also been found to be typical for Perga and Neodiprion (Carne, 1965 and L.F. Wilson, 1975).

There are several factors which influence in the female's choise of the individual host, such as: host height, canopy size, localization, exposure to sun and wind, physical aspect of foliage, health state, history of previous infestations and presence of egg clusters. Oligophagous species as Perga spp and Neodiprion spp have a further complication in that they have to select between different suitable host species, usually within the same plant genus. Dielocerus diasi prefers larger trees, and never attacks small saplings. The same is true of Neodiprion spp, where the number of egg clusters per tree is directly proportional to the tree height (L.F. Wilson, 1975). But Perga affinis prefers young trees and regrowths, only attacking large trees in years of very high densities. Themos olfersii is extreme in only attacking low shrubs of E. pubescens less than 50cm high, totally avoiding the tall shrubs and trees.

Both T. olfersii and D. diasi avoid hosts with only old foliage and with foliage badly attacked by rust. Leaf width and shape have been shown to influence Perga affinis and Neodiprion spp in their choice: Perga females prefer trees with narrow, elongated, less waxy leaves, and Neodiprion females avoid trees with needles less than 2mm wide (Carne, 1965; Ghent, 1959).

D. diasi is more common in trees along roads and near towns than in undisturbed patches. The reason for this is unknown, but might be related to the absence of certain parasitoids in such areas (see Discussion on mortality in Chapter 6). Alternatively, it could be a response to a weakening of the trees in such disturbed areas, or else due to a higher visual exposure of these trees to flying female sawflies. Such an edge effect has also been found in Neodiprion sertifer, in this case probably due to the female preference for sun-exposed foliage (L.F. Wilson, 1975). Such effect has not been found in P. affinis, but instead there is a strong preference for trees situated near watercourses for these are more vigorous trees and produce more succulent foliage.

Neodiprion sawflies have a strong preference for weakened and desiccated host trees with low water content (Voute, 1957; Knerer & Atwood, 1973). Both Dielocerus and Perga have a preference for host trees which have been chronically attacked by the sawflies. It is common to find these chronically attacked trees heavily infested by sawflies whereas all neighbouring trees of the same species have no sawflies. Carne (1965) has attributed such strong preference to a vicious cycle which is established in these trees once they happen to be heavily attacked in a year of high sawfly densities: severely attacked trees loose most of their foliage and as a result produce abundant succulent new foliage in early summer which in turn is highly attractive to female sawflies and leads to repeated high infestation and a continuation of the cycle on and on. He found that these chronically infested trees do not owe their susceptibility simply to an intrinsic higher attractiveness, but to the chance occurence of an initial severe attack during a year of high sawfly density. This same explanation could perhaps apply to D. diasi. According to Carne (1965) such chronic infestations may be terminated by:

1) the extreme weakening or death of the tree;
2) a general decline of the sawfly abundance in the area; or
3) the severe defoliation by summer-active defoliating insects, making new foliage unavailable to the female sawflies.

The situation with T. olfersii is quite different due to the small size of hosts selected. Hosts heavily infested during the spring generation of this sawfly will have very few, if any, undamaged leaves by the time the females of the summer generation are on the wing, and so will not be selected. As the low shrubs of Eriotheca pubescens which T. olfersii females prefer have their aerial parts totally burnt every year during the dry season, the size of the epicormic canopy each spring is most probably proportional to the amount of energy which the plant managed to accumulate in the roots during the rainy season. It seems probable, though not tested, that heavily infested shrubs produce smaller canopies in the following spring than lightly, or uninfested shrubs. As egg cluster density was found to be proportional to canopy size, these heavily infested shrubs will be less attacked in the following year.

Again an interesting question is whether there is any evidence that adult females have a gregarious tendency to group their egg clusters in a few trees, not only because of differences in intrinsic attractiveness of the trees, but because they are attracted to trees which already have other females and egg clusters. I could not find any such suggestion in the sawfly literature. Nevertheless, such clustering of females and egg clusters due to a gregarious nature of the adult female sawflies would be very difficult to distinguish from contagious distribution due only to higher intrinsic attractiveness of some individual hosts, or due to a tendency of females to select the tree where they grew on. I believe, however, that I have found evidence supporting the idea of mutual attraction of adult females in D. diasi and T. olfersii. One line of evidence which has been presented in this Chapter is the frequent occurrence of several females (4 to 8 in T. olfersii and 10 to 20 in D. diasi) which select the same host plant simultaneously in the same day to lay their egg clusters, ignoring neighbouring hosts which have been found equally attractive by other females in other days. In view of the low population densities of both sawflies, such a high degree of clustering of females is so improbable that I do not think it could be explained only by differences in host attractiveness (see Chapter 6 for further discussion).

5.C.6 SPATIAL DISTRIBUTION OF THE SAWFLIES BETWEEN PATCHES OF HOST PLANTS

Most patches of Eriotheca pubescens and Sclerolobium aureum in the Federal District were devoid of sawflies, or had only very low density populations of T. olfersii and D. diasi, respectively during the years of study. But some patches, on the other hand, had relatively high density populations of these sawflies. The reasons for this very uneven distribution of both sawflies among the patches of host plants are unknown. Several factors might be involved, such as:

1) age and height structure composition of host plants in each patch;
2) prevalence of fire during the dry season;
3) prevalence of other defoliators and leaf diseases competing for the same hosts;
4) prevalence of potential predators and parasitoids;
5) wind exposure;
6) proximity to human settlements and roads;
7) proximity to other patches of host plants; and
8) dispersal power of the adult female sawflies.

Of these, the only ones which are apparently relevant for both sawflies are the prevalence of certain parasitoids (specially the egg parasitoid Chrysocharis sp), the proximity of other patches and the dispersal power of adult females. In addition, the prevalence of fire is certainly very important for T. olfersii but not for D. diasi and the proximity to human settlements and roads is an important factor for D. diasi but not for T. olfersii.

The distance between one patch of host plants to the next (degree of isolation) interacts with the dispersal capacity of the adult female sawfly. Unfortunately virtually nothing is known about their flight capacity. Benson (1950) comments on the absence of sawflies from oceanic islands such as Hawaii, Seychelles, Samoa and Galapagos, and their rarity in New Zealand, Madagascar and Madeira, as evidence of their poor dispersal power. D.R. Smith (1969a) reported only 7 or 9 species of sawflies in all the West Indies. Benson also contended that most sawflies are too large or too heavy in relation to their surface area to be commonly dispersed by air currents. Nevertheless, both Benson (1950) and Malaise (1945) called attention to the large numbers of lowland sawflies which are blown upwards along high mountain ranges. The only mention in the literature of large swarms of sawflies crossing relatively long distances refer to Athalia rosae (L.) and Athalia cordata Lepeletier, the first reported to cross the English Channel toward England (Benson, 1950). It is possible that large and heavy sawflies as the females of T. olfersii and D. diasi have a relatively small dispersal power, presenting thus a rather low rate of colonization of isolated patches of host plants. Carne (1965) found that the following factors affected the distribution of Perga affinis between different sites: age composition of host plants, host species composition, tree density, litter cover, soil type, ground vegetation, distance to watercourses, flooding and waterlogging prevalence, prevalence of summer-active defoliators of host plants, and prevalence of a Trigonalid parasitoid. Malaise (1945) and Schwerdtfeger (1970) called attention to the role played by ants in limiting sawfly distribution and abundance specially in the tropics (see also Jeanne, 1980).

5.C.7 LIMITS TO THE TOTAL RANGE OF DISTRIBUTION

Most probably the range of distribution of both T. olfersii and D. diasi is limited by that of their host plants, which in their turn are limited to the Cerrado biome which covers most of Central Brazil highlands (see Chapter 3). Presently T. olfersii is known from the Brazilian states of Mato Grosso, Goiás, Federal District and São Paulo, and D. diasi is known from Mato Grosso, Goiás and Federal District. Climatic factors might also restrict their range to only part of the range of their hosts. This was shown by Carne (1965) to apply to Perga a. affinis, which is restricted to a range with average monthly rainfall of between 36 and 56mm (between October and March) and average monthly temperature of between 17 and 22°C (between October and March).

CHAPTER 6. OVIPOSITION AND MATERNAL CARE

METHODS

Adult females and egg clusters were studied mainly in the field in completely natural situations. Female behaviour was recorded in notebooks and by photographs. Simple experimental manipulations (see text) were done to test the female's defensive reactions after she had laid her eggs, both in the field and in the laboratory. Adults in the field were observed at frequent short intervals, each observation lasting from a few seconds to several minutes, depending on the activity of the insect.

Newly-emerged virgin females and postreproductive females, reared in the laboratory or collected in the field, were fixed in Dietrich Solution and later dissected under the microscope and their ovaries examined.

The mortality of postreproductive females and their broods was measured by directly following the development and survival of marked females and broods in the field at daily or thrice weekly intervals. Egg mortality was also obtained by inspecting the scars of hatched egg clusters under the microscope, and by sleeving the egg clusters about half-way through their development to obtain the parasitoids which emerged from them.

6.A. THEMOS OLFERSII

6.A.1 DESCRIPTION OF EGG LAYING AND EGG CLUSTER

Each female lays all her eggs on a single leaflet of the host plant, on the same day, all very close together forming a very compact egg cluster. *Themos* females lay their eggs on the superior (adaxial) surface of the chosen leaflet, grouping all the eggs in a small area roughly circular and about 15mm in diameter. A few rare cases of egg clusters laid on the inferior (abaxial) surface of the leaflet were recorded. Each egg is laid with a slightly inclined upright orientation, and partially immersed in the parenchyma through a semi-circular horseshoe-shaped slit 1.2 to 1.8mm long by 2 to 2.5mm across opened by the female. A semi-circular portion of the superior epidermis is lifted at each slit cut by the female forming a lid beside each portion of parenchyma thus exposed. One such epidermal lid adheres to the side of each egg laid, thus helping to support the egg upright. The egg inclines away from this lid, and most of the egg stays above the leaflet's surface. The eggs are inclined toward the centre of the circle of eggs, arranged in rows and spaced about 1-2mm one from another. The egg clusters are laid half way between the midrib and one of the lateral margins of the leaflet, usually closer to the leaflet apex and lateral margin (Figures 6.1-6.2).

During the incubation period of 3 weeks (see Chapter 4) the eggs absorb large quantities of water from the host leaflet and their volume multiplies several times. As a consequence the eggs come to touch each other inside the cluster and most of the gaps which existed between them at the start now disappear (Figure 6.2).

No detailed observation was made on the egg-laying behaviour of T. olfersii. There was great variability as to the time of day when females started to lay their eggs, ranging from about 1000h to 1700h. The total time required for laying all the eggs in the cluster was relatively short, about one hour or so.

While laying each new egg, the female always maintains her body above those already laid. While cutting the horseshoe-shaped lids on the upper epidermis of the leaflet, the female rocks her body from side to side. I could not see if the female injected any liquid inside the cuts she makes on the leaflet.

6.A.2 FERTILITY AND EGG CLUSTER SIZE

Female T. olfersii emerge from their cocoons with their ovaries fully occupied by large eggs of a fairly constant size. The eggs fill most of the abdominal cavity. The average number of eggs per female is only 27 (Table 6.I). The eggs are yellow, elliptical, and are on average 2.0mm long by 1.6mm wide.

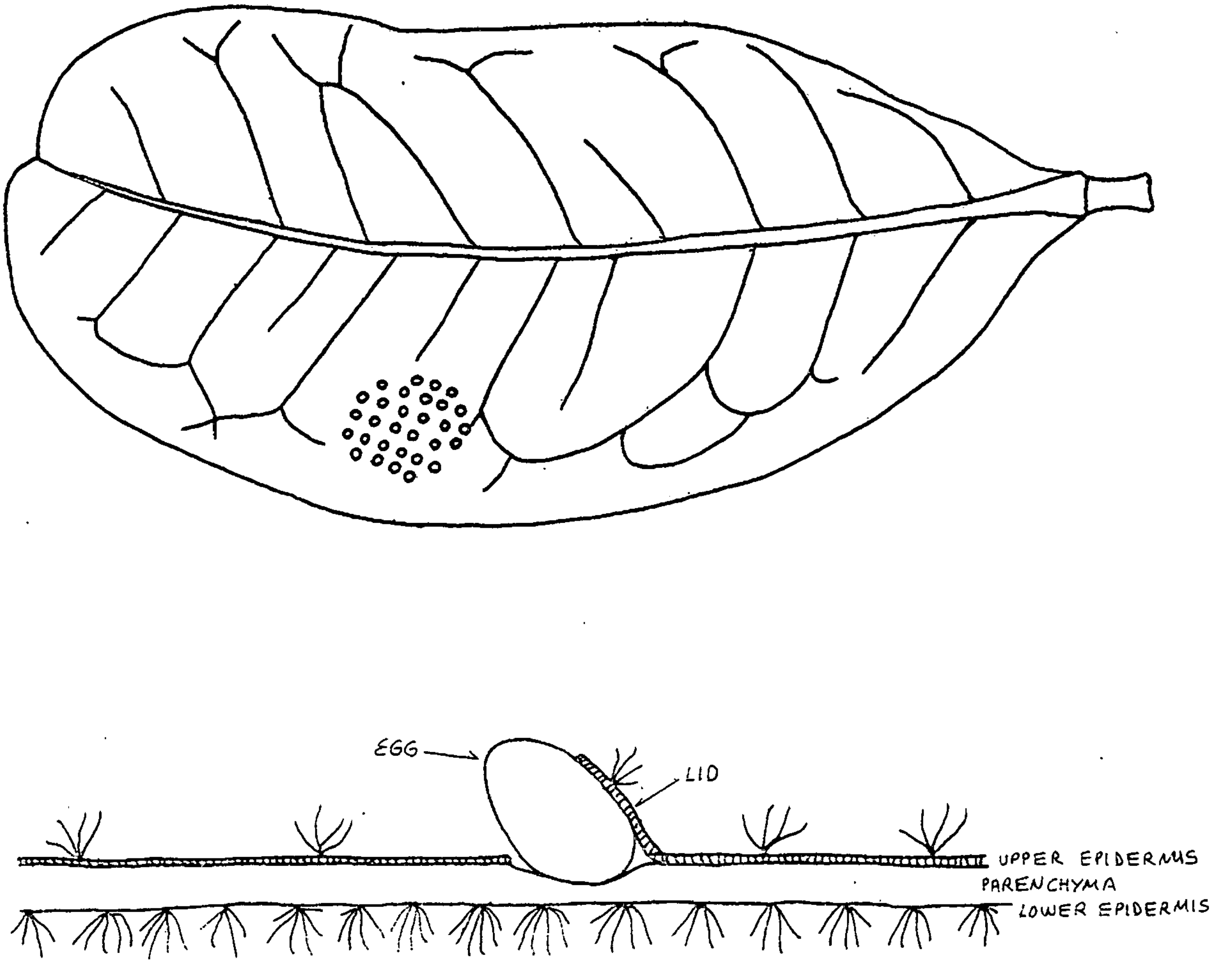


FIGURE 6.1. Top: egg cluster of *Themos olfersii* on a leaflet of *Eriotheca pubescens*, viewed from above, natural size. Bottom: a cross section of a single egg adhered to the lid which the female cuts on the upper epidermis, enlarged 10X.

FIGURE 6.2. Top: Recently laid egg cluster of *T. olfersii*. The female was partially removed to show the eggs. Note the space between the young eggs. Bottom: *T. olfersii* eggs halfway through their development. Note their swelling and the embryos inside them.

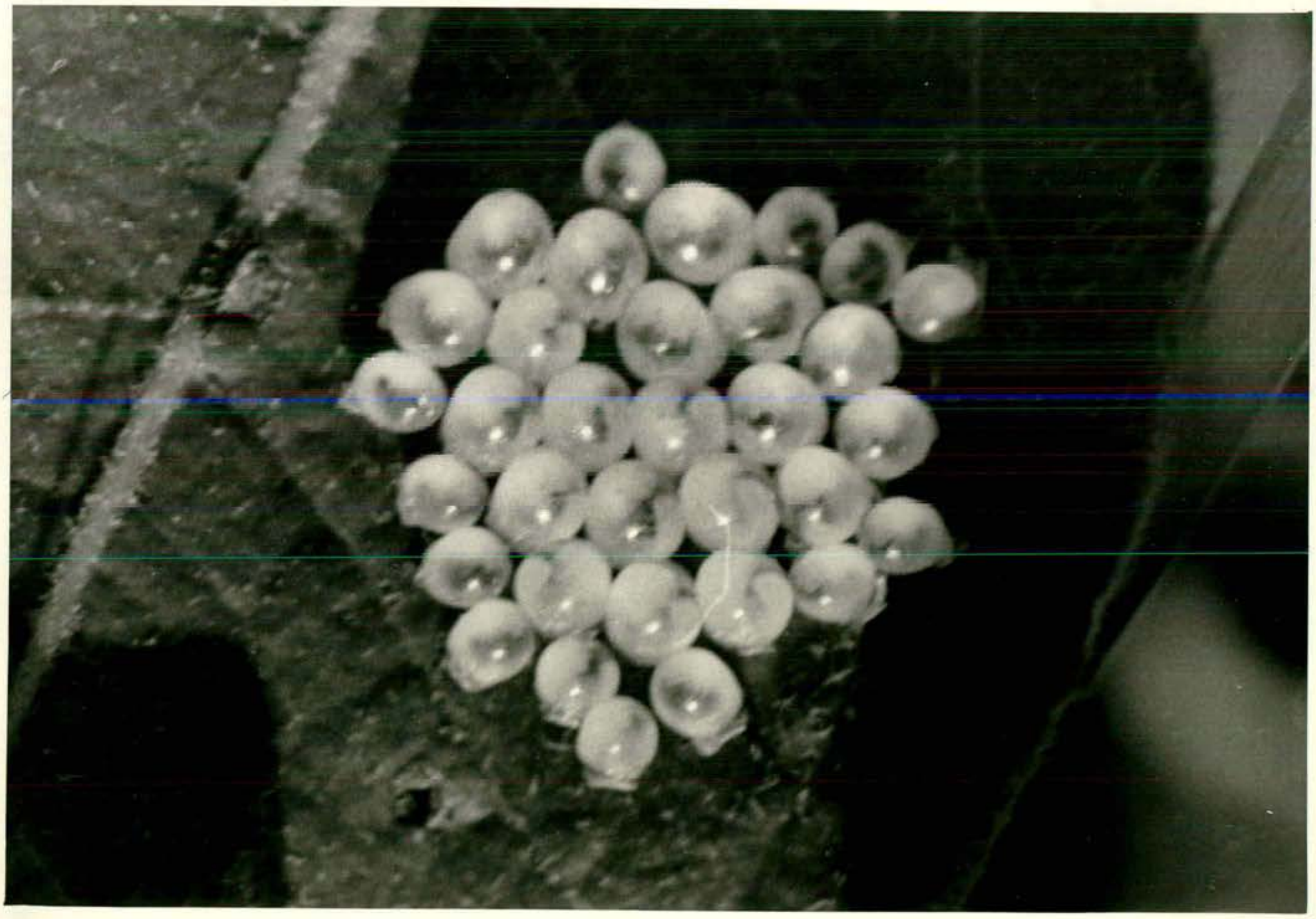


TABLE 6.I

Number of eggs in newly emerged females, number of eggs per cluster and number of eggs not laid per female in Themos olfersii and Dielocerus diasi.

	NO. OF FEMALES AND CLUSTERS STUDIED (N)	AVERAGE ($\bar{x}$)	STANDARD DEVIATION	RANGE OF VARIATION
THEMOS OLFERSII:				
EGGS IN FEMALES	4	27.50	-	23-30
EGGS PER CLUSTER	88	27.19	5.27	15-38
EGGS NOT LAID	21	0*	-	-
DIELOCERUS DIASI:				
EGGS IN FEMALES	30	75.67	11.18	45-95
EGGS PER CLUSTER	43	75.81	11.98	39-93
EGGS NOT LAID	11**	1.09	1.58	0-4

* except one female which had laid only 17 eggs and retained 9 eggs in her ovaries.

** seven females out of 11 had no egg left in their ovaries.

Each female produces only one egg cluster in her life. The average number of eggs laid per cluster is also 27 (Table 6.I), which means that most females lay all the eggs they have, although occasionally a female may retain several eggs in her ovaries (Table 6.I). These retained eggs are not laid afterwards.

The average number of eggs laid per cluster remained constant throughout the spring generation (Figure 6.3). and apparently also during the summer generation. There were, however, small but significant differences on the average number of eggs laid per cluster between the spring and the summer generations of 1977/78 in site one. The summer generation had an average of 30 eggs per cluster, 20% larger than the average of 25 eggs per cluster of the spring generation. The frequency distribution of the number of eggs laid per cluster approaches a normal distribution, but shows some indication of bimodality, more evident in some generations than in others, with very few clusters with 24 and 25 eggs (Figure 6.4).

6.A.3 EGG MORTALITY

The average total mortality for <u>Themos</u> during the egg stage ranged from 18 to 29% in different generations, with a mean of 24%.

Twenty four percent of the egg clusters lost more than 30% of their eggs, 15% lost more than 90%, and 11% of the egg clusters were totally lost. Egg clusters with total losses account for more than 60% of all the eggs lost in the population. On the other hand, 76% of the egg clusters lost less than 30% of their eggs, and more than half of these did not loose any (Figure 6.5). So, 63% of the egg clusters had very high survival rates (>90%), 13% had good survival rates (70-90%), 15% had very low survival rates (<10%) and only 9% had intermediate low survival rates (10-70%) - producing a U-shaped curve. Therefore, egg clusters escaping very high mortality (>90%) lost only 11% of their eggs in average.

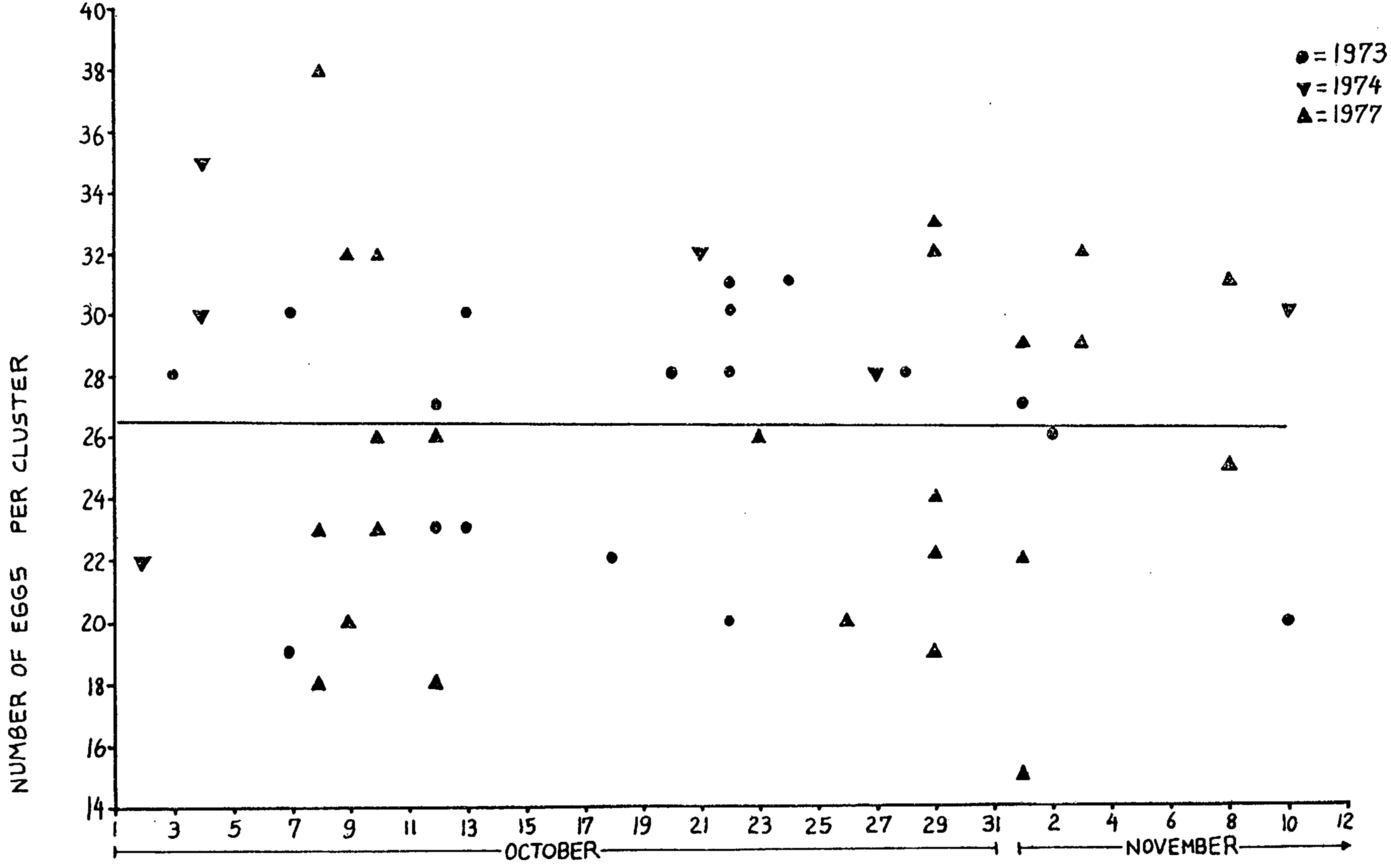


FIGURE 6.3. Constancy in the average number of eggs per cluster during the spring generation of *T. olfersii* at study site 1. The figures are plotted at the time when the clusters were laid. The regression line of eggs per cluster aginst time is presented. N = 49 egg clusters.

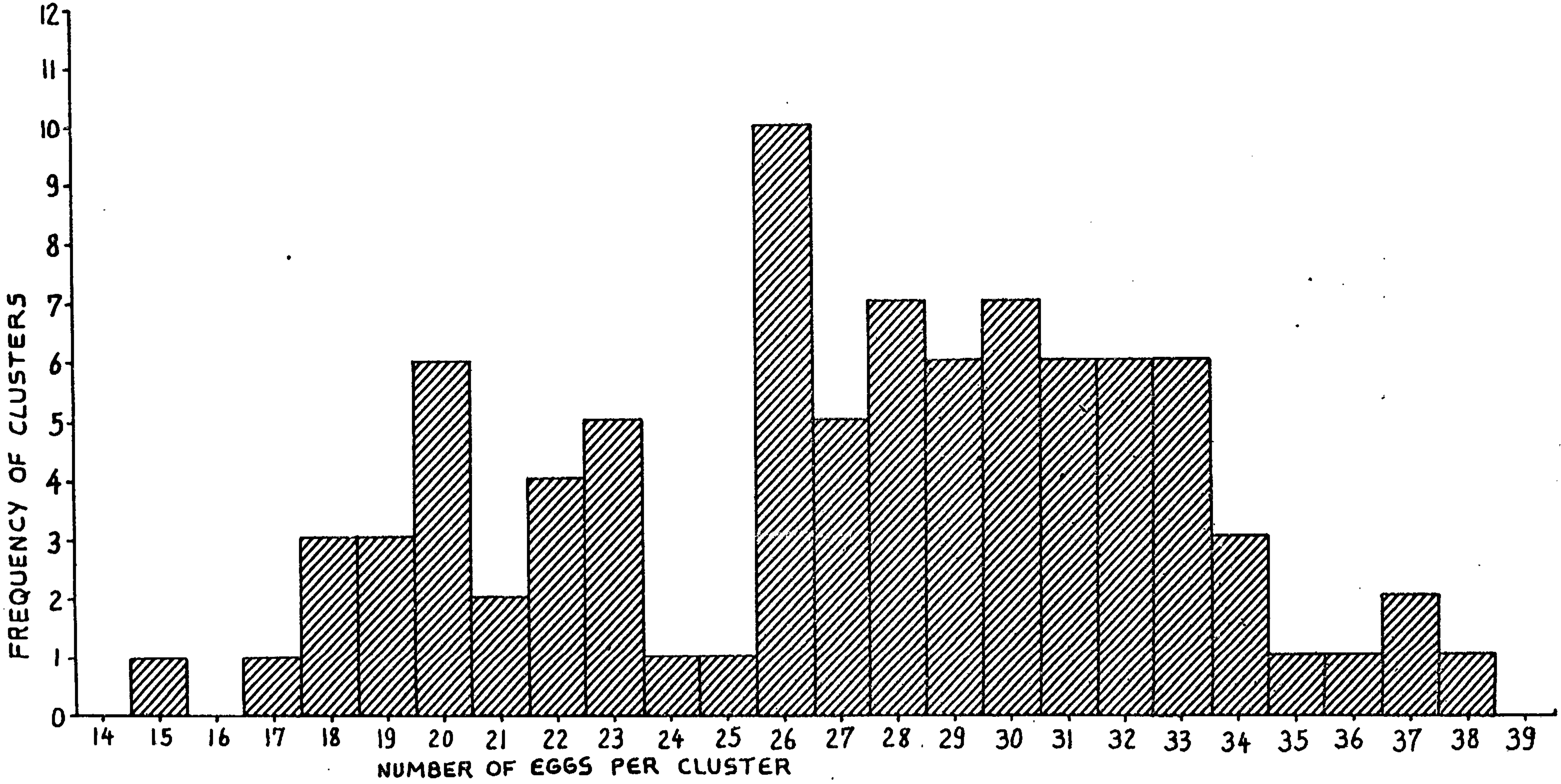


FIGURE 6.4. Frequency distribution of number of eggs per cluster in Themos olfersii. N = 88 egg clusters.

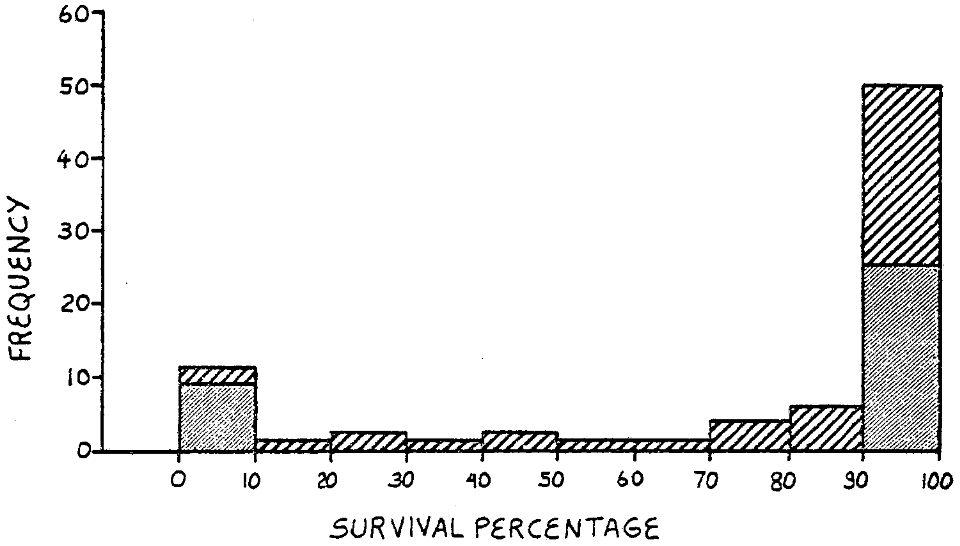


FIGURE 6.5. Frequency distribution of the percentage of egg cluster survival for <u>T. olfersii</u>. Sum of 4 generations: 1973, 1974 and 1978. The frequencies of 0% and 100% are shown shaded. N = 79 clusters.

The causes of Themos eggs mortality were: parasitism by Chrysocharis sp (Hymenoptera, Chalcidoidea, Eulophidae); predation by a lacewing larva (Neuroptera, Chrysopidae, genus still undetermined); predation where whole eggs are removed (unknown agent); leaflet drying due to other Themos larvae feeding on the egg bearing leaflet (intraspecific competition); leaflet fall; and unknown causes (eggs dry). The attack by Chrysocharis, Themos larvae and leaflet fall usually kill all the eggs in the clusters where they occur. The lacewing larva kills only part of the egg cluster, but, as it usually continues the attack on the newly emerged larvae, it frequently kills the whole brood too. The egg-stealing predator kills only a small number of the eggs. Most egg clusters had one or two eggs which failed to develop and became dry due to unknown causes (perhaps desiccation)(Table 6.II).

The most prevalent cause of mortality in the areas studied was Chrysocharis sp, which was responsible for half of the eggs killed (Table 6.II). Even so it only killed in average 11% of the egg clusters available. This parasitoid was more prevalent in the summer generations. The host eggs are attacked in a very early stage of development only. One parasitoid develops inside each host egg, and the development time until the adult parasitoid emerges takes about one month. Some 15 days after being parasitised, the egg's colour start to change becoming dark brown. They do not grow as large as unparasitised eggs and their surface become uneven and corrugated, giving a putrid appearance. The three clusters attacked by this Eulophid in the summer of 1978 at site 1 were all located in the very same shrub.

The lacewing larvae attack the eggs with their long hollow mandibles, sucking out most of the egg's fluids. The eggs shrink and then dry. It is difficult to determine the mortality cause once the egg is shrunk and dry. In Table 6.II only those eggs which were actually seen being attacked are ascribed to the lacewing, but probably a large proportion of the egg deaths classified as unknown causes were in fact due to lacewing larva. This predator might have been responsible for the killing of up to 6-8% of the eggs. It was found to be common at study sites 1 and 2 during the rainy season on low bushes.

TABLE 6.II

Mortality of *Themos olfersii* eggs at study sites One and Two in different years.

	1973+1974	1977	1978	Total
NO. CLUSTERS STUDIED	34	22	24	80
TOTAL NO. EGGS	884	572	708	2164
NO. EGGS KILLED BY:				
Chrysocharis sp (Hym., Eulophidae)	82(9%)	74(13%)	89(13%)	245(11%)
lacewing larva (Neur.,Chrysopidae)	-	17(3%)	30(4%)	47(2%)
unknown predator (stealer)	39(5%)	16(3%)	7(1%)	62(3%)
Themos olfersii larvae	-	-	27(4%)	27(1%)
leaflet fall	-	-	20(3%)	20(1%)
unknown causes	37(4%)	60(10%)	21(3%)	118(6%)
TOTAL MORTALITY	158(18%)	167(29%)	194(27%)	519(24%)

Another predator, never seen, attacked the clusters by removing a few eggs completely. It would appear to have chewing mandibles for it was able to remove the eggs. My suspicions fall upon ants, as several species were common in the areas studied.

The only instance witnessed of mortality due to the fall of the leaflet happened with the only egg cluster laid on a small young leaflet just 4cm long.

Only once were Theros larvae seen to feed on a leaflet which also had a developing batch of conspecific eggs on it. This happened at the beginning of the 1978 summer generation when a female chose for egg-laying a shrub which still had a group of large larvae of the spring generation. The larvae ate most of the leaflets of the shrub including the one with the new egg cluster. They did not eat the eggs but as the remaining portion of the leaflet dried, so did the eggs.

6.A.4 FEMALE LONGEVITY AND MORTALITY

The mortality rate of T. olfersii females during their short prereproductive period (see Chapter 5) is not known, but is apparently small. Postreproductive females have a relatively long life span of up to 5 weeks despite the fact that they do not feed at all. As the incubation period of their eggs takes about 3 weeks this means the adult females can outlive the hatching of their eggs.

Not all females, however, survive until their eggs hatch. In the spring generations of 1973 and 1974 at site 1, 80% of the observed females outlived the hatching of their eggs (N = 43 females). But in the spring and summer of 1977/78 only 60% of the observed females outlived the hatching of their eggs (N = 28 females). There was no significant difference between the average number of eggs laid by females outliving the hatching of their eggs (long lived females) and those females which died before their eggs hatched (short lived females).

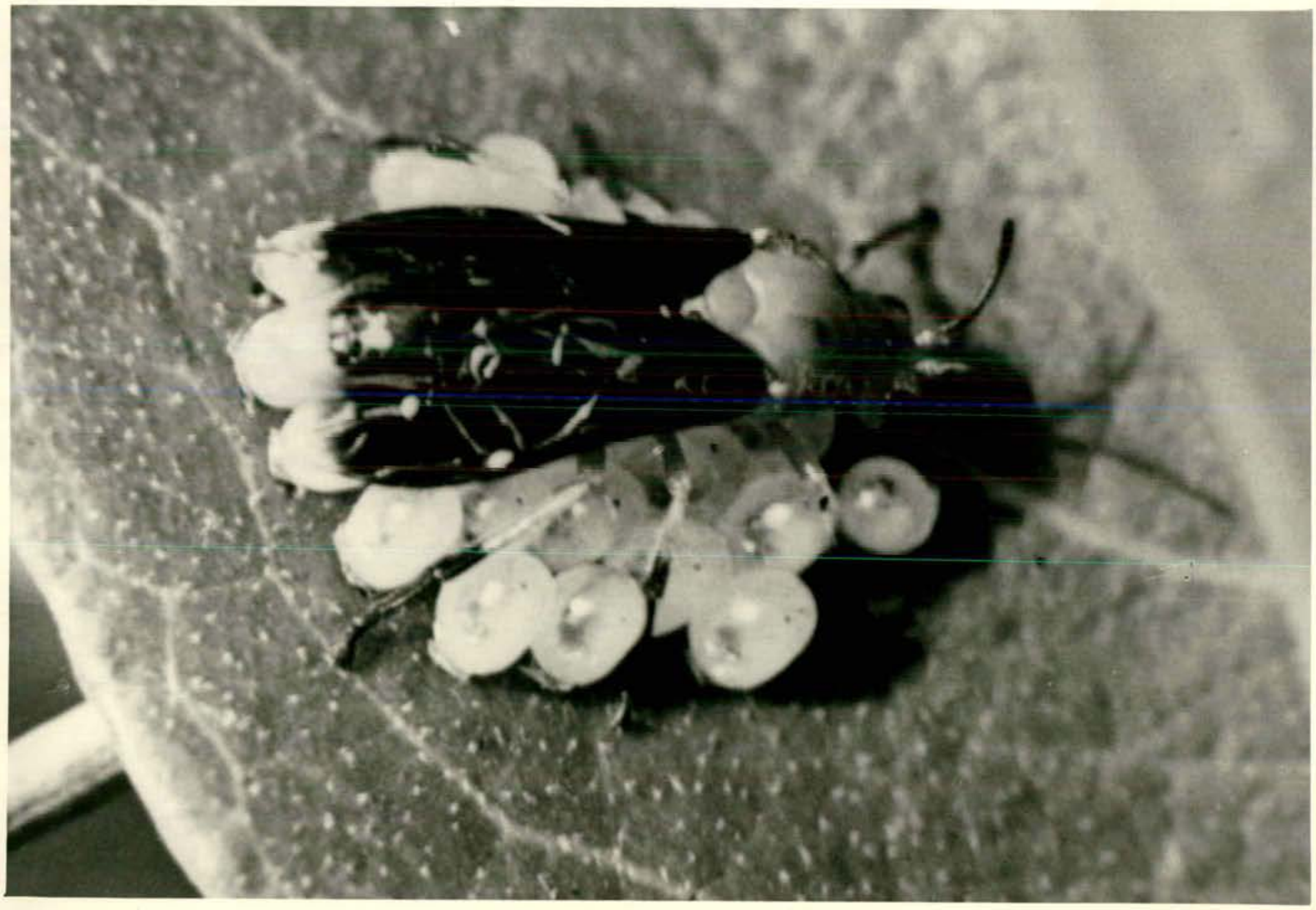
Most females died apparently after depleting their resources and their bodies usually fell to the ground just below the leaflet with the egg cluster. The female's dead body remains intact there for several weeks. Occasionally a dead female may remain attached to the leaflet hanging down supported by a firm grip made by her tarsal claws. Predation on T. olfersii females was very low. Less than 5% of them were apparently killed by predators: their bodies were found either cut into pieces of decapitated, beside their egg cluster or on the ground just below it. The identity of the predator(s) is not known yet. No incidence of disease or parasitism was detected on adult females.

6.A.5 MATERNAL CARE FOR EGGS

Since the time the eggs are laid and until the newly born larvae migrate out of the egg cluster site towards the base of the leaflet, the female maintains herself permanently straddled over her egg cluster. She sits astride the eggs with the axis of her body exactly over the centre of the circle of eggs and the tarsi of her six legs firmly grip the surface of the leaflet just outside the circumference of the cluster. The female maintains a position parallel to the leaflet's surface, her wings are closed over her abdomen, her mandibles remain closed facing down towards the leaflet surface, and her antennae remain at about right angles to each other both facing forward and inclined upward at about 45 degrees. I shall call this the "Egg Cluster Straddling Stance" (Figures 6.6).

While over her egg cluster in the Straddling Stance the female does not assume any constant orientation in relation to the rest of the leaflet - she may face the leaflet's margin, the midrib or any other direction. Whatever her orientation, the female maintains it for long periods of time without moving at all. Rarely some females did move away from egg cluster, but only to come back shortly afterwards to reassume the Straddling Stance. In a random sample of observations (N = 313 observations) on the positioning of several different T. olfersii females with eggs, the females were found at the Egg Cluster Straddling Stance in 97% of the observations.

FIGURE 6.6 (this and next plate). _Themos_ _olfersii_ females guarding their eggs in the Egg Cluster Straddling Stance.



Females found away from their eggs were either standing still on the underside of the leaflet with eggs, or just beside the egg cluster, or on another leaf of a different plant contiguous to the egg bearing leaflet, or else were wandering over neighbouring leaflets. In most of these cases the females were standing still on the underside of the egg bearing leaflet, in many cases exactly underneath the egg cluster. One female consistently prefered to stay on the underside of the egg bearing leaflet exactly underneath its egg cluster, but from time to time visited her eggs on the superior side of the leaflet assuming the Egg Cluster Straddling Stance, returning soon afterwards to the underside of the leaflet. Her egg cluster was directly exposed to the hot sun, whereas most egg clusters are protected from direct sun by the shade provided by neighbouring leaflets. Therefore, it seems possible that this and other females which behaved similarly go to the underside of the egg bearing leaflet to avoid excess of sun exposure. If disturbed, these females immediately returned to sit over their egg cluster.

It is very difficult to remove by force the females from the top of their egg clusters because their tarsal claws provide them with a very strong grip on the leaflet's surface. Females removed from their egg clusters promptly returned to straddle over their eggs if set free near their eggs.

While over her eggs (Straddling Stance) *T. olfersii* females react to visual,tactile and vibration stimuli (see below) with several different displays which involve changes in her body posture, body movements, wing movement and change in positioning, change in head orientation, mandibles movement, and leg flexion and change of grip. During all these displays the females remain over the egg cluster all the time. Most of these displays do not involve a change in the grip points of the tarsal claws. Some involve only a change in posture while others involve active behaviour patterns. At least 13 different displays have so far been recorded for *T. olfersii* females guarding their eggs. They are described below:

(1) BODY ROTATION - The female turns around over the egg cluster changing her grip points, so that she will face the direction from which the stimulus came or is coming. Wings and mandibles remain closed. In fact, except for the leg movements, there is no change in the posture of the rest of the body (Figure 6.7).

(2) OPEN MANDIBLES/BODY ADVANCE - The female pushes forward her forelegs and swings her body forward without changing the grip points of the middle and hind legs, raises her wings partially up, raises her head pointing her mandibles forward and opens her mandibles widely. If she comes, by doing so, in contact with any object or animal she tries to bite it. If successful she pulls her head downwards with her mandibles closed on it. Females maintain this forward stance as long as the stimulus remains near (Figures 6.7 and 6.9).

(3) WING BUZZING - The female lowers her head while raising her abdomen without changing the grip points of her legs, spreads her wings open and vibrates them forcefully back and forward producing a loud buzzing sound which is clearly audible several metres away and lasts for about 1 second. She may produce several short buzzes as long as the stimulus is still present (Figures 6.7 and 6.8).

(4) UNILATERAL FOREWING BLOW - The female turns her body sideways, without changing the grip points of her legs, so that her head is turned away from the source of stimulus, while at the same time spreading her wings open and pushing them forward with force in a fast movement, advancing more the wings on the side closest to the source of stimulus so as to hit it forcefully while producing a short buzzing sound. Her mandibles are kept closed and directed downwards (relaxed posture). The female immediately returns to her original Straddling Stance after the blow. She may repeat the Forewing Blow several times in a row if the stimulus is still present (Figure 6.7).

(5) BODY UP AND DOWN - The female raises and lowers her body alternatively and continuously for a few seconds. The upward movement is sudden and abrupt while the downward movement is slower and smoother. She maintains her body always parallel to the leaflet's surface, the wings closed over the abdomen, her mandibles closed and

FIGURE 6.7. Defensive displays exhibited by _T.olfersii_ females when guarding their eggs. Magnified 2X. 1 = Body Rotation, 2 = Open Mandibles/Body Advance, 3 = Wing Buzzing, 4 = Unilateral Forewing Blow, 5 = Lateral Body Bending, 6 = Lateral Body Bending/Wings Up, 7 = Body Up and Down, 8 = Abdomen Up and Down/Wings Spread, 9 = Body Up, 10 = Body Up/Wings Up, 11 = Forewings Down/Hindwings Up, 12 = Wings Spread, 13 = Body Down

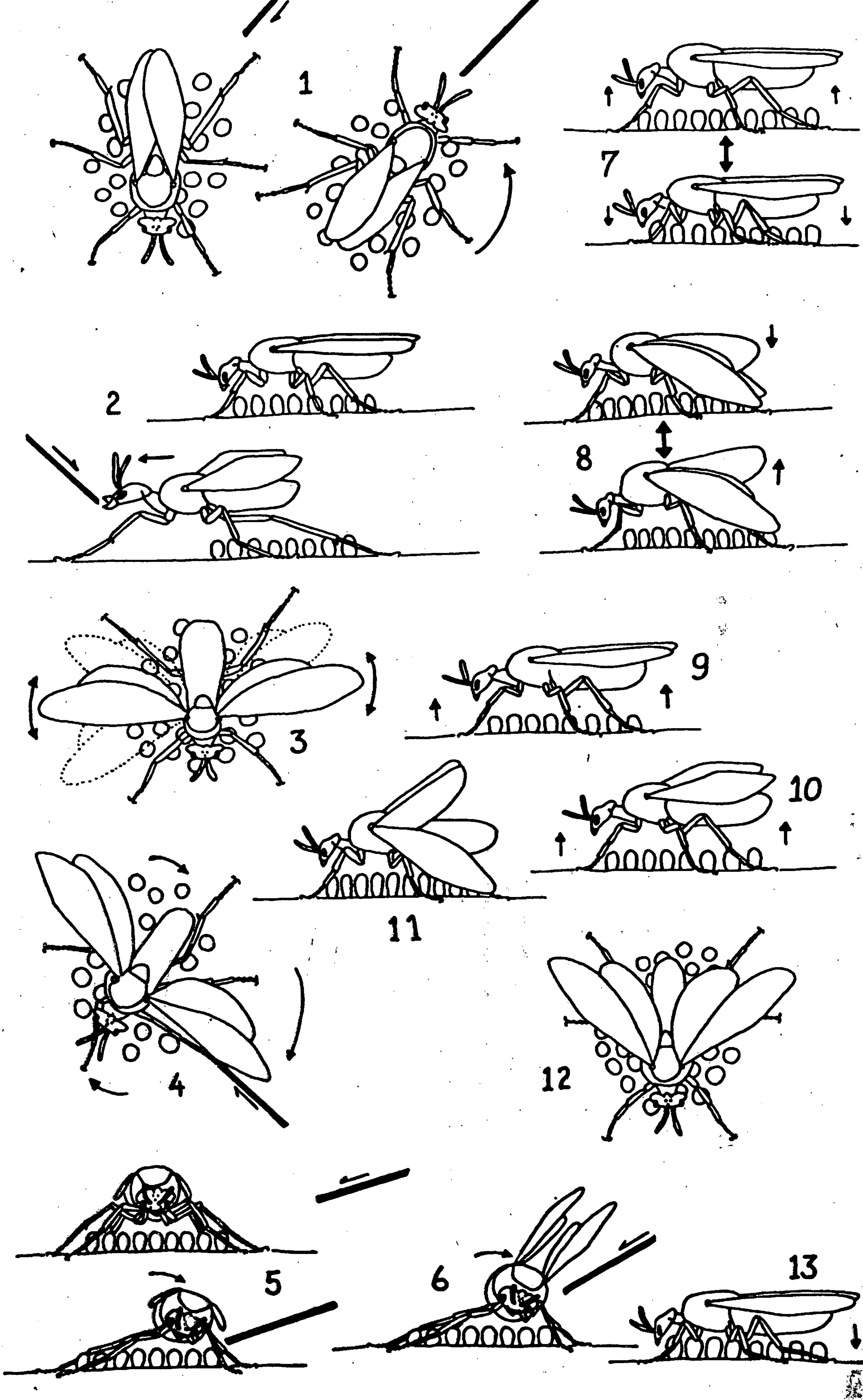

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FIGURE 6.8. Wing Buzzing defensive display of *T.olfersii* females guarding their eggs.

FIGURE 6.9. Two defensive displays of egg-brooding female <u>T.olfersii</u>. Top: Body Down defensive display; Bottom: Open Mandibles / Body Advance defensive display .

and directed downwards (relaxed posture) and does not change the grip points of her legs (Figure 6.7).

(6) ABDOMEN UP AND DOWN/WINGS SPREAD - The female spreads her wings partially forward and downward while raising and lowering her abdomen alternatively and continuously for a few seconds or minutes, maintaining her head always close to the eggs. Her mandibles are kept closed and facing downward (relaxed posture), and she does not change the grip points of her legs (Figure 6.7).

(7) LATERAL BODY BENDING - The female bends all her body to one side until contacting the eggs at the edge of the egg cluster and almost contacting the leaflet's epidermis just outside the egg cluster circle so as to intercept the approach of the source of stimulus from that side, therefore, using her thorax and abdomen as a shield. She maintains her wings closed over her abdomen, and her mandibles closed and directed ventrally (relaxed posture). The female varies the extension of her lateral bending according to the proximity of the source of stimulus. She immediately returns to her original Straddling Stance once the source of stimulus backs aways (Figure 6.7).

(8) LATERAL BODY BENDING/WINGS UP - The female behaves just as described for Lateral Body Bending, but the wings of both sides are held up parallel to each other and are inclined toward the source of stimulus. She may vary the inclination and spreading of her wings according to the proximity of the source of stimulus (Figure 6.7).

(9) BODY UP - The female raises her body parallel to the leaflet's surface without changing the grips of her legs, and remains immobile in this elevated posture for several minutes. The wings are kept closed over the abdomen and the mandibles are also kept closed and directed ventrally (relaxed posture). She may continue in this posture for some time after the stimulus has disappeared (Figure 6.7).

(10) BODY UP/WINGS UP - The female behaves just as described for Body Up, but the wings are now partially opened and raised (Figure 6.7).

(11) BODY DOWN - 'The female lowers her body parallel to the leaflet's surface until she touches her eggs with the ventre of her body, without changing the grips of her legs, and remains immobile in this lowered posture for several minutes. The wings are kept closed over the abdomen and the mandibles are also kept closed and directed ventrally (relaxed posture). This posture may be sustained for some time after the stimulus has disappeared (Figure 6.9).

(12) WINGS SPREAD - The female spreads her wings fully open inclining them slightly downward over her eggs such that the anterior margin of the forewing makes an angle of about 60° with her body axis, without changing the posture of the rest of the body. She remains immobile in this new posture for several minutes, even after the stimulus has disappeared (Figure 6.7).

(13) FOREWINGS DOWN/HINDWINGS UP - The female extends her forewings partially forward and downward over her eggs such that its anterior margin makes an angle of about 30° with her body axis, while at the same time she raises both hindwings upright until they meet each other above her abdomen. The posture of the rest of her body is not changed. She remains immobile in this new posture for several minutes, even after the stimulus has disappeared (Figure 6.7).

Most of these displays, except the last two, involve flexing of the legs either to rotate, bend, lift, lower, incline or turn the body, but only the first two involve changes in the grip points of the tarsal claws. Only display no. 2 involves the use of the mandibles, but the wings are much used either as a postural component of the total display or as the major component of an active behaviour pattern (nos. 3 and 4) or as the sole postural component of a static behaviour (nos. 12 and 13). The antennae however, are not used in any of these displays.

The most frequent display was always Wing Buzzing followed by Lateral Body Bending, Open Mandibles/Body Advance, Body Rotation, Unilateral Forewing Blow and Body Up/Wings Up. The other displays were less frequently observed, although some were exhibited in high frequencies by individual females.

As for the stimuli which trigger the above described displays, the females were found to react to vibration of her leaflet, visual and tactile stimuli. When any part of the egg bearing shrub is struck by a sharp knock, specially if close to the female, she always reacts with Wing Buzzing, and will repeat her display as often as she is stimulated. She also reacts with Wing Buzzing to the approach of a person within 1 or ½ metre to her egg cluster. I am not sure whether in this case the stimulus is perceived visually or through substrate vibration. The female may also react to the close approach of a person and a gentle touching of the leaflet she is in with the Body Down display.

The female reacts to visual stimuli, such as the approach of a small object (not in contact with the leaflet) or insect, with several different displays according to the orientation from which the stimulus comes: if it comes from behind she reacts with Body Rotation followed usually by Open Mandibles/Body Advance; if it comes laterally she may also react with Body Rotation followed by Open Mandibles/Body Advance, or she may react with Lateral Body Bending, with or without Wings Up; if it comes frontally she usually reacts with Open Mandibles/Body Advance; and if it comes from above she usually reacts with Abdomen Up & Down/Wings Spread. She may also react to such visual stimuli with Wing Buzzing and Unilateral Forewing Blow occasionally.

The female reacts to tactile stimuli, such as being touched by an object or insect, with several different displays according to the part of her body which is stimulated: if her head is touched she reacts with Open Mandibles/Body Advance; if her front legs are touched she reacts with Unilateral Forewing Blow; if her middle legs or lateral portion of her thorax or abdomen are touched she reacts with either Body Rotation followed usually by Open Mandibles/Body Advance or with Lateral Body Bending, with or without Wings Up. She may also react to tactile stimuli with Body Up, with or without Wings Up, Wings Spread, Body Up & Down, and Forewing Down/Hindwing Up - but it is not known whether each has a specific stimulus.

6.A.6 MATERNAL CARE FOR LARVAE

Newly born larvae remain within the egg cluster circle for a few hours and the female remains over them in the Straddling Stance (Figure 6.10). But when most newly born larvae leave the egg cluster site and migrate to the leaflet's base where they start to feed on the leaflet edge (see Chapter 7), the female also moves and reestablishes herself over the group of larvae on the inferior side of the leaflet near the edge and close to the petiole. Here the female remains with her wings spread and lowered, her legs evenly spread, her body parallel to the leaflet's surface, and her mandibles closed and directed ventrally (relaxed posture): the "Larval Straddling Stance" (Figure 6. 10). The female stays over her larvae for several hours. However, as the larvae proceed eating the leaflet they gradually move away from the leaflet's base and advance toward its apex (see Chapter 7). The female, however, stays behind at the leaflet's base where she adopts a new stance on the inferior side of the leaflet's petiole, facing away from the leaflet with her larvae. She maintains her wings closed over her abdomen, her mandibles closed and directed ventrally (relaxed posture), and her antennae facing forward at about right angles to each other and partially upward at about 45^{o}. I shall call this the "Leaflet Base Vigilance Stance".
When the larvae finish feeding on the egg bearing leaflet they move to the next leaflet on the same leaf, and the female, if still alive, follows them and establishes herself at the petiole of the neighbouring leaflet again taking up the Leaflet Base Vigilance Stance.

On over 92% of random observations (N = 74) on the positioning of several different T. olfersii females with larvae, the females were found either straddled over their larvae or at the leaflet's petiole (Vigilance Stance). Females found elsewhere were either found immobile on another part of the egg bearing leaflet or on a neighbouring leaflet on the same leaf, or were found moving around on the egg bearing leaflet or on a neighbouring leaflet on the same leaf.

FIGURE 6.10 (this and next plate). T.olfersii females guarding their young larvae. This plate:(top)=at the egg cluster site, and (bottom)=near the leaflet's base where the larvae are starting to feed. Next plate: If disturbed at this stage, the female reacts by raising her head and openning her mandibles.

The presence of two egg clusters on neighbouring leaflets of a same leaf, a rare phenomenon, occasionally disturbed the female's positioning after her larvae moved away from the leaflet's base. One of the females may abandon its Vigilance Stance at the base of the leaflet with her larvae and join the other female in a Vigilance Stance at the base of the neighbouring leaflet. Nevertheless, as the leaves of Eriotheca are palmate, the petioles of the individual leaflets are very close to each other, and therefore both females still remain close to their larvae.

While at the Leaflet Base Vigilance Stance near her larvae T. olfersii females react to stimuli (see below) with several different displays similar to those reported for egg guarding females. Some of these displays are in fact the same or slightly modified compared with displays exhibited while guarding the eggs, but others are new. During these displays the female usually does not leave her post at the base of the leaflet, unless she is very disturbed in which case she moves closer to her larvae and usually sits astride a number of them in a Larval Straddling Stance. At least 8 different displays were recorded up to now for T. olfersii females guarding their larvae. These are described below:

(1) OPEN MANDIBLES/BODY ADVANCE - as in egg guarding period.

(2) WING BUZZING - as in egg guarding period.

(3) UNILATERAL FOREWING BLOW - as in egg guarding period.

(4) LATERAL BODY BENDING - as in egg guarding period.

(5) BODY UP & DOWN/WINGS SPREAD - as in Body Up & Down during the egg guarding period but here the wings are also employed being partially spread forward and downwards.

(6) BODY UP/WINGS SPREAD - a combination of the Body Up and Wings Spread displays exhibited during the egg guarding period.

(7) ABDOMEN UP/WINGS SPREAD - not observed yet during the egg guarding period, but similar to the already described Wings Spread modified here by the inclination of the body so that the abdomen is raised and the head is lowered, as in Wing Buzzing. She remains immobile in this posture for several seconds or minutes, even after the stimulus has disappeared.

(8) ABDOMEN SCRATCHING - not observed and probably not performed during the egg guarding period. The female lowers her abdomen until it touches the surface of the leaflet's petiole and then scratches the tip (?ovipositor) back and forth against it. She may persist in this behaviour for several seconds. The wings are kept closed over the abdomen, and the mandibles are also kept closed and directed ventrally (relaxed posture). She does not change the grip of her legs.

Of the eight displays mentioned above, 4 are identical to displays exhibited during the egg guarding period, 3 represent different combinations of displays already described for the egg guarding period, and only 1 represents a new different display not found during the egg guarding period (Abdomen Scratching). The body structures most used in these displays are the legs (all have leg flexing, but only one, no. 1, changes grip points), and wings (4 use them in passive postures, and 2 use them in active vibration). Other body structures less used are the mandibles (only in no. 1) and the abdomen ventral tip, ?ovipositor (only in no. 8). The most frequent display was always Wing Buzzing.

The females were found to react to visual and tactile stimuli, to substrate vibration and whenever their larvae were disturbed. Wing Buzzing was used in all these situations, but specially when the egg bearing shrub was struck by a sharp knock or when a person approached within 1 or ½ metre to her leaf. Occasionally females react to substract vibration with Abdomen Up/Wings Spread or Body Up & Down/Wings Spread displays.

The female reacts to visual stimuli, such as the approach of an insect, with Wing Buzzing, Unilateral Forewing Blow or Open Mandibles/Body Advance. She reacts to tactile stimuli, such as being touched by a small object or insect, with Wing Buzzing, Lateral Body Bending, Unilateral Forewing Blow or Open Mandibles/Body Advance according to the position of the source of stimulus.

When their larvae were disturbed by some stimulus and reacted with their own displays (see Chapter 7), the females themselves reacted with Wing Buzzing or Body Up/Wings Spread, or else moved closer to them and sometimes sat astride over some of the larvae adopting the Larval Straddling Stance. I do not know what stimulus causes the female to display with Abdomen Scratching.

6.A.7 MATERNAL CARE VERSUS BROOD MORTALITY FACTORS

Egg-guarding and larvae-guarding females always reacted to the approach of other insects such as bugs and flies and including potential predators as ants. According to the distance of the approaching insect, female T. olfersii reacted by orientating toward it, performing a defensive display (such as Wing Buzzing and Lateral Body Bending), or attacking the insect with an offensive display (such as Unilateral Forewing Blow or Open Mandibles/Body Advance). Females straddled over their eggs are very well positioned to protect their eggs, and females at the Leaflet Base Vigilance Stance are also specially well positioned to intercept any insect which might try to climb to the leaflet with the larvae coming crawling up the twig.

Eggs and larvae protected by their mothers are nevertheless susceptible to attack by lacewing larvae. Such larvae approach the egg cluster from behind the female and remain several millimetres away from the cluster. With their long hollow mandibles they pierce and suck the contents of several eggs, one at a time. Clusters without females had a larger proportion of their eggs destroyed by this predator than those with their mother, which indicates that the female sawfly is able to give some protection to its eggs against the lacewing larvae. However, in the few interactions witnessed between egg-guarding female sawflies and lacewing larvae, the sawfly did not react with any display as she seemed to be unaware of the presence of the predator.

Egg clusters protected by their mother are easily attacked by Chrysocharis sp resulting usually in 100% parasitism of the sawfly eggs within the clusters discovered by this parasitoid. This parasitoid attacks the eggs shortly after they are laid, while they are still in the early stage of development. In the few opportunities when the parasitoid was seen attacking the sawfly's eggs in the field, the female Chrysocharis was seen approaching, walking around and over the sawfly's eggs at a slow pace and for long periods of time without eliciting any reaction by the female sawfly. The sawflies gave no sign that they were aware of the parasitoid. Chrysocharis females explored their host's eggs with their antennae, striking them quickly and alternatively on the egg's surface. The parasitoid hid between the sawfly's eggs inside the cluster every time I tried to collect them with a brush. In all the cases observed, the female sawflies continued to straddle on top of their eggs and to display when disturbed, despite the fact that all their eggs were parasitized and became dark brown in colour.

Females also continued to sit astride over their egg cluster and display when disturbed, even when all their eggs were dead due to desiccation. Females in the laboratory did not remove a white mold which grew over their eggs when kept in containers with saturated water. Females do not, in any way, help their larvae to feed.

The absence of the mother female does not affect egg development. Egg clusters which lost their mother at an early stage, in the field, developed normally and hatched in about 23 days, just as did those with the mother present. Neither does the mother's absence affect the development of the young larvae. Larvae which emerged after their mother had died had a normal development.

6.B DIELOCERUS DIASI

6.B.1 DESCRIPTION OF EGG LAYING BEHAVIOUR AND EGG CLUSTER

Each female lays all her eggs in just one leaflet of the host plant, on the same day, all close together forming an egg cluster. The eggs are laid within the parenchyma of the leaflet, each one inside an individual pocket, where they lay horizontally, parallel to the leaflet's plane. The egg pockets are made by the female's saw-like ovipositor, which penetrates the leaflet through narrow slits cut through the leaflet's inferior (abaxial) epidermis. Each egg pocket consists of a semi-circular narrow space, 2.5mm long by 2mm wide, just underneath the inferior epidermis. These egg pockets are located in those portions of the leaflet's blade free from larger veins, spaced about 1mm from each other forming irregular rows parallel to the secondary veins, 2 or 3 rows between each two neighbouring secondary veins. The longest axis of the egg pockets usually is parallel to the nearest secondary vein.

After an egg is laid inside an egg pocket, the leaflet's inferior epidermis protudes above the place where the egg is, forming a small lump. The egg does not affect the superior (adaxial) epidermis, however, for it is further away from the egg and much thicker than the lower epidermis. A dark green exudate appears over the narrow slit after the female withdraws her ovipositor from it. This exudate quickly dries and hardens, sealing off the egg pocket from the outside world. After a few days it becomes red colored and acquires a resinous appearance. I do not know whether this exudate comes from the leaflet or is secreted by the female (Figures 6.11 and 6.12).

The eggs within a cluster are not distributed uniformily throughout the whole leaflet, but rather concentrate in one of the halves of the leaflet determined by the midrib, which coincides with the core area of the buzzing displays performed by the female during the 24-hour long period which precedes egg-laying. For example, of 14 egg clusters taken at one time, half had all the eggs on just one side of the midrib, 6 clusters had more than 80% of their eggs on one side of the midrib and only one cluster approached an even distribution of the eggs between the two sides of the midrib.

During the incubation period of 2 weeks (see Chapter 4) the eggs absorb large quantities of water from the host leaflet and grow several times larger in volume. As a consequence they eventually burst open the lower epidermis of the leaflet just above them, forming a transverse, triradial or tetraradial slit (Figure 6.13).

D. diasi females start to lay their eggs between 1100h and 1200h on the day after choosing their egg-laying site. To lay an egg, the female first positions herself on the leaflet's lower surface between two secondary veins, parallel to them, and faces the leaflet's base. She firmly grasps the leaflet's hairy surface

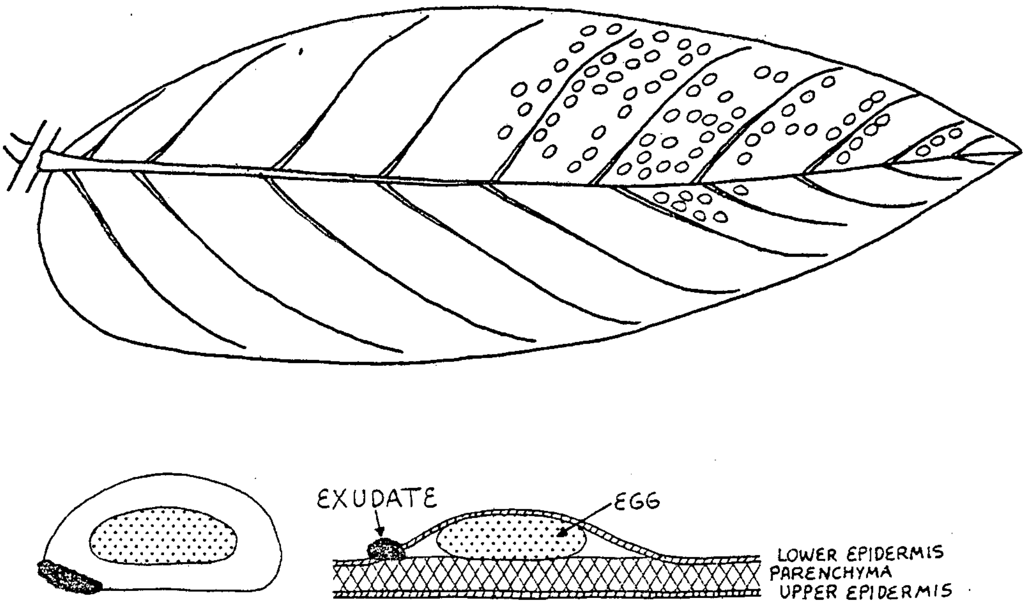
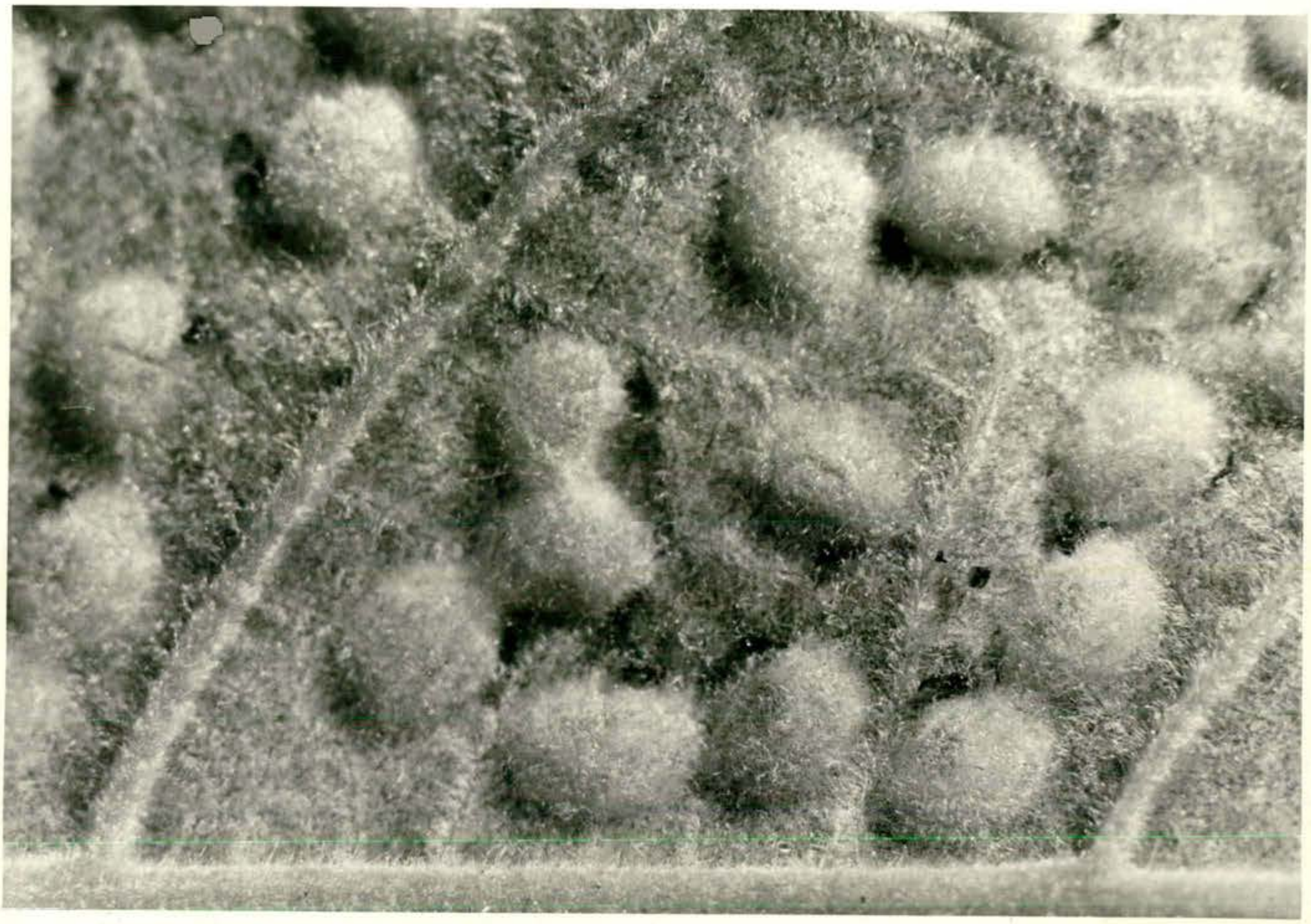


FIGURE 6.11. Top: egg cluster of Dielocerus diasi on a leaflet of Sclerolobium aureum, viewed from beneath, natural size. Bottom: a top view and a cross section of one egg pocket, enlarged 10X.

FIGURE 6.12. Egg pockets of D. diasi. Note the dark marks beside each pocket, sealing the incisions made by the female to open the pockets.



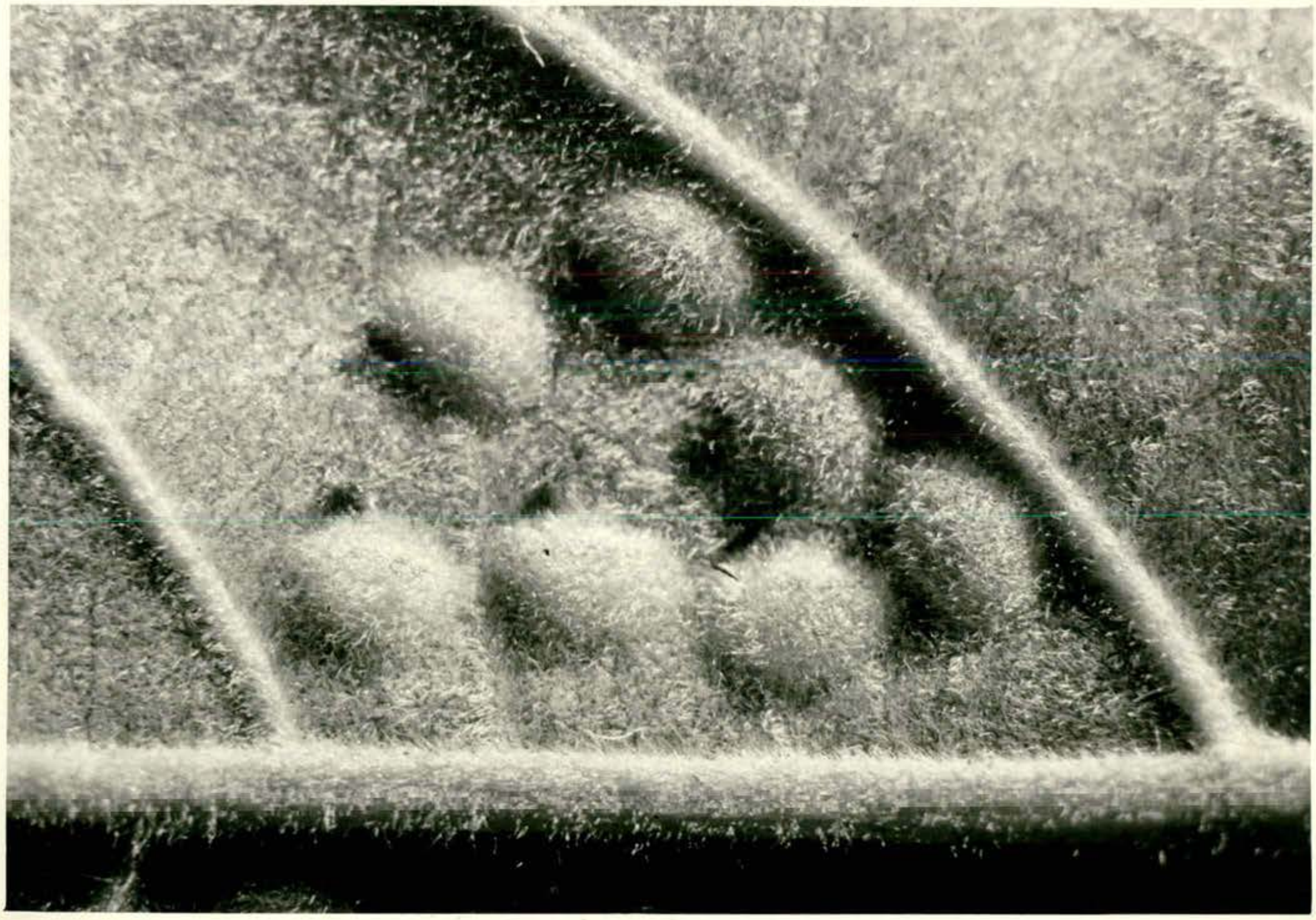


FIGURE 6.13. Swollen (top) and hatched (bottom) eggs of *D.diasi* showing how the lower epidermis of the leaflet above each pocket bursted due to the eggs' pressure.

with all her six legs and curves her abdomen downward to touch its tip on the leaflet's surface. The ovipositor is then exposed a little and is forced against the leaflet's cuticle, so that it cuts a narrow straight slit about 1mm long, usually at a distance of 2-3mm from the nearest secondary vein. This slit is made parallel to the female's longitudinal axis. By rocking the whole body from side to side, slowly but continuously, the ovipositor is slowly introduced inside the leaflet's blade just underneath the lower epidermis. While doing this, the whole body is kept slightly inclined so that the sawfly's sagittal plane makes an angle of about 110° with the leaflet's plane where the ovipositor is penetrating. The wings are kept partially open all the time.

The ovipositor initially penetrates laterally, perpendicularly in relation to the sawfly's longitudinal axis, and then after penetrating fully into the slit it is bent forward until it is parallel to the sawfly's longitudinal axis. In this way a semicircular pocket is opened, with its straight margin closest to the female and its curved margin closest to the nearest secondary vein, so that the pocket's longest axis is parallel to the female's longitudinal axis. This process takes about one minute. Once the pocket is finished, the female's abdomen is pushed against the leaflet's surface and an egg is passed through the ovipositor into the pocket, as the ovipositor is withdrawn in a curved backward movement. I could not see if the female injected any liquid inside the pocket together with the egg. After totally removing her ovipositor from the slit, which is done in a few seconds, the female moves away without turning her head to inspect the slit. The whole operation to lay one egg lasts only 80-85 seconds.

Frequently, in the intervals between finishing to lay one egg and beginning to lay the next, the females lift the anterior part of the body and vibrate their wings forcefully producing a loud buzzing which can be heard from more than 10 metres away. The total activity of laying all the mature eggs which the female has takes about 2 or 3 hours, varying according to the number of eggs laid by each female. Most females finish egg-laying between 1400h and 1500h (Figures 6.14).

FIGURE 6.14. Female *D.diasi* laying eggs on the underside of a leaflet of *S.aureum*.

6.B.2 FERTILITY AND EGG CLUSTER SIZE

Females emerge from cocoon with their ovaries full of large mature eggs of a fairly uniform size. The ovaries occupy most of the abdominal cavity. The average number of eggs per female D. diasi is 76 (Table 6.I). Each female has 16 ovarioles in each ovary (32 in all), united at their distal end by the terminal filaments. Each ovariole has usually 2 or 3 mature eggs, but sometimes may have only one. There is no gradation in size of eggs inside the ovarioles. The average size of the mature egg is 2.1mm long by 1.2mm wide. They are yellow and slightly kidney-shaped. The collaterial glands are highly branched and open into a large reservoir (Figure 6.15).

Each female produces only one egg cluster in her life. The average number of eggs laid per cluster is also 76 (Table 6.I), which means that females usually lay all the mature eggs they have, although a few females were found to retain up to 4 mature eggs (Table 6.I). These retained eggs are not laid afterwards.

The frequency distribution of the number of eggs per cluster plus number of eggs per newly emerged females (Figure 6. 16) is asymmetric (skewed) with a sharp upper limit around 95 eggs and a long tail at the other side, down to only 39 eggs. But if we leave aside those females which produced less than 54 eggs (only 7% of the females), it can be seen that the rest (93%) approach a normal distribution.

6.B.3 EGG MORTALITY

The total mortality of Dielocerus diasi during the egg stage is low and averaged 25% in a sample of 38 egg clusters collected in different localities around Brasília (Table 6.III and Figure 6.17). Only at one specific occasion, described below, was the general egg mortality much above this figure due to parasitism.

In general, only about one fourth of the egg clusters had more than 20% mortality and only 15% had more than 60% mortality. Only about 11% of the egg clusters lost more than 90% of their eggs.

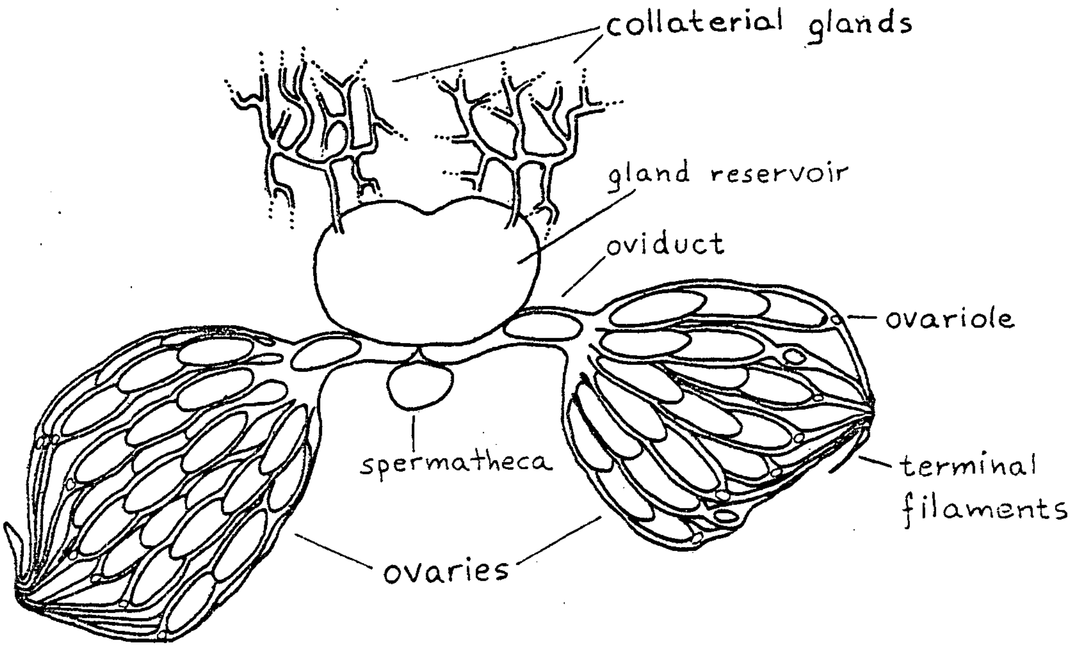


FIGURE 6.15. Female reproductive system of D.diasi. The ovaries are shown rotated from their original positions.

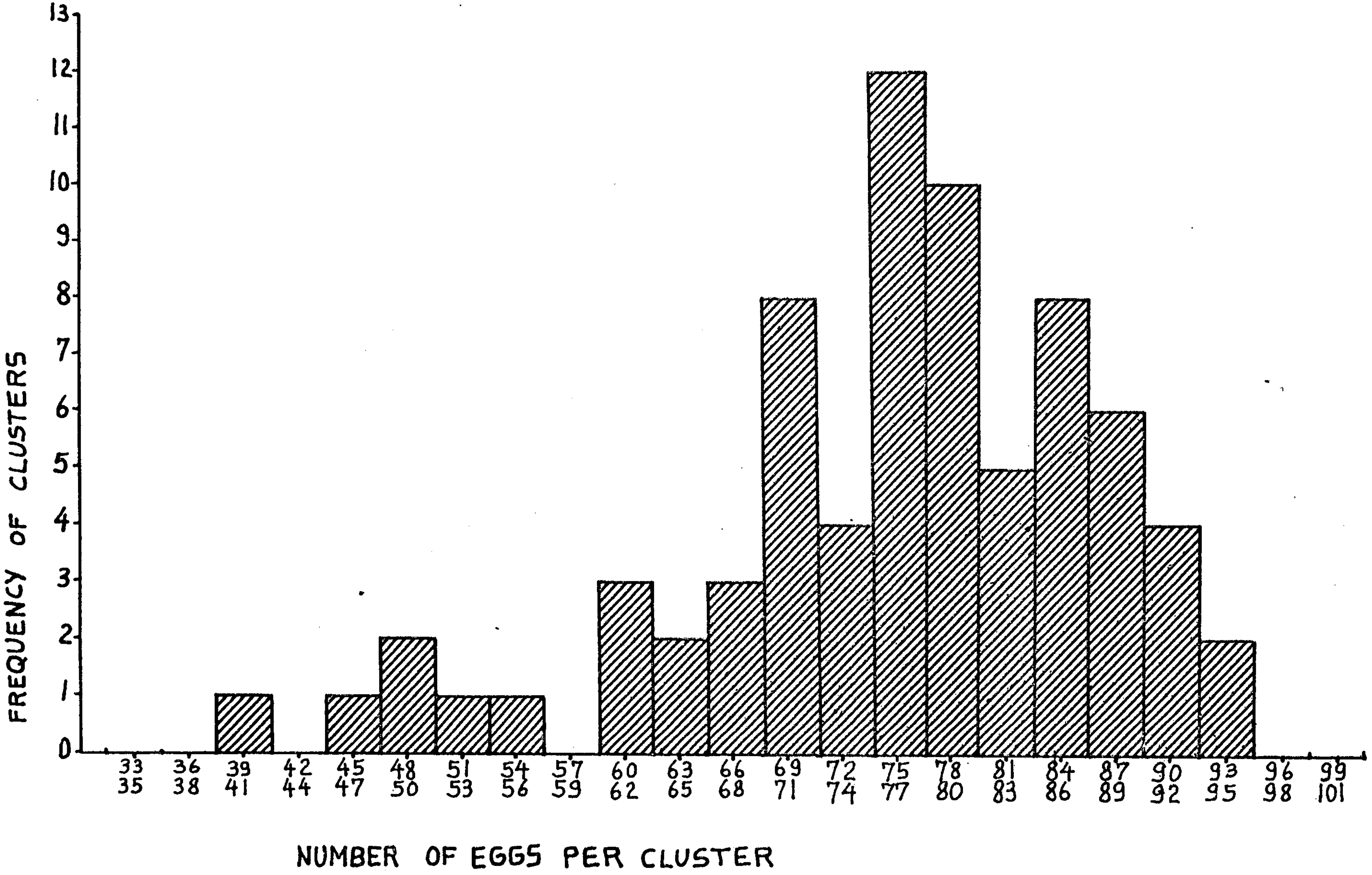


FIGURE 6.16. Frequency distribution of number of eggs per cluster and number of eggs in ovaries of newly emerged females in D.diasi, plotted together. Class interval of 3. N=73 egg clusters plus females.

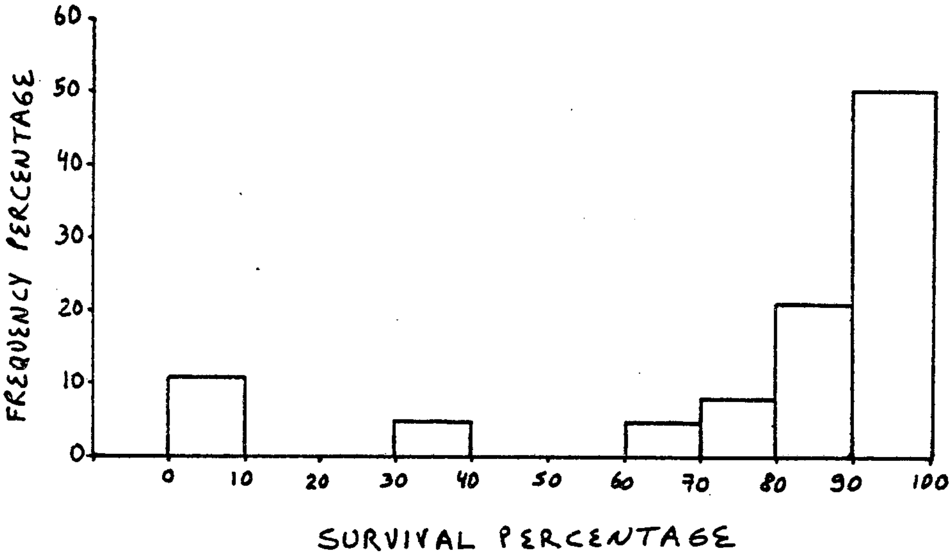


Figure 6.17. Frequency percentage distribution of egg cluster survival percentage for Dielocerus diasi around Brasília in 1976. N = 38 clusters.

TABLE 6.III

Mortality of *Dielocerus diasi* eggs around Brasília in a sample of 38 egg clusters (with 2,857 eggs) from different sites in 1976.

mortality factors	total number and (percentage) of eggs killed	number and (percentage) of egg clusters affected	percentage of eggs killed per affected egg cluster	
			Average	Range variation
Chrysocharis sp (Eulophidae)	168 (5.9%)	7 (18.4%)	32%	4 - 85%
unknown parasitoid (?)	37 (1.3%)	3 (7.9%)	16%	4 - 43%
Dielocerus diasi larvae	16 (0.6%)	2 (5.3%)	11%	8 - 13%
leaflet fall	226 (7.9%)	3 (7.9%)	100%	100%
unknown causes (? desiccation)	257 (9.0%)	34 (90%)	10%	2 - 24%
TOTAL MORTALITY	704 (24.6%)			2 - 100%

Most egg clusters, about three fourths, however, had less than 20% mortality, and about half of all egg clusters had less than 10% mortality. In other words, 50% of the egg clusters had very high survival rates (>90%), 29% had good survival rates (70-90%), 11% had very low survival rates (<10%)and only 10% had intermediate low survival rates (10-70%) - producing a U-shaped survival curve, as in Themos (Figure 6.17). Therefore, egg clusters escaping very high mortality (>90%) lost only 15% of their eggs on average.

The causes of Dielocerus egg mortality were: parasitism by the same species of Chrysocharis (Hym., Eulophidae) which parasitizes Themos eggs; apparent parasitism by another unknown microhymenopteran; leaflet drying due to other Dielocerus larvae feeding on the egg-bearing leaflet (intraspecific competition); leaflet fall; and drying due to unknown causes.

The most common mortality factor was egg drying due to unknown causes, which affected most egg clusters, but killed only a small number of eggs in each cluster, 10% in average. In most of these cases the eggs failed to grow by absorbing water from the host leaf. The second most important mortality factor was leaflet falling, which affected only a small percentage of the egg clusters (8%), but killed all the eggs of those clusters affected - its occurrence resulted in the complete destruction of the total reproductive effort of the females involved.

Another important mortality factor was Chrysocharis sp. Only 18% of the egg clusters were attacked by this parasitoid in most sites, which killed between 4 and 85% of the eggs in affected clusters, with an average of only 32% per cluster. Only one parasitoid developed from each sawfly egg. Parasitised eggs become dark brown and are easily identified, after the parasitoid emerges, by the presence of a thick vitreous dark brown/black shiny lining to the egg pocket. This Eulophid was rare or absent in most patches of Dielocerus studied, but was more prevalent at sites 14 and 15 at RECOR. Its incidence there increased greatly when the Dielocerus population was increased artificially in 1978 by the periodical introduction of several groups of larvae and masses of cocoons collected in other sites. Initially the sawfly population increased steadily, but within a few months the incidence of *Chrysocharis* sp increased greatly, killing most of the egg clusters. Virtually 100% of the eggs in affected clusters were destroyed by the parasitoid. After one year the population density of *Dielocerus* at sites 14 and 15 was smaller than the original. Therefore, the incidence of *Chrysocharis* sp on *D. diasi* eggs is apparently correlated with the host's density, i.e., the greater the density of the sawfly the higher the incidence of this Eulophid. The occurrence of this parasitoid in high incidence resulted in the complete destruction of the total reproductive effort of the female sawflies involved.

A small number of eggs in a few egg clusters were apparently killed by another, still unknown, parasitoid. This was evidenced by the presence of a characteristic light brown cylindrical membrane inside the egg pocket. Further information is needed here to elucidate this observation.

No direct predation on *Dielocerus* eggs was ever observed, but invasion of egg-bearing leaflets by other *Dielocerus* larvae was not rare in chronically infested trees. These larvae eat only part of the egg-bearing leaflet, but not those parts with eggs. However, this caused some parts of the remaining portion of the leaflet to dry, and those eggs near the eaten parts of the leaflet usually wilt and die. However, only about 10% of the eggs of affected clusters die due to this intraspecific competition.

6.B.4 FEMALE LONGEVITY AND DISTASTEFULNESS

The mortality rate of *D. diasi* females during their short pre-reproductive period (see Chapter 5) is not known, but is apparently small. Post-reproductive females have a relatively long life span of up to 4 weeks despite the fact that they do not feed at all, as adults, like *T. olfersii* females. As the incubation period of their eggs takes about 2 weeks this means that the adult females can outlive the hatching of their eggs. Most observed females, in fact, outlived the hatching of their eggs for 11 to 14 days.

Most females died apparently after exhausting their resources but their bodies remained attached by the tarsal claws to the rachis of the compound leaf where they laid their eggs. Dead females remained intact in this position for several weeks.

A few females, however, died just before or shortly after the hatching of their eggs, and their bodies disappeared. They might have been killed by predators such as Mantids or Reduviid bugs which were found in numbers on the host trees. No incidence of disease or parasitism was detected on adult females.

Several live adult *D. diasi* females were presented in the laboratory to the following predators: adult toads, *Bufo* sp; adult and young scorpions, *Tityus trivittatus* and *T. mattogrossensis*; adult centipedes, *Scolopendra viridicornis*; adult bird-eating spiders, *Acanthoscurria atrox*; adult black widow spiders, *Latrodectus curacaviensis*; and a colony of the large hunting ant, *Dinoponera gigantea*. All these predators had been kept in large terrariums for a few months feeding on soft-bodied insects. None of these predators ate the sawflies, and only two, the *Scolopendra* and the *Dinoponera*, killed them. All the others only approached the sawflies, but then avoided them.

6.B.5 MATERNAL CARE FOR EGGS

Since the eggs are laid and until the newly born larvae migrate out of the egg-bearing leaflet (see Chapter 7), the female remains on the egg-bearing leaflet, usually motionless. When not active, the female remains on the underside of the leaflet, with her body parallel to the leaflet's surface, her six legs spread evenly apart and all grasping the leaflet's surface with their tarsal claws, her wings spread laterally such that the front margin of the forewings make an angle of 30-40° with the body axis projecting backward and slightly lowered, her head in the relaxed posture with mandibles closed and facing ventrally, and antennae spread apart from each other bent sideways and slightly inclined forward and upward or backward and upward. However, she may position and orientate herself in different ways while adopting this motionless posture. Most of the time the female positions herself at the base of the leaflet, on its underside, facing the leaf's rachis, with her head over the leaflet's petiole and her body over and parallel to the leaflet's midrib, and her front tarsal claws gripping the leaflet's basal margin. I shall call this the "Leaflet Base Vigilance Stance" (Figure 6.19). Other times the female positions herself over some of her eggs, on the underside of the leaflet, while her body may be orientated in any direction, but most often toward the leaflet's base or a source of stimulus. I shall call this the "Eggs Straddling Stance" (Figure 6.18). Less often the female positions herself beside the leaflet's margin, specially at the apex, on the underside of the leaflet, usually with her body perpendicular to the leaflet's margin and her head facing outward, and her front tarsal claws gripping the leaflet's margin. I shall call this the "Leaflet Margin Vigilance Stance".

Females in the Leaflet Base Vigilance Stance or in the Eggs Straddling Stance remain motionless for long periods of time, several hours or days, if not disturbed. However, they often, specially during the earlier part of the incubation period, alternate shorter motionless periods at Leaflet Base Vigilance Stance or at Eggs Straddling Stance with short periods of zigzag and circular walking over their eggs, on the underside of the leaflet. They keep their wings partially spread, as in the motionless posture, and their head in the relaxed posture with their mandibles closed and facing ventrally while walking. I shall call this activity "Walking Over Eggs". Such walks usually last only for a few seconds and are often initiated without any apparent external stimulus. Most females spend most of their time motionless at the Leaflet Base Vigilance Stance, occasionally interrupted by short periods when they alternate Walking Over Eggs with Eggs Straddling Stance and Leaflet Margin Vigilance Stance.

Egg-guarding *D. diasi* females never fly or abandon their egg-bearing leaflet when disturbed by external stimuli. Females react to stimuli (see below) with several different activities and displays

FIGURE 6.18. Female *D.diasi* in the Eggs Straddling Stance.

FIGURE 6.19. Female D.diasi in the Leaflet Base Vigilance Stance at the time of the egg hatching.

which involve changes in positioning, orientation, body posture, body movements, use of mandibles and wings. At least 11 different displays and changes in positioning were recorded up to now for D. diasi females reacting to external stimuli. They are described below:

(1) WALKING OVER EGGS - as described above. The female approaches the source of stimulus.

(2) EGGS STRADDLING STANCE - as described above. The female approaches and faces the source of stimulus.

(3) LEAFLET MARGIN VIGILANCE STANCE - as described above. The female approaches and faces the source of stimulus.

(4) WING BUZZING - The female lifts her head and thorax and lowers her abdomen until almost touching its lower tip on the leaflet's surface. The head is maintained in the relaxed posture with the mandibles closed and facing ventrally, the antennae remain spread apart directed sideways and slightly forward and upward. The wings are spread open and vibrated forcefully back and forth producing a loud buzzing sound which is audible several metres away and may last several seconds.

(5) WING BUZZING/MANDIBLES OPEN - as above but in addition the mandibles are opened widely and projected forward.

(6) WINGS UP/MANDIBLES OPEN - The female maintains her body parallel to the leaflet's surface, lifts her wings partially up, opens her mandibles widely and projects them forward.

(7) UNILATERAL FOREWING BLOW - as described for T. olfersii.

(8) WALKING OVER EGGS/WING BUZZING/MANDIBLES OPEN - a sommatory of Walking Over Eggs and Wing Buzzing/Mandibles Open displays.

(9) BITING/UNILATERAL FOREWING BLOW - While displaying with her mandibles open in displays no. 5, 6 and 8, if the female comes in contact with any object or animal which is disturbing her, she tries to bite it. If successful she pulls her head downwards with

her mandibles closed on it while at the same time striking it with an Unilateral Forewing Blow.

(10) WINGS FORWARD - The female spreads her wings foreward until the front margin of the forewings become perpendicular to the main body axis, maintaining them slightly lowered. Her body remains parallel to the leaflet's surface and her head in the relaxed posture with mandibles closed facing ventrally.

(11) WINGS UP & DOWN - The female maintains her body parallel to the leaflet's surface and her head in the relaxed posture while suddenly lifting her wings partially up in a fast movement amd subsequently lowering them again in a slower movement. She may repeat this movement several times in a sequence.

All these displays and movements involve the use of the wings, either in buzzing movements or as postural components of static or active displays. The legs are used in six of these behaviours either to walk, incline or rotate the body, but they are not used in five of these displays. Only four of these behaviours involve the use of the mandibles, whereas the antennae are not utilized in any of them.

The most frequent reactions are always to walk toward the eggs to assume the Eggs Straddling Stance, Walking Over Eggs and Wing Buzzing. These three behaviours may occur in sequence in reaction to a single stimulus. Leaflet Margin Vigilance Stance, Unilateral Forewing Blow and Walking Over Eggs/Wing Buzzing/Mandibles Open come next in frequency. The other displays were less frequently observed.

D. diasi females guarding their eggs were found to react to visual, sonore and tactile stimuli and vibration of the egg-bearing leaflet. Females usually did not react to vibration of the egg-bearing leaflet, but occasionally reacted with either Wing Buzzing, Wings Up & Down, Walking Over Eggs or Eggs Straddling Stance. Females readily react to visual stimuli of various kinds such as the approach of a person 1 or ½ metre away from her, the close approach of insects on the egg-bearing leaflet, including other adult females and larvae of D. diasi, and the incidence of a beam of light on her during the night. The most common reactions to visual stimuli are Eggs Straddling Stance, Walking Over Eggs, Leaflet Margin Vigilance Stance and Wing Buzzing, and less frequently Unilateral Forewing Blow, Wing Buzzing/Mandibles Open, Wings Up/ Mandibles Open and Walking Over Eggs/Wing Buzzing/Mandibles Open.

The females also reacted readily to the buzzing sound produced by nearby pre-reproductive females by either Walking Over Eggs, Eggs Straddling Stance, Leaflet Margin Vigilance Stance or Wing Buzzing, or more often by a combination of the above displays.

Females usually did not react to tactile stimuli unless they were touched on the front leg or the head, in which case they reacted with Unilateral Forewing Blow to the first and with Wings Up/ Mandibles Open followed by Biting/Unilateral Forewing Blow to the second.

6.B.6 MATERNAL CARE FOR LARVAE

The newly born larvae remain at the egg cluster site for a few hours, readily clustering themselves into tight small groups, while the female remains at her Leaflet Base Vigilance Stance (Figure 6.19). When most larvae have emerged they migrate to the leaflet's base and proceeding out of the egg-bearing leaflet through the petiole and rachis they reach the youngest leaflets at the apex of the same compound leaf, where they start feeding (see Chapter 7). As the females are usually positioned over the petiole of the egg-bearing leaflet, when their larvae migrate out of this leaflet they necessarily come into contact with them. In such cases, the females always reacted by walking out of the leaflet onto the rachis, turning toward the base of the rachis and walking 40 to 80mm down along the rachis. Here, on the underside of the rachis and between the junctions of the two pairs of leaflets next to the egg-bearing leaflet basally, the female establishes herself parallel to the rachis and facing the rachis' base, grasping it with all her six tarsal claws, with her wings partially spread and slightly lowered (such that the frontal margin of the forewings make an angle of 30-40° with the body axis projecting backwards) and her head in the relaxed posture with mandibles closed and facing ventrally. This is the "Midrachis Vigilance Stance" (Figure 6.20).

A few days later, after they have eaten partially or totally the apical two or four younger leaflets of the egg-bearing compound leaf, the larvae migrate down the rachis and up the branch onto another compound leaf just above the first. As most females are still alive at this stage, the larvae will come again into contact with their mother on the rachis about half way between the apex and base of the rachis. When the leading migrating larvae touch her, she immediately moves forward along the rachis about 20mm towards the rachis' base with no agitation and making no noise. As the larvae continue migrating they soon reach her again, and again she immediately moves forward another 20mm or so. This sequence of events continues until the female reaches the base of the rachis on its underside. Here she stays as the larvae moving along the upper side of the rachis finally reach the branch and climb it to the next compound leaf.

At the base of the rachis of the compound leaf where she had laid her eggs, the female remains motionless with her body parallel to the plant's surface, her wings partially spread laterally and slightly lowered (such that the frontal margin of the forewings make an angle of 30-40° with the main body axis projecting backward) and her head in the relaxed posture with her mandibles closed and facing ventrally. She may orientate herself toward any direction but usually faces down toward the base of the rachis, and occasionally she may position herself out of the rachis' base on the branch itself but always close to the rachis' junction. The female which was found most distant from the base of her selected compound leaf was situated 12cm away along the branch. Less often, the female at this stage positions herself on the underside of the rachis a few centimetres away from its base, sometimes as far away up the rachis as the junction of the first basal pair of leaflets. This is the "Compound-Leaf Base Vigilance Stance" (Figure 6.20).

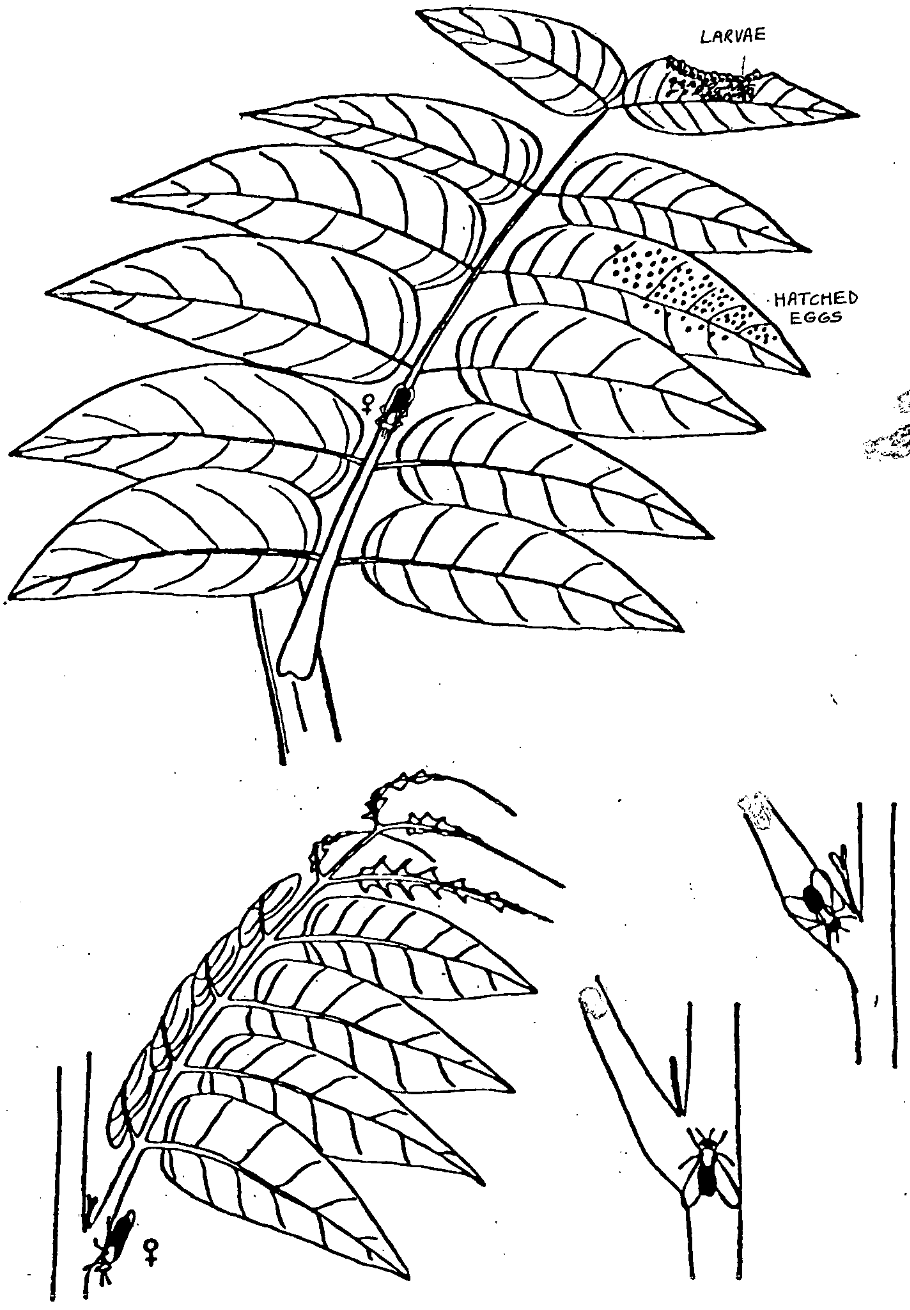


FIGURE 6.20. Top: Position of *D.diasi* female on the middle of the rachis (Midrachis Vigilance Stance) while its larvae are still feeding in their first compound leaf. Bottom: Position of *D.diasi* females on the base of the rachis of their egg-bearing compound leaf (Compound Leaf Base Vigilance Stance) after their larvae migrated out of their first comound leaf.

If not disturbed, the females remain motionless for days in their Vigilance Stances at the Midrachis or Compound Leaf Base. They do not usually react to stimuli such as vibration of the Compound Leaf, other D. diasi buzzing nearby, and being touched. They do react, however, to some visual stimuli such as the approach of a person within ½ metre and the close approach of an insect, and also to strong tactile stimuli specially on the head and front legs. Their reactions were always restricted, involving only the Wing Buzzing and the Unilateral Forewing Blow displays. They never tried to approach their larvae when disturbed. Most females died either when at the Midrachis or the Compound Leaf Base Vigilance Stances, and maintained these postures after death for several weeks supported by the firm grip of their tarsi.

6.B.7 MATERNAL CARE VERSUS BROOD MORTALITY FACTORS

Egg-guarding and larvae-guarding females always reacted to the approach of other insects, including potential predators. The females were standing most of the time at the base of the leaflet, on the rachis or at the base of the compound leaf, well positioned to intercept any insect which might try to climb the leaf or leaflet with eggs or larvae. The usual reactions to approaching insects coming from the branch up the leaf through the rachis were Wing Buzzing, Unilateral Forewing Blow, Wings Up/Mandibles Open and Biting/Unilateral Forewing Blow. Egg-guarding females reacted to insects or other animals approaching the eggs from the air by leaving their Leaflet Base Vigilance Stance and approaching and orientating toward the threat adopting the Eggs Straddling Stance, Leaflet Margin Vigilance Stance or Walking Over Eggs, together with or followed by defensive displays such as Wing Buzzing, Unilateral Forewing Blow, Wing Buzzing/Mandibles Open, Wings Up/Mandibles Open and Wings Up & Down. Larvae-guarding females, however, never left their Vigilance post at the Midrachis or Compound leaf base to approach any insect or other animal coming from the air. Their only reactions were alarm displays (Wing Buzzing and Unilateral Forewing Blow).

Egg clusters protected by their mother, however, are easily attacked by Chrysocharis sp resulting often in 100% parasitism of the sawfly eggs within the clusters discovered by this parasitoid. There is no evidence that the maternal care offers any protection to her eggs against this parasitoid. As I never saw the adult females of this parasitoid in the act of attacking the eggs of D. diasi, I do not know whether the female sawfly attempts to intercept the parasitoid. Females which had their egg cluster totally destroyed by this parasitoid still continued to protect it when disturbed.

Egg-guarding females react to the approach of non-related conspecific larvae but are unable to prevent them from invading their egg-bearing leaflet and feeding on it. The females react by adopting the Eggs Straddling Stance and Walking Over Eggs approaching the larvae frequently and facing them. When the invading larvae leave her egg-bearing leaflet the female goes back to her Leaflet Base Vigilance Stance. One case was observed, however, in which the female was apparently confused by the invasion of her egg-bearing leaflet by small first instar non-related D. diasi larvae. The female reacted moving out of her egg-bearing leaflet, walking with agitation over the rachis near the junction of her egg-bearing leaflet and over the base of the leaflet opposite her egg-bearing leaflet for a few minutes, and then establishing herself on the rachis below the junction of her egg-bearing leaflet, with her wings partially spread and her head facing the base of the rachis in the Midrachis Vigilance Stance. Hours later, however, she returned to her leaflet and alternated between Leaflet Base Vigilance Stance and Eggs Straddling Stance.

The female does not, in any way, help the larvae to emerge from the egg or to feed. They also do not clean their eggs and larvae and are unable to prevent their eggs and larvae from desiccating. The absence of the mother does not affect the egg and larval development. Eggs and larvae which lost their mother in the field at an early stage had a normal development.

6.C DISCUSSION

6.C.1 EGG LAYING PATTERN

The first careful and detailed observations on sawfly oviposition behaviour and ovipositor structure and mechanism of action were made about two and a half centuries ago by the famous pioneer entomologists Vallisnieri (1725) and Réaumur (1740), both working with Argid sawflies, Arge pagana(Panzer) and Arge ochropus (Gmelin) respectively (see Morice, 1912). After these, a number of other species were studied but detailed accounts are available for only a few species: Chapman(1914) on Trichiosoma lucorum (L.) and Bibolini (1967) on Cimbex lutea (L.) (both Cimbicidae); Carne (1962) and Tait (1962) on Perga affinis Kirby (Pergidae); Ghent (1955, 1959) and Ghent and Wallace (1958) on Neodiprion spp (Diprionidae); Morice (1912) and Chapman (1915) on Phymatocera aterrima (Klug), Chapman (1918) on Trichiocampus viminalis (Fallén), Delmas (1926) on Pristiphora conjugata (Dahlbom) and Keir (1936) on Thrinax spp (all Tenthredinidae). There is no modern detailed account on the oviposition behaviour for any Argid species. All that is available for this family are succinct descriptions of the oviposition behaviour and descriptions of the eggs laid on the host plants. This is also all that is offered here regarding D. diasi and T. olfersii.

The egg laying behaviour of D. diasi is similar to that described for other species which also lay their eggs inside individual pockets inside the leaf blade (see e.g. Chapman, 1914 and Delmas, 1926). Tozawa (1940) gives a good description and illustration of an egg pocket inside the leaf blade. The egg laying behaviour of T. olfersii, however, although not described here in any detail, is evidently very different from that of most Tenthredinoid sawflies, although not unique (see below).

Most sawflies lay their eggs orientated and positioned in a consistent manner, e.g. along the leaf edge. To do this the females are guided by structures in the host substrate such as the leaf's margin, midrib, major lateral veins and petiole. These structures serve either as grip points for the tarsal claws and/or mandibles, or to guide the female's sheath scopae at the lower tip of her abdomen (e.g. Carne, 1962; Delmas, 1926; Ermolenko, 1975; Ghent, 1959). D. diasi females orientate themselves parallel to and between two lateral secondary veins, always facing the leaflet's base, before laying each egg. It should be pointed out here that D. diasi females always lay their eggs in the portion of the leaflet where they concentrated their "territorial" displays during the pre-reproductive period (the core area of displaying). I do not know which features T. olfersii females utilize as reference points for positioning and orientating their eggs.

Tenthredinoid sawfly eggs always absorb some water from the plant tissue, and usually double or treble in volume. The eggs die if prevented from absorbing water. For this reason, some authors have compared sawfly eggpockets with galls, calling them "procecidia" (e.g. Delmas, 1926). It is no surprise, therefore, to find that sawfly eggs are always laid spaced from each other, even when laid in compact clusters or rows. This spacing is very critical in compact circular clusters such as that of T. olfersii where those eggs in the centre of the cluster could be squeezed by those surrounding them if there were no such spacing. Ghent (1959) discovered that Neodiprion sertifer females exhibit a stereotyped pattern of leg movements associated with the cutting of the egg pockets which results in a regular spacing between the eggs laid in a row in each pine needle, the magnitude of the spacing depending on the needle's width. Given that all authors have always pointed out that once female sawflies start to lay their eggs they are not easily disturbed, which is also valid for both species studied here, it is possible that all sawflies which lay their eggs in clusters exhibit stereotyped patterns of leg movement.

Very little is known regarding whether the female sawfly injects any substance into the slit opened in the plant together with her egg. Some early authors (e.g. Vallisnieri, 1725; Réaumur, 1740) believed the female also injects a liquid together with the egg inside the egg pocket which would prevent the leaf's tissues from destroying the egg, but there is no proof yet for this. Carne (1962) reported that female *Perga affinis* secretes a fluid, produced in her accessory glands, during the egg laying process which he believes "may serve to lubricate the lancets and egg duct and possibly to seal the leaf incision". The substance which was described in this paper to seal the incision made by *D. diasi* females in the leaflet's epidermis could have been produced and secreted by the female sawfly. This needs to be verified. All sawfly females have collaterial glands and large gland reservoirs which are connected with the ovipositor, and the substances produced by these glands are almost certainly utilized during egg laying in one way or another. There is no evidence that any mother-produced secretion is necessary for the normal development of the egg. Female *Diprion pini* (L.) secretes a froth substance to cover her eggs (Cebalos & Zarco, 1952) giving them some protection against parasitoids (Eichhorn & Pschorn-Walcher, 1976).

Tenthredinoid sawflies exhibit great diversity regarding the positioning of their eggs. Several species lay their eggs in the host's twig (e.g. *Arge ochropus* and *A. pagana* (Ermolenko, 1975) (Argidae), *Acordulecera* and *Haplostegus* (Pyenson, 1940)(Pergidae), *Phymatocera* (Morice, 1912)(Tenthredinidae)); rachis and petiole (e.g. *Didymia* (Dias & Smith, in prep.)(Argidae), *Trichiocampus* (Downes, 1925)(Tenthredinidae)); leaf's midrib (e.g. *Syzygonia* (Marques, 1933) and *Haplostegus* (Pyenson, 1940)(Pergidae), *Eriocampa* (Mackay & Wellington, 1977)(Tenthredinidae)); leaf's lateral veins (e.g. *Croesus* (Caccamo, 1966) and *Nematus* (Ermolenko, 1972) (Tenthredinidae)); leaf's blade along the edge (e.g. *Arge*, *Aprosthema*, *Schizocerella*, *Sterictiphora* (all Argidae)(Ermolenko, 1975; Conde, 1934; Webster & Mally, 1900; Scheibelreiter, 1973), *Cimbex*, *Corynis*, *Palaeocimbex*, *Trichiosoma* (all Cimbicidae) (Bibolini, 1967; Greathead, 1978; Bodenheimer, 1932; Chapman, 1914), *Lophyrotoma* (Tryon, 1921) and *Polyclonus* (Moore, 1957)(both Pergidae), *Pristiphora* (Delmas, 1926) and *Athalia* (Dhillon, 1966) (both Tenthredinidae)); leaf's blade away from the edge (e.g. *Atomacera* (Tippins, 1965), *Sphacophilus* (Ross, 1933), *Dielocerus* and *Themos* (this study) and *Sericoceros* (Martorell, 1941)(all Argidae), *Perga* (Carne, 1962), *Pseudoperga* (Brittlebank, 1888), *Philomastix* (Leask, 1944a), and *Phylacteophaga* (Farell & New, 1980) (all Pergidae), *Metapedias* (Pyenson, 1940), *Caliroa* (Carl, 1972), *Amauronematus* (Vikberg & Kontuniemi, 1971), *Ametastegia* (Dustan, 1916) and *Nematus* (Ermolenko & Kozak, 1979)(all Tenthredinidae)); needle (all Diprionidae and several Nematinae (Tenthredinidae)).

Tenthredinoid sawflies also exhibit great diversity regarding the manner in which the egg is placed in the host plant. Most species lay their eggs parallel to the plant substrate surface inside egg pockets (e.g. *D. diasi*), others lay them parallel to the substrate surface partially inside shallow slits (e.g. *Croesus septentrionalis* (L.)(Caccamo, 1966)), others lay them parallel to the substrate surface with just a small portion inside very shallow slits (e.g. *Nematus melanaspis* Hartig (Ermolenko & Kozak, 1979)), and a few lay their eggs more or less perpendicular to the substrate surface, either with the basal third of the egg imbedded in a deep slit (e.g. *Brachythops wüstneii* (Konow)(Ermolenko, 1975)), or with the base of the egg just slightly imbedded in a large semi-circular slit and with the lifted portion of the leaf epidermis helping to support the egg upright (e.g. *Themos olfersii*), or with only the basal tip of the egg imbedded in a very small slit (e.g. *Sericoceros krugii* (Cresson)(Martorell, 1941) and *Syzygonia cyanocephala* Klug (Marques, 1933)).

However, these eggs laid perpendicular to the plant substrate are certainly more exposed to predators and parasites than those eggs laid parallel to the plant's surface totally imbedded within the plant. Why some sawflies have abandoned the safe mechanism of inserting the egg inside the plant substrate in egg pockets to lay the egg almost completely exposed on the plant's surface is difficult to understand. Perhaps the reason is that laying their eggs perpendicular to the plant's surface has enabled the female to concentrate all her eggs in a very compact cluster, small enough to enable her to sit astride over them to better protect them. Thus maternal care with female straddling over her cluster of perpendicular eggs occurs in *Themos*, *Sericoceros* and *Syzygonia*. The significance of perpendicular egg laying in *Brachythops*, which has no maternal care and no egg clustering, is unknown.

Other sawflies have evolved compact egg clusters by different means: (1) compound egg pocket - several eggs are laid side by side within one large egg pocket (known only for *Arge berberidis* (Schrank) (see Ermolenko, 1972)); (2) egg pod - several eggs are laid together side by side within one large egg chamber, although each egg is inserted through a separate slit (known only for the Pergids *Perga* (see Carne, 1962), *Pseudoperga* (see Brittlebank, 1888) and *Lophyrotoma* (see Tryon, 1921)); (3) row of contiguous slits - several eggs are laid together in a rwo (e.g. *Phymatocera aterrima* (Klug)(Morice, 1912), *Croesus septentrionalis* (Caccamo, 1966), *Eriocampa ovata* (L.)(Mackay & Wellington, 1977), *Gilpinia socia* (Klug)(Knerer, 1977), *Haplostegus epimelas* Konow (Pyenson, 1940), *Arge pagana* (Panzer)(Scheilbelreiter, 1973)); (4) circular cluster of horizontal eggs - several eggs are laid very close to each other but in individual slits, laying parallel to the plant's substrate (e.g. Nematus melanaspis Hartig (Ermolenko & Kozak, 1979), and probably Philomastix nancarrowi Froggatt (Leask, 1944a - the author did not indicate clearly the orientation of the eggs inside the cluster).

The most common type of egg clustering, however, is to lay the eggs in individual slits or pockets close to each other forming rows (e.g. Neodiprion spp (Atwood & Peck, 1943 and Ghent, 1959), Arge spp (Ermolenko, 1975), Pristiphora spp (Delmas, 1926), Polyclonus (Moore, 1957) and Dielocerus diasi (this study)). Such type of egg laying results in clusters not so compact as those discussed in the above paragraphs.

A large number of sawfly species usually lay their eggs singly or in small groups of 2 or 3 eggs per leaf, distributing their eggs over a large number of hosts. These include all studied Cimbicidae, most Tenthredinidae, some Diprionidae, some Pergidae and some Argidae. On the other hand, a smaller number of sawfly species lay their eggs in clusters, either compact or loose clusters, distributing their eggs between a few or only one host. These include most Argidae, most Pergidae, most Diprionidae, many Tenthred--nidae of the subfamily Nematinae (but few Tenthredinidae in the other subfamilies), and no Cimbicidae.

Egg clustering occurs in species where larval aggregation is advantageous for defence against predators and parasitoids (Ford, 1962; Labine, 1968; Lyons, 1962; Prop, 1960; Tostowaryk, 1972). In an attempt to classify the different egg-laying strategies of Tenthredinoid sawflies in terms of clustering of eggs, 4 major groups can be easily identified: (1) all eggs in one host/all grouped in a compact cluster in just one leaf or leaflet (known only for Dielocerus and Themos (this work) and Sericoceros (Martorell, 1941)(all Argidae), and Pseudoperga (Lewis, 1836), Philomastix (Leask, 1944a) and Syzygonia (Marques, 1933)(all Pergidae)); (2) all eggs in one host/all grouped in one loose cluster in one shoot - the eggs are distributed between several neighbouring leaves within one branch, one or several eggs per leaf (e.g. many species of Neodiprion (Atwood & Peck, 1943), Gilpinia (Knerer, 1977), Nesodiprion (Beaver & Laosunthorn, 1975), Diprion (Eliescu, 1932), Microdiprion (Mallach, 1974) (all Diprionidae), Perga (Carne, 1962 and 1965)(Pergidae)); (3) eggs distributed between a few distinct hosts/eggs grouped into a few clusters (e.g. many species of Arge (Ermolenko, 1975; Tozawa, 1940), Atomacera (Tippins, 1965), Sphacophilus (Ross, 1933)

(Argidae), Lophyrotoma (Tryon, 1921), Polyclonus (Moore, 1957), Haplostegus (Pyenson, 1940)(Pergidae), Croesus (Caccamo, 1966), Eriocampa (Mackay & Wellington, 1977), Trichiocampus (Downes, 1925), Pristiphora (Martelli, 1954)(Tenthridinidae)); (4) eggs distributed between several distinct hosts/eggs laid singly or 2 or 3 per leaf and branch (e.g. Acordulecera (Pyenson, 1940), Phylacteophaga (Farell & New, 1980)(Pergidae), Zenarge (Moore, 1962), Schizocerella (Gorske et al., 1977)(Argidae), Gilpinia (Prop, 1960), Athalia (Dhillon, 1966), Metapedias (Pyenson, 1940), Caliroa (Lahille, 1909)(Tenthredinidae), Cimbex (Bibolini, 1967), Corynis (Scheibelreiter, 1979), Palaeocimbex (Bodenheimer, 1932)(Cimbicidae)).

There is no simple general correlation between egg clustering, maternal care and fertility among the Tenthredinoid sawflies. Egg clustering is found among species with the lowest fertility in the group which lay only 25-35 eggs per female (Pseudoperga lewisi (Brittlebank, 1888), Philomastix nancarrowi (Leask, 1944a), Sericoceros krugii (Zwaluwenberg, 1918; Martorell, 1941) and Themos olfersii (this study)), among species with medium fertility which lay 70-90 eggs per female (Syzygonia cyanocephala (Marques, 1933), Themos vigilax (Malaise, 1949), Themos sp (Dias, in prep.a), Dielocerus diasi (this study))and among those species with the highest fertility in the group, which lay about 200 eggs per female (Croesus septentrionalis (Caccamo, 1966), Croesus japonicus (Iwata, 1958), Trichiocampus populi (Iwata, 1958)). All species mentioned in the first two groups, lowest fertility and medium fertility, cluster all their eggs in just one compact cluster and exhibit maternal care. But those mentioned in the highest fertility group and others not mentioned in the medium fertility group (such as Pristiphora conjugata (Martelli, 1954), Neodiprion pratti (Bobb, 1972), N. fulviceps (Dahlsten, 1967), N. sertifer (Pschorn-Walcher, 1970; Hardy & Allen, 1975)) either group their eggs into a few separate compact clusters or cluster all their eggs in just one loose cluster over several leaves on a single shoot, in both cases without maternal care.

In the other extreme, species which lay isolated single eggs can be found throughout the fertility range: low fertility (e.g. Caliroa cerasi (Lahille, 1909; Brèthes, 1919; Carl, 1972)), medium fertility (e.g. Palaeocimbex quadrimaculata (Bodenheimer, 1932), Corynis similis (Scheibelreiter, 1979), Cimbex lutea (Bibolini, 1967), Athalia proxima (Dhillon, 1966)), and highest fertility (e.g. Zenarge turneri (Moore, 1962), Waldheimia japonicus (Iwata, 1958)). None of these exhibit maternal care.

The difference in egg cluster size observed between T.olfersii, P. lewisi, P. nancarrowi and S. krugii at one side with low fertility around 30 eggs per cluster, and T. vigilax, T. sp. n., D. diasi and S. cyanocephala at the other hand with medium fertility around 80 eggs per cluster, is most probably due to differences in hatching larval size requirements correlated with differences in hostleaf thickness and toughness. Those species, as T. olfersii, attacking hosts with thick and tough leaves need to lay large eggs which will produce large hatching larvae, and because the energy commited to reproduction is limited this can only be achieved by reducing the number of eggs laid (Labine, 1968).

6.C.2 EGG CLUSTER SIZE AND FERTILITY

Larval gregariousness can usually only occur in species where the females lay their eggs together in just one or a few clusters. Larval group size, thus, is very much dependent upon the egg cluster size, which in turn is dependent upon several factors, the most important of which are the female fecundity, egg maturation pattern, size of leaf where eggs are laid and whether or not the female is fertilized by a male.

Fecundity is very variable among sawflies and horntails. It is broadly directly proportional to the number of ovarioles and to the size of the adult female, and inversely proportional to the egg size/adult size ratio. Thus the lowest fecundity is found among species of Orussidae and Pamphiliidae, which have, respectively, only 8 and 12 to 16 ovarioles per female producing in average only about 15 and 18 to 25 eggs per female, each egg with a length of 10 to 28mm and 1.5 and 3.9mm (Cooper, 1953; Eidt, 1969; Forsius, 1920; Iwata, 1958; Roberti, 1951). On the other extreme are the large species of horntails (Siricidae) which have 60 to 160 ovarioles per female, producing in average 250 to 650 (sometimes up to 1200) eggs per female, each egg with a length of 1.2 to 1.8mm (Forsius, 1920; Iwata, 1958; Spradbery, 1977). The egg length/adult female length ratio is about 0.5 to 1.0 for Orussus sayii (Orussidae), 0.2 to 0.3 for Acantholyda nemoralis (Pamphiliidae) and only 0.03 to 0.1 for Urocerus gigas (Siricidae).

Tenthredinoid sawflies are in between these extremes, most species producing in average between 50 and 80 eggs per female. Following is a Table with a brief summary of the available data on female fertility for the different families of Tenthredinoidea:

TABLE 6.IV

FAMILY	NUMBER OF OVARIOLES	AVERAGE NUMBER OF EGGS LAID PER FEMALE	AVERAGE EGG LENGTH
ARGIDAE	20-32	27-190	0.7-2.1mm
PERGIDAE	16-20	35-80	1.0-3.5mm
CIMBICIDAE	20-42	30-100	1.3-2.8mm
DIPRIONIDAE	44-46	46-120	0.9-2.1mm
TENTHREDINIDAE	10-60	25-200	0.35-3.0mm

RANGE OF FEMALE FERTILITY AND EGG SIZE AMONG TENTHREDINOID SAWFLIES

The Tenthredinidae being the largest and best studied family of this group exhibits the greatest variability. It should be kept in mind that the data presently available for the other four families is very incomplete and certainly not totally representative for all the species in each of these families.

If we take into consideration the primary sex ratio per egg cluster (see Chapter 5) and the number of generations per year (see Chapter 4) the effective fecundity of each species may be calculated, i.e. the potential number of females which would be produced by direct descent from a single female in one year in the absence of mortality. The formula is

$$\text{Effective Fecundity} = \left(\begin{array}{c}\text{average egg}\\ \text{cluster size}\end{array} \times \begin{array}{c}\text{proportion of females}\\ \text{in the brood}\end{array} \right)^{\begin{array}{l}\text{number of gener-}\\ \text{ations per year}\end{array}}$$

Therefore, *Themos olfersii* has an effective fecundity = $(27 \times 0.66)^2$ = 324 females per year, whereas *Dielocerus diasi* has an effective fecundity = $(76 \times 0.75)^4$ = 10,556,000 females per year. It is evident, then, that while *D. diasi* comes nearer the r pole of the r-K spectrum of reproductive strategy, *T. olfersii* comes close to the K pole. If the population density of both species is in equilibrium, not increasing or decreasing significantly along the years, this means that in each generation only one adult female descendant is produced by each reproducing female in average. This would require a higher mortality for *D. diasi* broods, aroung 98.25% in average (56/57 females) than for *T. olfersii* broods, around 94.44% in average (17/18 females) per generation.

Themos olfersii and *Dielocerus diasi*, then, have relatively large eggs (2.0 x 1.6mm and 2.1 x 1.2mm respectively) compared to most Tenthridinoids, but whereas the fecundity of *D. diasi* (average of 76 eggs per female) is situated at about the average range for most Tenthredinoids, that of *T. olfersii* (average of only 27 eggs per female) is at the lowest limit of fertility in this superfamily. This is very interesting as *T. olfersii* adult females are slightly larger than *D. diasi* females. Even though *T. olfersii* eggs are significantly larger than those of *D. diasi*, it is evident that *D. diasi* females invest much more energy in egg production than does *T. olfersii*. The following Table summarizes these data:

TABLE 6.V

	T.OLFERSII	D.DIASI	RATIO T.OLFERSII/ D.DIASI
EGG LENGTH (mm)	2.0	2.1	0.95
ADULT FEMALE LENGTH (mm)	15	14	1.1
EGG LENGTH/FEMALE LENGTH	0.13	0.15	0.87
EGG VOLUME (mm^3)	2.7	1.6	1.7
ADULT FEMALE VOLUME (mm^3)	200	180	1.1
EGG VOLUME/FEMALE VOLUME	0.013	0.009	1.4
NUMBER EGGS PER FEMALE	27	76	0.36
EGG VOLUME x NO. EGGS (mm^3)	73	122	0.6
EGG VOLUME x NO. EGGS/FEMALE VOL.	0.37	0.68	0.5

EGG PRODUCTION INVESTMENT OF T. OLFERSII AND D. DIASI

The question which arises then is: why do Themos olfersii females not invest as much as Dielocerus diasi in egg production? This question is still more puzzling if we consider that two other species of Themos, T. vigilax Malaise and T. sp. n. (D.R. Smith, in prep.), which are about the same size as T. olfersii, lay about 80 eggs per cluster (Malaise, 1949 and Dias, in prep.a).

Part of the answer might be in that T. olfersii invests more energy in maternal care than D. diasi does. Another reason is that perhaps T. olfersii eggs are proportionally much richer in yolk than those of D. diasi, so that T. olfersii females in toto might be investing comparable amounts of energy in egg production. There is evidence for this in that there is a huge difference in size between the first instar larvae of both species: Themos olfersii larvae have a head volume 13 times those of D. diasi. In fact, first instar larvae of T. olfersii are about the size of fourth instar larvae of D. diasi. Accordingly, the incubation period for T. olfersii eggs is one and a half times longer than that for D. diasi.

But as the sawfly eggs apparently absorb only water from the host leaf during their development and do not take up any nutrients, and as the difference in egg volume (*Themos olfersii* eggs are only 1.7 x bigger than those of *D. diasi*) seems to me to be insufficient to account alone for the difference in first instar larval size, I suggest that there is also some qualitative difference in the eggs' yolk contents.

Sawflies, butterflies and moths resemble each other as the energy invested in reproduction is supplied mainly or solely by the reserves built up during the larval feeding phase. Therefore, "the amount of time alloted to larval feeding (by life history pattern, by environmental conditions, etc.), the efficiency of larval feeding, and the availability of the foodplant must be significant determinants of the amount of energy expended on reproduction" (Labine, 1968).

The apparent reason for the evolution of this great difference in first instar larval size is that each species coevolved with very different host plants, specially in terms of leaflet toughness and width. The leaflets of *T. olfersii*'s host plant, *Eriotheca pubescens*, are much harder and 2.5 x thicker on average than the leaflets of *D. diasi*'s host plant, *Sclerolobium aureum*. The leaf-edge of *E. pubescens* is even thicker, being 4 x wider than the edge of *S. aureum*. The first instar larvae of D. diasi are clearly unable to open their mandibles wide enough to bite through the leaves of *E. pubescens*. As a corroboration, the leaves of the host plant of *Themos* sp. n., *Luhea* sp. (Tiliaceae, Dias, in prep.a), are much thinner and softer than those of *E. pubescens*, and are comparable to those of *S. aureum*.

Female fecundity within a species is also very correlated with body size: the larger the female, the larger the number of eggs. This has been shown, for example, for Siricid horntails (Spradbery, 1977) and Diprionid sawflies (Lyons, 1970; Hard, 1976). But body size, in its turn, is correlated with the amount of food eaten in the larval stage and inversely correlated with the length of the cocoon stage (diapause)(Carne, 1969). Partial starvation in the larval stage has been shown to reduce the adult female fecundity in the larch sawfly Pristiphora erichsonii (Heron, 1955 and 1966) and in some Neodiprion sawflies (Lyons,1970; Hard, 1971). The temperature during the larval and cocoon periods was also found to be directly related to female fecundity in Neodiprion swainei (Campbell and Sullivan, 1963: Philogène and Benjamin, 1971).

The large variation in female fecundity observed among the females of both T. olfersii and D. diasi could be caused by differences in the amount of food ingested during the larval stage. The adult female body size is very variable in T. olfersii and several instances were observed where T. olfersii larvae finished eating all the available leaves in the host plant before they had attained their full size. These semi-starved larvae probably produced smaller than average adults, which might explain the apparent bimodal tendency found in the frequency distribution of the number of eggs per cluster in T. olfersii. There is clearly an abrupt upper limit (near 96) in the number of eggs per female in D. diasi which is approached by only some females if every one of the 32 ovarioles produce 3 eggs each. But there is a long tail at the other side of the frequency distribution curve, which means that there is not a fixed lower limit but rather a very variable one, probably linked with the degree of food deprivation suffered by each larva.

Another important factor in altering female fecundity is whether or not the sawfly entered in diapause or extended diapause during the prepupal stage within the cocoon, and for how long. Adult females of the spring generation of T. olfersii, which had no diapause, exhibited a 20% higher average fecundity in relation to the summer generation adult females which stood in diapause for about 7 months during the dry season. This effect should be expected to be even more pronounced in D. diasi as it was found that extended diapause of 1 to 2 years is not rare in this species (see Chapter 4).

Egg maturation pattern varies among the different groups of sawflies. Females from several groups of Tenthredinoid sawflies emerge from the cocoon with all the eggs which will be laid already mature. This type of maturation, which we could call Early-Maturation, is characteristic of the following groups of Tenthredinoid sawflies: Perginae, Philomastiginae, Pergulinae and Syzygoniinae (Pergidae); Dielocerinae, Theminae, Zenarginae, several Arginae and several Sterictiphorinae (Argidae); Diprioninae (Diprionidae) and Nematinae (Tenthredinidae). Accordingly, adult females of these groups do not feed at all, but may drink some water. Some species in these groups have reduced mouthparts: Philomastix spp, Syzygonia sp and Themos spp (Benson, 1938a). Even so the longevity of some of these females is very high by sawfly standards: up to 4 or 6 weeks. Most of these species lay all their eggs in one big cluster in just one leaf (when this is big enough) or in several neighbouring leaves in the same shoot, giving rise to gregarious lervae (see for example Carne, 1962; Caccamo, 1966; Dusaussoy & Geri, 1966; Ghent 1955 and 1959; Marques, 1933; Martorell, 1941; Regas-Williams & Habeck, 1979; Tozawa, 1940; L.F. Wilson, 1975). Several species in these groups exhibit maternal care behaviour.

Early egg maturation is advantageous in allowing the female to shorten her egg laying period therefore minimizing the danger of dying before finishing or even starting to lay her eggs. However, females emerging with their egg complement fully or mostly mature are heavy and consequently weak fliers. This restricts their participation in the search for mates, which tends to delay their mating and therefore offset the initial advantage (Labine, 1968). Therefore species with early egg maturation must rely mainly on the males for mate finding. The females of these species may facilitate the males' search by staying in localized dense populations as in Euphydrias editha (Labine, 1968) or by releasing sex-pheromones as in most moths (Jacobson, 1972) and some sawflies (Jewett, Matsumura & Coppel, 1976). Females of several species of sawfly, however, avoid this problem by starting to lay their eggs without mating, producing all-male progenies until they mate.

On the other hand, females from several other groups of Tenthredinoid sawflies emerge from the cocoon with most of their eggs immature, which will only mature a few days after emergence. This Delayed-Maturation is characteristic of the following groups of Tenthredinoid sawflies: some Arginae and some Sterictiphorinae (Argidae), all Cimbicidae, and Tenthredininae, Blennocampinae and Selandriinae (Tenthredinidae). Adult females from these groups feed voraciously on nectar and pollen(most species, see Benson, 1950; Ermolenko, 1972 and 1975; Schedl, 1976; Verzhutskii, 1966), honey dew (Schizocerella, Weires & Chiang, 1973), flower petals (Corynis and Dolerus, Benson, 1950; and Sciapteryx, Ermolenko, 1961), leaves (Sciapteryx, Ermolenko, 1961; Cimbex, E.L. Smith, 1970b; Macrophya, Chawner, 1921), leaf pubescence (Arge, Ermolenko, 1975; Sphacophilus, Ross, 1933; Nematus, Ross, 1933 and E.L. Smith, 1970b; Euura, E.L. Smith, 1970b), twig sap (Cimbex, Bibolini, 1967), or prey on other insects (most Tenthredininae, Benson, 1950; Hobby, 1932a,b; and Wolf, 1968; some Dolerini and Allantini, Benson, 1950; and Cimbicinae, Benson, 1950 and E.L. Smith, 1970b), or even on faeces produced by sawfly larvae (Tenthredo, Wolf, 1968). The Tenthredininae and Cimbicinae are voracious predators of other insects, and have large mandibles (Benson, 1938a). Several species which feed on nectar and pollen have very long mouthparts: Coryninae, Thrichorhachinae and Pterygophorinae (Benson, 1938a), and Euryinae (Benson, 1934). Several Ptiliini (Argidae, Sterictiphorinae) also have long mouthparts and probably also feed on flowers too. The adult female longevity in these groups where the adults feed is surprisingly small - usually less than two weeks (Benson, 1950; Verzhutskii, 1966). These females lay their eggs in a few days, dispersing them among several leaves and separate plants, usually only one or two per leaf, not forming clusters. The larvae of these species, thus, are bound to be solitary. No species of this group is known to exhibit maternal care.

There are still some groups of tropical and meridional subtropical Argidae, Pergidae, Cimbicidae and Tenthredinidae for which no information is available on the adult behaviour and egg maturation pattern.

Evidently, both species studied here, Themos olfersii and Dielocerus diasi, belong to the first of the two groups mentioned above: Early Maturation.

The size of the leaf or leaflet chosen for egg laying in relation to the female fecundity can also limit the number of eggs laid per leaf but not the size of the cluster. This applies specially to those species which attack conifers and pinnate or bipinnate broad leaves with small leaflets and also to those which lay their eggs only along the leaf margin or large veins of broad leaves. In both species studied here the size of the egg cluster is not affected by the size of the leaflet. See, for example, Carne (1962) and Tozawa (1940) for instances of leaf size limiting egg cluster size in Perga affinis and Arge similis respectively.

Yet another factor which may also alter the number of eggs laid per female is whether or not she is fertilized by a male. Moore (1962) and Tozawa (1940) have observed that unfertilized females of Zenarge turneri and Arge similis, respectively, lay less eggs than fertilized females (see also Bobb, 1972).

6.C.3 MATERNAL CARE IN THE SAWFLIES

Maternal care is a rare phenomenon among Tenthredinoid sawflies, at least in the Holoarctic region where they have been better studied. From the several hundred species of Holoarctic sawflies which have been studied biologically so far, only three have been found to exhibit some sort of maternal care. Two of these, the nearctic Diprionids Neodiprion lecontei (Fitch) and N. nanulus Schedl, exhibit only what could be interpreted as primordial maternal care behaviour: the postreproductive females stay at the base of the needle where they laid their last eggs and die a few days afterwards without providing any active protection to the eggs when disturbed. These females always position themselves facing the twig. There is no evidence that these females provide any protection to their eggs, but as these behaviours were not studied in any detail nothing can be concluded without further studies. In both these species the females lay all their eggs in just one large cluster at the apex of only one shoot of the host pine tree, distributing the eggs through several neighbouring needles, several eggs in a row per needle.

As this primordial maternal care has been reported only once and briefly for each Neodiprion species mentioned above, I shall quote the original descriptions. Thus, for N. lecontei Benjamin (1955) described that "when the egg supply is exhausted, the female walks to the base of the needle in which her last eggs were laid. As if to guard her egg batch, she remains there in the shelter of the small twig until she dies or is captured by ants or some other predator. Females live an average of 4.5 days with a range of 2 to 17 days". He also presented a photograph to illustrate this behaviour (Benjamin, 1955 - Figure 3a). As for N. nanulus nanulus, Kapler and Benjamin (1960) said that "after oviposition is completed, the female crawls to the base of the needle, and usually remains facing the twig until death occurs".

But whereas the incubation period of N. lecontei eggs is relatively short, 15 to 26 days (Benjamin, 1955), that of N.n.nanulus is very long as this sawfly overwinters in the egg stage (Atwood & Peck, 1943; Kapler & Benjamin, 1960). It is obvious, then, that such primordial maternal care, if benefitial to the eggs, will be of more significance to N. lecontei as the female's postreproductive life span will overlap with that of the eggs for a much greater extent in this species. Both species have highly gregarious larvae. Apparently, the postreproductive females of all the other 20 or so studied species of Neodiprion do not remain with the egg cluster after finishing egg-laying.

The only other record of maternal care for a Holoarctic Tenthredinoid sawfly refers to Pachynematus itoi Okutani (Tenthredinidae, Nematinae) which feeds on larch in alpine Europe and Japan and in Siberia. In this species the female remains over the egg cluster until the eggs hatch and maintains her wings outstretched as a display during the whole period (Pschorn-Walcher & Zinner, 1971). As this behaviour has been described only once and briefly, I shall quote the original description by Pschorn-Walcher and Zinner (1971): "Nach unseren Beobachtungen Bleibt das Weibchen mit abgespreizten Flügeln über dem Gelege sitzen, bis die Junglarven geschlüpft sind. Wurde es im Käfig von den Eiern weggenommen, so kletterte es alsbald wieder den zweig hinauf, um sich ernent beim Eigelege festzusetzen. Auch im Freiland haben wir einmal ein Weibchen über den Eiern sitzen angetroffen". There is no reported direct evidence of beneficial effect of this behaviour to the survival of the eggs, but it is evident that *P. itoi* females have gone a step further than the *Neodiprion* females to provide protection to her brood by staying over their eggs for a longer period (until larval emergence) and by using their wings spread open in display. Evidently more study is needed on *P.itoi* female's post-reproductive behaviour to understand its function. No other studied species of *Pachynematus*, among the 70 or so known, exhibits similar behaviour.

On the other hand, in the Temperate and Subtropical regions of the Southern Hemisphere (New Zealand, southern Australia, South Africa, Chile, Argentina, Uruguay and southern Brazil) the frequency of occurrence of maternal care in the Tenthredinoid sawflies is unknown as very few species have been studied biologically so far. However, three species of *Pseudoperga*, *P. lewisi* (Westwood), *P. guerini* (Westwood) and an unidentified species from Canberra, which are commonly misrefered in the literature as species of *Perga*, from temperate and subtropical southeastern Australia (from southern Queensland to South Australia, Victoria and Tasmania) have been found to exhibit very elaborate and prolonged maternal care behaviour.

Ever since the publication of Lewis' famous paper of 1836, *Pseudoperga lewisi* became the classical example of maternal care among the sawflies. Since then a number of other papers appeared dealing with the biology and specially the maternal care behaviour of this sawfly (Lewis, 1839; Brittlebank, 1888; Froggatt, 1890 and 1901; Blackbourn, 1930; and Norris, 1970). This sawfly has only one generation per year, the eggs being found in April (Autumn). Each female lays only 30-40 eggs in the leaf of an Eucalyptus species forming a compact cluster. The egg incubation period lasts about 30 days and the postreproductive female may live up to 48 days without feeding (see Brittlebank, 1888). Since finishing laying her eggs and until they hatch, the female remains seated straddled over her eggs with outstretched legs and partially open wings. The female continues to sit over her brood after her larvae emerge from the eggpod and follows the larvae from leaf to leaf as they migrate to new feeding sites (Lewis, 1836; Brittlebank 1888; Froggatt, 1901; Blackbourn, 1930; see also photograph of female sitting over her larvae in Norris (1970, figure 5.41).

P. lewisi females removed from their eggpod crawl back to sit over them again, but they can not distinguish their own eggs from non-related conspecific ones and readily accept to guard eggs which are not theirs (Lewis, 1836; Froggatt, 1901). When disturbed, the females never move away from over their brood and never fly, no matter how much disturbed they are (Lewis, 1836; Blackbourn, 1930), but rather they react with defensive or threatening displays and with aggressive behaviour. Blackbourn (1930) saw females reacting with a display of raising their bodies and opening their mandibles, Lewis (1836) observed females trying to bite any object approaching them, and Froggatt (1901) saw females reacting with a display in which the females turn their abdomens up, open their mandibles and vibrate their wings producing a buzzing sound. Lewis (1836) reported observing occasionally females deserting their own eggs to join a neighbouring female with eggs. The larvae are highly gregarious throughout their life. Lewis (1836) believed the main function of P. lewisi maternal care is to protect the brood from predators and parasitoids, and he observed that the female does not help the young larvae to emerge from the eggpod and to start feeding on the host leaf, and also that broods deprived from their mother at an early stage developed normally.

Only a short note has been published on the maternal care behaviour of Pseudoperga guerini. It is quoted here: P. guerini "may be seen tending its eggs or young larvae on sapling growth about March and April, but I once took an example similarly occupied at Ringwood, Victoria, in the middle of November" (F.E. Wilson, 1932). Morrow et al. (1976) gave further details on the biology of this sawfly, dealing with the larval gregarious behaviour. A third unidentified species of Pseudoperga from Canberra, A.C.T., Australia, also exhibits maternal care behaviour (see photograph of female sitting over her larvae, taken by Thomas Eisner, in Herreid II, 1977, figure 12.17). Biological information is available for only one of the remaining 6 species of Pseudoperga, P. belinda (Kirby), but only regarding its larvae and cocoons and nothing about its reproductive behaviour (see Raff, 1930 and 1934).

All the other known cases of maternal care in sawflies occur in the tropics of South America, West Indies and northern Australia and are confined to two families of sawflies only, Pergidae and Argidae. In Australia, another genus of Pergid sawflies besides Pseudoperga is known to exhibit maternal care: Philomastix which occurs in tropical northeastern Australia. Only two species have been described in this genus, P. nancarrowi Froggatt from north Queensland and P. macleaii (Westwood) in north New South Wales, but only the first has had its reproductive behaviour studied. See Froggatt (1901) for some information on the biology of the latter. The biology of P. nancarrowi was studied by Leask (1944a). As the maternal care of this sawfly which feeds on the compound-leaved wild raspberry, Rubus rosaefolius Sm. and R. hillii F. Muell, approaches closely to that exhibited by Dielocerus diasi, I shall quote Leask's observations more extensively: "In the middle of May, the adult deposits her eggs on the under side of the tip of the terminal leaf (= leaflet) of a composite stalklet (= compound leaf). Usually from 30 to 40 eggs are deposited in a close group placed athwart the midrib... After ovipositing, the female retires to the junction of that leaf (= leaflet) with its stem (= rachis) (Fig. A,1), where she remains with wings outspread, clinging upside down, the head invariably directed toward the centre of the plant (= leaf base). Several days later the eggs hatch, and within two days the tiny larvae have destroyed this terminal leaf (= leaflet). They proceed to crawl along the under side of the stem (= rachis); on reaching the adult's legs they cross to the upper side. When a few larvae have reached the first pair of leaves (= leaflets) making their way out of their tips, the female moves forward to mark the way, stopping just short of the stem junctions (= on the rachis where the first pair of leaflets branches off). As the next larva reaches her middle leg, it may stop as though sensing the appendage; then almost imperceptibly she moves that leg forward, thus assisting the larvae on to the junction, when it readily makes its way up the leaf stalk (= leaflet's petiole). Finally, the adult takes up her position on the junction (Fig. A.2) with her hind leg actually straddling two of the larvae, where she remains night and day, rain and fine until the larvae move forward to the second pair of leaves (= leaflets); she then waits on the second junction (Fig. A,3). When touched she shakes vigorously from side to side, as though to frighten off the intruder. When the three pairs of leaves (= leaflets) are eaten, the rapidly-growing larvae (Fig. B,4) and the adult (Fig. B,5) move down the plant, making towards its centre, the female now taking up her position on the junction of the branchlet (= compound leaf) with the main stem, there to await the move to the next branchlet. At this stage, or any earlier one, the female may die; six adults were observed on these food-plants, dead and fixed on the stem junctions (= on the rachis where leaflet pairs branch off), with larvae in various stages of development..... These observations cover eight individual adults examined for a period of fifteen days until violently inclement weather destroyed many insects" (Leask, 1944a).

Yet another genus of Pergid sawfly is known to exhibit maternal care behaviour: Syzygonia (also refered to in the literature as Bergiana), which occurs in tropical southeastern Brazil. There is only one species described, S. cyanocephala Klug which was studied biologically by Marques (1933). This sawfly attacks several species of Tibouchina (Melastomataceae), and lays its eggs in compact clusters of about 80 eggs on the underside of the host leaf in the base of the midrib. The egg incubation period lasts 10-12 days and the postreproductive females outlive the hatching of their eggs for a few days. The female remains over or near her eggs and young larvae, with her wings partly opened, and protects her brood against parasitoid wasps by vibrating her wings forcefully. I quote here a translation of the original description: "The female, after finishing the egglaying, remains positioned over her eggs (Figure A,3) or near them, where she stays until their hatching (Figure A,5). She does this to protect her eggs from the attack of certain microhymenopterans, their parasites. For, when the latter, in a slow and treacherous flight, try to approach the eggs, the female (sawfly) vibrates, with some energy, her wings, in order to repel them". The female, "when disturbed, has the habit of ejecting, through the anus, some quantities of a semi-pasty substance, of a light brown colour (meconium). And, although possessing relatively large wings, she rarely uses them, living, the few remaining days she has after laying her eggs, near her eggs or newly emerged larvae, to whom she dispenses careful protection" (Marques, 1933; see also Figure A,3).

Looking now at the Argidae, 10 species belonging to 5 tropical American genera have been reported to exhibit maternal care behaviour, but apart from the two species treated in the present study very little is known on their behaviour. Benson (1938a) recorded maternal care in three species from Brazil, Pachylota audouini Westwood, Digelasinus diversipes (Kirby) and Dielocerus formosus (Klug); but gave no detail of their behaviour and did not give the source of these observations either. He said that "the social habit of Dielocerus Curtis, Digelasinus Malaise and Pachylota Westwood remind one of Perga Leach (Pergidae)(meaning Pseudoperga Guérin); in all four genera the female sits over and protects her young, which, in the Argidae, finally build their cocoons massed together within a communal covering". And he further refered to

Pachylota as follows: "Larvae social, building a communal nest, the female sitting over and protecting them". The maternal care of Dielocerus diasi Smith has been studied in the present work (see also Dias, 1976).

Three brazilian species of Themos are known to exhibit maternal care behaviour: T. olfersii (Klug), T. vigilax (Malaise) and T.sp.n. (D.R. Smith, in prep.). All these species lay their eggs in compact circular clusters and the females sit astride over them. The behaviour of T. vigilax was briefly recorded by Malaise (1949): "both females were each sitting on the underside of a leaf, on which they had deposited 68 and 87 reddish yellow eggs respectively. Even in death the females tried to protect their eggs with their bodies. The new name vigilax alludes to their watching". One female T. sp.n. from Barueri, São Paulo (deposited in the Museu de Zoologia da Universidade de São Paulo) was collected by K. Lenko sitting on top of a compact egg cluster with about 80 eggs on a leaf of Luehea sp (Tiliaceae)(see D.R. Smith, in prep., and Dias, in prep.a). The maternal care behaviour of T. olfersii has been studied in the present work (see also Dias, 1975).

Finally, three species of Sericoceros from northern South America, Central America and the West Indies are also known or suspected to exhibit maternal care behaviour: S. alternator (Norton), S. gibba (Klug) and S. krugii (Cresson); but no detail is available for such behaviour in these species. Maternal care is suspected to exist in S. alternator in Guatemala due to Cameron's report of 1883: "Mr Champion sends along with the female a small bit of the leaf of an oak, on the lower side of which are arranged sixteen eggs in four rows. The eggs are about 1mm in length, of the usual shape, pinkish in colour, and are but slightly embedded in the leaf, from which they stand erect". S. gibba was found in Colombia sitting astride over her compact egg cluster on leaves of Triplaris sp (Polygonaceae). providing them with some protection but dying shortly after the eggs hatch (F. Schremmer, pers. information). Martorell (1941) recorded the maternal care of S. krugii in Puerto Rico as follows: "During oviposition the females do not move from the egg-mass, even if disturbed. Oviposition takes many hours and even after the last egg of a cluster is laid the females stay over the egg-mass as if they were brooding the eggs". This species lays only 15 to 40 large 2mm long eggs in compact circular clusters.

In all, 18 species of Tenthredinoid sawflies belonging to 10 genera in 4 families have been recorded so far exhibiting some kind of maternal care behaviour, most of them belonging to tropical species of Argidae and Pergidae. As most tropical sawflies are still waiting to be studied, it seems safe to assume that the actual number of sawfly species with maternal care is much higher than the above figure. In particular, the following species are strong candidates for having maternal care: the remaining species of Themos (9), of Pachylota (1), of Dielocerus (3), of Digelasinus (2), of Sericoceros (18), of Pseudoperga (6), of Philomastix (1), and the species in those genera closely related to those above mentioned, Topotrita (3), Mallerina (1), Parasyzygonia (2), and Incalia (3). These would represent another 49 species.

So far maternal care is known in 4 of the 10 subfamilies of Argidae (sensu Benson, 1938a)(Dielocerinae, Pachylotinae, Theminae and Sericocerini in the Sterictiphorinae) and in 3 of the 14 subfamilies of Pergidae (sensu Benson, 1938a)(Perginae, Philomastiginae and Syzygoniinae). However, as very little or nothing is known about the reproductive behaviour of the sawflies in most of the remaining subfamilies of these two families, it is not improbable that maternal care behaviour will also be found in at least some species in these other groups.

Judging by our present incomplete knowledge of the reproductive behaviour of Tenthredinoid sawflies, maternal care has evolved at least 9 times independently among the members of this group: once in the Diprionidae (some Neodiprion), once in the Tenthredinidae (some Pachynematus, in the Nematinae), 3 times among the Pergidae (Pseudoperga in Perginae, Philomastix in Philomastiginae, and Syzygonia in Syzygoniinae), and 4 times among the Argidae (Dielocerus and Digelasinus together in Dielocerinae, Pachylota in Pachylotinae, *Themos* in Theminae, and *Sericoceros* in the Sericocerini in Sterictiphorinae).

Out of the 18 species discussed above which are known to exhibit maternal care behaviour, 13 remain virtually unknown biologically, at least in terms of the adult reproductive behaviour. All that is known about them is them is that they have some kind of maternal care toward their eggs or eggs and young larvae, and in some cases something about the female positioning in relation to her brood is also known. Only 5 species are better known, although much still remains to be studied and understood about their maternal care: 2 Pergids from Australia, *Pseudoperga lewisi* and *Philomastix nancarrowi*, and 1 Pergid and 2 Argids from Brazil, *Syzygonia cyanocephala*, *Dielocerus diasi* and *Themos olfersii*.

In the following species the female's common egg-guarding posture is to straddle over them motionless, usually with wings partly opened: *T. olfersii*, *Sericoceros krugii*, *S. gibba*, *Syzygonia cyanocephala* and *Pseudoperga lewisi*. Most probably all the other species of *Themos*, *Sericoceros* and *Pseudoperga* also adopt the same posture. On the other hand, Leaf or Leaflet Base Vigilance Stance, where the female remains at the base of the egg-bearing leaf or leaflet and facing the petiole or rachis, is the female's common egg-guarding posture in *Dielocerus diasi*, *Philomastix nancarrowi*, *Neodiprion lecontei* and *N. nanulus*. Most probably the other species of *Dielocerus* and *Philomastix* also adopt the same posture. The information available for the other species is insufficient regarding this matter.

In the following species the female guards not only the eggs but also the young larvae for a few days up to 2 or 3 weeks: *Themos olfersii*, *Dielocerus diasi*, *Pachylota audouini*, *Syzygonia cyanocephala*, *Philomastix nancarrowi*, *Pseudoperga lewisi*, *P. guerini* and *Pseudoperga* sp. - Of these *T. olfersii*, *D. diasi*, *P. nancarrowi*, *P. lewisi* and *Pseudoperga* sp are known to have females which change their position in response to their larvae's movements from leaf to leaf to feed.

The following species are known to react with defensive displays and aggressive behaviours when disturbed: *T. olfersii*, *D. diasi*, *S.*

cyanocephala, P. lewisi and P. nancarrowi. No information is available on this matter regarding the other species. Only some of the displays exhibited by the above mentioned species have been recorded however. Thus, S. cyanocephala may buzz her wings (against approaching parasitoid wasps) and eject a jet of meconium; P. nancarrowi may shake her body vigorously from side to side (when touched); P. lewisi may raise her body while opening her mandibles, may attempt to bite any approaching object, and may raise her abdomen while opening her mandibles and buzzing her wings; while D. diasi and T. olfersii were recorded in the present work to react with at least 11 and 18 different displays, aggressive actions and changes in positioning, respectively.

Wings play the major role in most of the known displays exhibited by brood-guarding sawfly females, and most of the species known to exhibit maternal care have large conspicuous all black or yellowish infuscated wings or hyaline wings with dark transversal bands, which probably helps to increase the visual effectiveness of these displays.

The only parts of the body used by sawfly females to attack disturbing objects or animals are the wings and mandibles.

D. diasi has apparently a higher irritability threshold compared with T. olfersii, as a higher dose of stimulation is usually needed to trigger the defensive reactions of the former, specially in terms of tactile and substrate vibration stimuli. This is perhaps not surprising as D. diasi females are much more exposed, than those of T. olfersii, to strong wind for they live high up in the tree canopy, such that they are constantly subjected to substract vibration and tactile stimuli caused by the wind. T. olfersii, on the other hand, lives in hard leaves near the ground where she is not affected by the wind, where most substract vibration and tactile stimuli will probably be caused by other animals, potential predators. D. diasi females, however, were very sensitive to the buzzing sound produced by other nearby conspecific females, to which they reacted with different displays and changes in positioning. This might also apply to T. olfersii, but was not verified. Such behaviour certainly plays an important role in preventing newcoming females from selecting for their oviposition sites leaves too close to those already bearing eggs.

All the sawfly species known so far to exhibit maternal care have also aposematic colouration in the adult, involving different combinations of bright orange or red with or without parts in black or bluish black, and are therefore highly conspicuous specially against the green background of the host plant. Most probably these sawflies are also distasteful to predators in the adult stage. This was confirmed in this study for D. diasi, at least. The described defensive displays exhibited by these females help to increase the conspicuousness of their warning colouration to alert potential predators about their distasteful nature. As pointed out by Hamilton (1964), the behaviour of a postreproductive female must be entirely altruistic. Blest (1963) showed that whereas for cryptic palatable species it is altruistic for the adult to die soon after laying all its own eggs for this decreases the density of cryptic individuals, therefore minimizing the chances of some of them being discovered by a predator thus revealing the trick and exposing the other members of the population to the experienced predator, the opposite happens with the aposematic distasteful species. In the latter, it is altruistic for the adult to prolong its postreproductive life for this increases the density of aposematic individuals, therefore enabling postreproductive individuals to act as decoys, in place of prereproductive adults, for the naive predators so that they may learn the aposematic warning colouration (Blest, 1963). Therefore, by prolonging their postreproductive lives, aposematic sawflies may gain in inclusive fitness for increasing the safety of neighbouring prereproductive females, including their relatives, against certain predators. The habit of dead females remaining in the host canopy attached by their tarsal claws for several weeks, found in D. diasi, P. nancarrowi, T. vigilax and occasionally in T. olfersii, appears to be a further adaptation to prolong the presence of the postreproductive individuals near the prereproductive ones.

In fact, while most sawflies have edible adults which are much attacked by birds (see e.g. Carne, 1969; Verzhutskii, 1966;

Buckner & Turnock, 1965) and are short lived - usually less than 7 days - (see e.g. Gorske et al., 1977; Moore, 1962; Regas-Williams & Habeck, 1979; Tozawa, 1940; Verzhutskii, 1966), those which exhibit maternal care and are believed to be distasteful have relatively long adult postreproductive life in the female sex - between 2 and 7 weeks.

Most sawflies do not exhibit maternal care, for they have evolved toward delayed egg maturation, adult feeding, short adult life, eggs laid singly or in small groups and spread through a number of individual hosts, and solitary larvae. It is easy to see that in this type of reproductive strategy there is no room for maternal care. As mentioned earlier, all studied Cimbicids, most Tenthredinidae (except some Nematinae), and several Argids (many Arginae and Sterictiphorinae) share this strategy in broad terms. Maternal care behaviour will only pay for species with low adult mortality, adults which dispense feeding, compact egg clustering, high egg predation, and gregarious larvae.

Despite all similarities between the Symphyta and the Lepidoptera, only one case of maternal care is known among the latter: the Philippine butterfly Hypolimnas antelope (Cramer) lays up to 200 eggs in just one compact batch and protect them by sitting astride over them and displaying with her wings (Johnston & Medicielo, 1979). Most butterflies lay their eggs singly, with only a minority, mainly tropical, laying their eggs in large compact clusters (Labine, 1968).

6.C.4 MATERNAL CARE AND BROOD MORTALITY

Total mortality during the egg stage varies considerably from one locality to another and from year to year in the same species, but averages between 30 and 70% in the best studied species, e.g. 30% for Pristiphora erichsonii (Hartig) in Manitoba, Canada (Ives, 1976); 50% for Perga affinis affinis Kirby in New South Wales, Australia (Carne, 1969); 40% for Athalia proxima (Klug) in tropical India (Dhillon, 1966); 35% for Diprion pini (L.) in France (Geri & Dusaussoy, 1966) and Switzerland (Eichhorn & Pschorn-Walcher, 1976); 40% for Neodiprion sertifer (Geoffr.) in Switzerland (Pschorn-Walcher,

1970) and in Ontario, Canada (Lyons & Sullivan, 1974). There are, however, reports of lower rates of egg mortality in other species of sawflies, e.g. 7% for Pikonema alaskensis (Rohwer) in Minnesota, U.S.A. (Houseweart & Kulman, 1976). Rasnitsyn (1969) claims that in general egg mortality is below 20% among Tenthredinoid sawflies, and that reported instances of higher egg mortality were obtained only at times when a sharp decrease occurred in the sawfly population. The data quoted above indicates that this is not so.

Common mortality factors during the egg and early larval stages are: low temperature, desiccation, predation, parasitism, destruction by other phytophagous insects, destruction by conspecific larvae, leaf fall, fungal disease, failure to escape from the egg pocket, and failure to establish a feeding site. However, once the female has selected her egg-laying site and laid her eggs there is nothing she can do to protect her brood against low temperature, desiccation and leaf fall, except for covering her eggs with a protective secretion against the first two. But, at least theoretically, post-reproductive sawfly females could protect their offsprings against the other mortality factors mentioned above through maternal care of the eggs and young larvae.

Egg clustering results in a tendency for the young to die or survive together as a brood, i.e. the entire progeny either survives or does not. This was found with T. olfersii and D. diasi broods, specially during the egg and larval stages, where U-shaped survival frequency curves are the rule. Such contagious mortality increases the variance of the number of surviving offsprings per female and this may considerably reduce the effective population size (Crow & Morton, 1955). The two sawflies studied here, in fact, represent examples of the situation pointed out by the above mentioned authors as being rare where the entire lifetime progeny of a parent remains together until maturity.

What is the relative importance of each type of mortality factor during the egg stage of the sawfly?

Sawfly eggs, as those of other insects, are subject to the attack of many kinds of predators and parasitoids, but thanks to the adult female's effort in inserting the eggs inside the plant tissue, the eggs of most sawflies are not so exposed to predators and parasitoids as those of bugs, butterflies and moths, for example. It is not surprising to find, therefore, that egg mortality due to predation is rare among Tenthredinoid sawflies. The rare cases of predation on sawfly eggs reported in the literature involve the following predators: trips (Thysanoptera)(Marlatt, 1896; Knechtel, 1931); Pentatomid, Anthocorid and Reduviid bugs (Heteroptera) (Chapman, 1922; Dusaussoy & Geri, 1966; Sitowski, 1925); snakeflies (Megaloptera, Raphidiidae)(Lang, 1897); and birds (Carne, 1969). Lacewings (Neuroptera, Chrysopidae) are reported in the present work attacking T. olfersii eggs. No predation was observed on D. diasi eggs.

Egg predation has never been considered a major mortality factor for any of the best studied sawflies. It is unlikely, therefore, that egg predation would provide any strong selective pressure for the evolution of maternal care among Tenthredinoid sawflies, unless the predation rate increased significantly. It is worth pointing out that 7 of the 10 genera of sawflies known to exhibit maternal care are restricted to the tropics where predation pressure is known to be higher than in the Temperate regions (see e.g. Jeanne, 1980 regarding ants), and also that 4 of these genera (Philomastix, Syzygonia, Sericoceros and Themos) lay their eggs externally on the leaf's surface where they are much more exposed to predators than the eggs of most other sawflies which introduce their eggs totally inside the host plant tissue. So it seems possible that maternal care has only evolved in those groups of sawfly where for one reason or another egg predation assumed a major role in the total egg mortality. It has been shown in some other groups of insects that maternal care can greatly increase the survival of offsprings during the egg and early larval stages by giving them effective protection against predators (see e.g. Eberhard, 1975; Eickwort, in press; Wood, 1974-76). This hypothesis, however, would have to be tested in the case of the sawflies by removing the females in the field from a number of egg clusters, and the observed incidence of predation would be compared with controls where the females remained with their broods.

Most sawflies are subject to the attack of parasitoids during their egg stage. All records refer to parasitoids belonging to the order Hymenoptera. These involve the following families: Trichogrammatidae (e.g. Carl, 1972; Cheng & LeRoux, 1969; Scheibelreiter, 1973), Mymaridae (e.g. Marcovitch, 1916), Scelionidae (e.g. Scheidter, 1919) and most specially Eulophidae. Several genera of Eulophids have been recorded attacking sawfly eggs: e.g. *Achrysocharella*, *Dipriocampe*, *Derostenus* and *Closterocerus* attack Diprionid eggs (see Dahlsten, 1967; Eichhorn & Pschorn-Walcher, 1976; Krombein *et al.*, 1979; Pschorn-Walcher & Eichhorn, 1973); *Teleopterus*, *Closterocerus* and *Chrysocharis* attack Tenthredinid eggs (see Krombein et al., 1979; Scheibelreiter, 1973); *Achrysocharis*, *Chrysocharis*, *Cirrospilus* and *Ootetrasticoides* attack Argid eggs (Marcovitch, 1916; Regas-Williams & Habeck, 1979; Tozawa, 1940; and this study). Most of these parasitoids are not host specific but rather parasitize many insects from several different families and orders: e.g. *Chrysocharis* and *Cirrospilus* attack eggs and larvae of phytophagous insects, specially leaf-miners belonging to the orders Coleoptera, Lepidoptera, Diptera and Hymenoptera (Krombein et al., 1979). The genus *Chrysocharis* is here for the first time reported to attack the eggs of Argid sawflies.

The incidence of attack of such parasitoids varies from locality to locality and from year to year for the same species of sawfly, but it is generally low: e.g. 10% of *Arge similis* (Vollenhoven) eggs were attacked by *Ootetrastichoides habachi* Ii in Japan (Tozawa, 1940); 15% of *Diprion pini* (L.) eggs by *Achrysocharella ruforum* Krause in France (Geri & Dusaussoy, 1966) and in Switzerland (Eichhorn & Pschorn-Walcher, 1976); 2% of *Neodiprion fulviceps* (Cresson) eggs by *Derostenus* sp in California, USA (Dahlsten, 1967); 11% of *T. olfersii* eggs and 7% of *D. diasi* eggs by *Chrysocharis* sp in Central Brazil (this study).

The incidence of Eulophid parasitoids on sawfly eggs can be much higher, specially during outbreaks of the host sawfly: e.g. during outbreaks of *Diprion pini* in several parts of Europe, *Achrysocharella ruforum* has been reported destroying 80-100% (Besemer, 1942), 75% (Schwenke, 1964) and 94% (Urban, 1962) of the sawfly's eggs. In all these cases, the high incidence of the parasitoid brought about the termination of the sawfly outbreak. Therefore, these egg-parasitoids can act as delayed density-dependent factors, exerting their greatest influence during the breakdown phase of the host population (Eichhorn & Pschorn-Walcher, 1976; Pschorn-Walcher & Eichhorn, 1973). This phenomenon was observed, in a smaller scale, in the present study when an attempt to artificially increase the population of Dielocerus diasi at sites 14 and 15 in the Reserva Ecológica do IBGE failed due to a rapid increase in the incidence of Chrysocharis sp resulting in the total destruction of most egg clusters in both sites after an initial increase in the sawfly population.

The oviposition pattern of Achrysocharella spp and Dipriocampe spp attacking Diprionid sawflies which cluster their eggs is markedly aggregated, i.e. "once an egg-cluster of the host has been discovered by a parasite, the female of the latter usually stays with it until it has found most or all egg-bearing needles and laid an egg into virtually every host egg of all the egg-bearing needles discovered, as long as her egg supply is sufficient" (Eichhorn & Pschorn-Walcher, 1976). Therefore, most egg clusters of European Diprionid sawflies are either free of parasitoids or are heavily parasitized. This same type of aggregated oviposition pattern has been documented here for Chrysocharis sp attacking egg clusters of T. olfersii and D. diasi, and it is specially marked in T. olfersii with its smaller egg cluster size, where 100% parasitism is the rule for those egg clusters discovered by the parasitoid.

Therefore, egg parasitism can exert a strong selective pressure upon the sawflies, which, a priori, could lead to the evolution of maternal care behaviour in those sawflies which lay their eggs in cluster. However, the total inability of maternal care in T. olfersii and D. diasi to avoid or deter, not even partially, the attack of the Eulophid parasitoid on their eggs indicates that maternal care in these sawflies probably did not evolve as a defense against egg parasitoids. The failure of maternal care in these two sawflies is probably due mainly to the enormous 1,000 times fold difference in volume between the female sawfly and the very small 1.5mm long parasitoid, which makes it difficult for the sawfly to see and deter the parasitoid approaching. In the case of T. olfersii eggs, the female Chrysocharis sp can move about freely over the sawfly's egg cluster, directly under the sawfly's body, without the sawfly noticing it and there is nothing the sawfly can do about it even if it were aware of the parasitoid's presence. For the sawfly would have to move out from over the egg cluster and then turn around so that it could then threaten and attack the parasitoid with her mandibles and forewings. But field observations have shown that disturbed female sawflies may display in a variety of ways but never move out from their post over their egg cluster.

D. diasi's maternal care is also useless against the parasitoid as the eggs are distributed over a large area of the leaflet and the females spend most of their time at the base of the leaflet facing the petiole in the Leaflet Base Vigilance Stance. As all Eulophids, Trichogrammatids, Mymarids and Scelionids which parasitize the eggs of sawflies are very small, between 0.2 and 2mm long, there is no reason to believe that female sawflies in the past were more successful in protecting their eggs against these parasitoids than they are now. However, Marques (1933) reported that female Syzygonia cyanocephala Klug, which exhibits maternal care behaviour, were able to defend their eggs against a parasitoid wasp by buzzing their wings forcefully. Eberhard (1975), in the first critical study on the function of maternal care in non-eusocial insects, found that the net effect of the maternal care in the Pentatomid bug Antiteuchus tripterus against generalized egg predators is to greatly increase egg survival, but the net effect against two Scelionid parasitoid wasps is to decrease egg survival because these wasps rely on the adult bug's presence to find the eggs.

There is no evidence that brood-guarding female sawflies can help their larvae to emerge from their egg pocket or to establish their feeding site. There is also no evidence that they can protect their brood against desiccation, heavy rain and fungi. There is also no evidence that they may help to prevent larval dispersal for their gregarious larvae are strongly attracted to each other and do not disperse in the absence of the female.

Critical studies are needed to enable us to understand the function of maternal care in the sawflies, but available information indicates that its function in the sawflies may be to: (1) protect eggs and young larvae against predators; (2) protect neighbouring related adult females against predators through aposematic warning; and (3) attract other conspecific females to the same chosen host, but at the same time prevent other egg clusters from being laid on the same compound leaf or shoot.

CHAPTER 7. LARVAL GREGARIOUSNESS

MATERIALS AND METHODS

Larvae of all instars were fixated in Dietrich Solution and later dissected under the microscope. Drawings were made with a camera lucida attached to the microscope and the measurements were made with an ocular micrometric scale.

Larval groups were studied mainly in the field, but when convenient, the larvae were transferred to lower branches and shrubs to make observations easier. This applies specially to D. diasi larvae.

Larvae were marked individually with coloured enamel dots on the top of their heads for some observation sessions (acrylic dyes and coloured strings were found to be unsuitable). Larval behaviour was recorded in notebooks, with stopwatch, time tables, photographs and specially time-lapse cinematography. Simple experimental manipulations (see text) were done to test larval defensive reactions and spinning behaviour.

The mortality of larval sib-groups was obtained by directly following the development and survival of marked groups in the field in completely natural situations at daily or three times a week intervals.

A heavily infested tree (no. 3/2) was chosen for a detailed study of the spatial distribution and mortality of cocoons within one tree. The tree is located at the study site 3 at the University of Brasília campus, just beside a paved road, in an area of slightly disturbed Cerrado vegetation. It is a mature, medium sized tree with about 10 metres in height and 50cm in trunk diametre, and a typical S. aureum habitus of straight trunk and branches which branch off at all levels from 1 metre above the ground upward (Figure 3.6). This tree was first discovered in September of 1970 and has been under observation periodically ever since. In 1970 it was already heavily infested with about 150 cocoon masses of all sizes and ages on its trunk and branches.

In December 1978, all the cocoon masses were removed from this tree, including those that were still found on the ground around the tree trunk. In all, 628 cocoon masses of all ages, comprising about

20,000 individual cocoons, were found attached to the tree's trunk and main branches. The cocoon masses were removed in 4 different height groups: 6 to 4 metres above the ground, 4 to 2 metres, 2 to 0 metres, and those found on the ground. Each of these groups was divided into 3 gross age classes based on the external aspect of the communal covering envelope: (1) NEW COCOONS (paper-like top layer partially intact, white); (2) OLD COCOONS (paper-like top layer partially destroyed, gray); (3) VERY OLD COCOONS (paper-like top layer missing, sponge layer and cocoons dark gray, covered with moss and with marks of burnings). In all, 10 lots were thus obtained (all the cocoons found on the ground fell into one same lot: very old). A detailed description is given for 4 of these lots: 6 to 4 metres NEW, 6 to 4 metres OLD, 4 to 2 metres NEW, 4 to 2 metres OLD, with a total of 11,395 cocoons grouped into 359 cocoon masses. Among the very old there are 27 cocoon masses which were removed from the tree in September of 1970 and in August of 1972 (they were new by that time) and reared in the laboratory to record the emergence of adult sawflies and parasites.

Cocoon masses were examined and measured after the removal of the communal covering. The number of cocoons per cocoon mass was then obtained by direct counting as estimates based only on the overall size of the mass gave imprecise results.

Through repeated and careful examinations of the contents of closed and opened (occupant emerged) cocoons of D. diasi, a correlation was established between the characteristic remains and exit openings of the sawfly (both sexes easily separable) and its parasitoids, predators and commensals. Thereafter, data on the incidence of the different parasitoids, predators, commensals and survival of the adult sawfly through the cocoon stage was obtained by examination of the characteristic exit openings only. In cases of doubt, the contents of the cocoons were checked.

7.A+B DIELOCERUS DIASI AND THEMOS OLFERSII

7.1 LARVAL DESCRIPTION

The first instar larvae of Dielocerus diasi hatch from the egg weighing 2.33mg in average (N = 12 larvae of both sexes), are about 4.6mm long and have a maximum head width of 0.9mm in average (N = 34 larvae of both sexes). The body (Figure 7.1) is light green covered with many irregular black plates, most of them with one or more pointed conical tubercles, each ending with a short seta. Most of these plates are on the dorsal side of the body. Each abdominal segment has three transversal rows of black plates. The last tergum is covered by a large brown plate and armoured on the edge by a row of 10 stout black pointed tubercles. Four small prolegs are present on abdominal segments 3 to 6. The uropod is large and covered with short bristles. The thoracic legs are large, brown coloured, 5-segmented, covered with a few large setae, and each ends with one large curved sharply pointed claw and an equally large fleshy lobe.

The head (Figure 7.2) is round, mostly brown coloured, but paler on the front and ventral sides. It is covered with small setae, longer and denser between the antenna and the mandible where about 10 large setae are found on each side. The eye is large, round and black, and is surrounded by a circle of some 30 medium sized setae. The antenna has a single conical segment. The clypeus is slightly emarginated in the centre and has 2 setae on each side. The labrum has a deep central emargination and also 2 setae on each side, and its inner edge is covered with a row of small hairs.

The mandibles have oneseta each, have dark brown tips and are slightly asymmetric. The left mandible has 5 marginal teeth, whereas there are only 4 teeth on the right one. The 3 anterior teeth in both mandibles have each an inner longitudinal carena. The middle tooth of the left mandible has a particularly large and toothed carena. The maxillary palps are 4-segmented, and the labial palps are apparently 2-segmented. One small seta is present on each of the following segments of the maxilla: second segment of the palp, palpifer and stipes. The lacinia has about 5 strong spines.

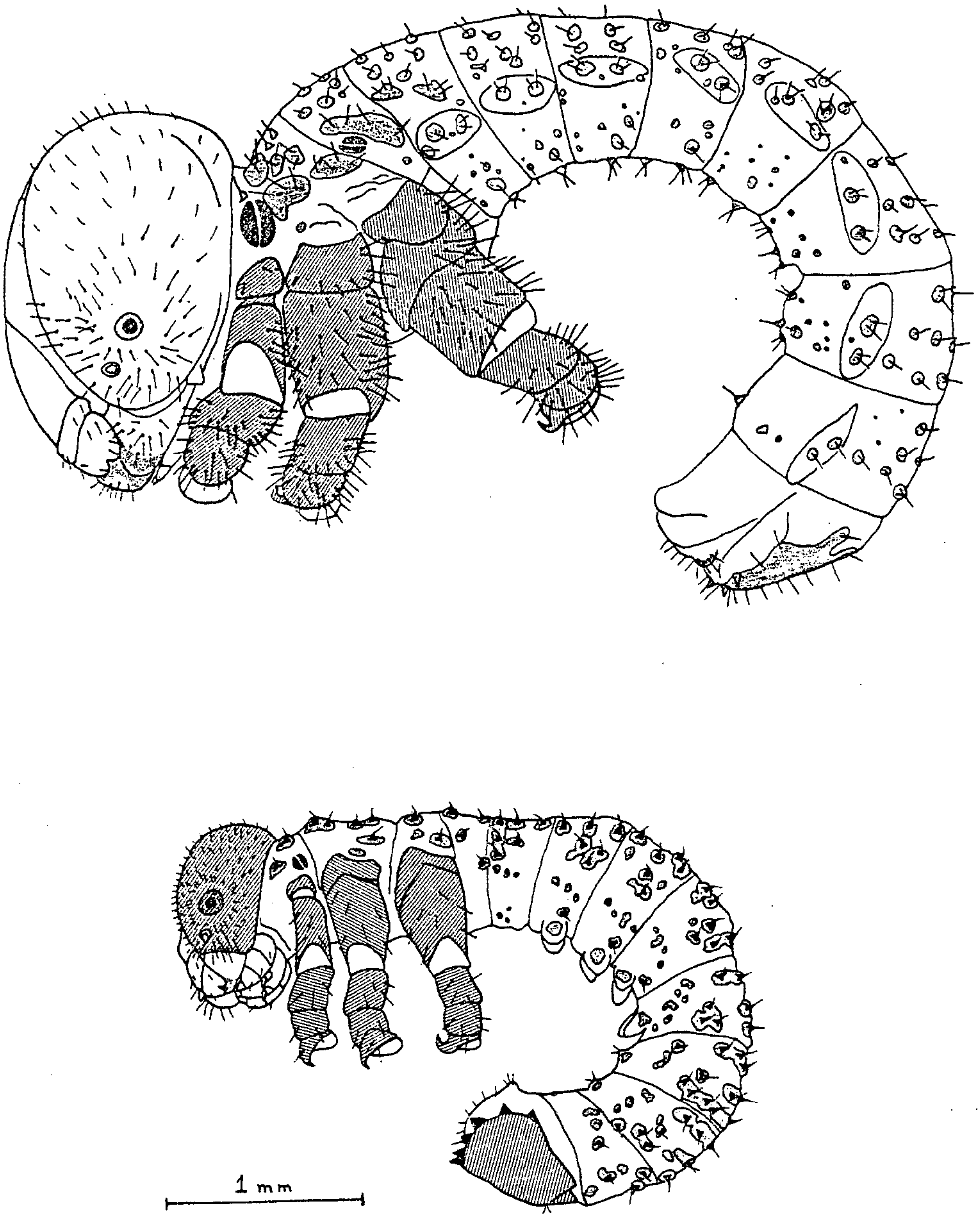


FIGURE 7.1. First instar larvae of *Themos olfersii* (top) and *Dielocerus diasi* (bottom). 25 X natural size.

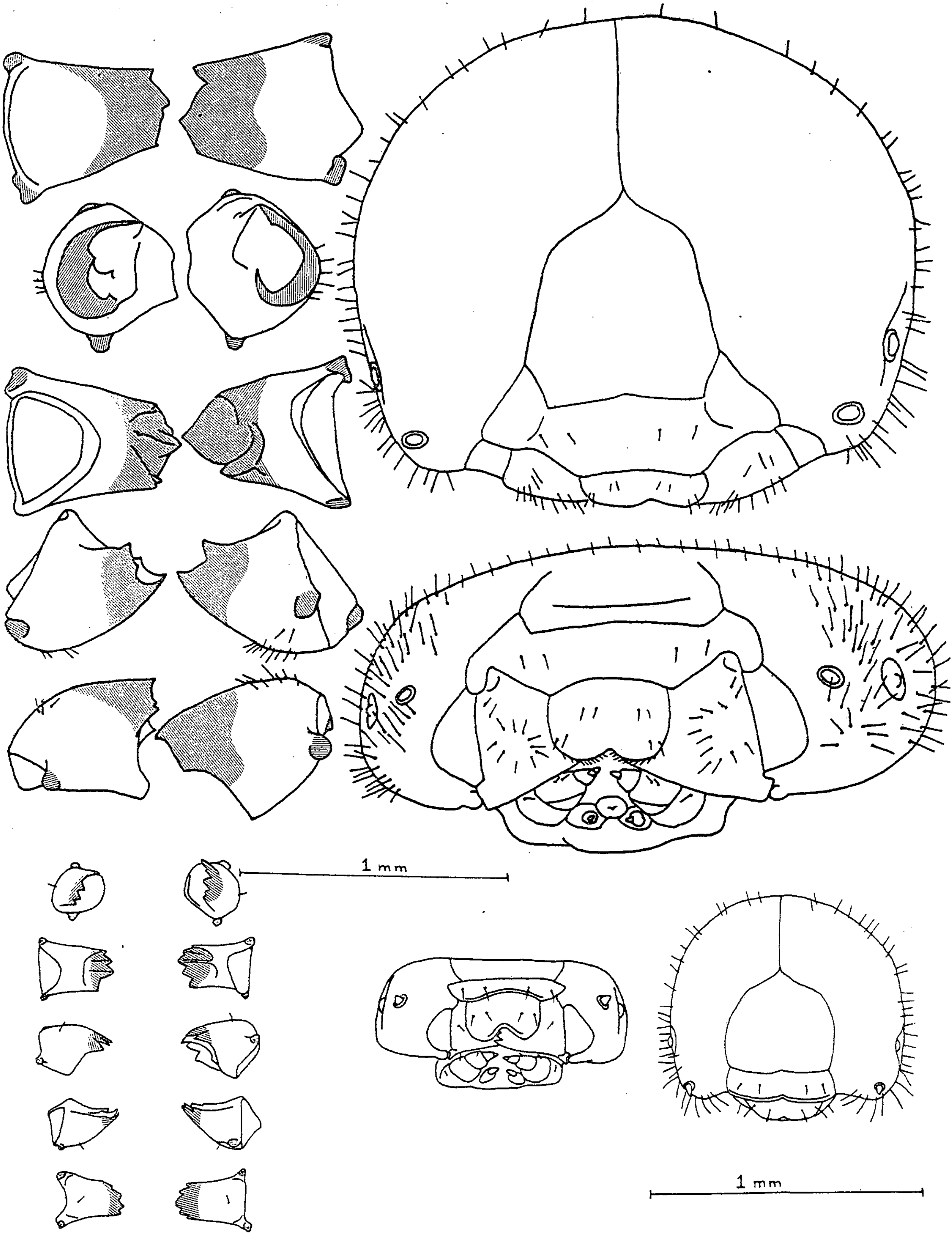


FIGURE 7.2. Front and vental view of head of the first instar larvae of *Themos olfersii* (top) and *Dielocerus diasi* (bottom). On the left different views of right and left mandibles of *T. olfersii* (top) and *D. diasi* (bottom). The orientations of the mandibles are, from top to bottom , for *T. olfersii*: ventral, distal, inner, anterior and posterior; and for *D. diasi*: distal, inner, posterior, anterior and ventral. 50 X natural size.

Larvae of the second instar onwards are similar to the first instar but have red head, a row of three groves on the prothoracic coxa and 12 tubercles on the supra-anal plate. Larvae of the third instar onwards progressively loose the brown colour of the supra-anal plate and thoracic legs. The antenna is also progressively flattened. The last two instars have a fifth proleg on the seventh abdominal segment. The head of the last instar differs from all the others in having a spotted pattern of red dots on an orange background on the front and top. The last instar larva has been described by D.R. Smith (1975).

The first instar larvae of Themos olfersii hatch from the egg with a very large size compared to Dielocerus (Figures 7.1 and 7.2). Their body is about 7.0mm long (only 1.5 times that of Dielocerus), but their head is much bigger: maximum width = 2.0mm (average of 51 larvae of both sexes)(2.2 X bigger than Dielocerus), frontal area = 3.14mm^2 (4.9 X bigger), volume = 3.14mm^3 (12.6 X bigger), mandible length = 0.68mm (2.5 X bigger), mandible base width = 0.58mm (2.4 X bigger), mandible ventral area = 0.25mm^2 (5.0 X bigger), mandible volume = 0.06mm^3 (15.0 X bigger), distance between articulation joints of the two mandibles = 1.07mm (2.4 X bigger). The body of Themos larvae is yellowish green and covered with numerous small brown plates, each with one or more tubercles, each ending with a strong seta. These brown plates are found all round the body, even on the underside. These plates are larger on the thorax. Each abdominal segment has three transversal rows of these conical plates. The plates on the dorsum have only one tubercle and seta, but those on the side of the ventre of the body have usually 2 to 4 tubercles and setae. The larger tubercles have only very small seta on their top, but have several long setae around them. The last tergum has less brown colour and only 4 to 6 strong tubercles on its edge, but there are several long hairs there. The uropod is big and has a large number of setae around the anus. There are no prolegs in the abdomen. The thoracic legs are very large, 5-segmented, brown coloured, and have a great number of long stiff setae. Each leg has one curved sharply pointed claw and a large fleshy lobe.

The head (Figure 7.2) is round, orange in colour, and covered with hairs. The hairs are more abundant around the eyes and antennae. The eye is very small and flattened. The antenna is single segmented and also flat. The clypeus is broad, slightly U-shaped and has two setae on each side. The labrum is strongly emarginated in the centre and has four setae on each side. The inner lower edge is covered with a thick row of small hairs. Each mandible has about 12 setae. The mandibles tips are dark brown. There is some asymmetry between the two mandibles. Both mandibles have only 3 teeth, but both lateral teeth of the right mandible are bifid. The right mandible also has a strong central carena on the inner side of the central tooth, ending with an inner tooth. The maxillary palps are 4-segmented, and have two setae on the second segment. The palpifer and stipes have one seta each. The galea is bare, conical and the lacinia has several long strong apparently unbranched spines. The labial palps are 3-segmented.

7.2 LARVAL SEXUAL DIMORPHISM AND GROWTH

Larvae of both species since hatching exhibit a clear size dimorphism, the females being larger than the males (Figure 7.3). This difference increases as the larvae grow. Last instar Dielocerus female larvae weigh twice as much as their cohort males: 692mg fresh weight in average (N = 20 larvae) as compared to 345mg fresh weight in average for the males (N = 20 larvae). At the same time the head volume of last instar female larvae is 1.7 times larger than in males: $22m^3$ against $13mm^3$. But the head width in females is only 1.2 times larger than in males: 3.86mm against 3.26mm (Table 7.I).

Dielocerus larvae go through seven instars (Figure 7.4), with an average increase in head width of 30% in each molt except the last which has an increase of only around 10% (Table 7.I). The overall increase in head width is about 4 X in females and 3.7 X in males. At the same time there is an overall 300 fold increase in weight in female larvae and only 150 fold increase in male larvae. Looking at the head volume there is a 80 fold increase in females and only 50 fold in males. The only instars to superimpose in terms

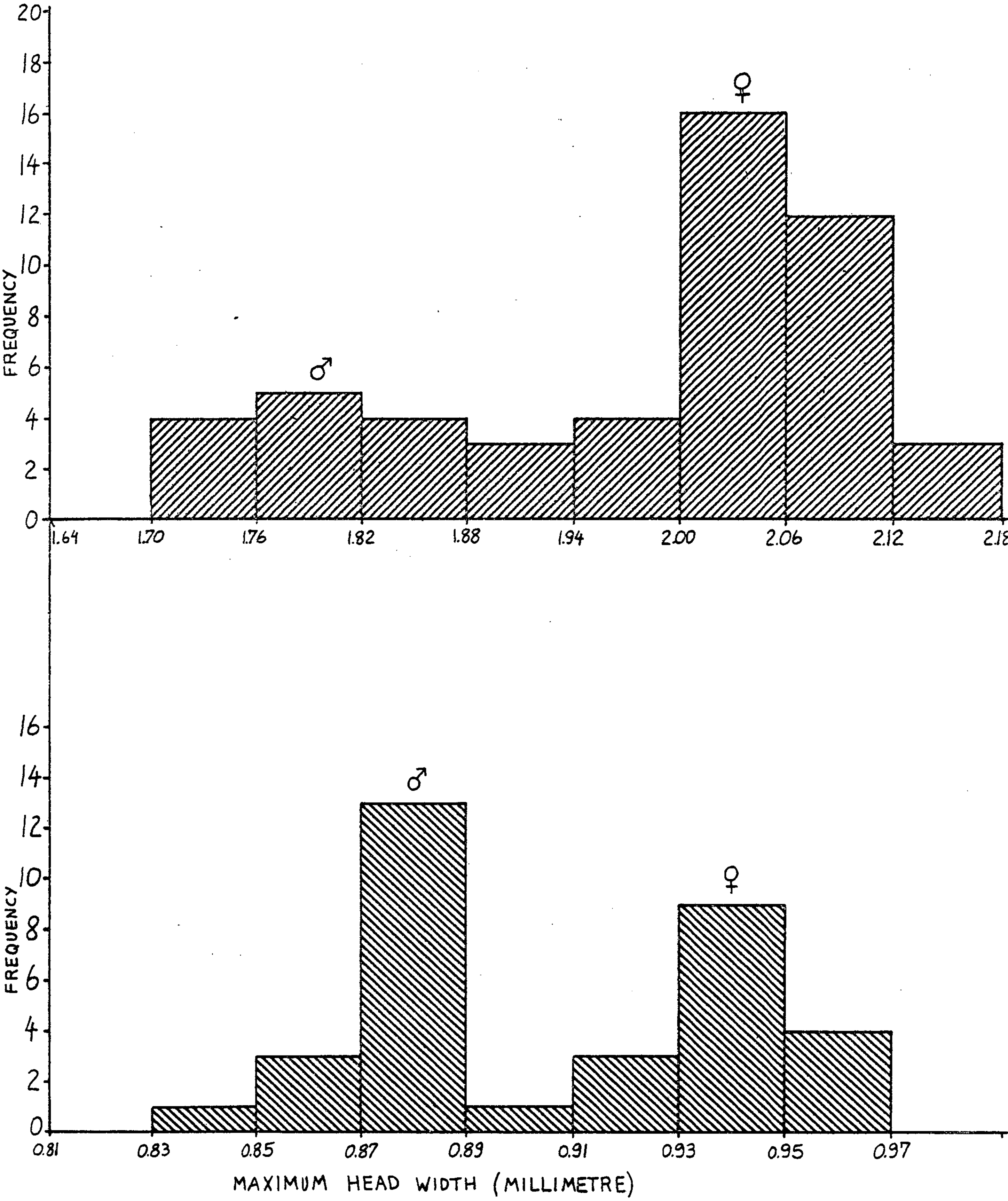


FIGURE 7.3. Frequency distribution of maximum head width of first instar larvae of Themos olfersii (top) and Dielocerus diasi (bottom) showing sexual dimorphism in size. N=51 larvae for T. olfersii and N=34 larvae for D. diasi.

FIGURE 7.4. Larval instars of *Dielocerus diasi*. Each frequency unit corresponds to 4 specimens. No quantitative measurements were made for the third instar. N=254 larvae.

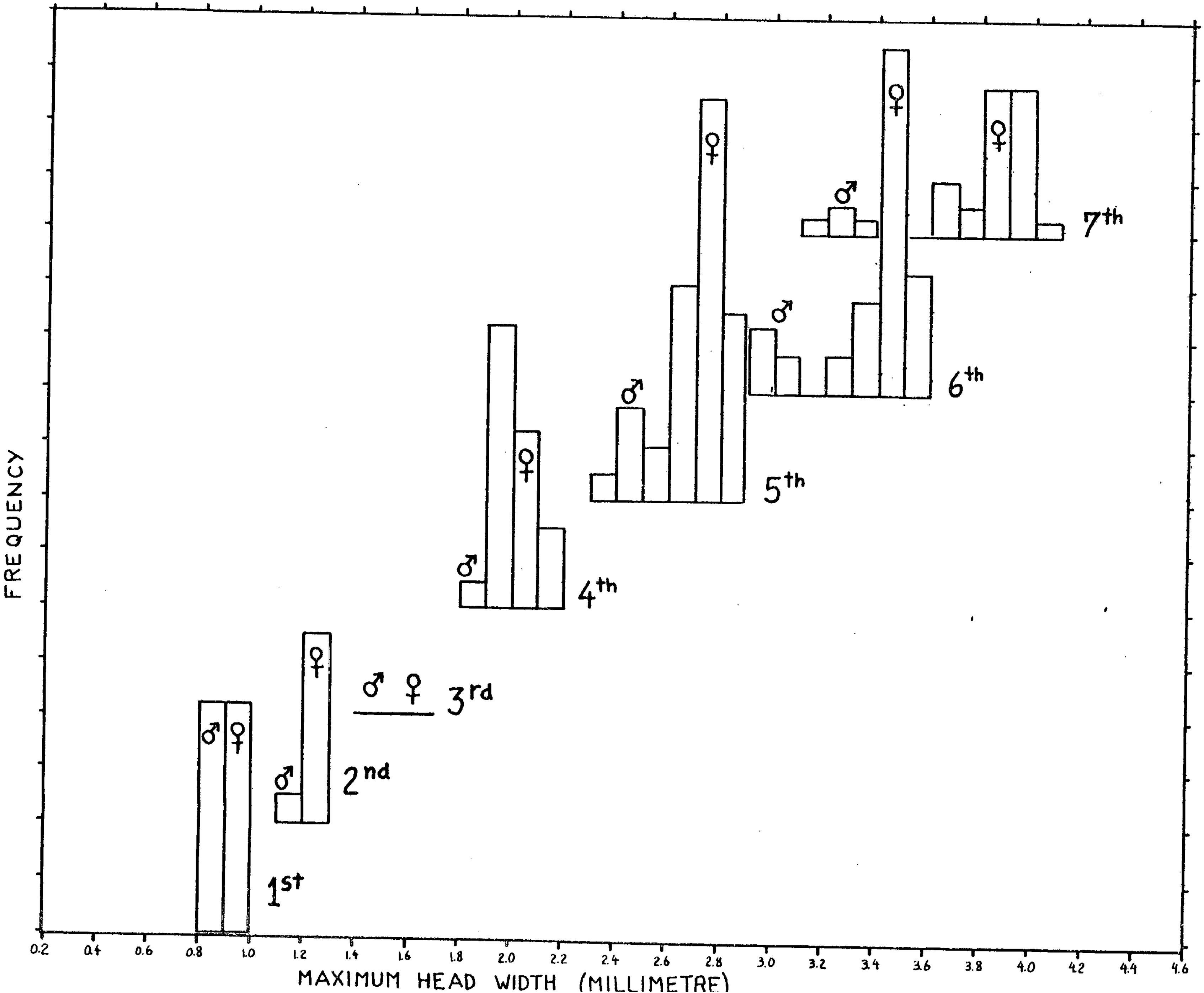

FREQUENCY
MAXIMUM HEAD WIDTH (MILLIMETRE)
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
3.0
3.2
3.4
3.6
3.8
4.0
4.2
4.4
4.6
♂ ♀
1st
♂
♀
2nd
♂ ♀ 3rd
♂
♀
4th
♂
♀
5th
♂
♀
6th
♂
♀
7th

TABLE 7.I

Larval instars of *Dielocerus diasi*, indicated by the maximum head width in millimetres of 254 larvae.

	LARVAL INSTARS													
	FIRST		SECOND		THIRD		FOURTH		FIFTH		SIXTH		SEVENTH	
	MALE	FEMALE	MALE	FEMALE	MALE	FEMALE	MALE	FEMALE	MALE	FEMALE	MALE	FEMALE	MALE	FEMALE
MEAN	0.88	0.95	1.19	1.27	1.50	1.60	1.91	2.04	2.47	2.74	3.00	3.44	3.26	3.86
STANDARD DEVIATION	0.02	0.02	0.04	0.01	-	-	0.05	0.07	0.07	0.07	0.04	0.08	0.08	0.12
MINIMUM	0.84	0.92	1.14	1.25	-	-	1.81	1.94	2.34	2.59	2.94	3.28	3.16	3.61
MAXIMUM	0.91	0.97	1.23	1.30	-	-	1.94	2.19	2.56	2.84	3.06	3.59	3.35	4.07
SAMPLE SIZES	18	16	4	13	1	1	9	33	11	62	8	45	4	29

The errors for the measurements are: ±0.01mm for the first and second instars, ±0.02mm for the fourth, fifth and sixth instars, and ±0.03mm for the seventh instar.

of head width are the last two where sixth instar female larvae and seventh instar male larvae partially overlap. But they can be readily separated by the colour pattern of the head. The last instar larvae of *T. olfersii* and *D. diasi* reach, respectively, a final length in the female sex of about 40mm and 32-35mm, and in the male sex of about 25mm and 25-29mm.

7.3 LARVAL COHESIVENESS

The larvae of both species are gregarious throughout their entire feeding stage. *Dielocerus* larvae in the early stages of development feed together in just one leaflet. But as they grow bigger they can not accommodate themselves in just one leaflet any more, and have therefore to spread among several neighbouring leaflets of the same compound leaf. *Themos* larval groups being much smaller always manage to feed together in just one leaflet. The larvae only leave the host plant canopy for cocooning. There is no migration from one host plant to another, even when the host is too heavily infested and the food supply is insufficient. The number of larvae per group varies greatly in both species. This is due to several causes: the great variability in the number of eggs per cluster and in the egg and larval mortality and also the coalescence of larval groups. It is common, specially in *Dielocerus*, for two or three groups of larvae to coalesce and thereafter feed and move together in the more heavily infested host plants. Even groups which are in different stages of development readily coalesce when they meet. Mixed groups of first or second instar larvae with large last instar larvae are commonly found. I never found *T. olfersii* larval groups with more than about 50 larvae. Most larval groups of *T. olfersii* and most young groups of *D. diasi* larvae were sibs-only groupings.

The larvae of both species consistently ignore suitable empty space available along the leaflets margins and pack tightly one against the other either one after the other forming compact queues or side by side forming compact circular masses. No larva moves away from her group for more than a few centimetres. Larvae left alone for some minutes soon stop feeding and start moving about, only stopping after coming close again to other conspecific larvae. Sib-larvae almost always remain together after migrations from one feeding site to the next. The only occasions observed when sib-larvae split during migrations were when they came into contact with another larval group while on the move: in most cases all the sib-larvae joined the second group of larvae, but in a few cases only part of the sib-larvae did so while the rest established themselves in a separate feeding site.

7.4 LARVAL MOVEMENTS

The larvae of both species use only their thoracic legs to hold to the host leaflet while feeding, three legs on each side of the leaflet along its edge in a horse-riding fashion. The abdomens are always kept arched back in a S-shape (Figure 7.12) or curved laterally and hidden on the underside of the leaflet (Figure 7.16). The abdominal prolegs are not utilized to make additional grips by _D. diasi_ larvae while moving during feeding bouts (see below).

However, in all other situations the larvae of _D. diasi_ make much use of their abdominal prolegs and uropod as gripping aids. The larva bends its abdomen around the edge of the leaflet, leaf rachis, stem or companion larva, gripping her support firmly with the tip of her abdomen and prolegs, as a prehensile tail. Once the abdominal grip is established the larva may set free the grips made with her thoracic legs, move her body forward a little and establish new grips with her thoracic legs slightly forward than before. She then releases her abdominal grip, pulls her abdomen slightly forward and establishes a new abdominal grip forward, and so forth (Figure 7.5). She also uses her abdominal grip to enable her to change direction along the leaflet edge or along the rachis or stem (Figure 7.5). Moulting _D. diasi_ larvae also use their abdominal grip to attach themselves to a twig or to the abdomen of another conspecific larva (Figure 7.6). _D. diasi_ larvae, therefore, possess a true prehensile abdominal tail. _T. olfersii_ larvae, on the other hand, lack such prehensile abdomen and merely bend their abdomen sideways when moving, without using them to grip the substrate.

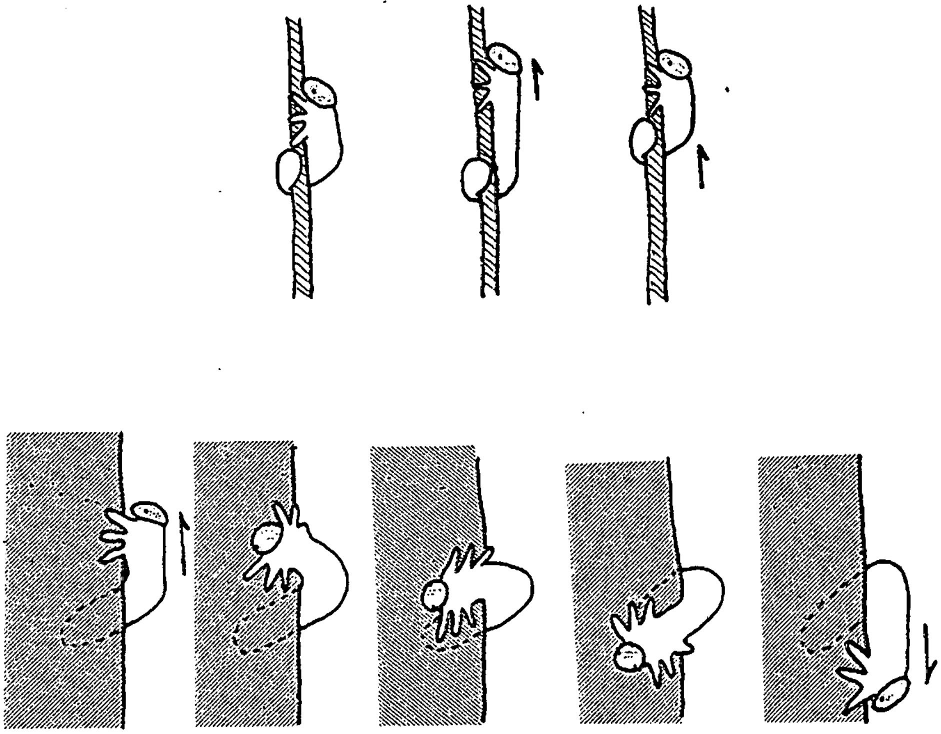
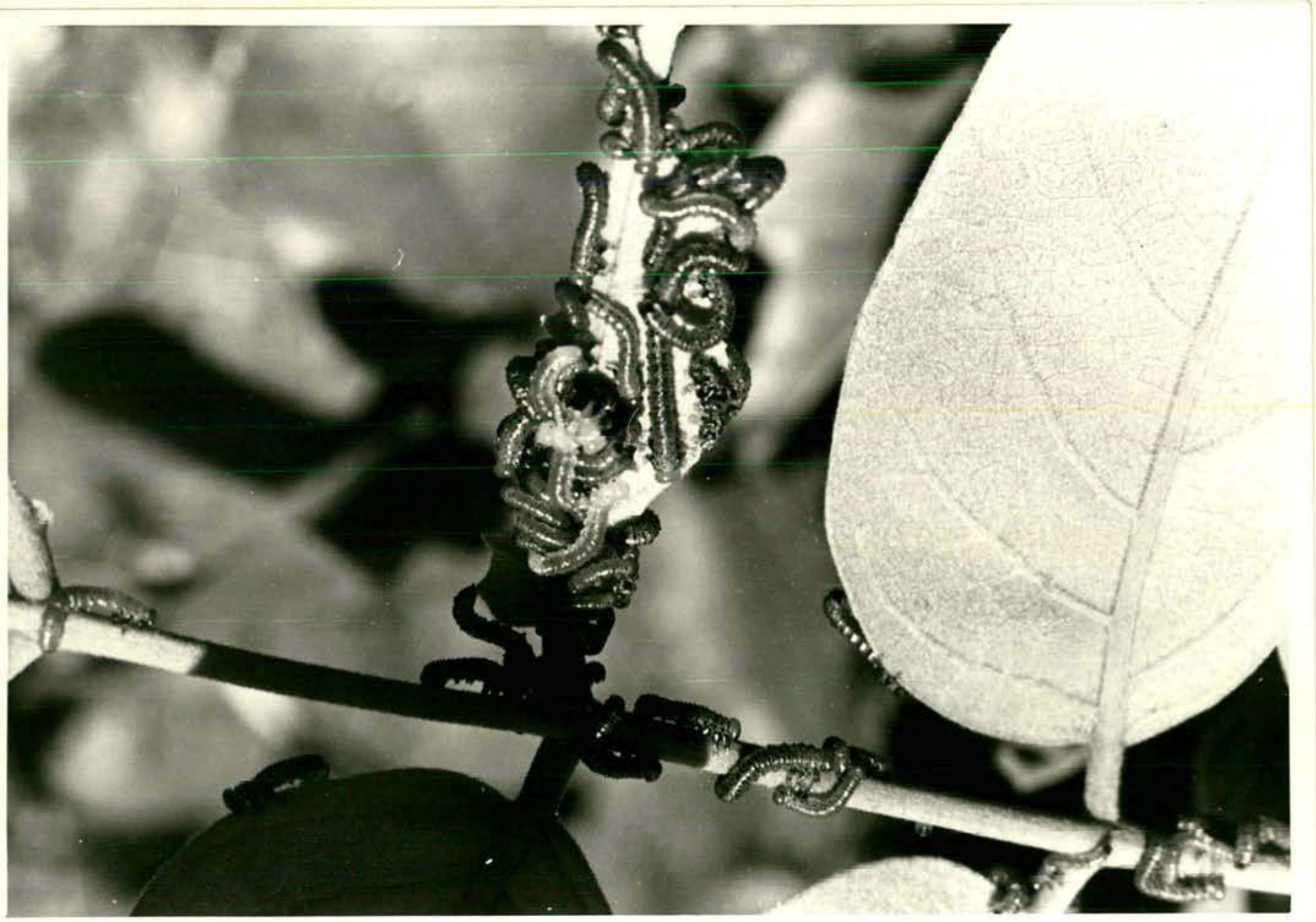


FIGURE 7.5. *D.diasi* larvae utilizing their prehensile abdomen to move along the twig (above) and turn 180° along a leaflet edge (below) (diagrammatic).

FIGURE 7.6. Dielocerus diasi larvae migrating from one feeding site to another. Note the use of the abdomen to grasp the twig.



When moving from place to place the larvae of both species always avoid the flat surfaces of the leaflets. They always move along the leaflet edge, rachis and stem where they can get a better grip, and they very often crawl over the bodies of the other larvae in the group (see below).

T. olfersii larvae only move to a new compound leaf after eating all the leaflets in the compound leaf they are in. They usually move to the nearest leaf when looking for a new feeding site. D. diasi larvae, on the other hand, frequently abandon a compound leaf after eating only the apical 2 or 4 leaflets leaving the basal leaflets either intact or just partially eaten, specially during their earlier stages. Older larval groups in heavily infested trees, frequently return to these partially eaten compound leaves and finish eating them. The migrations of D. diasi larvae from one compound leaf to the next feeding site are not randomly made but follow a typical pattern: after feeding on a number of leaflets in one compound leaf, the larvae migrate together down the leaf's rachis until they reach its base at its junction with the branch, and by climbing this branch they reach the next or the following next compound leaf along the branch, climb the rachis of the said compound leaf and feed on some of its leaflets starting from the youngest ones at the distal end of the rachis and then moving towards its base. This pattern is repeated until they finally reach the uppermost and youngest compound leaves at the distal end of the branch. Then they migrate all the way down this branch without stopping at any missed compound leaf until they meet a junction with another major branch which they climb until they reach its lowermost compound leaf and start feeding on its apical leaflets. The pattern then repeats itself again. Older larvae, however, do not follow so strictly this pattern.

When migrating towards a new feeding site, the larvae of D. diasi keep close together but do not maintain prolonged contact with each other and do not move consistently in the same direction. As the whole group progresses forward, all the larvae keep moving back and forth within it in an apparently disorganized fashion and with no apparent constant leader larvae. The larvae apparently take turns in the role of leading larvae of the marching group, each one advancing yet further along the rachis or branch for a few centimetres but then turning back to the middle or back of the group. The moving larvae apparently leave behind a chemical trail, as larvae which are sometimes left well behind the rest of the group are able to find and rejoin the rest of the group dozens of minutes later by following exactly the same track taken by the rest of the group earlier (Figure 7.6).

7.5 LARVAL DEFENSIVE BEHAVIOUR

The larvae of both species react readily to visual and tactile stimuli such as abrupt movements of an object or hand at less than 1m from them, an insect flying past them at close range (including adult female sawflies of the same species), the approach of an insect crawling on the leaf near them, a sharp knock on the branch where they are feeding, and being touched by an object or animal. Their first and most common reaction to these stimuli is to exhibit a defensive display in which all the larvae in the group lift their abdomens all the way up until they are upright or slightly forward and then lower them back to their original position. This abdomen movement is done by all larvae in the group at the same time, synchronously. Once stimulated the larvae stop feeding but do not lift their heads or move their thoracic legs' grips. During this display, the shiny black spot which the larvae of both species have on the dorsum of the last abdominal segment becomes very evident enhancing the larva's conspicuousness. I shall coin this the "Synchronous Abdomens Up" display.

The two species differ in some details of this display. _T. olfersii_ larvae maintain their abdomens upright for several seconds and then slowly lower them back to their original position, and they lift back their abdomens every time the stimulus is repeated, but when much disturbed they maintain their abdomens upright for longer periods of time and eject a large drop of a yellow viscous liquid from the tip of their abdomen, supposedly repellent to the other animals (Figure 7.7). The drop of viscous liquid usually remains attached to the tip of the larva's abdomen for a long time. D. diasi larvae, on the other hand, lift their abdomens abruptly and less than a second later lower them back only to lift them abruptly again, without being further stimulated, maintaining them erect this time for a longer period. They will repeat their display as many times as they are stimulated. Younger D. diasi larvae exhibit a fast abdominal movement and maintain their abdomens straight upright, whereas the older larvae exhibit a slower response and maintain their abdomens inclined backwards and curved at the end. Only if they are much disturbed by touching do D. diasi larvae eject a large drop of a yellow viscous liquid from the tip of their abdomen, supposedly repellent to other animals (Figure 7.8). The drop of viscous liquid usually remains attached to the tip of the larva's abdomen for a long time. D. diasi last instar larvae reacted to having their abdomens pinched with human fingers or forceps by discharging a strong jet of the yellow viscous fluid through their abdomen tip (Figure 7.9).

The larvae of both species also react to being touched on their heads by lifting their abdomens and arching them forward over their thorax until the tip of their abdomens touch the larvae's heads. With their abdomen's tip, then, they try to hit forcefully the offender. At this moment they usually eject a drop of the yellow viscous liquid and attempt to hit the offender with it (Figure 7.9). I shall call this the "Abdomen Forward" defensive reaction. D. diasi are more active in the use of their abdomen during this reaction than T. olfersii larvae.

Young T. olfersii larvae occasionally react to touching stimuli by releasing their grip on the host leaflet and dropping to the ground, while old T. olfersii larvae sometimes react to touching stimuli by rolling their body laterally.

T. olfersii larvae react to bad weather conditions such as heavy rains and strong winds and occasionally to darkness by aggregating tightly on the underside of the leaflet forming a compact mass, with

FIGURE 7.7. Defensive display of *Themos olfersii* larvae. Note the dark spot and drop of defensive liquid at the tip of their abdomens.

FIGURE 7.8. Defensive display of *Dielocerus diasi* larvae. Note the dark spot at the tip of their abdomen.

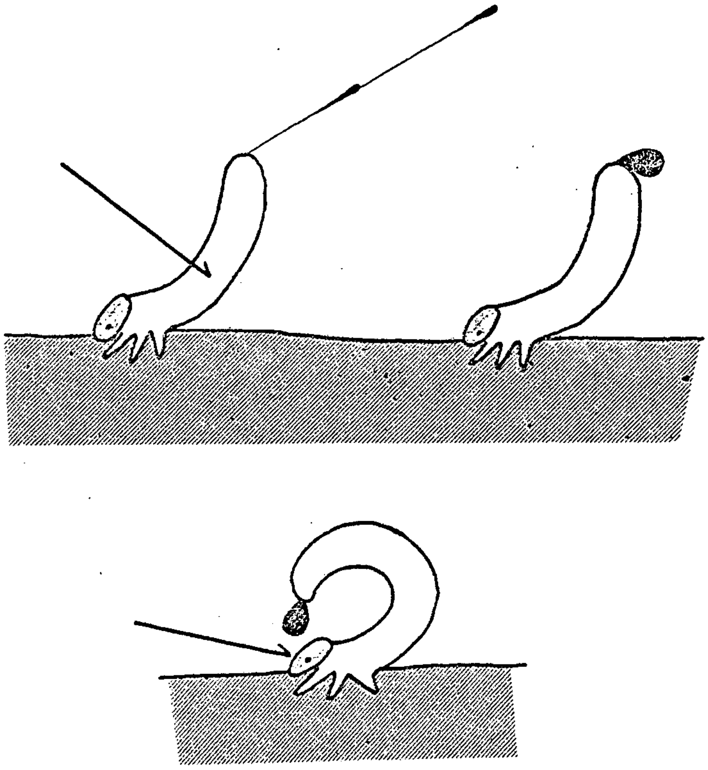


FIGURE 7.9. Typical larval postures for both species when ejecting the defensive liquid at the tip of their abdomen.

their heads facing outwards and their abdomens arched backwards toward the centre of the group. The smaller larvae in the group, males or younger larvae, remain in the centre of the larval mass (Figure 7.10).

One female Spilochalcis sp (Hym., Chalcididae) was observed in the field while she attacked a group of half-grown, 15mm long, D. diasi larvae. The parasitoid approached the larvae walking slowly on the same leaflet where the larvae were feeding. The parasitoid immediately stopped, or even moved backwards a little, every time the larvae reacted with their "Synchronous Abdomens Up" display. But as soon as the larvae quieted down, the parasitoid wasp moved slowly forward yet closer to them, and so on until the wasp came very near them and touched one of the larvae with its antennae. As the larvae reacted again with their Synchronous Abdomens Up display the parasitoid retreated a little, only to approach and touch again with its antennae the same or another larva nearby. The Chalcidoid continued with this slow advance-and-retreat approach until it could touch one larva without triggering her defensive reaction. When this happened, the parasitoid quickly jumped onto the thorax and head of the larva and immobilized the larva's abdomen with one of her large hind legs, gripping it between her hind femur and tibia. She usually also immobilized with her other hind leg the larva closest to the one she was attacking. She then introduced her ovipositor inside the larva's thorax, in its dorsal side just behind the head. It took about 90 seconds for the wasp to lay one egg in the larva after jumping onto it. The wasp then released the larva and proceeded to approach other larvae in the same way as described above.

7.6 LARVAL GROUP FEEDING BEHAVIOUR

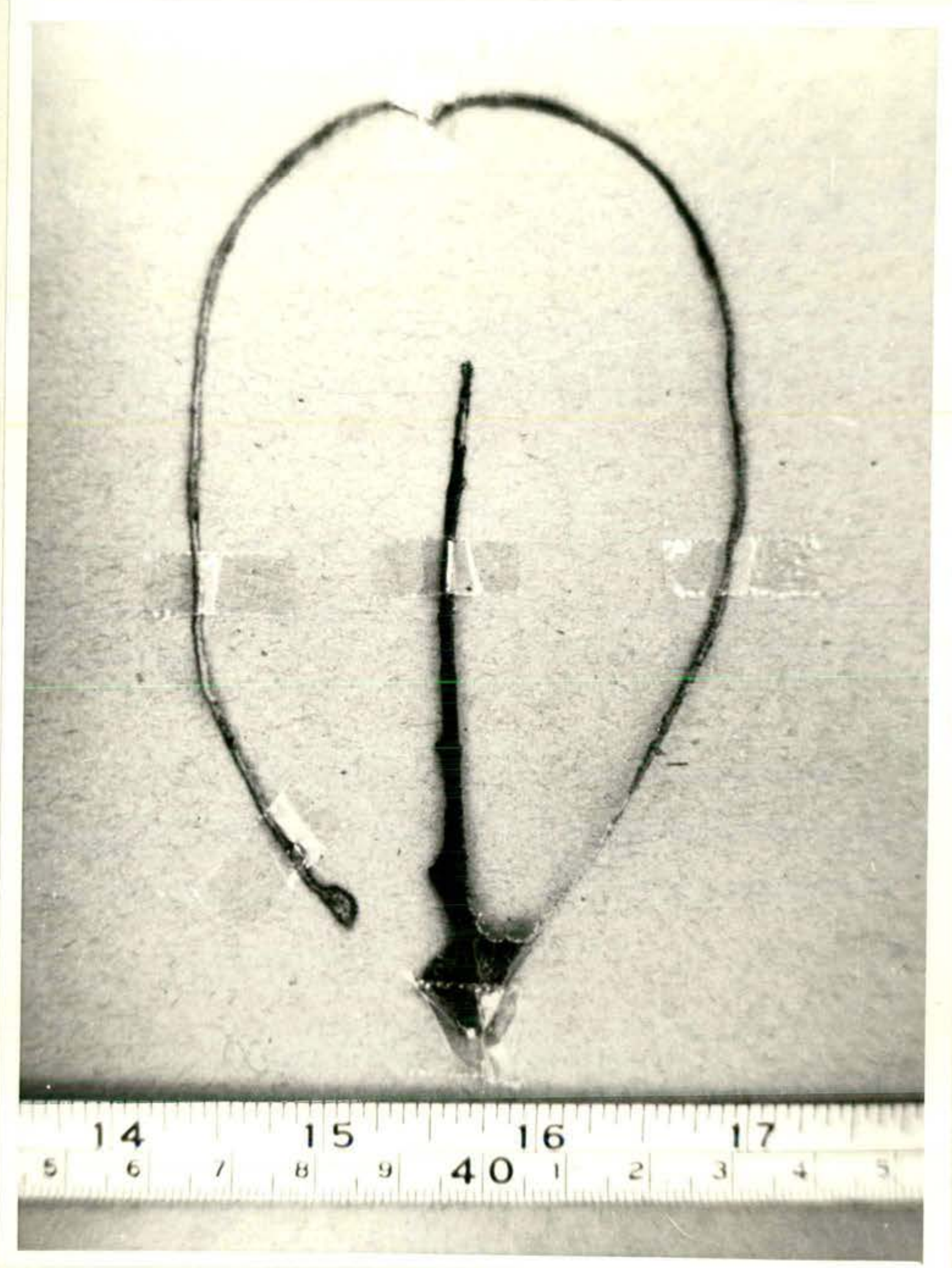
The larvae of both species always feed together in compact aggregations. They feed during the whole day and at least during the first half of the night in days with full moon. I do not know whether they continue feeding during the second half of these nights, and whether they feed during the dark nights with little or no moonshine.

FIGURE 7.10. *Themos olfersii* larvae massed together in a compact cluster on the underside of their leaflet in response to heavy rains.

The newly-born first instar larvae of the two species differ in respect to the manner they follow to begin feeding. T. olfersii always start to feed on the leaflet where they were born. The young larvae initially move singly back and forth along the leaflet's edge for several hours, and eventually cluster along the leaflet's edge near the base of the leaflet. Here they work together to chew off a piece of the tough and thick curved margin of the leaflet of about 10mm long. The smallest number of larvae observed working together to do this was of six. In this way they gain access to the edible leaflet blade which they start feeding right away in a compact formation, one behind the other. The late emerging sib-larvae join the rest here at the same feeding site. The young T. olfersii larvae of the first two instars do not eat the leaflet's margin and midrib, but eat everything between them progressively from the leaflet's base toward the apex. Here they bite through the thin apical portion of the midrib and start feeding on the second half of the leaflet's blade, moving now from the leaflet's apex towards its base. When they reach the base of the leaflet again they stop feeding and move to the nearest leaflet in the same compound leaf, starting the same way as before by chewing through the leaflet's margin near its base and repeating the same feeding pattern described above. Therefore, Eriotheca pubescens leaflets eaten by young T. olfersii larvae have a very characteristic aspect, having almost the whole leaflet margin and midrib intact (Figure 7. 11).

Newly-born D. diasi larvae, on the other hand, never eat the leaflet where they were born, but instead they always migrate together to the youngest leaflet at the apex of the same compound leaf where they were born. In this apical leaflet the larvae move about along the leaflet's edge for some time biting it occasionally, and eventually start to feed on it in a compact group usually at about halfway between the leaflet's base and apex (Figure 7. 12). The young D. diasi larvae avoid the thicker portions of the main lateral veins and also do not touch the midrib, but they do eat the whole leaflet's margin which is thin and tender. When they finish eating the whole leafblade on the first longitudinal half of the leaflet, they move on to the other half of the leaflet and start eating it along its median edge. The larvae always proceed from one of the lateral

FIGURE 7.11. Remains of an <u>Eriotheca pubescens</u> leaflet eaten by first instar <u>T.olfersii</u> larvae. The midrib and thicker edge are left almost intact. The small portion of the leaflet's edge, which the larvae had to crew off to gain access to the edible part of the leaflet's blade, can be seen near the leaflet's base. Upper scale in inches, lower scale in millimetres.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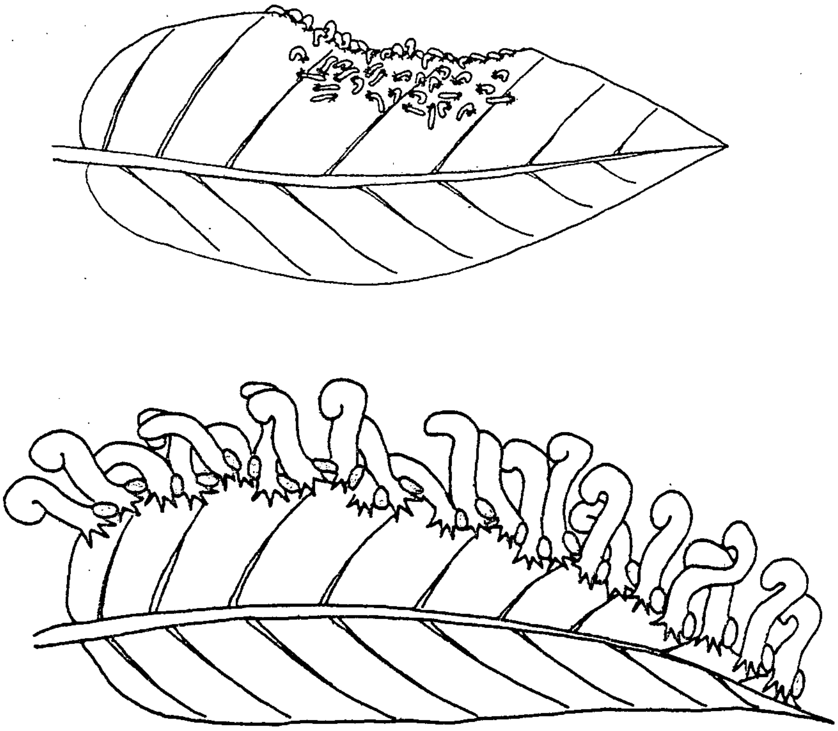


FIGURE 7.12. Group feeding in *D.diasi* larvae. Young larvae start feeding midway between the leaflet's base and apex (above). Non-feeding larvae stay away from the edge on the underside of the leaflet. The queue is always orientated toward the leaflet's apex.

margins towards the midrib as they feed. After finishing, or almost, to eat this first leaflet they migrate together to the opposite leaflet in the same apical pair, where they repeat the same feeding pattern. Sclerolobium aureum leaflets eaten by young D. diasi larvae are left with only the midrib and the basal stubs of the main lateral veins.

Older larvae of both species eat all the leaflet's margin, lateral veins and blade leaving only the basal stub of the midrib. It is common, however, in D. diasi for larval groups of all ages to abandon a leaflet halfway through, leaving the whole midrib intact plus the stubs of the major lateral veins and portions of leafblade between the lateral vein stubs, especially in the case of older tougher leaves (Figure 7.13). Heavily infested S. aureum trees may be completely defoliated by D. diasi larvae.
The same applies to E. pubescens shrubs attacked by T. olfersii larvae, but as the canopy size (number of leaves) is always small in these shrubs, very often only one or two larval sib-groups are enough to totally defoliate them.

The basic feeding pattern is the same for the larvae of both species at all stages of development. Each larva alternates periods of almost continuous feeding (meals), which may last dozens of of minutes or up to a few hours, with periods with no feeding (rests), which may last several minutes. Each meal is divided into several short periods of continuous feeding (feeds), which last several minutes, interrupted by even shorter periods with no feeding when the larva has to change her position in the feeding site and wait for a feeding site to become available (inter-feeds), which may last from a few seconds to several minutes. Each feed consists in a long alternating sequence of biting bouts, as the head is pushed backward and deeper into the leaflet's edge, and forward body movements, when there is no feeding. Figure 7.14 illustrates a typical feed sequence of a last instar D. diasi male larva. Here each biting bout lasted usually between 15 and 20 seconds, with a rate of one bite every 2 seconds, and each forward move lasted usually between 2 and 3 seconds. During each biting bout, a last

FIGURE 7.13. Remains of Sclerolobium aureum leaflets eaten by D.diasi larvae. Only the midribs are left intact.

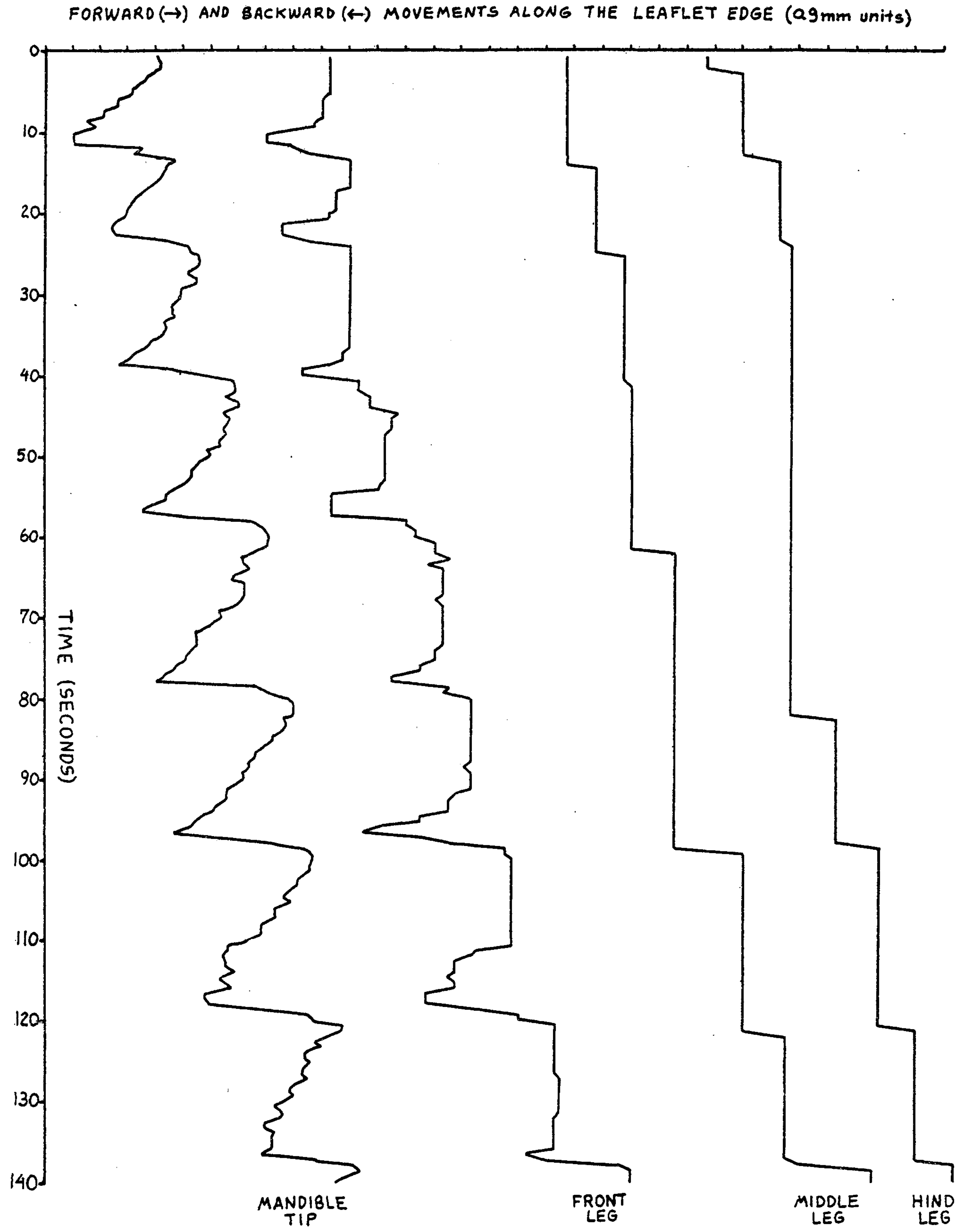


FIGURE 7.14. Feeding pattern of D.diasi larva. Typical sample of feeding pattern of a single male last instar larva. Frame by frame analysis of a 140 seconds sequence filmed with time-lapse cinematography at a speed of 1.5 frames per second. Only changes in the grip points of the tarsal claws and in position of the mandible tip are shown.

instar male D. diasi larva cuts and swallows a small narrow strip of the leaflet measuring about 3mm long and 0.5mm wide. As the larva pushes her head further backwards against the ventral side of her thorax, she also moves backward the grip of her forelegs, but never moves the grips of her middle and hind legs. When each biting bout finishes, the larva lifts her head and swings it forward usually about 45 degrees while pulling her body forward 1 or 2mm and moving the grip of her middle or hind legs or both also forward by the same extent (Figures 7.14).

As the larvae of both species feed along the leaflet's edge in a horse-riding fashion, they have only one plane of movement: the leaflet's edge. And just like a train moving in its track, these larvae can only move toward two directions: either toward the leaflet's apex or toward its base.

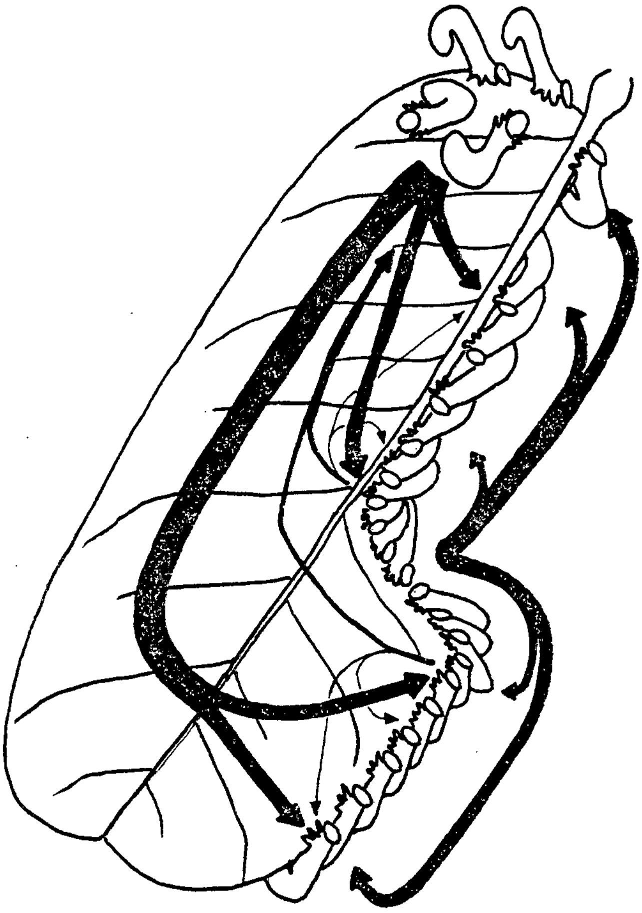
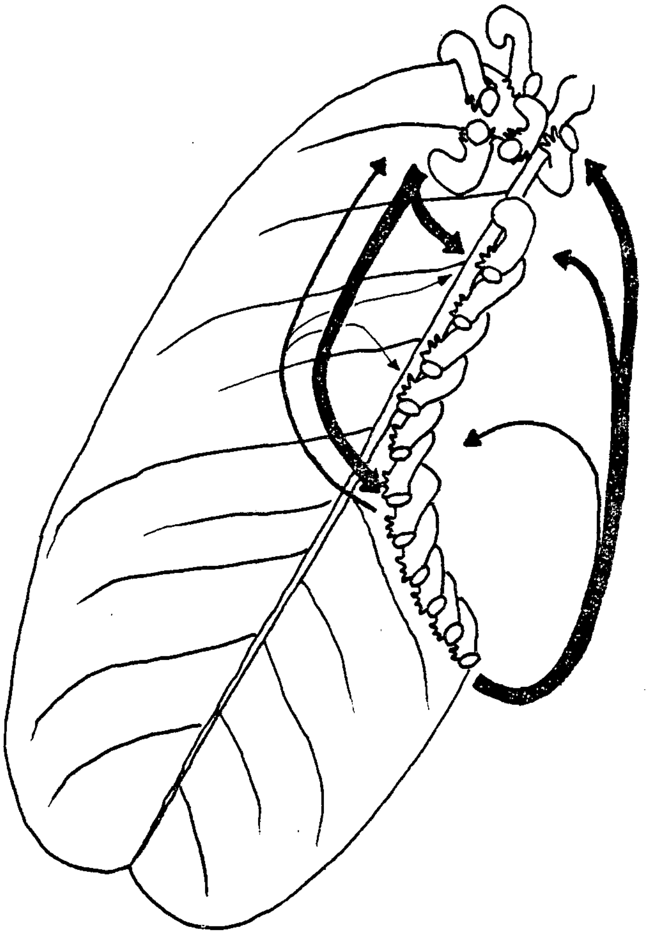
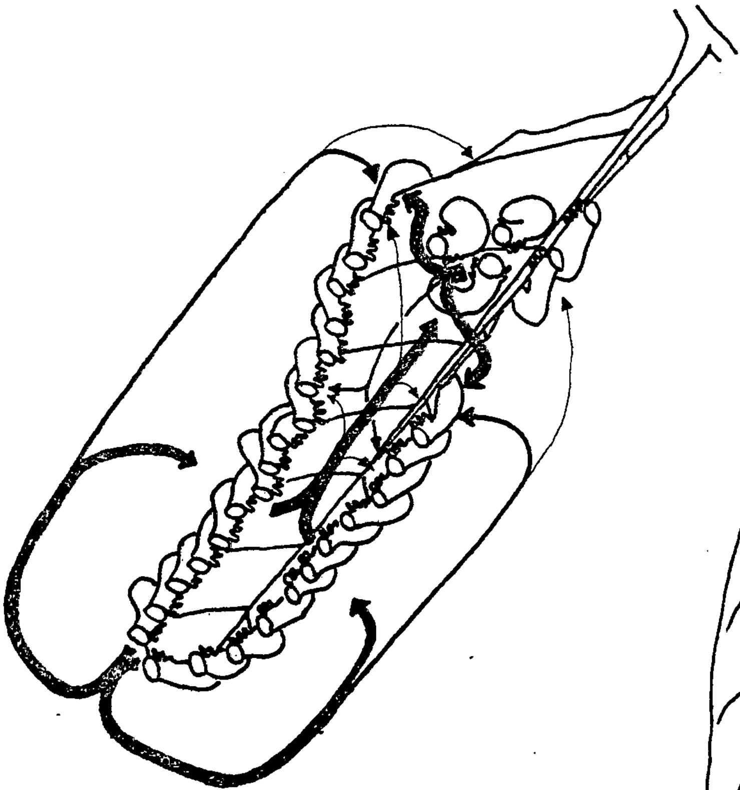
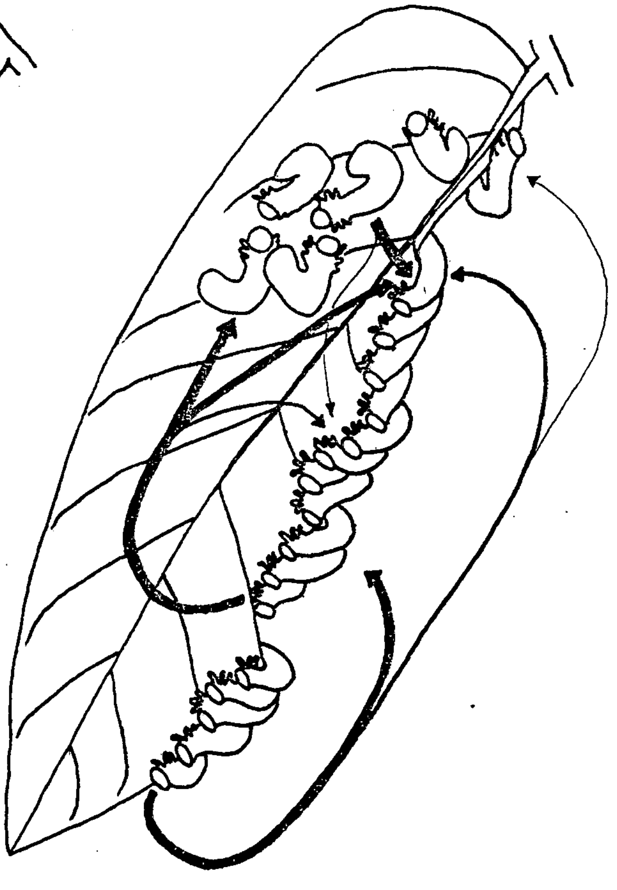
The larvae of both species always feed all together in compact formations, where all the larvae orientate toward the same direction, usually toward the leaflet's apex, forming a long compact queue along the leaflet's edge, with each larva pressing her head against the ventral part of the metathorax or first two abdominal segments of the larva immediately in front. Each larva in the queue alternates between biting bouts and forward moves, however the extent to which each larva moves forward after each biting bout depends on the moving pace of the larva in front. Therefore the activities of the larvae in the queue tend to synchronize, but as the feeding surface is never homogeneous because of the occurrence of thicker portions along the leaflet's margins, at the lateral veins and near the midrib, the pace of the larvae is not always constant and so the synchronism is never perfect. The whole group of larvae moves together slowly forward along the leaflet's edge toward its apex.

However, when the front larva in the queue reaches a patch along the leaflet's edge which is tougher and thicker than the feeding edge (this can be over a lateral vein, an intact portion of the leaflet's margin, the midrib or the leaflet's apex), she stops feeding, moves forward a few millimetres along the edge, turns around 180 degrees over the leaflet's edge with the help of an abdominal grip (in the case of D. diasi larvae) and then crawling over the bodies of the other larvae she moves to the rear of the queue. When she reaches the end of the queue, she moves a few millimetres or centimetres further along the leaflet's edge at the rear of the queue and then stops, and with the help of an abdominal grip (in the case of D. diasi larvae) she turns around 180 degrees over the leaflet's edge to face the same direction as the rest of the larvae and moves forward until she comes into contact with the larva at the rear of the queue. If the leaflet's edge here is suitable she immediately starts feeding again, thus beginning a new feeding bout. Each period of continuous feeding with alternating biting bouts and forward moves, from the time the larva begins feeding at the rear of the queue until she stops feeding and retreats from the front of the queue, constitutes one feed. And each short non-feeding period from the time the larva stops feeding at the front of the queue until she starts feeding again at its rear constitutes one inter-feed.

After passing through the queue several times in succession, i.e. after having several feeds in succession interrupted only by short inter-feeds, the larvae of both species move slightly away from the feeding queue, near the base of the leaflet and the rear of the queue, where they remain motionless for several minutes without feeding (rest). At any one time, there is always a number of larvae not feeding at the base of the leaflet while the great majority of the larvae in the group feed in the queue along the leaflet's margin. The proportion of non-feeding larvae to feeding larvae at any moment decreases as the larvae grow larger. The non-feeding larvae remain grouped together either along the leaflet's edge behind the rear of the queue or on the underside of the leaflet's blade near its base. At the end of the non-feeding period (rest), the larva rejoins the feeding queue usually by entering in the rear of the queue where she starts eating as she comes over a suitable part of the feeding edge. Each period of successive feeds between two "resting" periods constitutes one meal.

There are some complications in this apparently simple cyclic feeding system. The first is that the larva may interrupt her feed (i.e. move out from the queue) either from the front of the queue or from any other point in the middle of it. A preliminary sample of quantitative observations indicates that D. diasi larvae end half of their feeds at the front of the queue and half in the middle of it, whereas T. olfersii larvae end most (about 80%) of their feeds at the front of the queue and only about one fifth of the feeds in the middle of the queue. The second complication is that the larva may join the queue either by entering at its rear or by entering in any position in its middle (jumping in), which is accomplished either by occupying a vacant space in the middle of the queue (a rare event which occurs in those places where the feeding edge coincides with a lateral vein) or by forcing its passage, i.e. pressing one of the larvae in the queue so as to force it to move backwards therefore producing a vacant space in the queue. A preliminary sample of quantitative observations indicates that in both species about half the larvae entering the queue join at its rear while the others jump in its middle. These same observations show that in D. diasi most larvae coming out from the front of the queue reenter the queue by jumping in its middle, and just a few reenter the queue at its rear, while only a very few of these larvae join those at the non-feeding area. Most of those larvae coming out from the middle of the queue, however, either go to the non-feeding area or join the queue at its rear, while only a few of these larvae rejoin the queue by jumping in its middle (Figure 7.15). The situation is slightly different in T. olfersii, for most of its larvae coming out of the queue from its front either go to the non-feeding area or join the queue at its rear, while only a few of these larvae rejoins the queue by jumping in its middle. And most of those larvae coming out of the queue from its middle go to the non-feeding area, while only a few of these larvae rejoin the queue either at its rear or jumping in its middle (Figure 7.15). On the other hand, while "resting" T. olfersii larvae leave the non-feeding area and join the queue either by entering at its rear or by jumping in its

FIGURE 7.15. Queue-feeding systems of Dielocerus diasi larvae (above) and of Themos olfersii larvae (below). The diagrams on the left illustrate single-queue systems in both species while those diagrams on the right illustrate two-convergent-queues systems in both species. Those larvae out of the queues, near the leaflet's base are "resting". The arrows indicate the paths followed by the larvae to enter and to leave the queues. Their thickness is proportional to the relative frequency of each path.

middle, "resting" D. diasi larvae usually rejoin the queue by entering at its rear and only rarely by jumping in its middle (Figure 7.15).

The third complication, in the larval cyclic feeding system of these two sawflies, is that the leaflet's edge over which those larvae at the rear of the queue are frequently located are often unsuitable as feeding sites. This happens when the larvae at the rear of the queue are positioned over the midrib, the thick basal part of a lateral vein or the thick leaflet's margin. In this situation, the larvae at the rear of the queue are unable to feed and have to wait until those larvae in her front move sufficiently forward allowing her access to the edible part of the feeding edge. Therefore, in these circumstances the rear part of the queue actually constitutes a waiting queue. This situation is of rare occurrence in D. diasi larval groups, and when it does occur it usually affects only last 1 or 2 larvae at the rear of the queue. However, in T. olfersii larval groups this situation is so common that it is rare to find larval queues without a waiting queue, and usually the waiting queue contains about half the larvae in the queue so that only those larvae on the anterior half of the queue are actually feeding (Figure 7.15). Therefore, the entering of a larva in the queue does not usually coincide with the moment when the larva starts feeding in the queue.

A further complication is that very often the larvae of both species, instead of arranging themselves all in one unique queue, organize themselves into two separate queues in the same leaflet. This happens in D. diasi mainly in the large mixed larval groups and during the final stage of destruction of a leaflet when all the larvae cannot accommodate themselves in just one of the lateral margins of the leaflet and have therefore to occupy both lateral margins of the leaflet thus producing two parallel queues, both facing the leaflet's apex. As the larvae move forward while feeding, the two queues eventually meet and collide head-to-head at the leaflet's apex. In T. olfersii larvae, the two queues arrangement is more common than the single queue, but in this species the two queues are formed opposite to each other on the same side of the leaflet, with one queue partially over the midrib and facing the leaflet's apex and the other queue partially over the leaflet's intact margin and facing its base so that both queues meet and collide head-to-head halfway between the midrib and the leaflet's margin (Figures 7.16 and 7.17).

In the two-convergent-queues arrangement the larvae of both species behave just as described for the single queue situation, except that in the former the larvae in the front of the queues have to stop and cannot feed any more once they collide with the opposite queue and are, therefore, forced to leave the queue. Another difference is that larvae wishing to join the queue in the two-convergent-queues arrangement have a choice of two queues and must opt for one of them. Preliminary sampling of quantitative observations indicates that the larvae of both species "choose" randomly the queue to join in. In the case of T. olfersii larvae feeding in two-convergent-queues system, there are two waiting queues, one over the intact leaflet's margin and the other over the exposed midrib (Figure 7.15).

FIGURE 7.16. *D. diasi* last instar larvae feeding in two queues converging to and colliding at the leaflet's apex.

FIGURE 7.17. (this and the next plate). *T. olfersii* last instar larvae feeding in two queues converging to and colliding at about midway between the leaflet's apex and base. As the two queues collide one larva, after the other in the front, is forced out of the queue and moves to the rear of one of the two queues.

7.7 LARVAL MORTALITY

The average total mortality for the larval feeding period of Themos was around 57% of the larvae per larval sib-group (N = 26 larval groups of the 1977/78 spring and summer generations). There was no difference between the two generations. The mortality rate varies along the feeding period, being higher during the earlier stages and very small beyond the 20th day after hatching (Figure 7.18). The mortality curve varied greatly between the different larval groups. In 2 groups, out of the 26 observed, the mortality was virtually zero, whereas in 3 other groups the mortality reached 100% in a short time after hatching (Figure 7.19).

One fourth of the larval groups had a mortality percentage higher than 60%. However, the mortality in the 20 groups with a smaller rate reached a score of only 37% in average (Figure 7.18).

The observed mortality factors were: predation by the lacewing larvae (the same that attacked the eggs), internal parasitism and fungi. The lacewing larva was responsible for the early total mortality of at least two of the observed larval groups, and is suspected as being also responsible for the third instance of total early mortality seen. The larvae were killed just after hatching. Larvae killed by a white fungus were seen occasionally below clusters of medium to large sized larvae. More commonly found were pink coloured sluggish larvae which stayed apart from the rest of the group. These larvae were parasitized, but the parasite is still unknown. These larvae were more obvious in groups already halfway through their development.

There is no quantitative data available for Dielocerus, but an overall qualitative assessment indicates that the mortality is low during the larval feeding period.

7.8 COOPERATIVE COCOON SPINNING BEHAVIOUR IN DIELOCERUS DIASI

When the full grown last instar larvae of D. diasi finish eating, they migrate all together down the branches of their host tree. They move close together, one after the other forming a single continuous

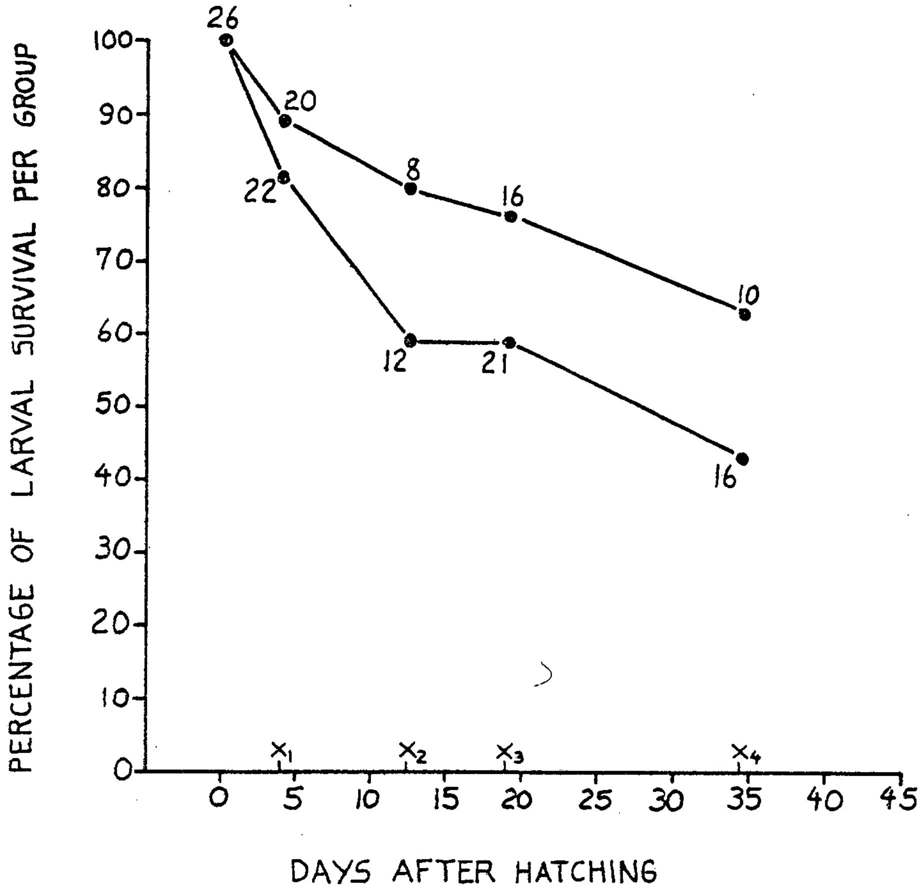


FIGURE 7.18. Average survival rate for Themos olfersii larvae represented as percentage of survival per group at different intervals of time after hatching (x_1=2 to 6 days; x_2=10 to 15; x_3=16 to 22; x_4=26 to 43 days). The data of the spring and summer generations of 1977/78 are summed here. The number of larval groups surveyed at each time interval is indicated beside the plotted points. The number of larvae hatching per cluster is taken as 100%. The lower curve is the overall average for the 26 larval groups observed. The upper curve is the average of 20 groups excluding the 6 groups with high early mortality.

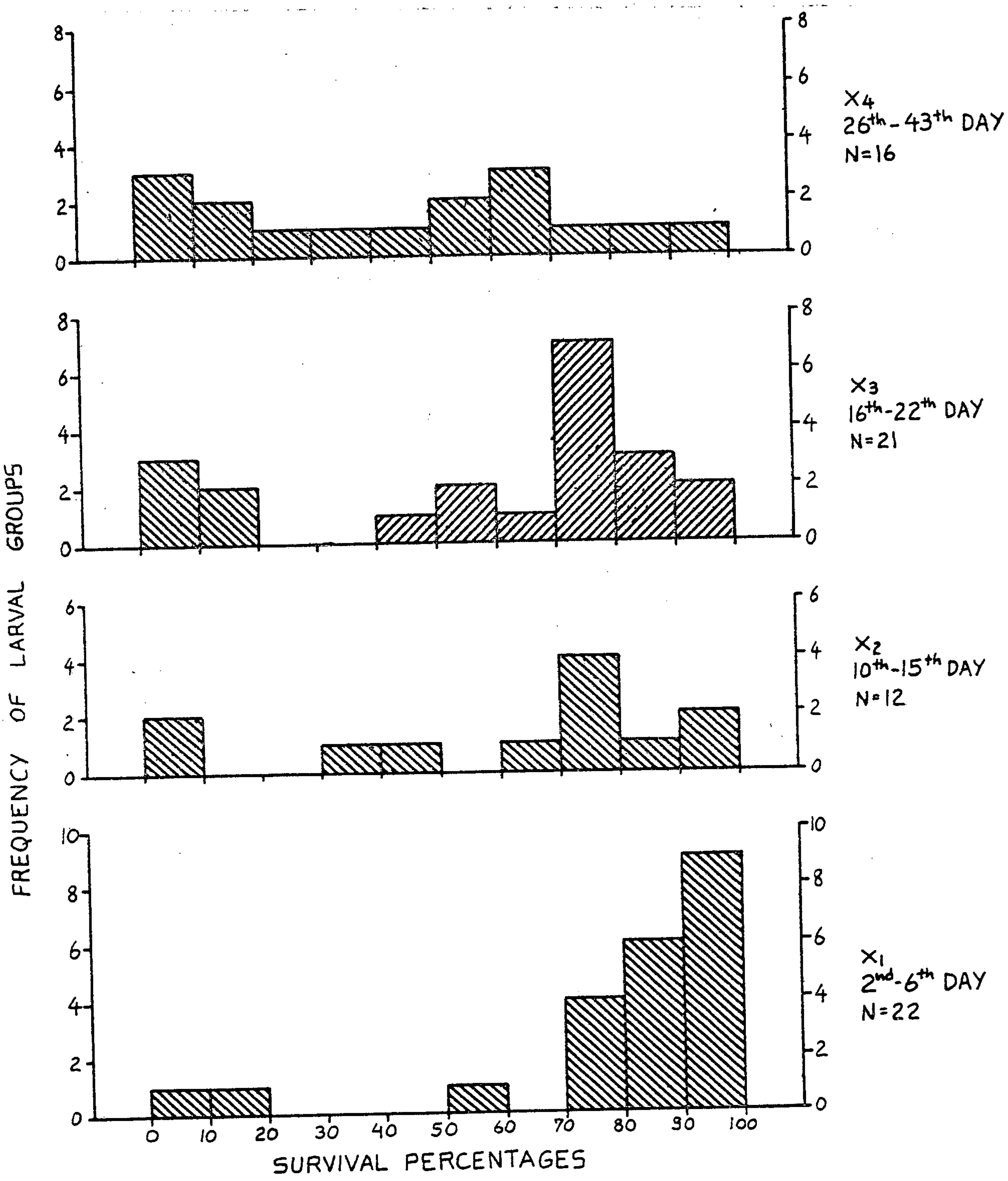


FIGURE 7.19. Frequency distribution of survival percentages for <u>Themos olfersii</u> larval groups at different periods of time ($x_1 - x_4$) from the day the larvae hatched.

queue in which each larva has its abdomen arched backward and with its tip bent to one side and turned in such a way that it grips with its uropod the thorax of the larva immediately behind it, on one side of its thorax usually between the second and third segment (Figure 7.20). These larvae move together in a slow pace without disconnecting the grips. Sometimes, when part of the group remains in the canopy feeding, the descending group may turn back and climb to the canopy until they reunite with the rest of the group, only to start descending again soon afterwards. Larval groups at this stage readily fuse with others if they come close to each other. In trees with high infestation, large groups with several hundred larvae may form. Groups with over 500 larvae have been found during this stage.

In the case of mixed feeding larval groups with larvae of different ages, when the older larvae at their proper time stop feeding and migrate down the tree to cocoon, the remaining younger larvae in the group may join them to cocoon even though they have not reached their final size. Thus, larvae which still had about 10 to 15 days of feeding yet to go have been observed to follow older larvae to cocoon. However, in cases when the difference in age between the larvae in mixed groups were greater than this, the younger larvae remained feeding at the tree canopy, or would only follow the older larvae for a short distance and then turn back to the canopy to continue feeding.

The descending group of larvae may stop at any point along the main branches and trunk of the host tree, from about 6 metres above the ground until the base of the trunk at ground level. There is a marked tendency for choosing a place near earlier spun coooon masses (see below). In their chosen place, the larvae remain almost motionless in a very compact assemblage gripping the bark with their thoracic legs and with their abdomen raised outwards and curved, such that only the abdomens are seen in the outside (Figure 7. 21). Here they stay for about two days, and during this period the larvae bite the rough cork of the bark making it into a smoother surface.

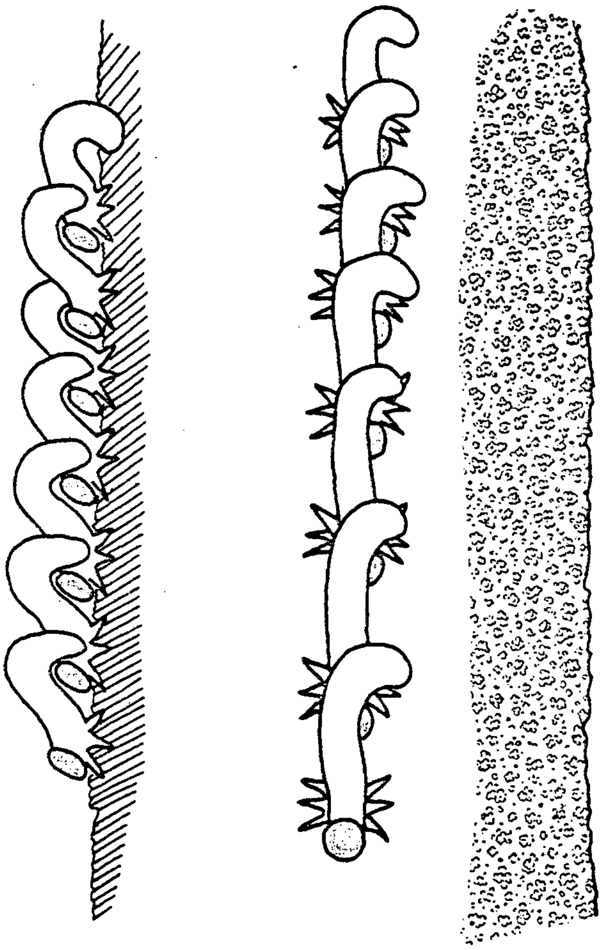


FIGURE 7.20. Fully grown D.diasi larvae migrating down the branches and trunk of its host tree in an Indian File pattern, side and superior views (diagrammatic).

FIGURE 7.21 (left). Fully grown *D.diasi* larvae clustered on the trunk of its tree, beside an old cocoon mass, just before spinning their own cocoons.

FIGURE 7.22 (right). The outer papery silk layer of the communal envelope removed to show large female *D.diasi* larvae clinging to its inner surface.

The larvae, then, start to secrete silk threads, specially along the edge of the larval mass against the bark. At this stage, some larvae leave the bark surface and climb on top of the other larvae where they obtain a new firm grip by bending the tip of their abdomen around the abdomen of other larvae which are fastened against the bark. In this way, some larvae are able to remain on top of the larval mass with their thoracic legs free so that they can turn their forebody freely in all directions including keeping their back against the back of the rest of the larvae so that their mouthparts project freely above the larval mass. These larvae start to spin over the rest of the larvae in the mass, including themselves, producing a thin translucent mesh of silk fibres covering loosely the whole mass of the larvae. As the spinning progresses, the spinner larvae are able to hold onto this thin silk covering wall with their thoracic legs so they can release their abdominal grip on other larvae and move about against this outer wall as they finish spinning it (Figure 7.22). After about one day of work, the larval mass becomes invisible under the very thin white papery silk envelope which is firmly fastened against the bark of the branch or trunk on all sides of the larval mass (Figure 7.23). Only female larvae were observed among those spinning the outer silk envelope.

After completing the spinning of the outer white cover, the larvae start secreting a different type of silk fibre: a much thicker brown-coloured coarser thread. This new silk is secreted against the outer cover and against the bark of the tree, specially along the periphery of the larval mass. But instead of forming a uniform and smooth unidimensional layer of silk as the outer cover, this new silk is spun in a very irregular manner such as to form a very thick sponge-like layer of coarse silk with about 10mm in width between the outer white cover and the larvae themselves (Figure 7.24). This coarse spongy layer of silk is apparently spun by all larvae in the group cooperatively. This spongy layer takes about one day to be spun.

Eventually, as no further space is left for them to move beneath the double layered communal silk covering wall, the larvae start to spin their own individual cocoons, usually in a very regular

FIGURE 7.23. Recently spun cocoon masses of *D.diasi* showing the finished outer papery silk layer of the communal envelope. Upper scale in inches and lower scale in millimetres.


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FIGURE 7.24. Two views of the spongy layer of silk of the communal envelope of *D. diasi* cocoon masses, seen from inside. Upper scale in inches and lower scale in millimetres.


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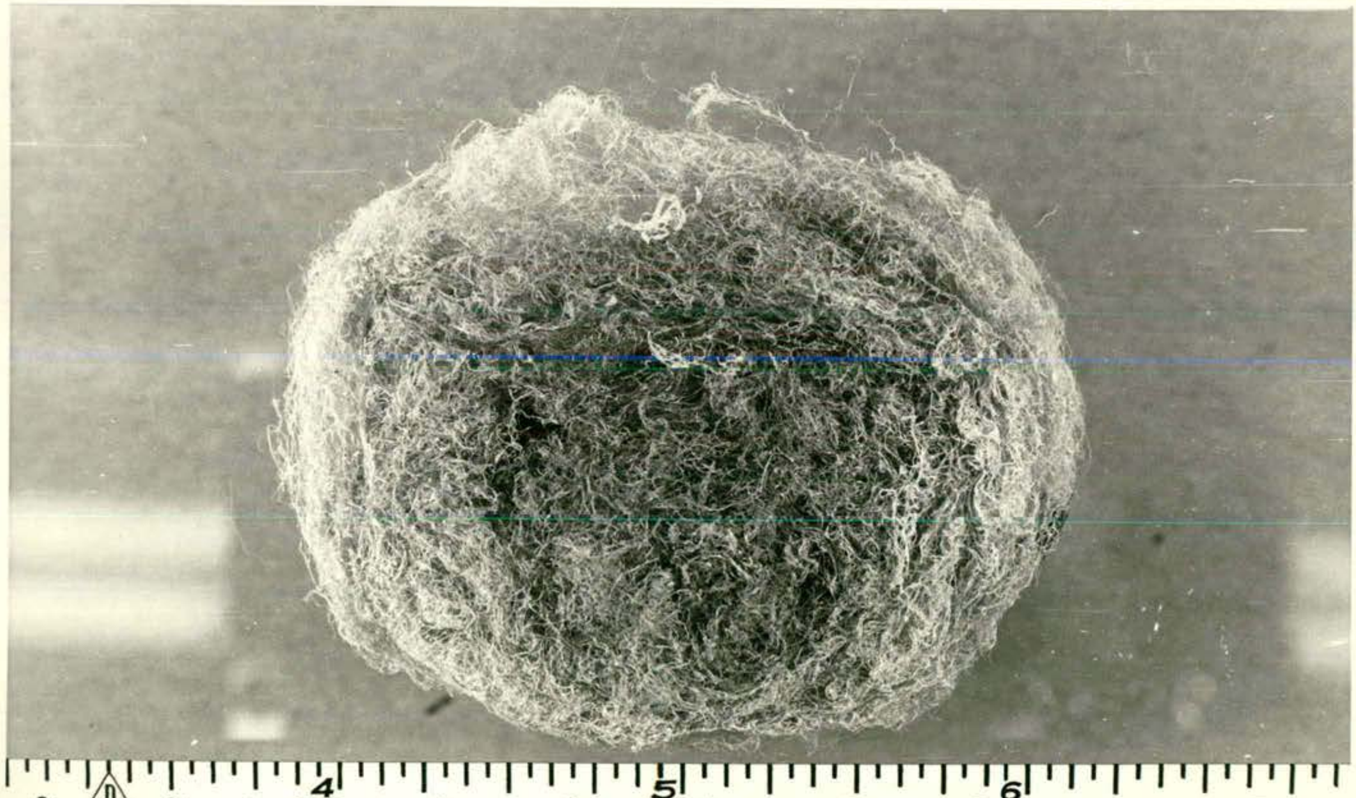
7 8 9 10 1 2 3 4 5 6


4 5 6
8 9 10 1 2 3 4 5 6 7

orientation one to another, parallel to each other and tightly packed such that the walls of each cocoon is firmly glued to those of its immediate neighbouring cocoons. The whole process, since the larvae leave the tree canopy and until they finish spinning their individual cocoons, takes about 5 days to complete.

When the double layered communal silk cover was removed experimentally from some larval groups before they had started to spin their own individual cocoons, the larvae failed to spin their own individual cocoon and remained motionless for several days. But as soon as an artificial cover made with gauze and cotton wool was provided for them, the larvae resumed their spinning behaviour and spun their individual cocoons normally (Figure 7.25).

All-male larval groups, produced artificially by removing the females, failed to spin the outer white papery silk layer of the communal cover but were able to spin a thinner spongy layer around them and to spin their own individual cocoons normally (Figure 7.26).

Small larval groups with less than four larvae spin cocoon masses without the outer white papery silk layer in the communal envelope, and single larvae fail to spin both the white papery and the spongy layers of silk around the cocoon wall proper, spinning only a few loose threads of coarse brown silk outside the cocoon wall.

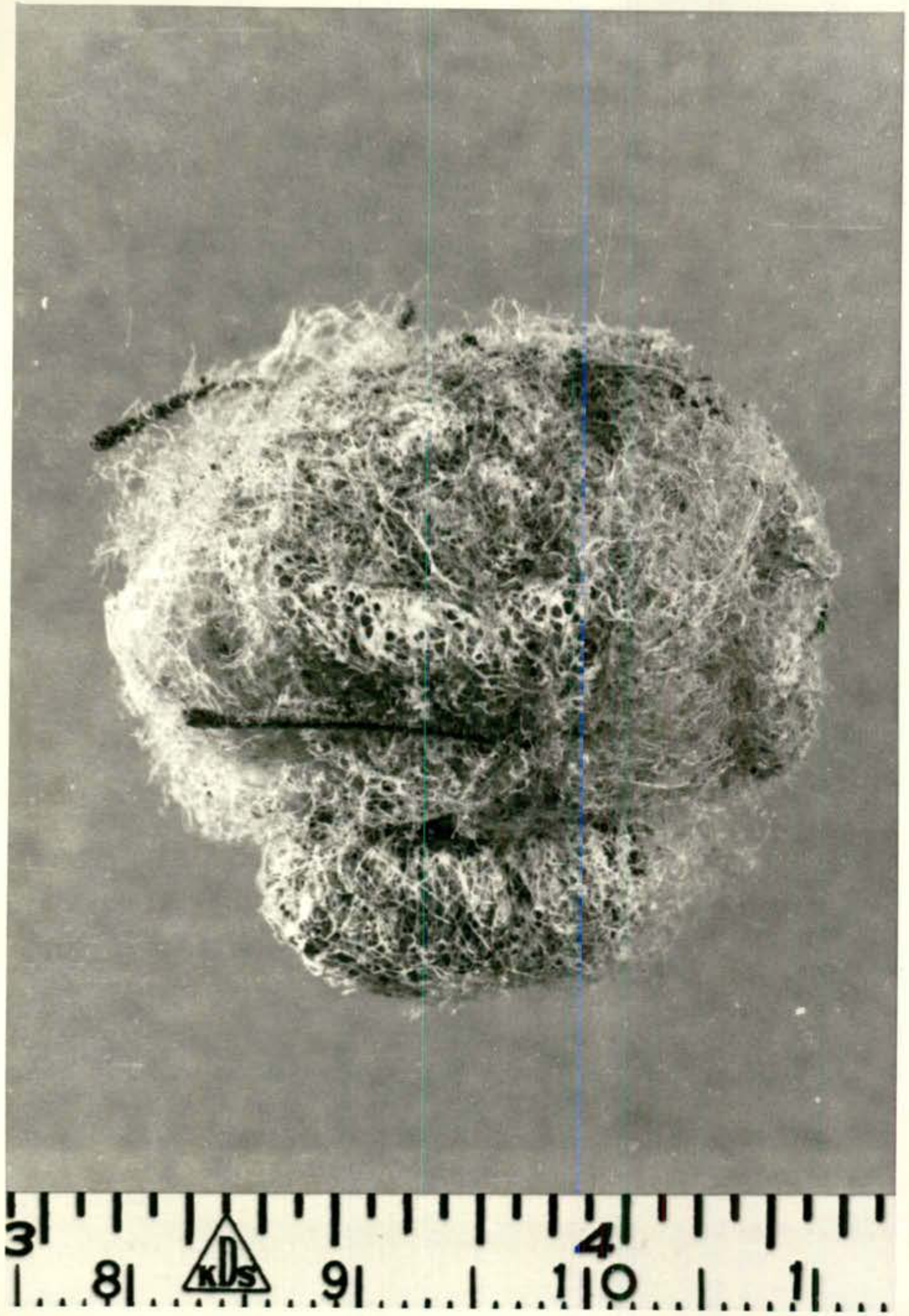
Themos olfersii full grown last instar larvae after finishing feeding also migrate together down the branches of the host shrub until they reach the ground where they look for a softer place to penetrate the soil, just beneath the shrub. The larvae usually penetrate through the same burrow in the ground, one after the other. Soil penetration and cocoon spinning takes a few days and was not studied.

7.9 COCOON DESCRIPTION

Themos cocoons are cylindric with both ends rounded, and have a very thin and flexible wall on which earth particles adhere to externally (Figure 7.28). The cocoons are always spun separate

FIGURE 7.25 (top). Cocoons spun by *D.diasi* larvae in an experimental situation where the communal silk envelope was removed before they spun their individual cocoons. The larvae interrupted their spinning for several days and only resumed it after an artificial cover of gauze and cotton wool was provided. Upper scale in inches and lower scale in millimetres.

FIGURE 7.26 (bottom). Cocoon mass spun by an all - male *D.diasi* group of larvae. Note the absence of the outer papery silk layer of the communal envelope. Scale on the left in inches and scale on the right in millimetres.



from one another, burrowed in the ground just below the host plant, 10 to 40mm below the surface. The cocoons are vertically orientated, loosely grouped.

Dielocerus cocoons are also cylindric but have a very thick and tough wall, which is difficult to cut even with a knife. The cocoons measure internally 15 to 17mm long and 5 to 8mm wide, and the wall is 0.1 to 0.2mm thick. But contrary to Themos, the cocoons are spun together in an orderly arrangement forming honeycomb-like masses covered with communal envelopes which are attached to the bark of the trunk and major branches of the host plant (Figure 7.27). The communal envelope is divided in two parts: an outer thin white paper-like layer and below a thick (up to 10mm high) spongy layer of thick long brownish silk threads. This cover is the result of a cooperative work of the larvae forming the group. Therefore, Dielocerus larvae produce much more silk than Themos, and accordingly have huge silk glands which occupy about 2/3 of the larval body cavity (Figure 7.29).

The structure of Dielocerus cocoon masses vary greatly according to the number of larvae forming the group (Figure 7.30). Groups with up to 7 larvae always align their cocoons parallel to the supporting surface, glueing the cocoon to the surface by its long side. The cocoons are glued to each other side by side (Parallel arrangement). Groups with more than 26 larvae always align their cocoons perpendicularly to the supporting surface, glueing the cocoon to the surface by one of its ends. The cocoons are glued to each other side by side in a honeycomb arrangement (Perpendicular arrangement). In both types of alignment the cocoon's longer axis is always parallel to the ground. Groups with 8 to 26 larvae vary greatly in their arrangement, and are in this respect greatly influenced by the geometry of the place chosen by the larval group to cocoon. These groups can have a parallel arrangement, sometimes with two or even three layers of cocoons forming a pile; or a perpendicular arrangement, specially when the group has settled beside another cocoon mass which gives them some lateral support; or a mixture of both types of arrangements forming two distinct

FIGURE 7.27. Old *D. diasi* cocoon masses without the communal cover, showing the honeycomb pattern of the individual cocoons. Upper scale in inches and lower scale in millimetres.

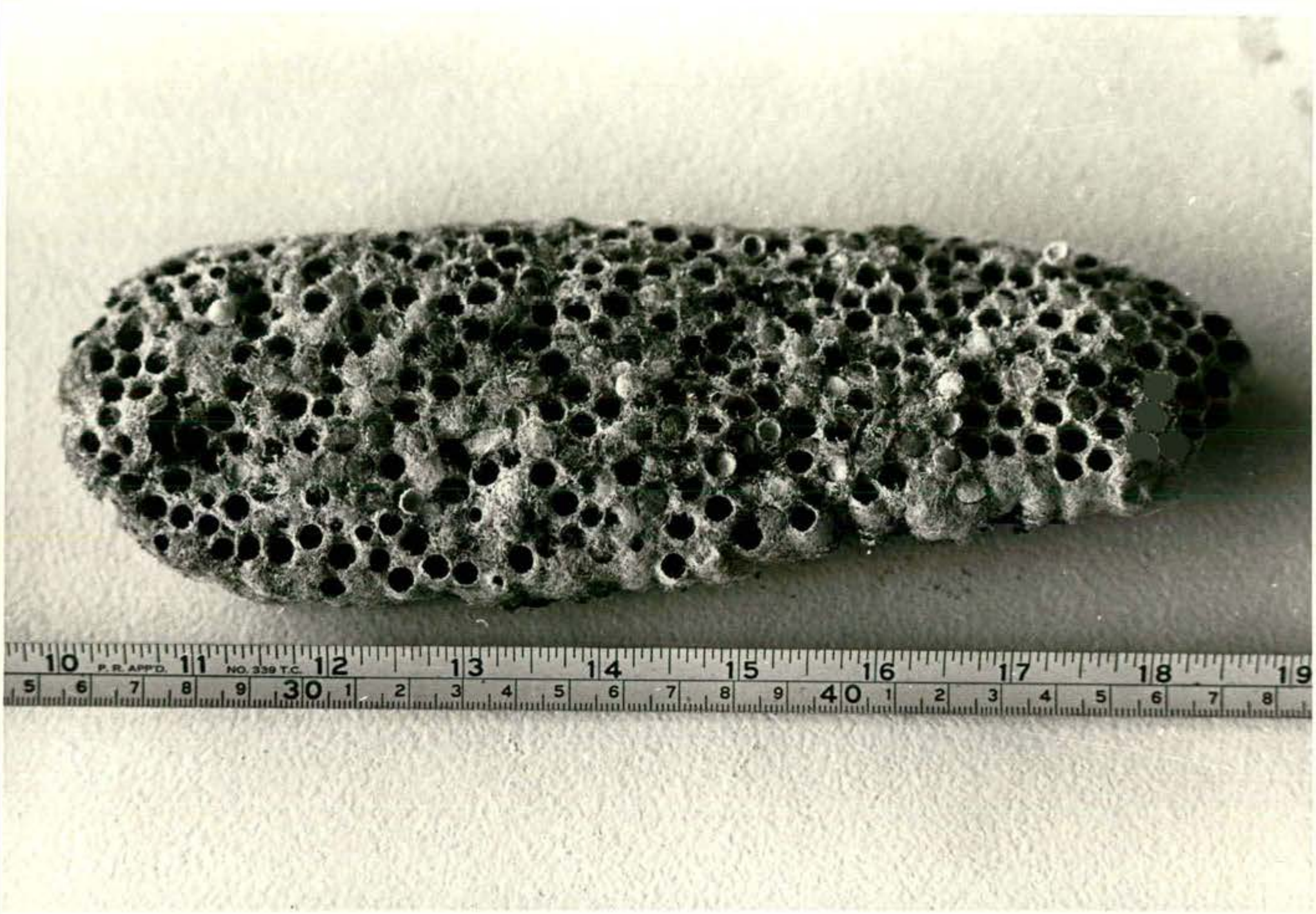

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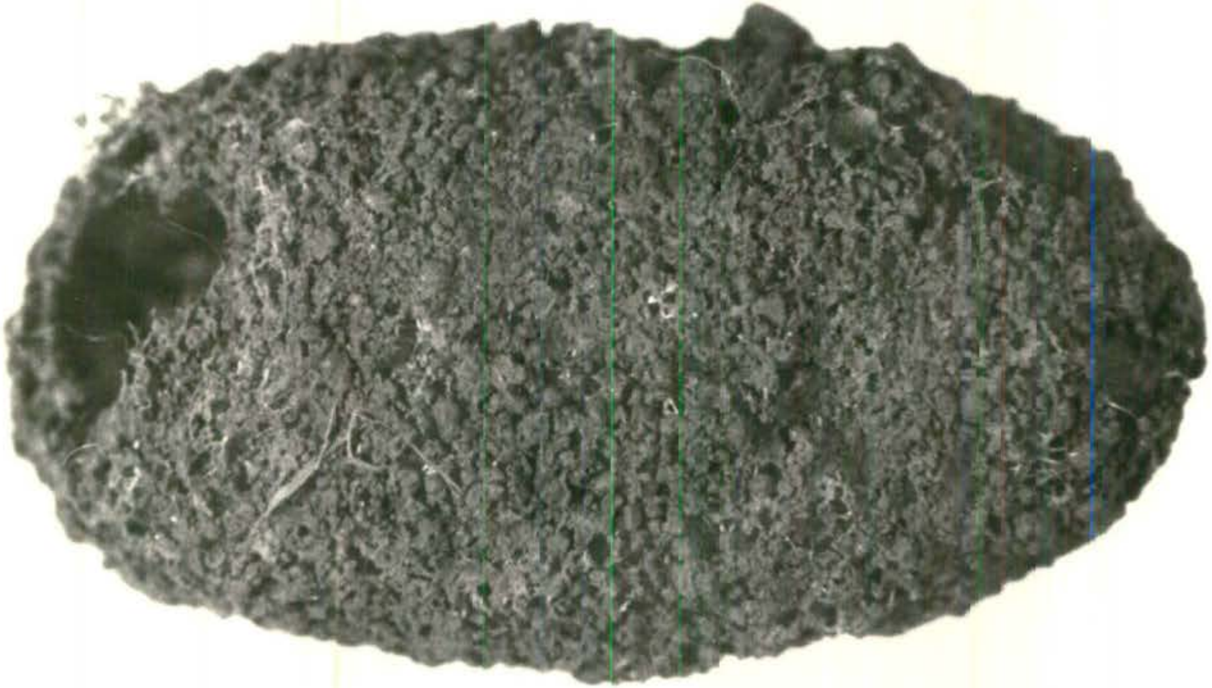
FIGURE 7.28. Cocoon of a Themos olfersii female, showing soil particles adhered to its outer surface and the exit hole at its apex. Magnified 10X.



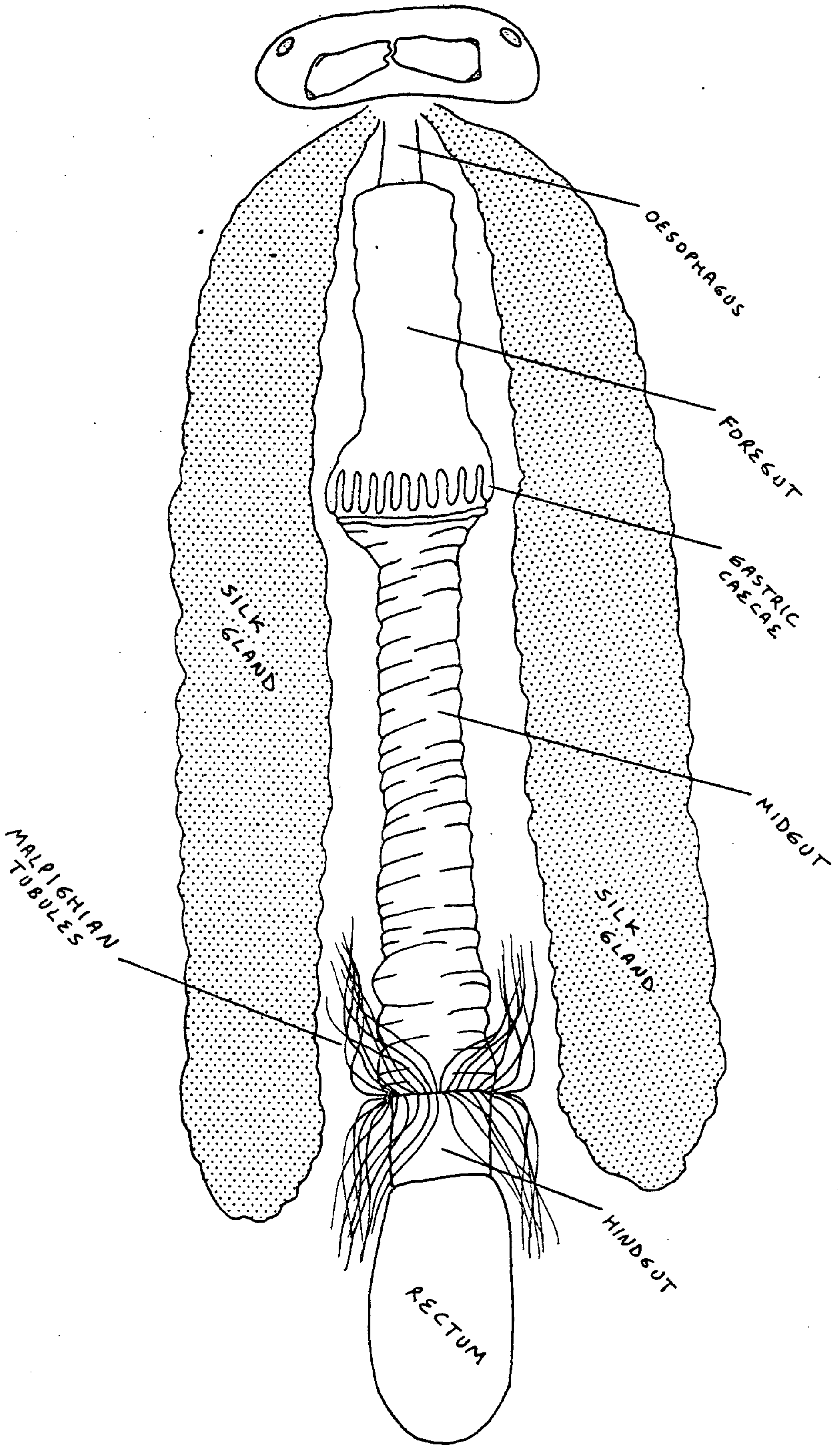


FIGURE 7.29. Last instar larva of *Dielocerus diasi* dissected to show its guts and the huge pair of silk glands (shaded), 8X natural size.

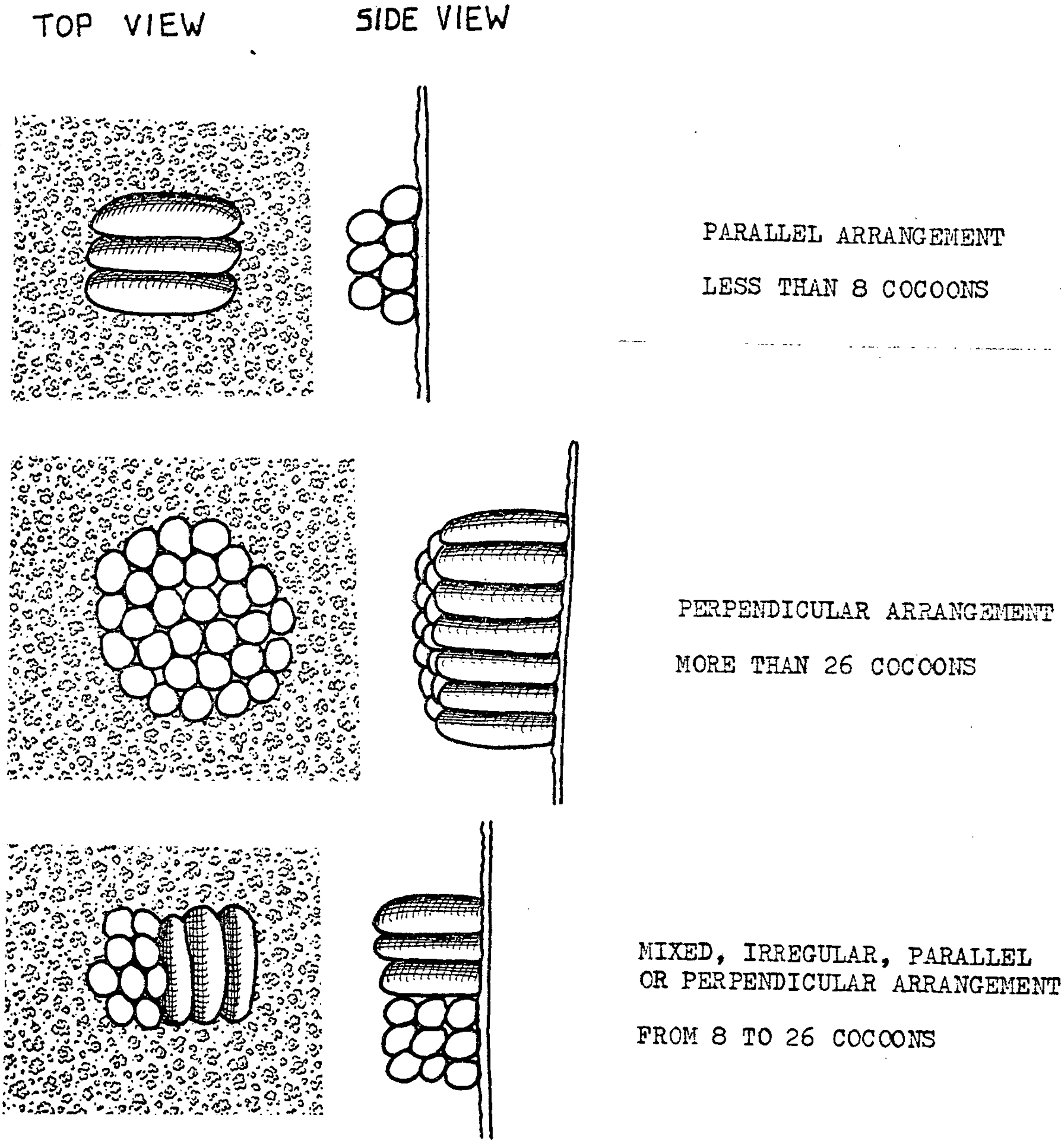


FIGURE 7.30.Different arangements of Dielocerus diasi cocoons when grouped into cocoon masses, according to the group size and existence of other cocoon masses nearby.

but united blocks; or even a disorganized arrangement with parallel, perpendicular and oblique cocoons mixted together.

The shape of the cocoons in a mass change from cylindric to polygonal. Those cocoons in a honeycomb arrangement surrounded by cocoons on all sides take a hexahedral or pentahedral form. The larvae inside perpendicular cocoons always face opposite the supporting substrate, but those inside parallel or irregular cocoons may face either side, for both sides are unobstructed.

7.10 SPATIAL DISTRIBUTION OF DIELOCERUS DIASI COCOONS WITHIN ONE HEAVILY INFESTED TREE

The distribution of the cocoon masses found in December of 1978 on tree no. 3/2 at study site no. 3 at the University of Brasília Campus is presented here. The total number of cocoon masses found and their distribution according to height and age classes is given in Table 7.II. About one third (32%) of all the 628 cocoon masses were classified as NEW, 38% as OLD and 30% as VERY OLD.

The cocoons were distributed from the base of the trunk to the main branches up to about 6 metres above the ground, where the branches had a diametre of at least 10cm. The majority of the cocoon masses were found between 1 and 5 metres above the ground, and specially between 2 and 4 metres where half (48%) of the cocoon masses were spun (Figure 7.31). In 1970, though, the greatest concentration of cocoons was between 1 and 3 metres above the ground. The great majority of the cocoons were facing the paved road (northeast), and were grouped around the main bifurcations of branches (see Figure 7.32). There was a strong agglutination tendency, thus, not only for the larvae to join each other to form large cocoon masses, but also for the masses to be built side by side forming large surfaces of continuous masses of cocoons (see Figures 7.32 and 7.33).

Of the total of 11,395 cocoons sorted out, only 38 (0.3%) were built alone, all the rest being grouped. Only 12.7% of the cocoons were spun in small groups of less than 20 cocoons each (Figure 7.34). The great majority of cocoons (73%) were built

TABLE 7.II

Distribution of the cocoon masses of *Dielocerus diasi* at the heavily infested tree no. 3/2 into height and age classes.

HEIGHT CLASS*	AGE CLASS	NUMBER OF COCOON MASSES	
0-2 METRES	NEW	45	156
	OLD	63	
	VERY OLD	48	
2-4 METRES	NEW	98	312
	OLD	119	
	VERY OLD	95	
4-6 METRES	NEW	70	187
	OLD	72	
	VERY OLD	45	
ON THE GROUND	VERY OLD	14	
TOTAL	NEW	213	669
	OLD	254	
	VERY OLD	202	

* height above the ground.

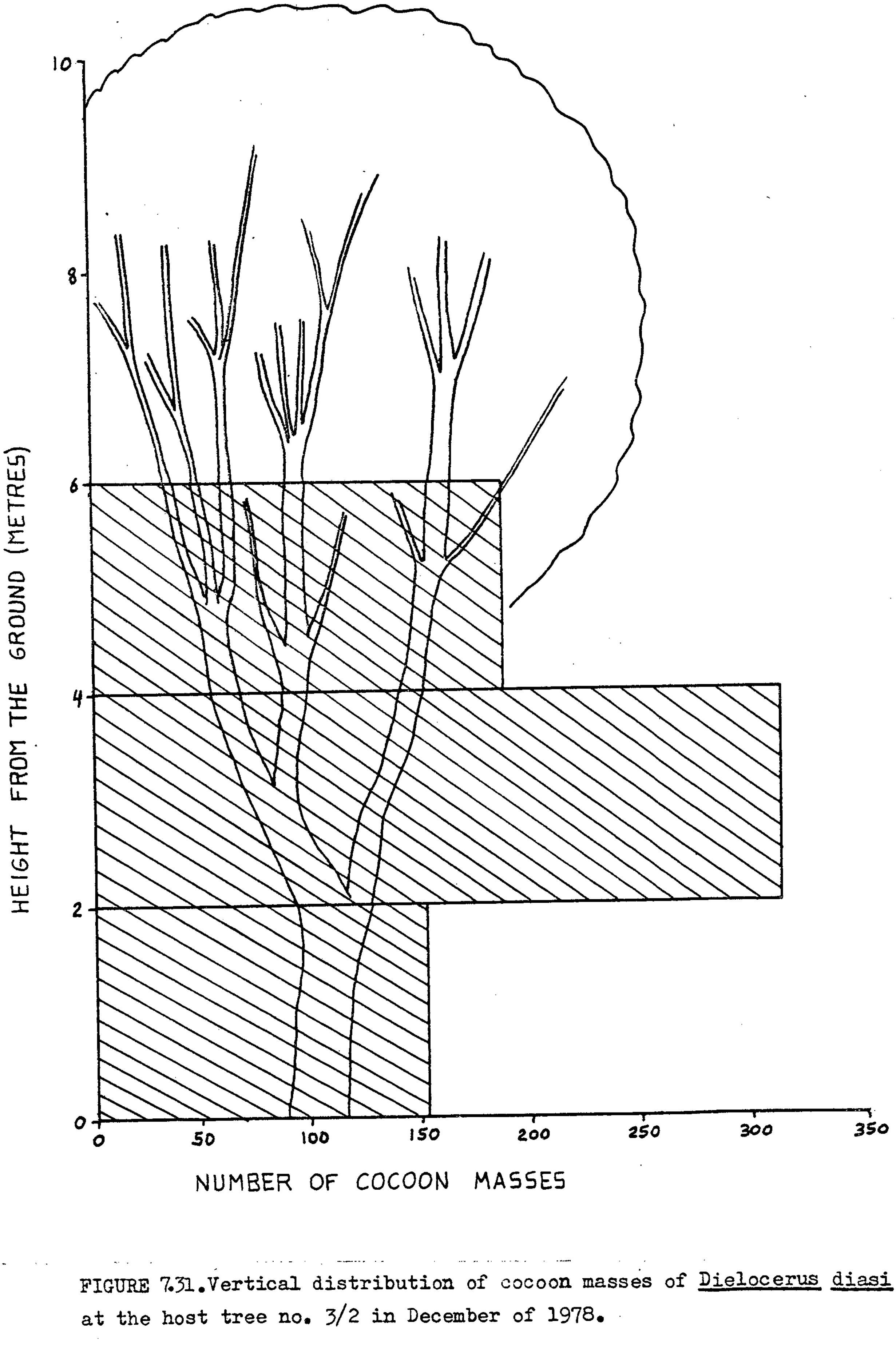


FIGURE 7.31. Vertical distribution of cocoon masses of Dielocerus diasi at the host tree no. 3/2 in December of 1978.

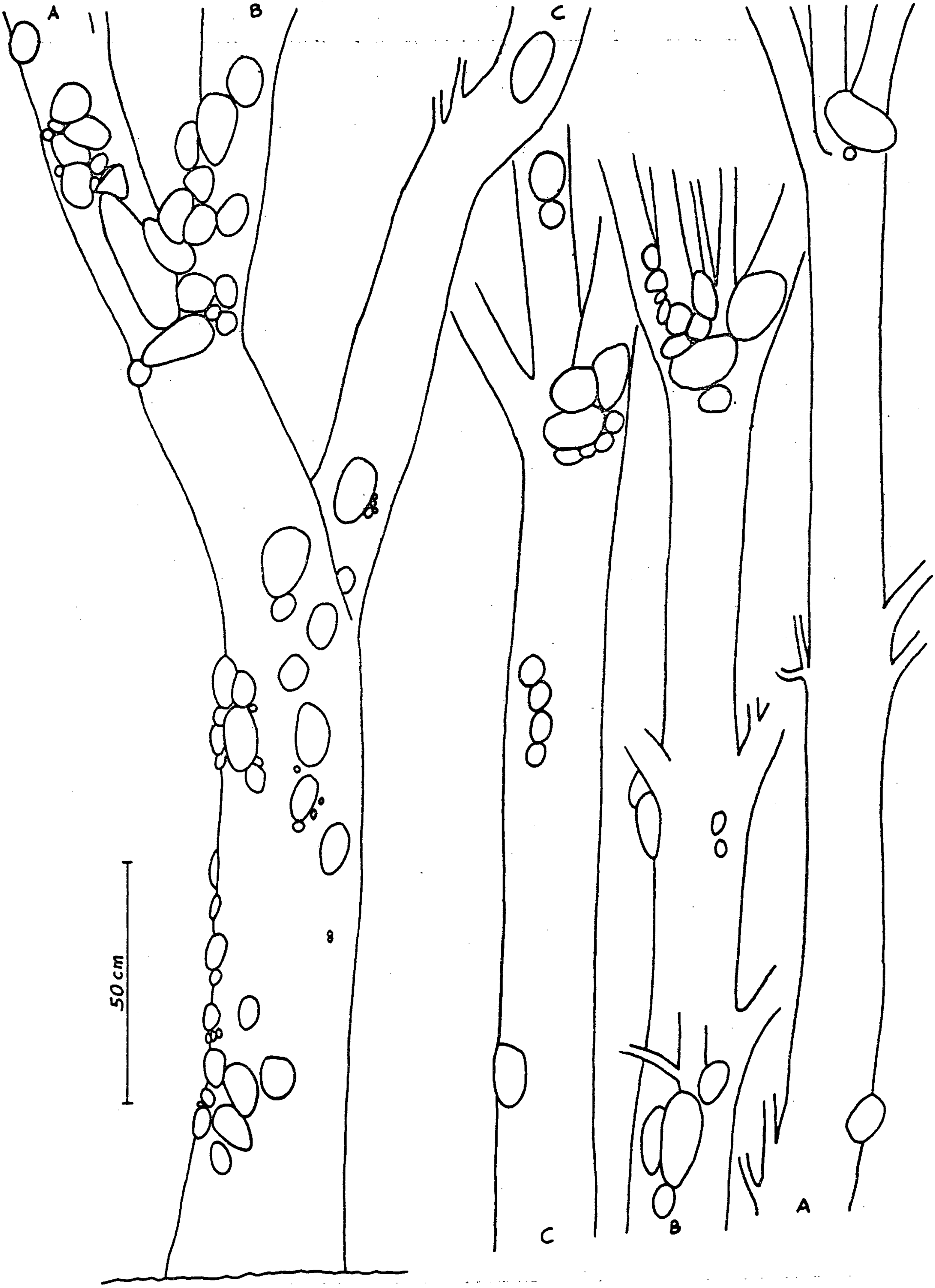


FIGURE 7.32. Distribution of cocoon masses of Dielocerus diasi at tree no. 3/2 in September of 1970.

FIGURE 7.33 (this and the next plate). Cocoon masses of *Dielocerus diasi* tightly clustered on the trunk and lower branches of heavily infested host trees.

in masses of 20 to 160 cocoons each. Among these, almost half belong to groups with 20 to 60 cocoons each. The modal class of frequency of cocoons per cocoon mass size grouped in classes of 20 is that of 20 to 40 cocoons per mass (Figure 7.34).

Looking at this from another perspective, the frequency distribution of cocoon masses (y) is negatively correlated with the number of cocoons per mass (x) (Figures 7.35 and 7.36). The best fitting curve is an inverse power curve ($y = 2306.75\ x^{-1.34}$, where x is the mean of each 10 x 10 class of x). The correlation coefficient, $r = -0.9667$, is highly significant at $\alpha = 0.001$. The standard error of estimate of y is $S_{y.x} = 0.2979$. The average number of cocoons per mass is 32. Most cocoon masses (68%) have less than 30 cocoons each; in fact, 40% have less than 10 cocoons each. Figure 7.37 gives details of the frequency distribution of cocoon masses according to the number of cocoons per mass for the initial interval of cocoon masses with 1 to 40 cocoons. The best fitting curve is also a negative power curve ($y = 27.11\ x^{-0.56}$), although it is somewhat different from the anterior. The correlation coefficient, $r = -0.7643$, is highly significant at $\alpha = 0.001$. But this correlation explains only 58% of the variance of y. The rest of the variance is probably due to random variation and perhaps a polymodal tendency.

Cocoon masses with 9, 10, 12, 13, 21, 25 and 31 cocoons each seem to have a higher frequency than expected by the negative power function (Figure 7.37). This is more evident when the data is plotted in x classes of 2 (Figure 7.38). It looks now that the total distribution is composed of several separate curves, that is, is polymodal. Bearing in mind that the large cocoon masses are the result of the coalescence of two or more larval sib-groups, and assuming that the egg and larval mortality for Dielocerus is similar to that found in Themos (25% in the egg stage and 50% in the larval stage), it would be expected that the mean larval sib-group size at the time of spinning the cocoon is about 30 larvae and therefore we would expect to find a clustering of higher frequencies of cocoon masses around this value. This value agrees with the overall average number of cocoons per cocoon

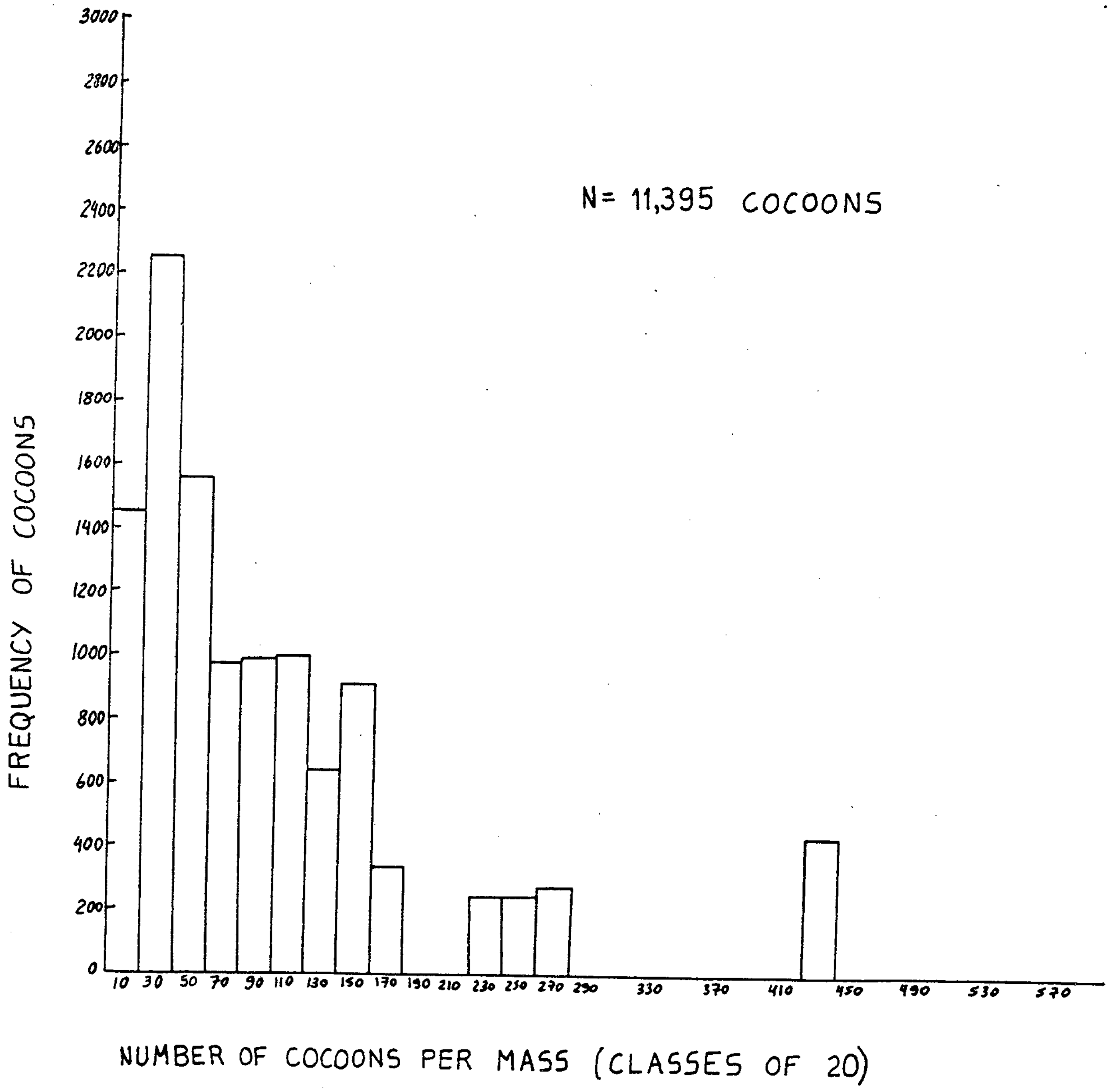


FIGURE 7.34. Frequency distribution of Dielocerus diasi cocoons at tree no. 3/2 in December of 1978 according to the size of their cocoon mass.

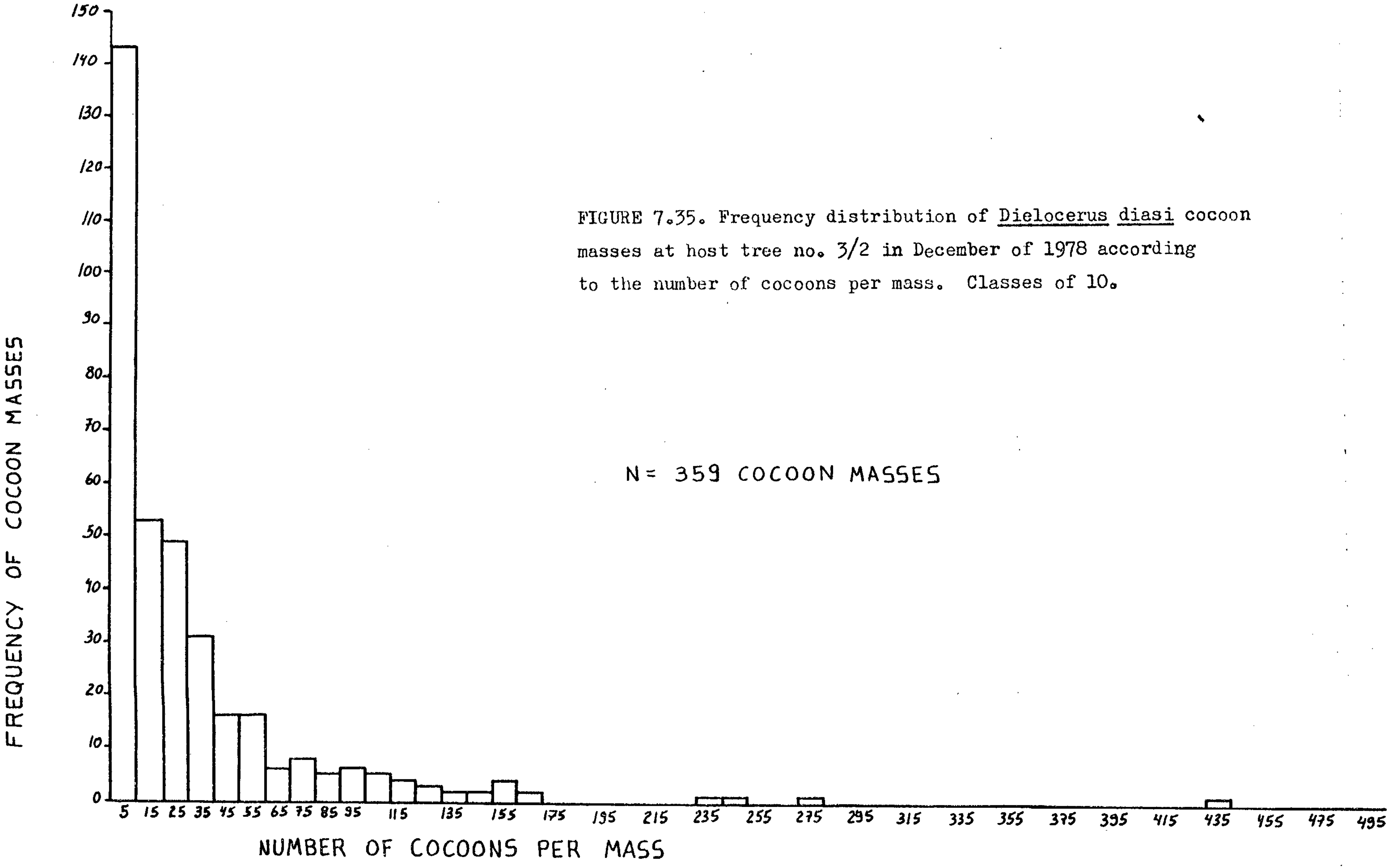


FIGURE 7.35. Frequency distribution of <u>Dielocerus diasi</u> cocoon masses at host tree no. 3/2 in December of 1978 according to the number of cocoons per mass. Classes of 10.

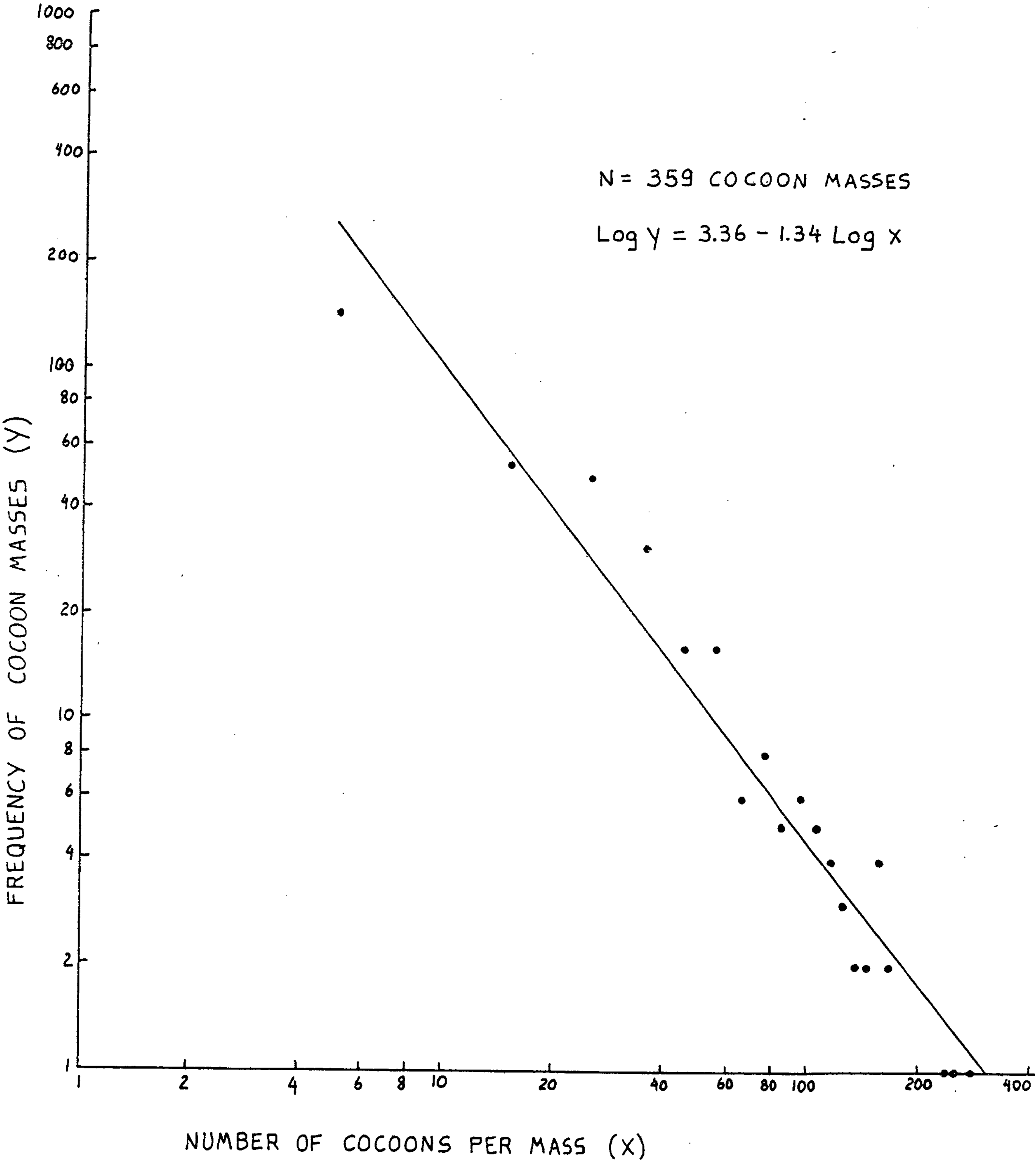


FIGURE 7.36. Regression line of the number of Dielocerus diasi cocoon masses at host tree no. 3/2 in December of 1978 on the number of cocoons per cocoon mass. Log X Log. Classes of 10.

FIGURE 7.37. Frequency distribution of <u>Dielocerus diasi</u> cocoon masses at host tree no. 3/2 in December of 1978 according to the number of cocoons per mass. Detail of the initial interval of cocoon masses with 1 to 40 cocoons. The best fitting power curve is indicated.

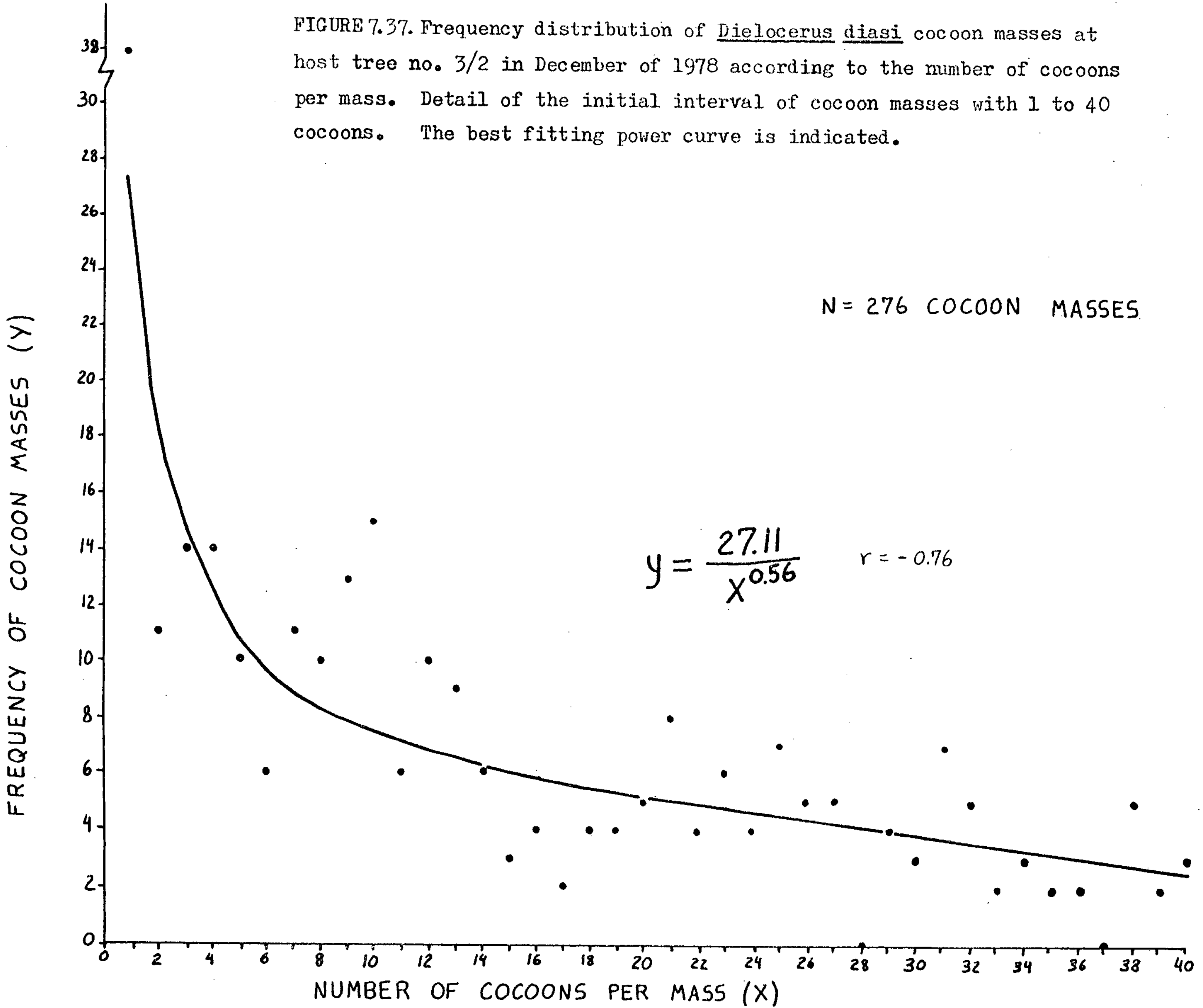
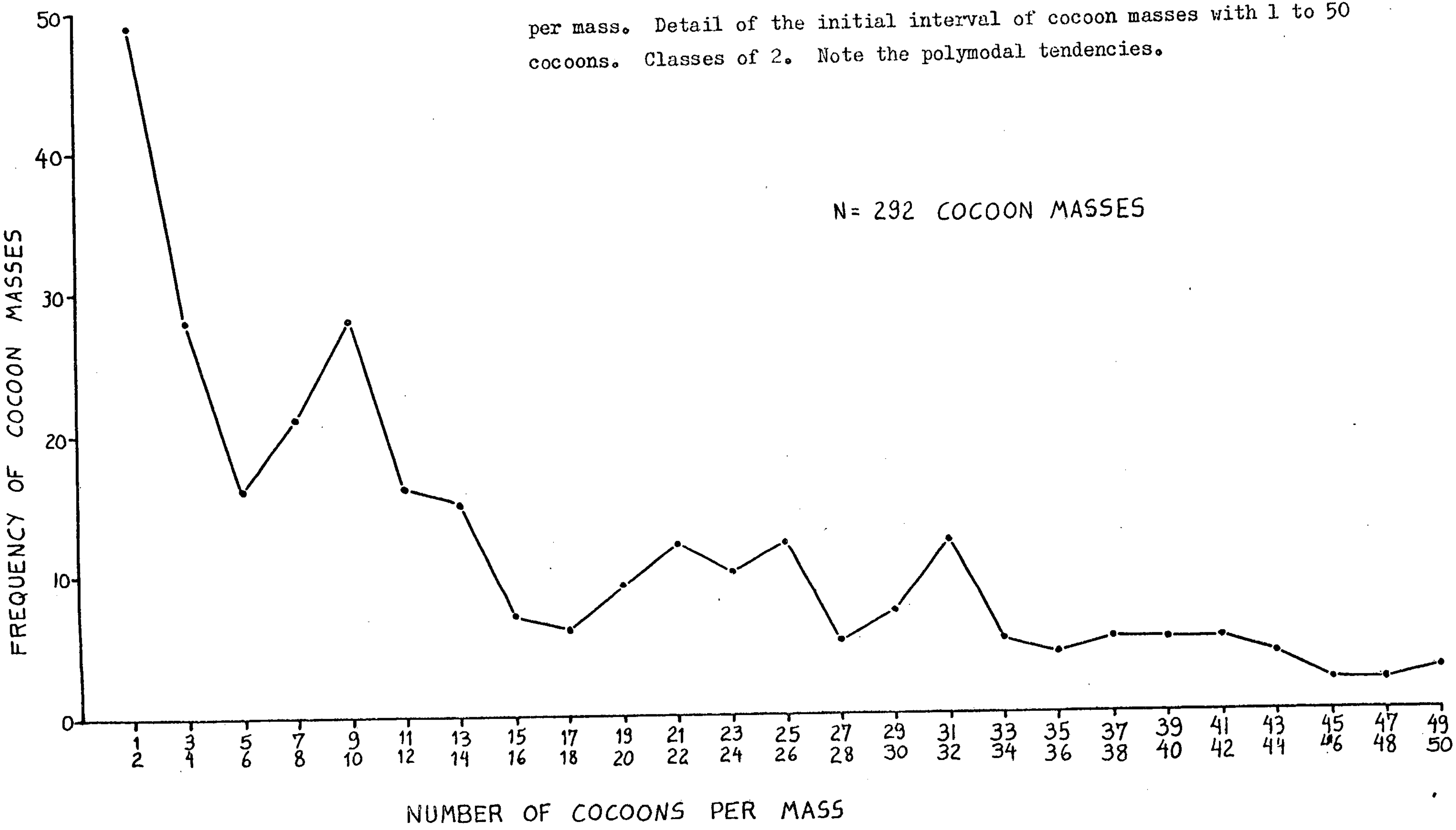


FIGURE 7.38. Frequency distribution of Dielocerus diasi cocoon masses at host tree no. 3/2 in December of 1978 according to the number of cocoons per mass. Detail of the initial interval of cocoon masses with 1 to 50 cocoons. Classes of 2. Note the polymodal tendencies.



mass in this sample (32 cocoons), and with the modal class of cocoon frequency according to cocoon mass size (see Figure 7.34) and indeed there is a higher frequency of cocoon masses with 21 to 32 cocoons compared to the frequencies of larger and immediately smaller cocoon masses.

Most of the cocoon masses with less than 15 cocoons each probably result from larval sib-groups which split into smaller groups, and the smallest cocoon masses of all might result from stray larvae. It is difficult to understand the high frequencies of cocoon masses with 9 and 10 cocoons each, unless this is due to a tendency of larval groups to split into two similar half groups. It would be logical to expect to find, thus, an overall polymodal distribution, with modal classes at multiple numbers of 30. Such is not the case however. But given the large variance in sib-group size, this is hardly unexpected.

Figure 7.39 shows how the cocoon arrangement patterns are related to the cocoon mass size. The frequency distribution of parallel plus irregular cocoon masses is strongly "J" shaped, whereas that of the perpendicular cocoon masses is probably polymodal with at least two modals evident at 30-36 and 114-120 cocoons per mass.

The size of the cocoon mass, represented by the area of the ellipse (x) obtained by multiplying the largest diametre by the smaller perpendicular diametre and by π and dividing by 4, is significantly positively correlated with the number of cocoons per mass (y): $y = 42.74x + 8.13$, $r = 0.9323$, $S_{y.x} = 17.6$, significant at $\alpha = 0.001$ (Figure 7.40). These diametre measurements were taken disregarding the external cover of the mass. However, the estimates of the number of cocoons per mass obtained from this correlation with the measured diametres of the cocoon masses have an error of up to 45% and are therefore very inaccurate. Perhaps the volume of the cocoon mass would yield better estimates.

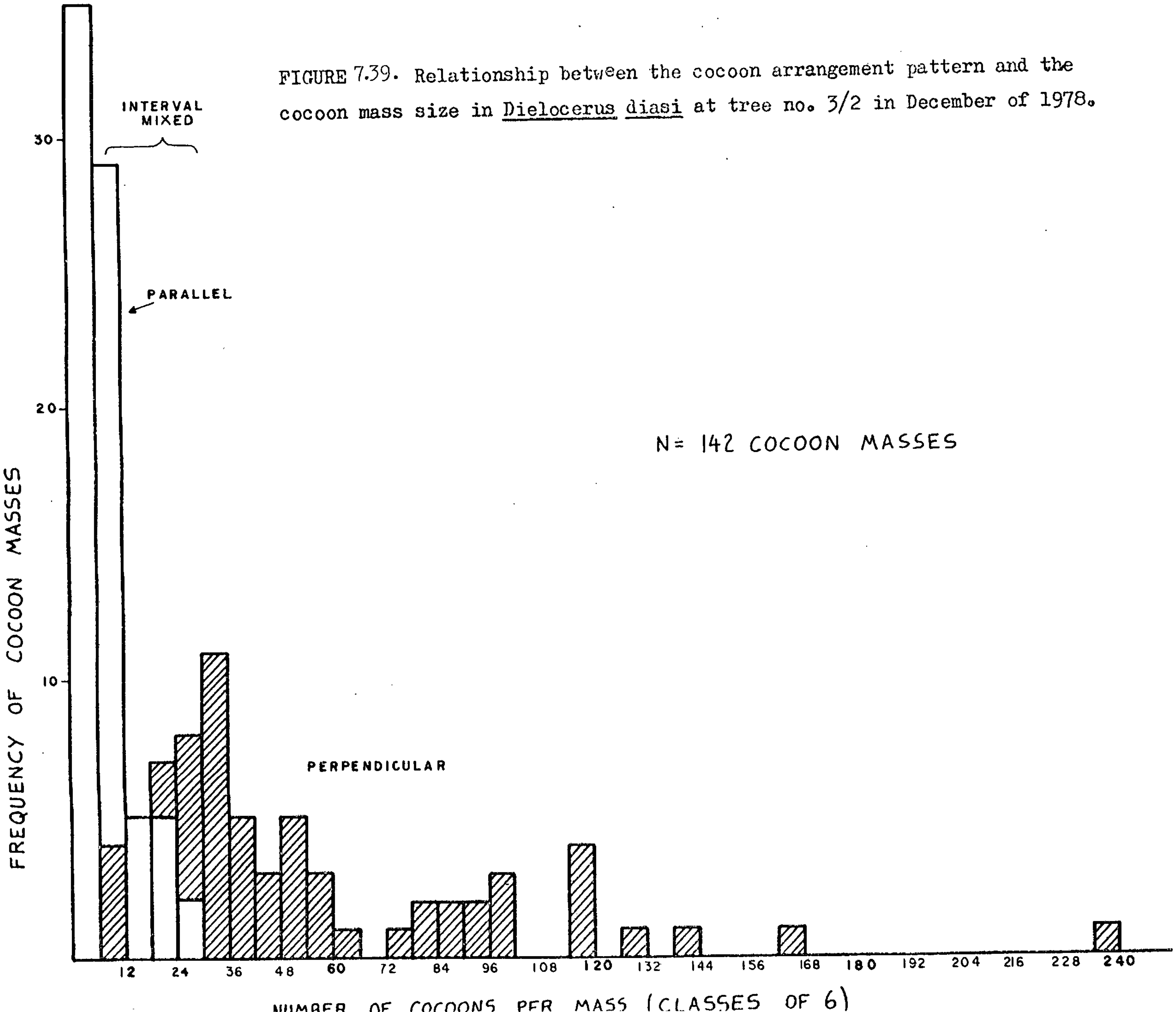


FIGURE 7.39. Relationship between the cocoon arrangement pattern and the cocoon mass size in *Dielocerus diasi* at tree no. 3/2 in December of 1978.

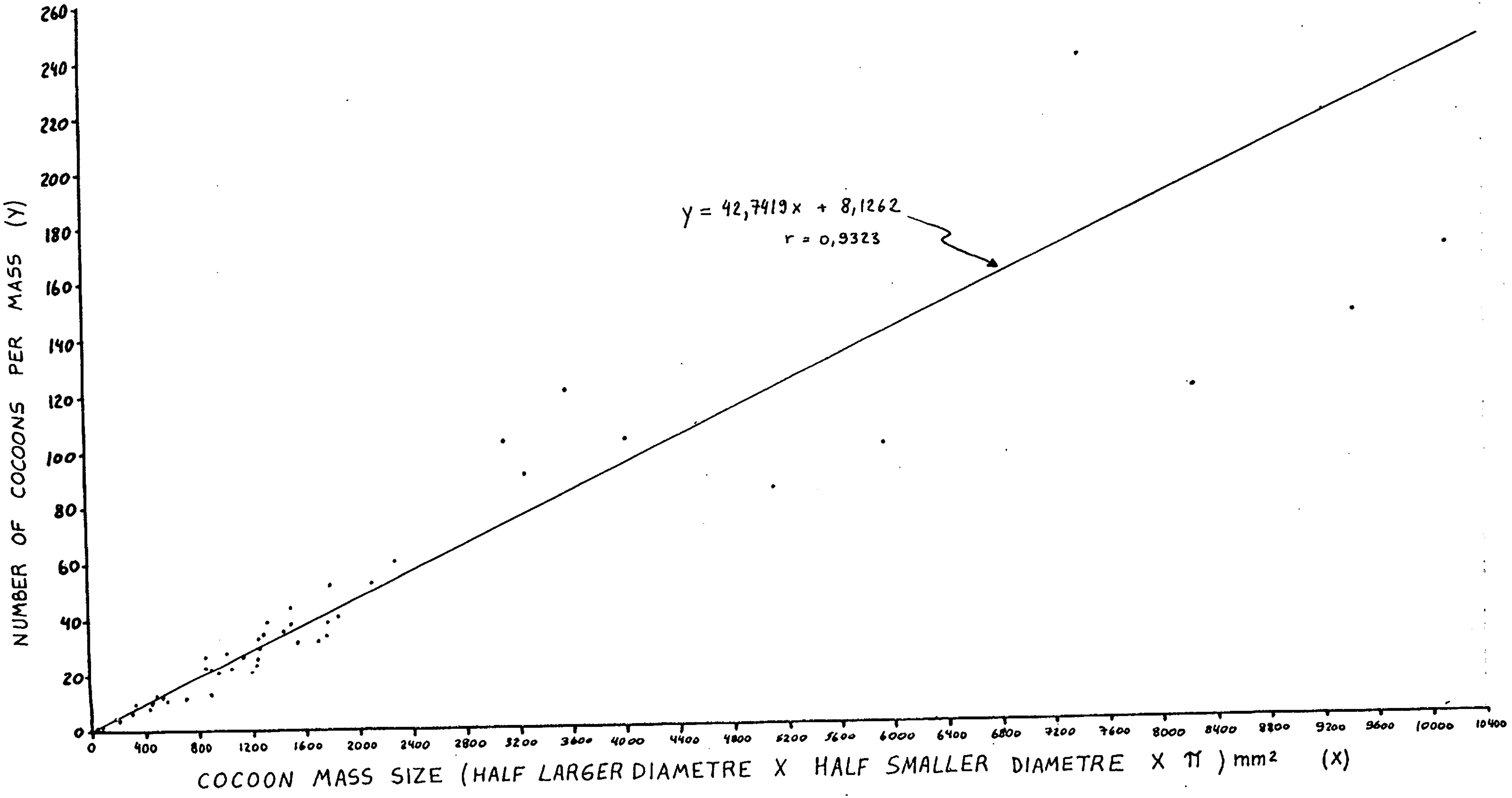


FIGURE 7.40. Correlation of the cocoon mass size (large diametre x smaller diametre in mm^2) with the number of cocoons per mass, in Dielocerus diasi.

7.11 COCOON MORTALITY

Virtually nothing was recorded about the mortality during the cocoon stage of Themos, except that there is a species of Tachinidae fly (Blondeliini, undetermined) which parasitizes the larvae and finishes its development inside the sawfly cocoon.

The average survival percentage of Dielocerus during the cocoon stage (from cocoon spinning until the emergence of the adult) at tree 3/2 was 25%. There is considerable variation on the percentage of survival per cocoon mass, ranging from zero to almost 100%. The frequency distribution (Figure 7.41) has an inverse power curve shape, with 36% of the cocoon masses having only 0 to 5% survival. Most of these cocoon masses with less than 5% survival have less than 10 cocoons per mass (63%). But removing all the cocoon masses with less than 10 cocoons each does not change the shape of the frequency distribution (Figure 7.41 top). This shows, however, that there is some relationship between the survival percentage per cocoon mass with the size of the cocoon mass, as 64% of all cocoon masses with less than 10 cocoons each have less than 5% survival as compared to only 20% of the cocoon masses with 10 or more cocoons per mass. However there is no significant correlation between the average percentage survival per cocoon mass with the number of cocoons per mass (Figure 7.42). Only single cocoons have an average survival significantly smaller than all the grouped ones: only 8%. This value falls outside the range with P = 99% based on all the other values. Cocoon masses with only two cocoons have a much higher survival percentage of 18%. The cocoon masses of the lot "2 to 4 metres/new" had a somewhat smaller average survival percentage of 19.3% as opposed to values between 25% and 27.5% for the other lots.

The major mortality factors and the average percentage of damage which they did to Dielocerus cocoons on tree 3/2 are given in Table 7.III. Six species of parasitoids were recorded emerging from the cocoons of Dielocerus: Spathimeigenia dieloceri

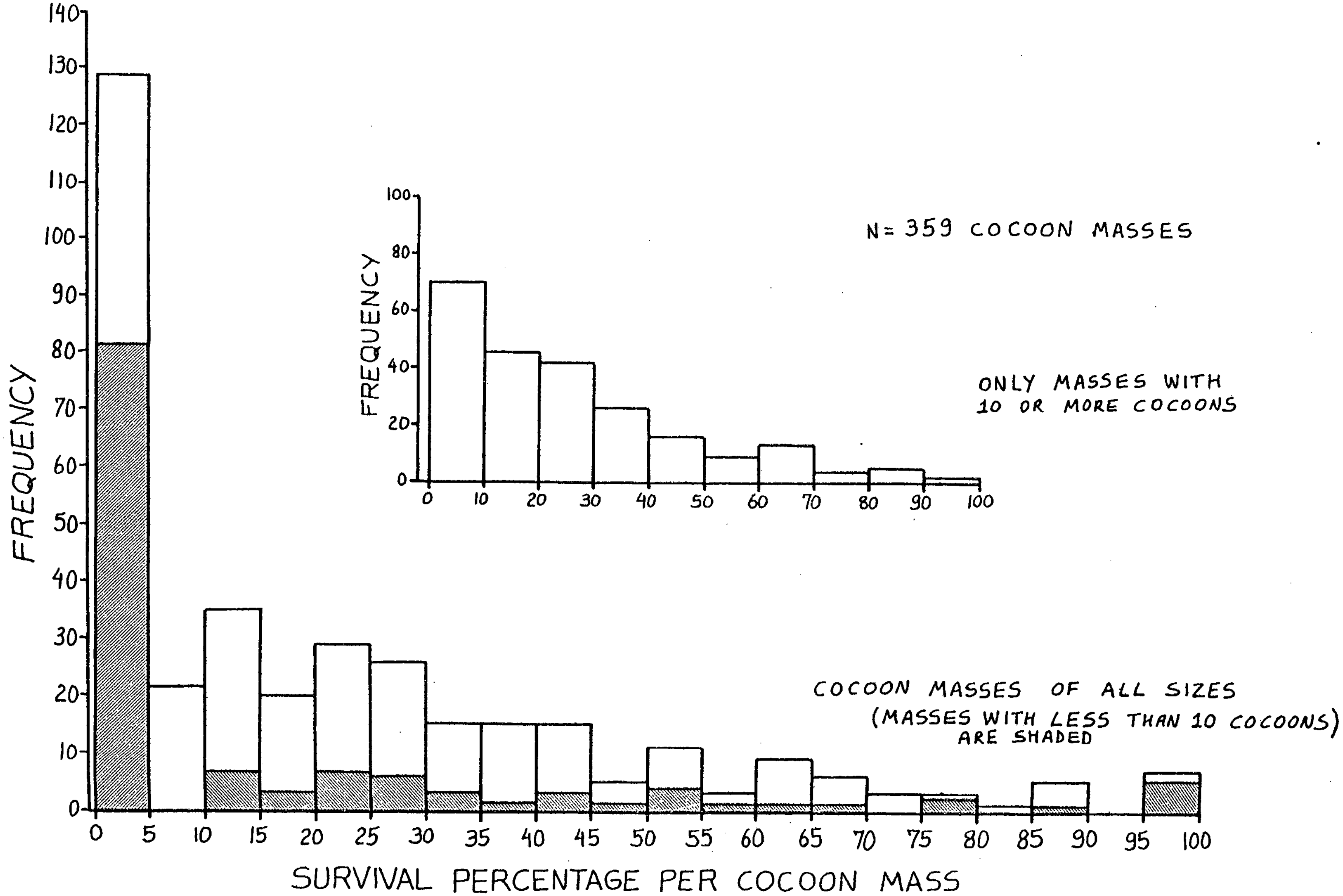


FIGURE 7.41. Frequency distribution of Dielocerus diasi survival percentage per cocoon mass in tree no. 3/2.

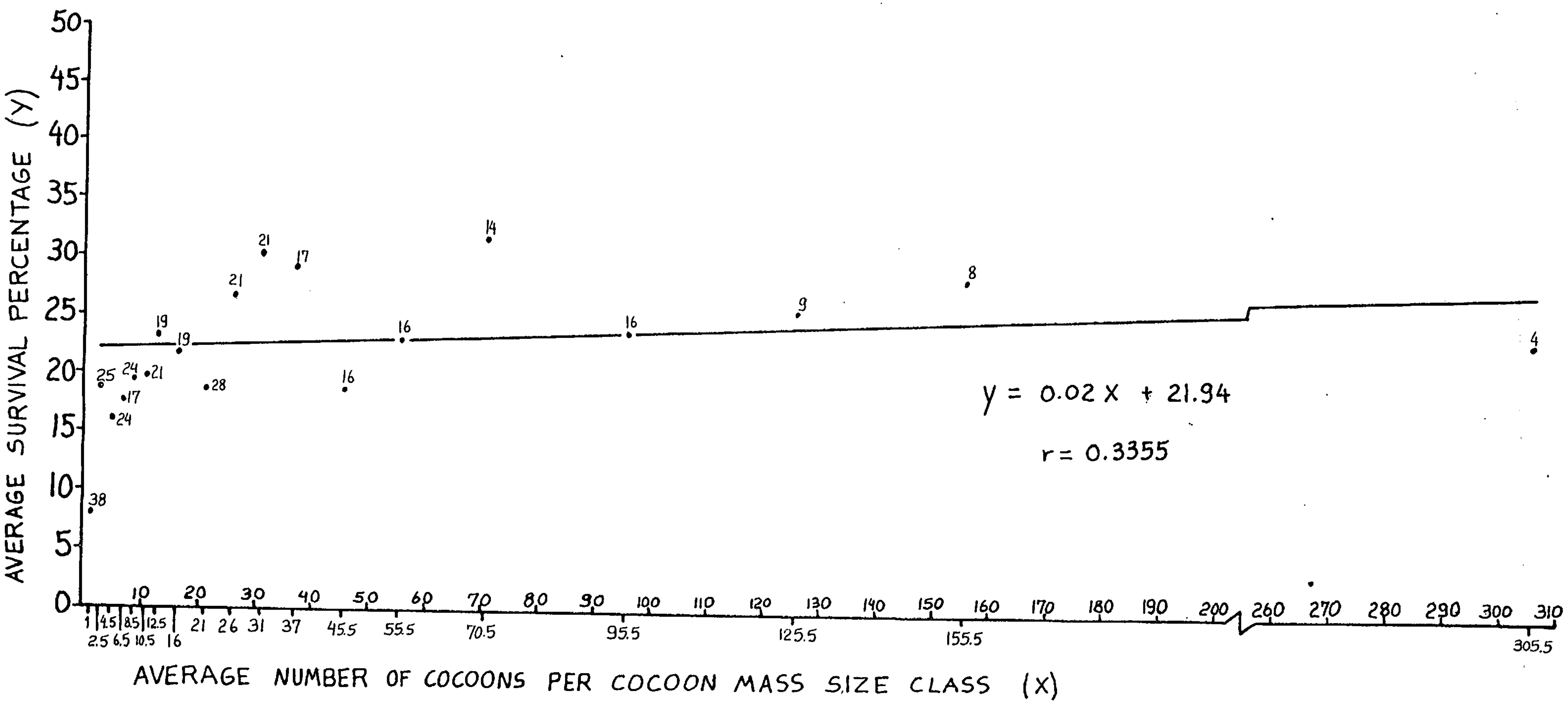


FIGURE 7.42. Relationship between the average survival percentage (y) of Dielocerus diasi per cocoon mass and the number of cocoons per cocoons mass (x). The cocoon masses are grouped in classes which increase in size with the size of the masses (single cocoons are not grouped, masses with 2 to 13 cocoons are grouped in classes of 2, those with 14 to 33 cocoons in classes of 5, those with 34 to 40 in a class of 7, those with 41 to 60 in classes of 10, those with 61 to 80 in a class of 20, those with 81 to 170 in classes of 30 and those with 171 to 440 in one class of 270). The average values are plotted at the average size of mass for each class. The number of cocoon masses in each class is indicated beside each plotted dot. The linear regression of y on x (except for single cocoons) is indicated. The correlation coefficient is not signifficant.

TABLE 7.III

Summary of the total percentages of *Dielocerus diasi* cocoons from which adult sawflies, parasitoids and moths emerged, and the estimates of the number of cocoons which were attacked by each parasitoid species and fungus plus desiccation, and an estimate of the percentage of sawfly larvae which were killed by each mortality factor for the 11,395 cocoons studied from tree no. 3/2.

MORTALITY FACTOR	No. & % EMERGED		ESTIMATED No. & % ATTACKED		ESTIMATED No. & % KILLED	
Spathimeignia dieloceri	3496	(31%)	6240	(55%)	6240	(55%)
Chalcidoids*	88	(0.8%)	250	(2.2%)	250	(2.2%)
Lymeon dieloceri	121	(1.1%)	340	(3.0%)	93	(0.8%)
predation*	55	(0.5%)	55	(0.5%)	24	(0.2%)
fungus + desiccation	3012	(26%)	4790	(42%)	1937	(17%)
Ectomyelois decolor	1779	(17%)	-		-	
TOTAL MORTALITY	8551	(75%)	8551	(75%)	8551	(75%)
Dielocerus diasi	2844	(25%)				

***Spilochalcis* sp., *Brachymeria* sp and unidentified Eupelmidae

**probably by the Campo Flicker, *Colaptes campestris* (Aves, Picidae)

(Townsend, 1942) and Pseudochaeta sp (both Diptera, Tachinidae), Brachymeria sp and Spilochalcis sp (both Hymenoptera, Chalcididae), an unidentified species of Eupelmidae (Hymenoptera, Chalcidoidae), and Lymeon dieloceri (Costa Lima, 1937) (Hymenoptera, Ichneumonidae). The species of Spathimeigenia, Spilochalcis and Lymeon are primary parasitoids of Dielocerus larvae. I do not know whether the Pseudochaeta, Brachymeria and Eupelmidae are primary or secondary parasitoids, or whether they parasitise one of the commensals which infest the older cocoon masses. From the several hundred cocoons reared in the laboratory only one adult Pseudochaeta sp and less than 10 Eupelmidae emerged. Only two out of 90 large cocoon masses reared in the laboratory were parasitised by Brachymeria sp, each producing only one adult parasitoid. But Brachymeria sp was not so rare at tree no. 3/2. Spilochalcis sp was more common, although still rare if compared with Spatimeigenia and Lymeon. Only three out of 90 large cocoon masses were parasitised by Spilochalcis sp, though one of them had 34 out of 57 cocoons parasitised by this Chalcidid. Adult Pseudochaeta, Brachymeria and unidentified Eupelmidae were never seen in the field, but one adult Spilochalcis was once seen attacking a group of third or fourth instar larvae to lay its eggs on them (see Chapter on larval behaviour). Cocoons attacked by Spilochalcis are easily recognized by the diametre of the round emergence lide (2.5 to 3.1mm) and by the nature of the remains inside the cocoon. The host sawfly larva is reduced to an unrecognizable round dark brown pasty ball with approximately 3mm in diametre, and the bottom fourth of the cocoon is filled with the brown fluid defecation of the parasitoid and covered by a thin membrane. The parasitoid pupa stands free above the defecation suspended by a thin petiole (Figure 7.43). Adult Chalcidoids emerged from less than 1% of the cocoons on tree 3/2. The cocoon masses from lot "2 to 4 metres/new" produced much less Chalcidoids than the other lots: only 0.2% compared with an average of 1% in the other lots.

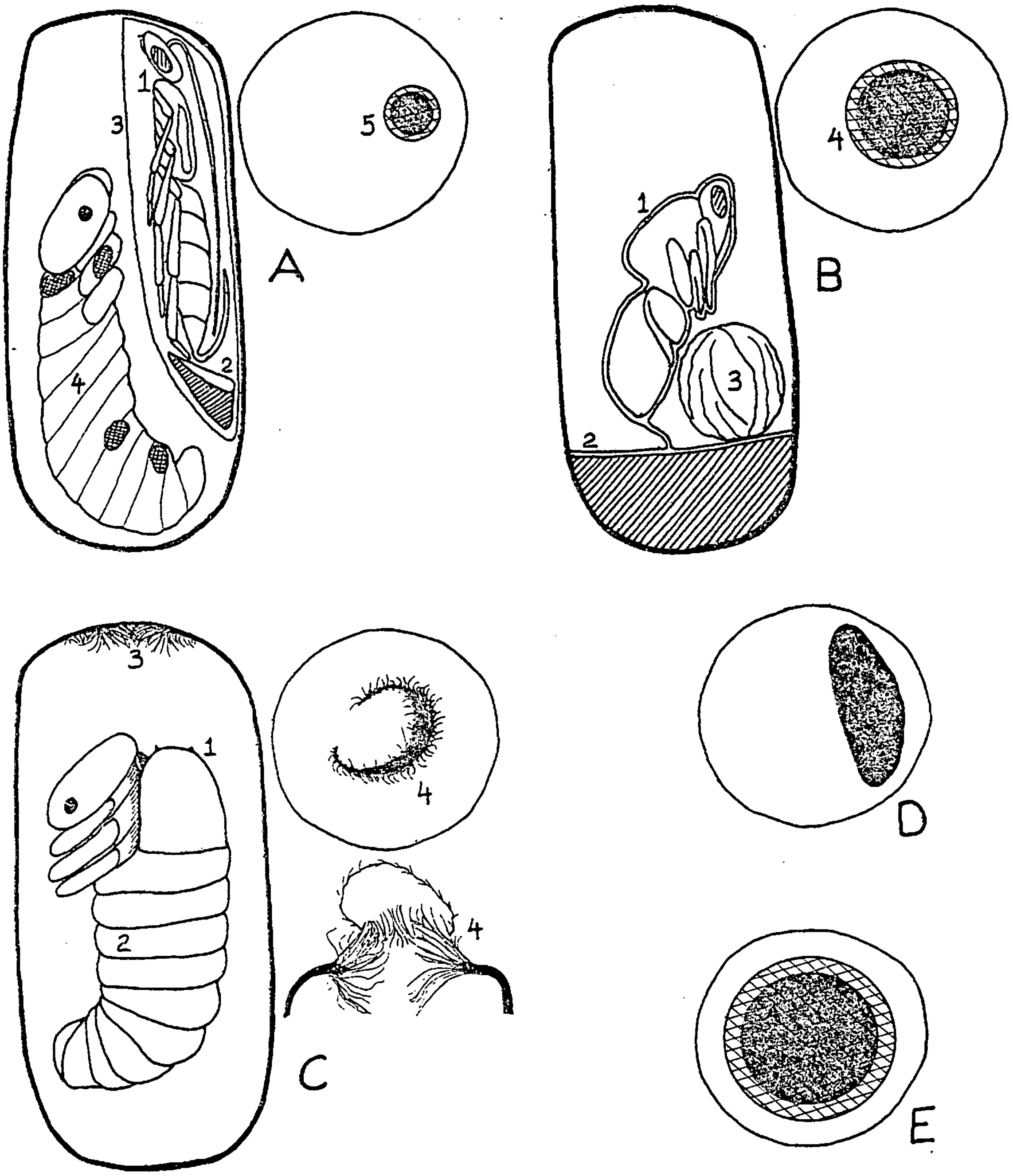


FIGURE 7.43. Cocoons of Dielocerus diasi attacked by parasitoids, showing their contents prior to emergence and also their emergence holes (top view). A) cocoon attacked by Lymeon dieloceri (Costa Lima)(Ichneumonidae), 1 = female pupa of parasitoid, 2 = parasitoid meconium, 3 = parasitoid silk cocoon, 4 = remains of sawfly larva, 5 = emergence holes (top view) (inner circle made by males and outer circle made by females); B) cocoon attacked by Spilochalcis sp (Chalcididae), 1 = parasitoid pupa, 2 = parasitoid meconium, 3 = remains of sawfly larva, 4 = emergence holes (top view) (inner circle made by males and outer circle made by females); C) cocoon attacked by Spathimeigenia dieloceri (Townsend)(Tachinidae), 1 = parasitoid pupa, 2 = remains of sawfly larva, 3 = sawfly cocoon wall scratched by parasitoid larva, 4 = emergence hole and lid, top and side view; D) emergence hole (top view) made by Ectomyelois decolor (Zeller)(Pyralidae), a scavenger; E) emergence holes (top view) made by Dielocerus diasi, inner circle by male sawflies and outer circle by female sawflies. All drawings on the same scale: 5X natural size.

Spathimeigenia dieloceri was by far the most important parasitoid of Dielocerus at tree 3/2, where 31% of the cocoons produced adult flies. Cocoons in lot "4 to 6 metres/new" were relatively more attacked (38%) than the others (28% to 30%). It was also the most prevalent parasitoid found in cocoon masses taken to the laboratory collected in several different localities in the Federal District. No adult fly of this species was ever seen in the field attacking the larvae, although it has been recorded in the literature that this fly attacks the host in the late larval stage. Several sib-groups had up to two-thirds of the larvae parasitised by this fly.

Cocoons attacked by Spathimeigenia can be easily recognized by the nature of the emergence aperture and of the remains inside the cocoon. The fly larva consumes only the fluids and inner structures of the host larva leaving the external skeleton intact but shrunken, and comes either totally or partially (through the dorsal membrane between the third thoracic and the first abdominal segments) out of the host larva to pupate (Figure 7.43). The puparium is cylindric and is on average 9 to 9.5mm long and 3.5 to 4mm wide. But before pupating, the fly larva scratches the inner surface of the cocoon's top making the wall here very thin. When emerging, the adult fly expands its ptilinum and with it presses against the top of the cocoon thus opening a semi-circular lid. This opening is very characteristic and makes it easy to detect cocoons attacked by this parasitoid (Figure 7.43). The adult fly seems to have difficulty in making its way through the spongy layer of the communal envelope, for it is common to find dead flies trapped in this layer of silk. Most flies in the same cocoon mass emerge through the very same opening in the outer paper-like cover.

Lymeon dieloceri was also a common parasite in most patches where Dielocerus occured. This Ichneumonid emerged from 19 of 90 large cocoon masses reared in the laboratory, and some of these cocoon masses had more than 80% of their cocoons parasitised by the Lymeon. But it was very rare at tree 3/2, where adults emerged from only about 1.5% of the cocoons. Cocoons from lot "2 to 4 metres/new" were less attacked (only 0.2%) than in other lots (1.1 to 1.5%). This parasitoid consumes the larva's fluids and inner structures and perforates the external cuticle in several places. After finishing feeding, the parasitoid larva crawls out of the host and spins a white papery silk cocoon on the corner of the host cocoon facing opposite the tree trunk, inside the host's cocoon. Inside its cocoon the Ichneumonid larva defecates producing a hard brown meconium. When emerging, the adult Lymeon opens a round narrow lid on the top of its host's cocoon. This lid has a diametre of 1.5mm for the females and 1.1mm for the males (Figure 7.43). As with the Tachinid fly, this parasitoid seems also to experience some difficulty in trespassing the spongy layer of the communal envelope, and it is not rare to find adult Lymeon dead trapped in the outer cover. Lymeon females are commonly seen in the field moving on top of newly spun cocoon masses. The females totally ignore mature Dielocerus larvae which are just beginning to spin their cocoons. As she moves on top of the cocoons, her antennae tap alternately the surface.

A further unknown species of parasitoid was recorded attacking the larvae of D. diasi killing them just after they finish spinning the outer papery white silk communal covering, but before they spin their individual cocoons. Each parasitoid makes its own small emergence hole in the outer covering wall of the larval mass. Several dozen parasitoids emerge from the same larval mass, leaving the outer papery wall full of small holes, giving it a sieve-like appearance. Only a few larval masses were found to be attacked by this parasitoid, none of them in tree no. 3/2.

No correlation was found between the average percentage of cocoons parasitized per cocoon mass at tree 3/2 with the number of cocoons per cocoon mass. As Spathimeigenia comprised about 95% of all parasites emerged, this lack of correlation applies specially to it. Unfortunately nothing can be said regarding the other parasitoids because of their very low frequencies (Figure 7.44).

Predation was always very low. In tree 3/2 only 0.5% of all the cocoons were destroyed by predators. Predator attacks were never witnessed, and the identity of the animal(s) responsible for these attacks is still not known, although heavy suspicion falls on

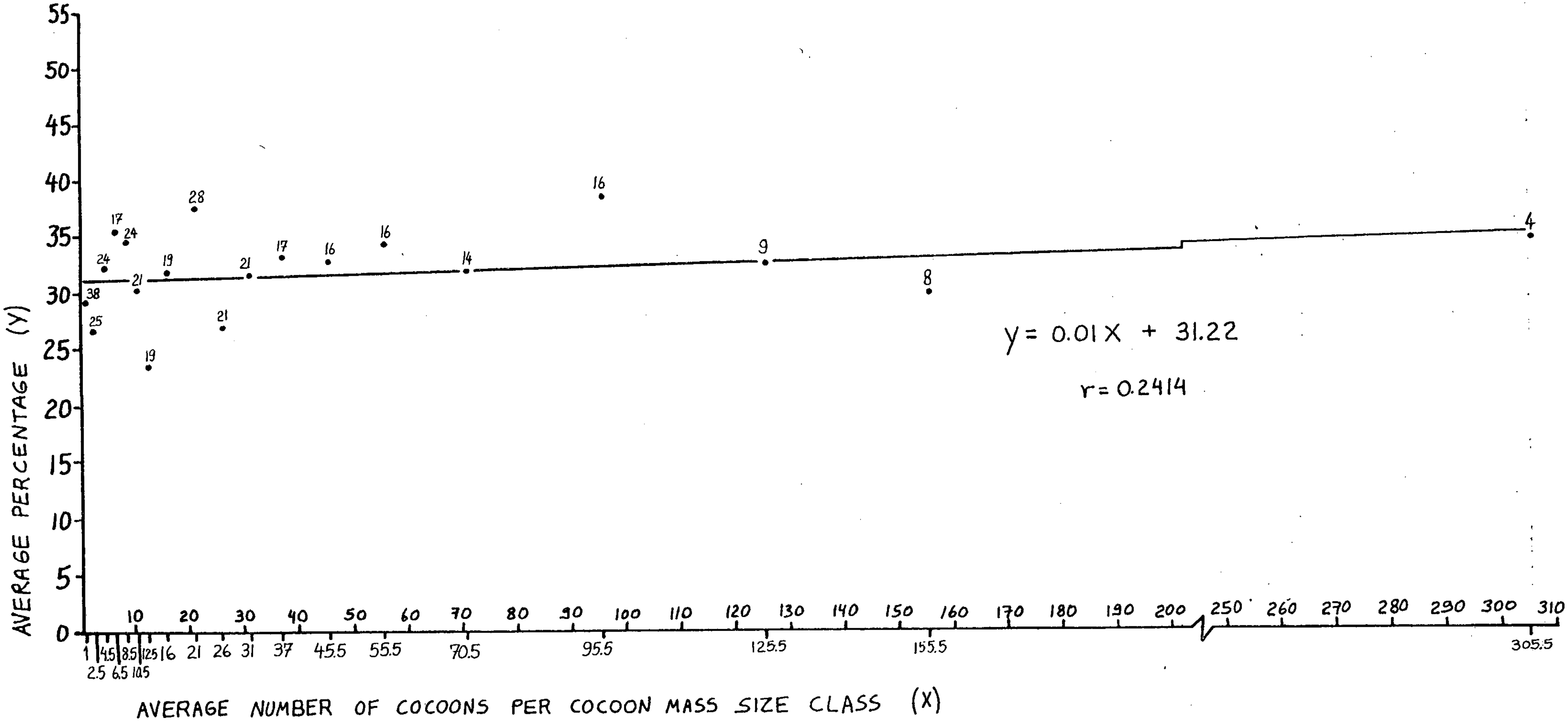


FIGURE 7.44. Relationship between the average total percentage of cocoons producing adult parasitoids (specially *Spathimeigenia dieloceri* = 95%) per cocoon mass (y) of *Dielocerus diasi* and the number of cocoons mass (x). The linear regression of y on x (including single cocoons) is indicated. The correlation coefficient is not significant. See figure 7.42 for additional explanation.

the common Campo Flicker, Colaptes campestris (Aves, Picidae). In all the cases of predation, only a few cocoons in each cocoon mass were destroyed, and the squeezed larvae could be found on the ground just below the cocoons, uneaten.

A large number of cocoons (26%) at tree 3/2 remained closed. Their prepupae were killed either by desiccation (specially in the dry season) or fungi (specially in the rainy season). The desiccated prepupae become shrunk and hard, while the cocoons attacked by molds become totally covered and filled with white mold. The incidence of molds and desiccation among cocoon masses varied greatly between the different lots, from 19% to 37%. In both height intervals studied, the oldest cocoon masses had less closed cocoons than the newer ones. There is no significant correlation between the average percentage of closed cocoons per cocoon mass with the number of cocoons per mass (Figure 7.45). Only single cocoons are significantly more susceptible to desiccation plus mold than grouped cocoons.

After the first adults emerge from the cocoon masses, these are colonized by larvae of a scavenger Pyralid moth, Ectomyelois decolor (Zeller) (Lepidoptera, Pyralidae, Phycitinae). These caterpillars eat the remains of exuviae and dead larvae inside the cocoons, and burrow passages from one cocoon to another with powerful mandibles. When full grown they pupate inside the sawfly's cocoon and either emerge through the lid opened by the adult sawfly or parasitoid which emerged from that cocoon before, or open their own irregular narrow slit, in the case of closed cocoons (Figure 7.43). Cocoon masses with high incidence of desiccated cocoons are prefered by the moth. As the time passes these heavily infested cocoon masses become so much mined, like a swiss cheese, rendering it impossible to collect information on the incidence of parasitoids in them, for the characteristic openings and remains of each species are destroyed. Nevertheless, the percentage of adult sawflies emerging from each cocoon mass can always be easily verified, because the sawflies' openings are

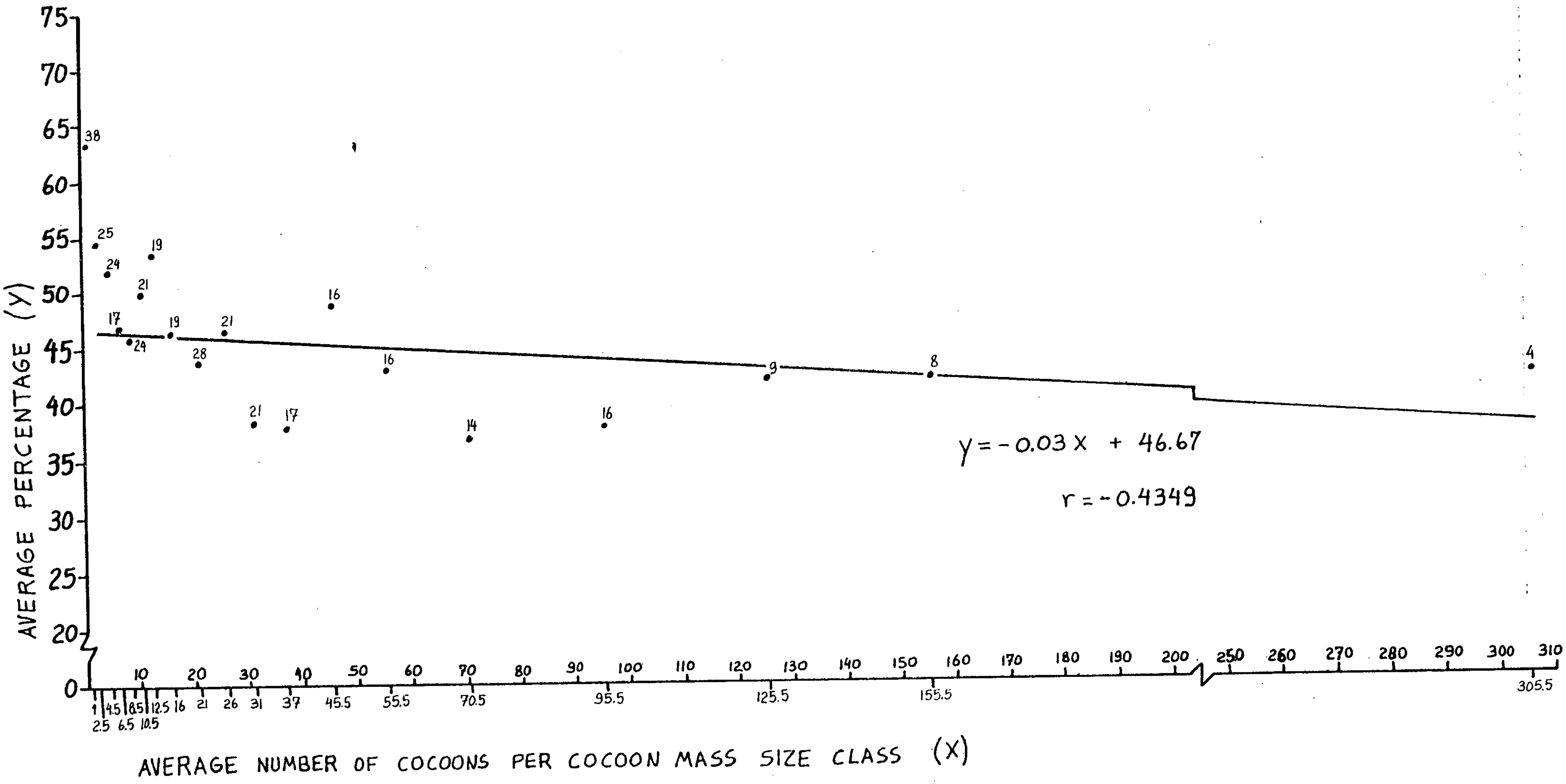


FIGURE 7.45. Relationship between the average percentage of closed cocoons (larvae killed by desiccation or fungus) per cocoon mass (y) of Dielocerus diasi and the number of cocoons per cocoon mass (x). Some of these closed cocoons were attacked by the scavenger moth Ectomyelois decolor. The linear regression of y on x (except for single cocoons) is indicated. The correlation coefficient is not significant. See figure 7.42 for additional explanation.

very wide and not disturbed by the moth. Therefore, the study of very old cocoon masses infested by this moth is very difficult.

About 17% of the cocoons on tree 3/2 had the characteristic moth opening. There was no difference between old and new cocoons in the "2 to 4 metres" lot: both had 14% of the cocoons with moth openings. But the difference between old and new cocoons in the "4 to 6 metres" lot was great: 24% of cocoons had moth openings in the old cocoons lot compared with only 9.4% in the new cocoons lot. But as the moth is only a scavenger, the sawfly larvae inside these 'moth opened' cocoons died of other causes: either desiccation, mold or <u>Lymeon</u> attack. Of all parasitoids, the moth decharacterize only the openings of <u>Lymeon</u>, for they are too narrow for the moth. Assuming that the moth has no preference for either closed or <u>Lymeon</u>- attacked cocoons, the death of the 1779 cocoons with moth openings in tree 3/2 should be attributed to desiccation plus mold and <u>Lymeon</u> in the proportion of 26:1.1. Therefore the estimated percentage of cocoons attacked by desiccation plus mold would raise to 41.4% and those attacked by <u>Lymeon</u> to 1.9%.

The incidence of mold and desiccation probably did not discriminate between healthy and parasitised larvae in the cocoons, and so the estimated percentage of cocoons parasitised by <u>Lymeon</u> could have been as high as 2.5%.

Only 6428 larvae (2844 producing <u>Dielocerus</u> adults, 3496 producing <u>Spathimeigenia</u> and 88 producing Chalcidoids) were not attached by mortality factors after they spun their cocoons. Therefore it can be seen that the percentage of larvae already parasitized before cocooning by <u>Spathimeigenia</u> was around 54%, and by the Chalcidoids around 1.5%. Taking into account the possibility of competition between the different parasitoids due to multiparasitism, and looking at the different possible outcomes, the estimated percentages of cocoons attacked by each parasitoid species, predator, desiccation plus mold were calculated (Table 7.III). This table also gives the estimated percentage of cocoons which were killed by the different mortality factors. By far the most important mortality agent at tree 3/2 was the Tachinid fly <u>Spathimeigenia</u>, responsible for killing just over half of the larvae of <u>Dielocerus</u> which spun their cocoons. Other parasitoids and predators were insignificant in this tree, but desiccation and mold attacked about 42% of the cocoons, being responsible for the death of about 17% of <u>Dielocerus</u> larvae in the cocoon. The sequence of attack of the several death factors can be better understood from Figure 7. 46.

Old <u>Dielocerus</u> cocoons are utilized by several small arthropods as shelter, nesting or feeding sites: spiders, pseudoscorpions, mites, springtails, booklice, ants, termites, mantids, moths, beetles, wasps and bees. <u>Ectomyelois</u> caterpillars are the ones that contribute most to the decay of the cocoon masses besides fire. After several years, the cocoon masses, specially those attacked by <u>Ectomyelois</u>, ants, termites, and fire, loose their grip to the bark and fall to the ground where they are rapidly decomposed, specially by termites and microorganisms.

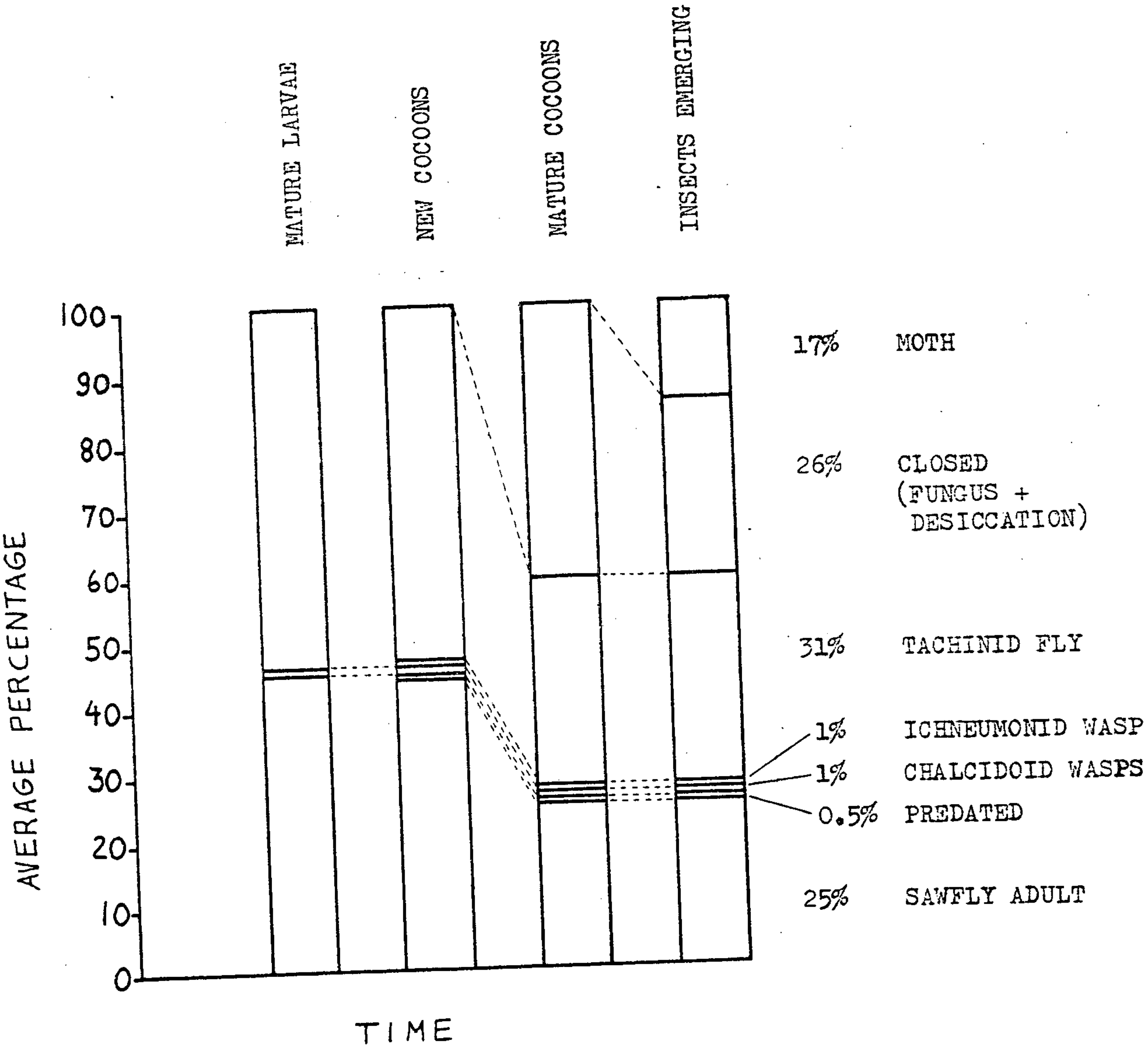


FIGURE 7.46. Sequence in which Dielocerus diasi cocoons were attacked by the different mortality factors on tree no. 3/2.

7.C DISCUSSION

The larval groups of Dielocerus diasi and Themos olfersii are two expressions of what Lindauer (1965) called "primitive communities". However they probably rate among the most socialized of such communities as not only the larvae are gregarious throughout their feeding stage but they exhibit considerable overlapping of generations, maternal care of eggs and young larvae and in the case of D. diasi the cocoons are also spun together under a communal cover. An average long-lived female of D. diasi spends about half of its approximately 100 day-long life overlapping with relatives from other generations (half of this with her mother and half with her own offsprings), and the other half is spent in sib-group associations with no overlapping of generations. For only one or two brief days in her life does she have a relatively solitary life (from the time she emerges as an adult from the cocoon until the time she lays her eggs), relatively because most of this time is spent near other adult females (some of which are closely related to her) and adult males which attempt to mate with her (some of which may also be closely related to her). The same applies to the slightly longer-lived (about 110 days) T. olfersii female, only that during the cocoon stage the individuals in a sib-group do not stay as close together as those of D. diasi.

Lindauer (1965) characterized primitive communities as those associations which have extensive coordination for moving, nest building and defence, gathering determined by mutual attraction and reciprocal sensorial stimulation, having frequently a temporary nature and being largely facultative and open. The communities of D. diasi and T. olfersii exhibit elaborate coordination of larval moving, feeding, defending, cocoon spinning (in D. diasi) and soil digging (T. olfersii), larval-larval and mother-offspring mutual attraction, and are of an open nature as they readily accept new members (other larvae or post-reproductive females). But, while the groupings are of a facultative nature in the sense that the individuals are able to live and develop alone, they are apparently less able to develop and survive against predators if they are alone. Their communities, as far as the immatures are concerned, are of a permanent nature which are only dissolved when the adults emerge from the cocoon.

Larval gregariousness is a common phenomenon among four groups of Tenthredinoid sawflies: Argids, Pergids, Diprionids and Nematines. The following genera in these groups are known to have species with gregarious larvae:

Argidae - *Arge* (Meirleire, 1969), *Dielocerus* (Curtis, 1844; Dias, 1976 and this study), *Digelasinus* (Benson, 1978a; Monte, 1946), *Dydimia* (Dias & Smith, in prep.), *Pachylota* (Benson, 1938a; Dias, in prep.b), *Pampsilota* (Togashi, 1975), *Sericoceros* (Martorell, 1941), *Sphacophilus* (Ross, 1933) and *Themos* (Klug, 1850; Dias, 1975 and this study); Pergidae - *Acordulecera* (MacGillivray, 1913), *Haplostegus* (Pyenson, 1940), *Lophyrotoma* (Tryon, 1921), *Perga* (Carne, 1959, 1962; Evans, 1934), *Pergagrapta* (Meyer-Rochow, 1972), *Perreyia* (Costa Lima, 1941; Camargo, 1956; ? Wheeler & Mann, 1923), *Philomastix* (Leask, 1944a), *Pseudoperga* (Lewis, 1836; Froggatt, 1901) and *Syzygonia* (Marques, 1933); Diprionidae - *Diprion* (Eliescu, 1932; Prop, 1960), *Gilpinia* (Beaver & Laosunthorn, 1974; Knerer, 1977; Pschorn-Walcher, 1962), *Microdiprion* (Pschorn-Walcher, 1962; Mallach, 1974), and *Neodiprion* (Atwood & Peck, 1943; Kalin & Knerer, 1977; Ghent, 1960; Lyons, 1962; Prop, 1960; Tostowaryk, 1972); and Nematine - *Croesus* (Benson, 1958; Caccamo, 1966), *Hemichroa* (Berland, 1947; Hopping, 1937), *Nematus* (Benson, 1950, 1958; Cameron, 1878; Miles, 1932), *Pachynematus* (Pschorn-Walcher & Zinnert, 1971), *Pikonema* (Atwood, 1962), *Pristiphora* (Atwood, 1962; Goidanich, 1956; Martelli, 1954) and *Trichiocampus* (Deegener, 1920; Downes, 1925; Goidanich, 1956).

The prehensile abdomen of *D. diasi* larvae must be very important for them as an extra protection against being blown away from the tree canopy by the wind. Several Cimbicid larvae are also known to have prehensile abdomens (see e.g. Bibolini, 1967; Ermolenko, 1975; Schedl, 1976). It is not surprising, however, that *T. olfersii* larvae lack a prehensile tail as they have no abdominal prolegs and feed in low bushes near the ground where they are not affected by the wind. This fact could also perhaps explain why these larvae do not attack hosts with tree habit. This is apparently the first larvae of Argidae reported to lack the abdominal prolegs, a phenomenon also known to occur in the larvae of the Australian Perginae and Philomastiginae (Benson, 1938a) and in several genera of leaf-mining sawflies.

D. diasi larvae exhibit two different patterns of migration: (1) the "Alternating Advances and Retreats" pattern, in which all the larvae alternate as temporary leaders and then retreat to the middle or end of the group in an apparently disorganized manner; and (2) the "Indian File" pattern in which there is only one constant leader larva and the other larvae align themselves one after the other in a continuous single queue with each larva maintaining constant body contact with the larvae immediately in front and behind her. The first pattern is observed during the frequent migrations from one leaflet to the next, in the same compound leaf or to another leaf, while the second pattern was only observed during the final migration down the tree to cocoon. *T. olfersii*'s larval migrations were not studied. Simultaneous group-migration also occurs in some other gregarious sawfly larvae. The Indian File pattern, with variations in details, has been recorded for the Pergids *Syzygonia cyanocephala* (Marques, 1933, Figure F), *Perga dorsalis* (Evans, 1934), *Perga affinis* (Carne, 1959 & 1962) and *Pergagrapta turneri* (Meyer-Rochow, 1972), the last three exhibiting sophisticated communications between the members of the colony by tapping the substract with the tip of their abdomens which is perceived by the others through the vibration of the substract. Carne (1962) observed that a few larvae regularly acted as leaders of the marching larvae. Another type of group-migration, similar to the Alternating Advances and Retreats pattern of *D. diasi*, but better described as a Broad-Column Amoeboid-fashion group-migration, has been recorded for the Pergids *Perga affinis* during their inter-tree migrations in the ground (Carne, 1959 & 1962), *Perreyia lepida* (Camargo, 1956 & Costa Lima, 1941) and unidentified Perreyids probably belonging to *Perreyia* (Wheeler & Mann, 1923; Dias, unpublished observations). This type of larval-mass-migration is similar to those exhibited by the army-worms (*Sciara* spp, Diptera, Mycetophilidae) (see e.g. Pocock, 1896; figure on page 54) and the processionary-caterpillars (*Thaumetopoa* spp, Lepidoptera, Thaumetopoeidae)(see e.g. Pickard-Cambridge, 1896; figure on page 106). The Indian File type of group-migration is also found in several groups of gregarious caterpillars (see e.g. Russi *et al.*, 1973).

The habit of turning the abdomens upward synchronously exhibited by *D. diasi* and *T. olfersii* larvae when disturbed, is widespread among the larvae of Diprionids (e.g. Prop, 1960), Pergids (e.g. Morrow *et al.*, 1976), Nematines (e.g. Benson, 1950 and Goidanich,

1956) and other Argids (e.g. Servadei, 1934). This display apparently works mainly to increase the larvae's conspicuousness, but it may also work as a direct threat to any predator or parasitoid in the case of the Nematines and the two studied Argids, for they use their abdomens to hit their enemies with blows and smear them with viscous supposedly repellent fluids produced by abdominal glands. The presence of a dark spot and a crown of stout tubercles on the dorsal anal plate at the tip of the abdomen of T. olfersii and D. diasi larvae most probably enhances the effectiveness of the Abdomens Up display to increase the larvae's conspicuousness and strength of their abdominal blows.

One difference between the Nematines and the two Argids is that the former secrete the viscous liquid from eversible glands situated in the ventral side of their abdominal segments (Benson, 1950; E.L. Smith, 1970b) while the latter secrete them from glands situated at the tip of their abdomens. Nematines and Argids are notorious for the great convergence which they exhibit in larval structure, colouring, distastefulness, feeding, defensive behaviours and parasitoids. None of the other Argid larvae studied so far, however, have been reported to eject defensive fluids from abdominal glands when disturbed, but Maxwell (1955) found ventral abdominal non-eversible glands on the first seven abdominal segments in some Nearctic species of Arge. Diprionid and Pergid sawflies are well known by their use of oral discharges of oily fluids, which they extract from the host plant and store in diverticular pouches in their foregut until they regurgitate it when attacked (Prop, 1960; Carne, 1962; Eisner et al., 1974; Morrow et al., 1976). These fluids discharged by the larvae are effective deterrents to predators, specially when produced by several larvae together (Eisner et al., 1974; Morrow et al., 1976; Tostowaryk, 1972). Tenthredinine and Dolerine larvae are also known to use oral discharges against their enemies (Benson, 1950), while the Cimbicids eject blood from lateral pores when disturbed (e.g. Bibolini, 1967).

The specialized strategy used by Spilochalcis sp (Chalcididae) when attacking the larvae of D. diasi to overcome their defensive reactions by inducing a stimulus habituation in the larval response to the parasitoid's approach and touch has also been found in other insects attacking gregarious sawfly larvae and caterpillars (see e.g. Arnold, 1971; Fintescu, 1927).

The leaf-eating Tenthredinoid sawflies have evolved several different methods to feed on them, including leaf-mining, gall-making and different types of external feeding such as leaf-rollers, one-surface feeders, and edge-feeders. The majority of the sawflies, including the two studied here, adopt the last method. There are basically three distinct types of edge-feeding: (1) forward horse-riding, where the larva straddles over the leaf's edge, with her body parallel to it and three thoracic legs on each side of it, and moves forward as she feeds (this is the method utilized by the two Argids studied here, and also by most other Argids, Nematines and Cimbicids); (2) backward horse-riding, where the larva straddles the leaf's edge aligned as in the first method but moves backward as she feeds (this is the method used by the needle-feeding Nematines and Diprionids); and (3) right-angle feeding, where the larva remains only on one side of the leaf with her body aligned perpendicularly to the leaf's edge and moves backward as she feeds (this is the characteristic method used by the Pergids). Gregarious edge-feeding sawfly larvae feeding together on the same leaf/leaflet (group-feeding) exhibit highly organized feeding which is apparently "aimed" at minimizing deleterious effects of intraspecific competition. Larvae adopting backward horse-riding or right-angle feeding align themselves side by side along the feeding edge and those larvae which cannot find a place at the feeding edge must wait their turn just behind the others (Carne, 1962; Evans, 1934; Ghent, 1960). On the other hand, the larvae adopting forward horse-riding align themselves all along the leaf's edge, one after the other forming a feeding queue and those larvae which cannot find a suitable place at the edible feeding edge must wait their turn just behind the others at the rear of the queue - the waiting queue. This is the situation in *D. diasi* and *T. olfersii* but is also known, though not described in detail, in a less compact arrangement in species of *Arge* (Berland, 1947; Servadei, 1934), *Sericoceros* (Martorell, 1941), *Sterictiphora* (Ross, 1933), *Pristiphora* (Goidanich, 1956) and *Croesus* (Caccamo, 1966). The last two have also been reported to exhibit the double-convergent-queues feeding system, described here for the two brazilian Argids.

Queue-feeding appears to be an efficient group-feeding method as it minimizes the loss of time when the larva is on the feeding edge by minimizing the frequency of head-head collisions between larvae moving on opposite directions. It has the additional advantage that no larva can monopolize any portion of the feeding edge for more than a few seconds, thus offering an equal opportunity for all the members of the group to exploit the best feeding edges. This probably increases each larva's own inclusive fitness as all or most of the larvae in the group are closely related (see below). However, the fact that jumping in the middle of the feeding queue occurs in _T. olfersii_ and _D. diasi_ damages this equality, as stronger larvae can force their way into the feeding queue, thus avoiding the waiting queue.

An interesting consequence of queue-feeding is that most feeds are terminated not by internal control but rather by external stimuli such as the arrival at an unsuitable portion of the leaflet's edge or the bumping against the head of another larva. Each meal, however, is apparently terminated by internal stimulation (? full crop) as larvae coming out of the queue to rest frequently come out from its middle before being forced to leave the feeding edge by external stimuli.

At the moment our knowledge on sawfly larval feeding is still very limited to permit comparisons with the better studied grasshoppers, caterpillars and Chrysomeloid larvae (see e.g. Bernays & Chapman, 1972 and 1974; Blaney, Chapman & Wilson, 1973; Hoekstra & Beenakkers, 1976; Ma, 1972; Scriber, 1977; Scriber & Feeny, 1979; Hsiao, 1974). The two Argids studied here, however, probably exhibit the most regular feeding pattern among the phytophagous leaf-biting insects feeding externally so far studied.

There is considerable variation among the Tenthredinoid sawflies on the type of silk secretion (Kenchington, 1969; Rudall & Kenchington, 1971), silk glands morphology (Kenchington, 1972; Maxwell, 1955), cocoon structure (Carne, 1962; Schedl & Klima, 1980), cocoon placement and clustering. Argid cocoons are either attached to the host's leaves - _Aprosthema_ and _Atomacera_ (summer generations only), _Eriglenum_, Sericoceros and Sphacophilus (Conde, 1934; Dias, unpubl.; Ross, 1933; Tippins, 1965); twigs - Arge, Dielocerus, Ptilia (Dias, unpubl.); thicker branches and trunk - Dielocerus, Digelasinus, Pachylota, Pampsilota, Sericoceros (Costa Lima, 1927; Curtis, 1844; Martorell, 1941; Monte, 1946; Togashi, 1975; Dias, unpubl.); in the leaf litter just below the host - Aprosthema and Atomacera (autumn generations only), Arge Sphacophilus (Chapman & Gould, 1929; Conde, 1934; Tozawa, 1940; Weiss & Lott, 1923); or buried in the soil a few centimetres below the surface, just below the host plant - Arge, Didymia, Schizocerella, Themos, Zenarge (Dias, 1975 and unpubl.; Moore, 1962; Servadei, 1934; Webster & Mally, 1900).

Most Argid cocoons are spun alone or in twins, but some are spun in small irregular groupings - Arge pagana (Meirleire, 1969), Arge flavicollis (Dias, unpubl.), Sericoceros krugii (Martorell, 1941) and Pampsilota nualsriae (Togashi, 1975). Only three Neotropical genera, Dielocerus, Digelasinus and Pachylota, are known to spin large cocoon masses in which the cocoons are tightly and regularly attached to each other in a honey-comb or spherical arrangement and covered by a thick communal envelope of silk. Elsewhere in the Tenthredinoidea, the only other sawflies known to spin large regular cocoon masses are the Australian Pergids of the genera Perga, Pergagrapta (only some species), Pseudoperga and Lophyrotoma (Carne, 1959 and 1962; Evans, 1934; Froggatt, 1890 and 1901; Tryon, 1921). These Pergids spin their cocoons vertically, buried in the soil just below the surface and adjacent to the host tree's trunk, tightly packed side by side in a honey-comb formation. They do not, however, spin any communal cover.

Isolated larvae of D. diasi are unable to spin the outer cover but succeed in spinning the inner wall of their cocoons, and male-only larval groups fail to spin the thin papery outer covering but spin the spongy layer of the communal cover and the inner wall of their individual cocoons. Therefore, although the spinning of the 2-layer communal envelope is a cooperative activity which larvae in very small groups or alone are unable to perform, the spinning of the outer papery layer of the communal cover appears to be mainly a female activity in which only a small proportion of the individuals in the group participate.

In view of the large quantities of silk which are spun by the larvae, it is amazing that D. diasi females still invest more energy in egg production than those of T. olfersii which secrete only a small amount of silk to spin their cocoons (see discussion in Chapter 6).

The function of the elaborate communal cover of the cocoon masses of Dielocerus, Digelasinus and Pachylota is unknown, but most probably it protects the sawflies against predators, parasitoids, fire and floods. The present study, however, failed to demonstrate any correlation between group size and survival of D. diasi during the cocoon stage, except for single cocoons which had a significantly lower survival rate in comparison with all other group sizes. However, as the major parasitoid of the cocoon stage of D. diasi, the Ichneumonid Lymeon dieloceri, occured only in small numbers in the cocoon samples utilized, further studies are needed.

By far the most important mortality factor of D. diasi during its larval stage was the parasitoid fly Spathimeigenia dieloceri (Tachinidae), which killed about half of all larvae.

The moth Ectomyelois decolor (Zeller)(Pyralidae) is reported here for the first time to feed as a scavenger on the remains of an insect cocoon. The species of this genus are known to feed on the seeds and fruits of several plants but specially on the pods of Leguminose plants, and on dried fruits in storage (Heinrich, 1956). Probably the seeds of the host of D. diasi, the leguminose tree Sclerolobium aureum, served as an intermediate host for the moth's attack on the sawfly's cocoons.

Assuming that T. olfersii and D. diasi reproduce by arrhenotoky, that females mate only once, that their populations are significantly inbred (mixture of OVP and LMC mating systems), and that their female-biased sex ratios are a consequence of this inbreeding alone (see discussions in Chapter 5), and given the fact that D. diasi has a more pronounced female-bias in their sex-ratio than T. olfersii, it follows that D. diasi populations are more inbred than those of T. olfersii and therefore the average relationships between larvae in fullsib-groups is higher in D. diasi than in T. olfersii (see Hamilton, 1967, 1972 and 1979). Therefore we would expect D. diasi larvae to be more cooperative and altruistic toward their sibs than the larvae of T. olfersii, and for the same reason we would also expect female larvae to be more cooperative and altruistic toward their sibs than the male larvae, in both species (see Hamilton, 1964 and West-Eberhard, 1975). At the moment, however, there is no evidence that D. diasi larvae are more cooperative and altruistic than those of T. olfersii, except perhaps for the fact that D. diasi larvae spin their cocoons packed together in a regular arrangement and covered by an elaborate 2-layer silk communal envelope which requires considerable cooperation and coordination, while T. olfersii larvae spin their cocoons separately. The only evidence so far that female larvae are more cooperative and altruistic than male larvae is that only female D. diasi larvae participate in the spinning of the outer papery layer of the communal cover of their cocoon masses. It is tempting to predict that male larvae are more prone to jump in the middle of the feeding queue while female larvae are more prone to give space for another larva to jump in the queue in her front, in both species, though more markedly in D. diasi, but this still remains to be confirmed in future studies.

CHAPTER 8. CONCLUSIONS

1. Dielocerus diasi is apparently monophagous on Sclerolobium (Leguminosae, Caesalpinoidea), specially on S. aureum (Tulasne) but is also found on S. paniculatum Vogel. Themos olfersii is apparently monophagous on Eriotheca pubescens (Mart. & Zucc.) (Bombacaceae).

2. So far, host plant information is available for about 120 species of Argidae belonging to 27 genera, i.e., about one fifth of known species and half of the described genera. Information is lacking for most Neotropical, Ethiopian, Oriental and Australian species. These 120 Argids have been recorded attacking plants of 27 families belonging to 19 orders of Dicotyledones (Angiospermae) and one family of Gymnospermae (Cupressaceae). The plant families attacked by the highest numbers of Argid genera are: Leguminosae (10 Argid genera, mostly American), Rosaceae (5 Argid genera, mainly Palaearctic) and Polygonaceae (5 Argid genera, widespread).

3. T. olfersii has only 2 generations per year, a spring generation from October to March and a summer generation from January to December. Its adults, eggs and feeding larvae are confined to the rainy season (October to March). Individuals of the spring generation complete their development in about 80 days, but those of the summer generation enter in prepupal diapause during the dry season for about 6 months. It is argued that this diapause is apparently induced by decreasing daylength and apparently terminated by increase in soil moisture with the first heavy rains of September. It is suggested that this diapause is an adaptation against frequent fires which burn all the lower Cerrado vegetation during the dry season. This species is particularly vulnerable to these fires as it develops on low shrubs near the ground. D. diasi has a different life cycle pattern, having 4 almost continuous generations per year. All its life stages are found throughout the year, though adults and eggs are rather rare during the early dry season (June and July). However, adults, eggs and young larvae are frequent during the peak of the dry season (August and September). Individuals during the rainy season generations complete their development in about 85 days. Development inside the cocoon is slower or briefly halted during the dry season. This species develops on high canopies usually 4 to 10 metres above the ground and

therefore escapes from most fires. This might explain why it does not have a dry season diapause as *T. olfersii*. However, in the laboratory, half of *D. diasi* larvae which spin their cocoons during the early dry season enter in prolonged diapause for one or two years.

4. Both species have female-biased secondary sex ratio, 2 females per male in *T. olfersii* during its larval stages (since the first instar) and 3 females per male in *D. diasi* during its early adult stage (just after emergence from cocoon) and also during its larval stages (since the first instar). Since the sex ratio in the first larval instar is already female-biased, it is assumed that the primary sex ratio is also female-biased. This is correlated with the occurrence of inbreeding in their populations promoted by their apparently small dispersal rate, and in *D. diasi* at least, by the male's behaviour of waiting beside their cocoon mass for the emergence of their sisters and attempting to copulate with them. It is suggested that male *D. diasi*, and probably also male *T. olfersii*, exhibit a mixed mating strategy involving mating on the natal host plant near their cocoons (Local Mate Competition model of Hamilton 1967) and flying to other hosts in the neighbourhood looking for females (Outbreeding Viscous Population model of Hamilton 1972). Female-biased sex ratio is apparently the rule rather than the exception among the Tenthredinoid sawflies. Female *D. diasi* and *T. olfersii* probably release a sex pheromone to attract their males, but conclusive evidence is needed. Female *D. diasi* mate only once during the first hours after emergence from cocoon, males are polygynous.

5. The females of both sawflies are very choosy in their selection of the oviposition site. They apparently utilize visual and sonorous stimuli to locate their hosts while flying, as they were seen visiting other plants which had similar foliage (similar sized and coloured leaves and canopy shape and height) but were *not their hosts*, and also because these females were found to be very sensitive to the buzzing sound produced by conspecific females vibrating their wings after they have become established on their chosen leaflet. Once landed on a host, they exhibit elaborate exploratory walking over the leaflets, apparently comparing certain qualities of the visited leaflets. They avoid leaves which already bear an egg cluster or an established female. They are very demanding in regard to the height, position, age, and health state of the egg laying site. *D. diasi* has a

preference for chronically infested host trees while *T. olfersii* prefers epicormic foliage (regrowth from fire damage). Females of both species tend to cluster in a few of the available hosts in a patch to lay their eggs, and it is suggested that the presence of one or more females in a host attracts others to the same plant. It is further suggested that prereproductive females are better protected against some predators when selecting hosts which already have other females (alive or dead) as the latter might serve as decoys to predators naive to their aposematic colouration.

6. *D. diasi* females spend about 24 hours on their chosen leaflet before laying their eggs, and during this period they display with wing-buzzing and walking in circles and zigzags on the underside of the leaflet. This behaviour has no parallel among studied sawflies, and is interpreted as a type of egg laying site territorial behaviour to prevent other females from laying their eggs in the same compound leaf. An alternative explanation is that this behaviour aims at attracting other females to join them at their chosen host. Further critical studies are needed to clarify this matter.

7. Both species are extreme semelparous, laying all their eggs clustered into just one host leaflet, but differ markedly in their fertility and manner of egg placement. *D. diasi* lays about 76 eggs spreading them throughout the leaflet, each one introduced into an individual pocket completely sealed off from the exterior; while *T. olfersii* lays only about 27 eggs tightly clustered into a small circle on the leaflet's superior surface, each one only slightly imbedded into the leaflet's parenchyma and standing nearly upright on the leaflet's surface. It is suggested that this difference in fertility is due to *T. olfersii*'s commitment to produce a larger first instar larva in response to the greater thickness and toughness of its host's leaflets. *T. olfersii*'s manner of egg placement lend them more vulnerable to predators while permitting at the same time a more intimate maternal care.

8. The females of both sawflies remain near their brood for up to 4 or 5 weeks until they die after depleting their energetic reserves. They do not feed in the adult stage. *T. olfersii* females sit astride over their egg clusters and newly-born larvae, while *D. diasi* females position themselves at the base of the egg-bearing leaflet, facing its

petiole, and from time to time walk toward and over and sit over their eggs. When disturbed by visual, tactile or sonorous stimuli they react with varied defensive displays and threatening reactions. So far, 18 different displays were described for T. olfersii females and 11 for D. diasi females. These displays involve much use of legs to change the total body position, orientation and posture, and also much use of the wings to change the sawfly's visual display, to hit an offender or to vibrate producing a loud buzzing sound. The mandibles are less often used, and only to threaten and attack an offender when much disturbed. There are several similarities and differences in displaying between the two species. It is argued that these displays probably evolved as a protection to the eggs and young larvae against predators. The females, however, are unable to protect their eggs against the attack of the parasitoid wasp Chrysocharis sp (Hym., Eulophidae). The females are specially disturbed by the following stimuli: the close approach of a person or insect, the buzzing sound produced by other conspecific females (at least in D. diasi) and sharp vibrations of their substract leaflet (specially in T. olfersii). D. diasi females exhibit a higher tolerance to substract vibration and other tactile stimuli which correlates with their greater exposure to strong winds than T. olfersii females. The females remain with their offsprings after they hatch, but at a greater distance and reacting less to disturbing stimuli and rarely approaching them again.

9. So far, 18 species of sawflies belonging to 10 genera (5 Argids: Dielocerus, Digelasinus, Pachylota, Themos and Sericoceros; 3 Pergids: Pseudoperga, Philomastix and Syzygonia; 1 Nematine: Pachynematus; and 1 Diprionidae: Neodiprion) are known in which the post-reproductive female remains beside her brood until she dies, apparently to protect her offspring against predators. Most of these species are tropical or subtropical, have low fertility, and lay their eggs exposed on the leaf's surface. Very little, however, is known about these behaviours and further studies are recommended.

10. The larvae of both species are highly gregarious forming compact sib-groups (and sometimes mixed sib-groups) throughout the feeding stage, and exhibit some coordination and cooperation for feeding, defense and moving from feeding site to feeding site and to cocooning site, and D. diasi also for spinning their cocoons together. Their

larval communities fit into Lindauer's "primitive communities" category of gregariousness, but probably rate among the most socialized of such communities. *D. diasi* larvae exhibit two different types of migration: the "Alternating Advances and Retreats" pattern in which each larva alternates as temporary leaders, and the "Indian File" pattern in which there is only one constant leader. The first occurs during inter-feeding sites migration in the tree's canopy and the second occurs during their final migration to the cocooning site. Similar migration patterns have already been described for several Pergid sawflies and many caterpillars. The larvae of both species exhibit a very conspicuous synchronized defensive display of lifting their abdomens and ejecting a viscous yellow fluid from anal glands, which seems to be effective against several other insects but fails against certain parasitoids: the Chalcidid *Spilochalcis* sp and the Tachinid fly *Spathimeigenia dieloceri* in the case of *D. diasi* larvae. The Chalcidid overcomes their defensive reactions by inducing a stimulus adaptation to the parasitoid's repeated slow approach and touch. The use of abdomens in defensive displays also occurs in other Argids, Pergids, Diprionids and Nematines, but the ejection of defensive liquid produced by abdominal glands occurs only in some Nematines and a few *Arge* spp.

11. The larvae of both species feed in compact queues along the leaflet's edge, exhibiting cyclic alternation of positions in the feeding edge and in the waiting queue at the rear of the feeding queue. This appears to be an efficient group-feeding method as it minimizes the loss of time caused by head-head collisions between larvae feeding and moving on opposite directions along the same feeding edge. It has an additional advantage in offering an equal opportunity to all members of the group to exploit the best feeding edges, which probably increases each larva's own inclusive fitness as all or most of the larvae within a group are closely related. However, this equality is broken by the fact that some larvae frequently attempt and some succeed to jump in the middle of the feeding queue, thus avoiding the waiting queue. The termination of each feed is determined by external stimuli. Further studies on this complex group-feeding mechanism are recommended, specially to see if there is any difference in behaviour between male and female larvae.

12. The two species differ markedly in their cocoon's structure and placement. T. *olfersii* spin their cocoons singly buried in the top soil just beneath their host, while *D. diasi* spin their cocoons together in large masses (usually fusing together several sib-groups), each cocoon regularly attached to the others forming a honeycomb-shaped structure which is enveloped by a thick double-layered communal silk cover, spun against the host's bark on its larger branches and trunk. Single *D. diasi* larvae are unable to spin this complex outer envelope, and male-only larval groups fail to spin the thin papery outer layer of this communal envelope, indicating this is a female job. The function of this elaborate communal cover is still unknown, but probably protects the cocoons against some predators, parasitoids, fire and floods. However, the Ichneumonid wasp *Lymeon dieloceri* succeeds in attacking the larvae inside these cocoon masses. No correlation was found between cocoon group size and sawfly survival, except for the single cocoons which had a significantly lower survival rate compared with the grouped cocoons. Further studies on populations subject to higher attack by *L. dieloceri* are needed to verify the effects of cocoon group size on the parasitoids incidence. Similar cocoon masses are known from other *Dielocerus* species and from two related Argid genera, *Digelasinus* and *Pachylota*. The Pergids *Perga*, *Pergagrapta*, *Pseudoperga* and *Lophyrotoma* also cluster their cocoons into regular honeycomb-shaped masses, buried in the soil, but do not spin any communal cover.

13. Based on their biology and immature stages morphology, I suggest that *Themos* and *Dielocerus* are better classified into separate tribes or subfamilies within the Argidae (as proposed already by Benson, 1938a, based on the adult morphology). However, in view of the remarkable similarities in their cocoon masses I suggest to include *Pachylota* Westwood in the subfamily Dielocerinae together with *Dielocerus* and *Digelasinus*. *Themos olfersii* is the first Argidae recorded to lack abdominal prolegs in the larval stages.

14. Both species suffer their heaviest mortality during their larval stage (feeding larva plus prepupa), about 70 - 90% of larvae die before pupating. The major mortality causes in *D. diasi* are parasitism by *Spathimeigenia dieloceri* (Townsend) (Diptera, Tachinidae) and by *Lymeon dieloceri* (Costa Lima)(Hym., Ichneumonidae), desiccation and

fungus attack in the cocoon masses; in T. olfersii the major mortality causes are predation by an unidentified lacewing larva (Neuroptera, Chrysopidae) and fungus attack during the feeding stages. Mortality during the egg stage is comparatively lower, averaging 25% in both species, but is very unevenly distributed among the clusters. The major mortality causes during this stage are the parasitism by Chrysocharis sp (Hym., Eulophidae) (in both species), predation by the above mentioned lacewing larva (in T. olfersii) and leaflet fall (in D. diasi). A minor mortality cause in both species is the drying of the eggs following the invasion of the egg-bearing leaflet by conspecific larvae. Mortality is very low during the adult stage in both species (for females).

CHAPTER 9. REFERENCES

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APPENDIX I. FURTHER LITERATURE ON THE BIOLOGY OF ARGID AND TROPICAL SAWFLIES.

The following notes are given as an aid to those wishing to know more about the biology of Argids and tropical sawflies.

A few other species of Argidae have received some attention, though considerably less than the two *Arge* mentioned in the introduction: *Arge berberidis* (Schrank) (Goureau, 1857; Brischke and Zaddach, 1863; Zirngiebl, 1932; Khodzhevanishvili, 1967; Ermolenko, 1975), *Arge clavicornis* (Fabricius) (Gobeil, 1937; Will, 1942; Wong, 1954; Raizenne, 1957; Ermolenko, 1975), *Arge gracilicornis* (Klug) (Brischke and Zaddach, 1863; Lindquist, 1937; Ermolenko, 1975), *Arge humeralis* (Beauvois) (Regas-Williams and Habeck, 1979), *Arge nigripes* (Retzius) (Pschorn-Walcher and Kriegl, 1965; Scheibelreiter, 1973; Ermolenko, 1975), *Arge pectoralis* (Leach) (Schwarz, 1909; Wong, 1954; Raizenne, 1957; Smirnoff, 1971), *Arge similis* (Vollenhoven)(Tozawa, 1940), *Arge pullata* (Zaddach)(Brischke and Zaddach, 1863; Vollenhoven, 1857-61; Ermolenko, 1975; Esbjerg, 1977), *Arge ustulata* (Linnaeus)(Brischke and Zaddach, 1863; Pschorn-Walcher and Kriegl, 1965; Ermolenko, 1975), *Atomacera debilis* (Say)(Dyar, 1900; Weiss and Lott, 1923; Lindquist and Trinnell, 1965), *Atomacera decepta* (Rohwer)(Dyar, 1900; Tippins, 1965), *Schizocerella pilicornis* (Holmgren)(Webster and Mally, 1900; Garlick, 1922; Force, 1965; Gomes de Lima, 1968; Gorske, Hopen and Randell, 1977), *Sericoceros krugii* (Cresson)(Zwaluwenberg, 1918; Wolcott, 1926; Martorell, 1941), *Sphacophilus apios* (Ross) (Ross, 1933), *Sphacophilus cellularis* (Say)(Riley and Howard, 1888; Marlatt, 1892; Chapman and Gould, 1929), *Sterictiphora geminata* (Gmelin)(Brischke and Zaddach, 1863; Scheibelreiter, 1973; Ermolenko, 1975) and *Zenarge turneri*(Rohwer)(Moore, 1962). Of these, only *Sericoceros krugii* is a tropical species (feeding on *Coccoloba* in Puerto Rico).

This situation is the same for all the other families of sawflies: very little is known about tropical species. The only other tropical sawflies for which we have some information on their biology are: *Nesodiprion biremis* (Konow) and *Gilpinia marshalli* (Forsius) (Diprionidae) which feed on pines in Thailand (Beaver and Laosunthorn, 1974 and 1975), *Zadiprion vallicola* (Rohwer) (Diprionidae) on pines in Southern Mexico (Hernandez, 1930; Olmedo, 1932; Mendiolea, 1942; Lara and Ortiz, 1969), *Zadiprion* sp on pine in Guatemala (Alvarado, 1939), *Metapedias pyensoni* Benson (Tenthredinidae) on Guava in Northeastern Brazil (Pyenson, 1940), *Athalia sjöstedti* (Forsius)(Tenthredinidae) on cabbage in East Africa (Bohlen, 1973), *Athalia proxima* (Klug) on mustard in India (Dhillon, 1966), *Syzygonia cyanocephala* Klug (Pergidae) on *Tibouchina* (Melastomataceae) in Southeastern Brazil (Marques, 1933), *Haplostegus epimelas* Konow (Pergidae) on Guava in Northeastern Brazil (Pyenson, 1940), *Acordulecera megacephala* (Benson)(Pergidae) on Guava in Northeastern Brazil (Pyenson, 1940), *Acordulecera* spp on potato in Peru and Bolivia (Wille, 1943; Munro, 1954; Carrasco, 1967), *Atomacera lepidula*(Konow) (Argidae) on *Ipomoea* (Convolvulaceae) in Trinidad (McCallan, 1953), and *Dielocerus formosus* (Klug) (Argidae) on *Inga* (Leguminosae) in Eastern Brazil (Curtis, 1844; F. Smith, 1866; Costa Lima, 1927; Monte, 1941). At present, there is no species of tropical sawfly which could be claimed to be well studied ecologically.

Some species of Argid sawflies have been studied in an attempt to control weed plants: *Arge humeralis* for the control of poison-ivy (*Rhus radicans* L.)(see Regas-Williams and Habeck, 1979), *Arge ochropus* and *Arge pagana* for the control of weed roses in New Zealand (see Scheilbelreiter, 1973), and *Schizocerella pilicornis* for the control of purslane (*Portulaca oleracea* L.)(see Force, 1965).

APPENDIX II. SUMMARY OF HOST PLANT ASSOCIATIONS OF ARGID SAWFLIES

PLANT ORDER & FAMILY	ARGID SAWFLY GENUS	SOURCE
GYMNOSPERMAE:		
CONIFERAE-		
CUPRESSACEAE	*Zenarge*	Moore, 1962.
ANGIOSPERMAE:		
DICOTYLEDONES:		
MAGNOLIIDAE-		
-RANUNCULALES		
BERBERIDACEAE	*Arge*	several, Ermolenko, 1975
HAMAMELIDAE-		
-HAMAMELIDALES		
HAMAMELIDACEAE	*Arge*	Raizenne, 1957
-FAGALES		
FAGACEAE	*Arge*	several, Lorenz & Kraus, 1957.
	Sericoceros (?)	Cameron, 1883.
BETULACEAE	*Arge*	several, Lorenz & Kraus, 1957.
CARYOPHYLLIDAE-		
-CARYOPHYLLALES		
PORTULACACEAE	*Schizocerella*	several, Webster & Mally, 1900.
-POLYGONALES		
POLYGONACEAE	*Arge*	Maxwell, 1955.
	Sterictiphora	Loth, 1913.
	Kokujewia	Benson, 1954.
	Pampsilota	Togashi, 1980.
	Sericoceros	several, Zwaluwenberg, 1918.
DILLENIIDAE-		
-MALVALES		
TILIACEAE	*Themos*	Dias, in prep.a
BOMBACACEAE	*Themos*	Dias, 1975.
MALVACEAE	*Atomacera*	several, Tippins, 1965.
	Brachyphatnus	D.R. Smith, pers.inf.
	Neoptilia	several, Cockerell, 1895.

PLANT ORDER & FAMILY	ARGID SAWFLY GENUS	SOURCE
ANGIOSPERMAE: DICOTYLEDONES: (continuation)		
-URTICALES		
ULMACEAE	Arge	Dyar, 1897.
	Aproceros	Okutani, 1967.
-LECYTHIDALES		
LECYTHIDACEAE	Ptilia	D.R. Smith, pers.inf.
-SALICALES		
SALICACEAE	Arge	several, Lorenz & Kraus, 1957.
-ERICALES		
ERICACEAE	Arge	Tozawa, 1940.
-EBENALES		
EBENACEAE	Arge	Pasteels, 1955.
SAPOTACEAE	Pachylota (?)	Dias, in prep.b
STYRACACEAE	Dielocerus	Dias & Smith, in prep.
ROSIDAE-		
-ROSALES		
ROSACEAE	Arge	several, Ermolenko, 1975.
	Alloscenia	Ermolenko, 1975.
	Aprosthema	Ermolenko, 1975.
	Aproceros	Togashi, 1968.
	Sterictiphora	several, Togashi, 1968.
CHRYSOBALANACEAE	Sericoceros	Zwaluwenberg, 1918.
-FABALES		
LEGUMINOSAE	Adurgoa	Dias, unpubl.
	Aprosthema	several, Conde, 1934.
	Atomacera	several, Weiss & Lott, 1923.
	Brachyphatnus	D.R. Smith, pers.inf.
	Dielocerus	Monte, 1941; Dias, 1976.
	Eriglenum	D.R. Smith, pers.inf.
	Hemidianeura (?)	D.R. Smith, pers.inf.

PLANT ORDER & FAMILY	ARGID SAWFLY GENUS	SOURCE
ANGIOSPERMAE: DICOTYLEDONES: (continuation)		
-FABALES		
LEGUMINOSAE	*Ptenus*	D.R. Smith, 1970.
	Sphacophilus	several, Ross, 1951; D.R. Smith, 1971.
	Subsymmia	Malaise, 1955.
-PROTEALES		
PROTEACEAE	*Trichorhachus*	Riek, 1970.
-SAPINDALES		
CONNARACEAE	*Didymia*	Dias & Smith, in prep.
	Ptilia	D.R. Smith, pers.inf.
ANACARDIACEAE	*Arge*	several, Burks, 1958; Regas-Williams & Habeck, 1979.
-EUPHORBIALES		
EUPHORBIACEAE	*Arge*	Ermolenko, 1975.
-GERANIALES		
GERANIACEAE	*Arge*	Pasteels, 1953.
ERYTHROXYLACEAE	*Digelasinus*	Costa Lima, 1937.
ASTERIDAE		
-POLEMONIALES		
CONVOLVULACEAE	*Atomacera*	McCallan, 1953.
	Sphacophilus	several, Riley & Howard, 1888.
-DIPSACALES		
CAPRIFOLIACEAE	*Arge*	Okutani, 1967.

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A detailed review of the host plant associations of Argid sawflies studied so far is in preparation.

The plant families are grouped according to the system of Stebbins (1974) which is based chiefly on the system of Cronquist (1968).

APPENDIX III. PUBLISHED WORKS

DIAS, B.F.S., 1975. Presocial behaviour in sawflies of Central Brazil. I. *Themos olfersii* (Klug)(Hym., Argidae). Studia Entomológica, Petropólis, Rio de Janeiro, **18**: 401-432. (in portuguese).

DIAS, B.F.S., 1976. Presocial behaviour in sawflies of Central Brazil. II. *Dielocerus diasi* Smith, 1975 (Hym., Argidae). Studia Entomológica, Petrópolis, Rio de Janeiro, **19**: 461-501 (in portuguese).

quando suas larvas são molestadas: zumbe; tenta morder; abre as asas e raspa a extremidade ventral do abdômen contra o galho. Sua reação mais freqüente é zumbir. A vespa-de-serra fica na base do folíolo até morrer e cair no chão. Muitas fêmeas morrem logo após a eclosão dos ovos, mas algumas vivem mais de 10 dias após a eclosão dos mesmos.

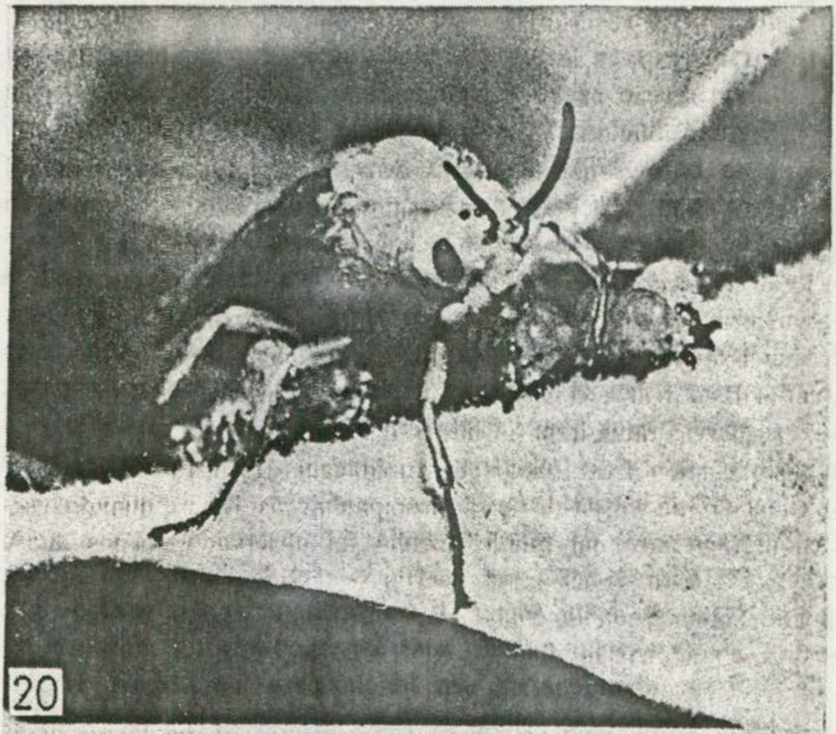
A vespa-de-serra observada que mais tempo viveu após a eclosão de seus ovos viveu entre 13 a 15 dias junto com suas larvas e as acompanhou para o folíolo ao lado quando estas, após terminarem de comer o primeiro folíolo, passaram para o segundo. Esta fêmea continuou a exibir comportamentos de defesa até as larvas atingirem o início do terceiro instar, quando já haviam comido três folíolos e terminavam o quarto. Esse comportamento da vespa-de-serra acompanhar as larvas quando estas migram para um folíolo vizinho foi observado apenas duas vezes. A outra fêmea a comportar-se assim mudou-se para o folíolo vizinho quando suas larvas, ainda no início do primeiro instar, abandonaram seu folíolo para juntarem-se às larvas de outra fêmea no folíolo ao lado.

Essa fêmea ficou na base do folíolo vizinho, na face dorsal deste, e continuou a apresentar as reações de defesa já referidas acima.

A presença de duas posturas em folíolos vizinhos parece atrapalhar, às vezes, o comportamento das vespas-de-serra. Uma fêmea abandonou seu folíolo, quando suas larvas jovens ainda comiam a primeira metade deste, e juntou-se a uma outra fêmea na base do folíolo vizinho. Aí ficou quieta ao lado da segunda fêmea e próxima às larvas desta, que se alimentavam deste folíolo.

Longevidade das fêmeas. Somando o período médio de cuidado maternal para com os ovos, cerca de 23 dias, e o período com as larvas, até 13 dias, a vespa-de-serra chega a ficar mais de um mês cuidando de sua prole. Maioria das fêmeas (81% dos casos observados) sobrevive à eclosão de seus ovos e permanece, como já foi dito acima, com suas larvas até morrer. Oito fêmeas morreram antes da eclosão dos ovos: duas com ovos novos e seis com ovos maduros.

No curso do presente trabalho, nunca foi visto esta Sínfita sendo predada ou atacada por algum animal, apesar de sua coloração vistosa e do longo tempo que fica exposta aos possíveis predadores. No entanto, três fêmeas (4% do total) morreram



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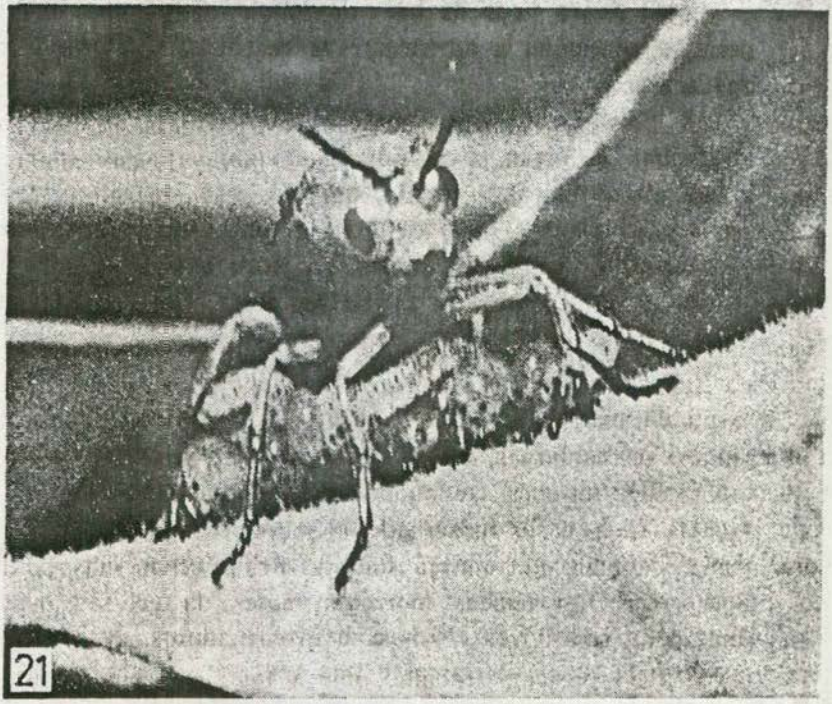

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Fig. 20. Fêmea sobre larvas novas na base do folíolo. As larvinhas iniciam a comer a margem grossa do folíolo. Fig. 21. Idem, a fêmea e as larvas reagem a uma batida no folíolo. A fêmea, após zumbir, abre as mandíbulas em atitude de ameaça. As larvas levantam seus abdômens em atitude de defesa.

Proteção aos ovos e às larvas recém-nascidas. As larvas recém-nascidas permanecem amontoadas junto aos ovos que ainda não eclodiram, debaixo da fêmea-mãe que continua a protegê-las assim como aos ovos (Fig. 14). Em poucas horas as larvas já estão totalmente esclerotizadas e migram para a base do folíolo onde iniciam a comer. Segundo foi observado oito vezes, os ovos não eclodem todos ao mesmo tempo e, assim, as primeiras larvas a nascerem terminam a esclerotização e migram para a base do folíolo antes que os últimos ovos eclodam. A vespa-de-serra nestes casos acompanha sempre as larvinhas que migram deixando para trás algumas vezes até nove ou dez ovos e as larvas mais novas.

Depois que as últimas larvas nascem e estão aptas para caminhar, juntam-se ao resto do grupo que já havia iniciado a comer.

As larvas recém-nascidas, antes de completar a esclerotização, são verde claras e muito moles. Certamente nesta fase o cuidado maternal é muito importante. Na base do folíolo a vespa-de-serra permanece sobre as larvas durante várias horas exibindo as mesmas reações de defesa descritas anteriormente para as fêmeas sobre os ovos (Figs. 15, 20 e 21).

Proteção às larvas. À medida em que as larvas vão comendo o folíolo e caminhando para o ápice deste, a fêmea não as acompanha, mas permanece, na maioria das vezes observadas, quieta na base do folíolo com a cabeça voltada para a base deste e geralmente em seu lado ventral (Figs. 16 e 17). De um total de 51 observações feitas desta fase, em apenas 5 dos casos a fêmea não estava no folíolo onde havia posto seus ovos, sendo que 4 destas observações referem-se a uma única fêmea, que após a eclosão nunca mais foi vista próxima das larvas. Em 90% dos casos, a vespa-de-serra estava próxima das larvas, nas seguintes posições: na base do folíolo com a postura, 30 vezes, sendo que geralmente a fêmea estava na face ventral do folíolo com sua cabeça voltada para a base deste; na base do folíolo vizinho àquele com a postura, 7 vezes, sendo que em pelo menos duas das ocasiões as suas larvas estavam também neste folíolo vizinho; no meio do folíolo com a postura, oito vezes, sendo que em 7 das ocasiões a fêmea estava na face ventral deste; no ápice do folíolo com a postura, uma vez.

Nesta fase a vespa-de-serra ainda apresenta vários comportamentos de defesa quando algo se aproxima do arbusto ou

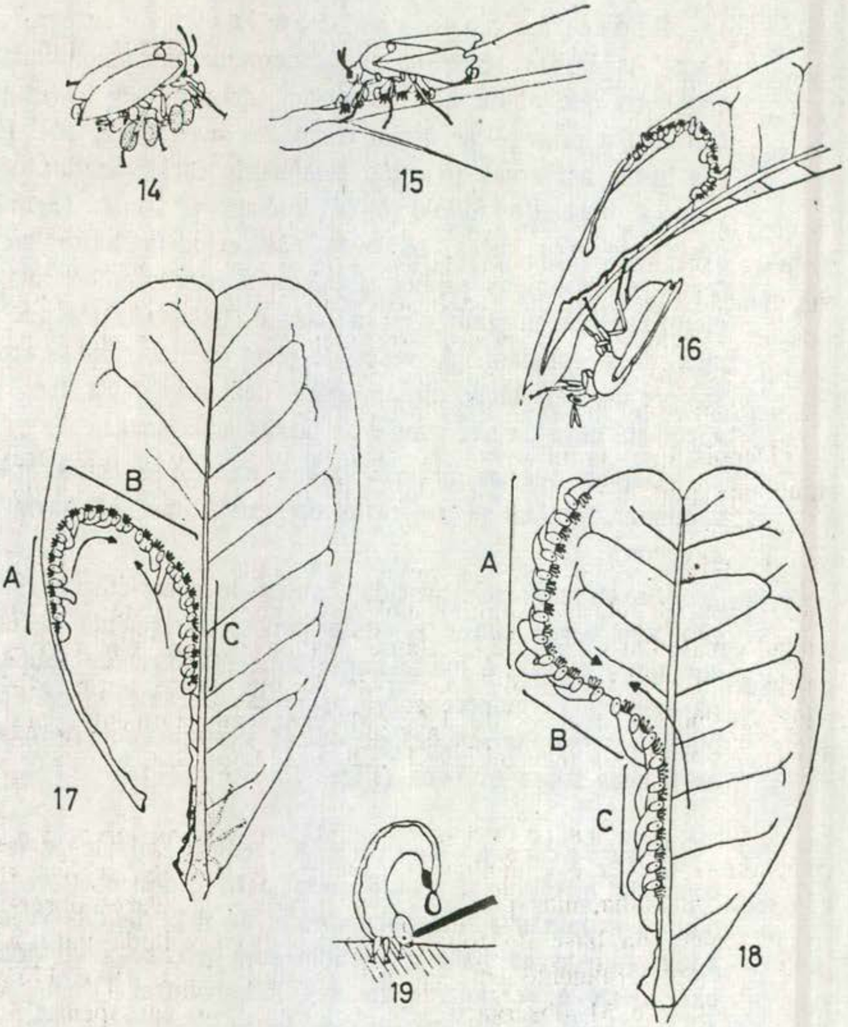


Fig. 14. Fêmea sobre os ovos e larvas recém-nascidas ainda não esclerotizadas. Fig. 15. Fêmea na base do foliolo sobre larvas jovens que iniciam a comer o foliolo. Fig. 16. Fêmea na base do foliolo, do lado ventral deste, enquanto suas larvas comem a lâmina foliar a certa distância da mãe. Fig. 17. Larvas jovens comendo foliolo no sistema de duas filas convergentes (setas). A fêmea está quieta na base do foliolo, do lado ventral deste (pontilhado). A = faixa de espera sobre a margem do foliolo; B = faixa de alimentação; C = faixa de espera sobre a nervura central. Fig. 18. Idem, larvas médias. Fig. 19. Larva curvando o abdomen para a frente e despejando gotas de liquido viscoso sobre o ofensor (palito). (original).

suas fêmeas: uma havia perdido seis ovos e outra cerca de 13. A terceira postura, cuja fêmea morrera dias antes, havia perdido 21 ovos. Em todos os ovos mortos referidos acima os embriões estavam no meio ou no fim de seu desenvolvimento.

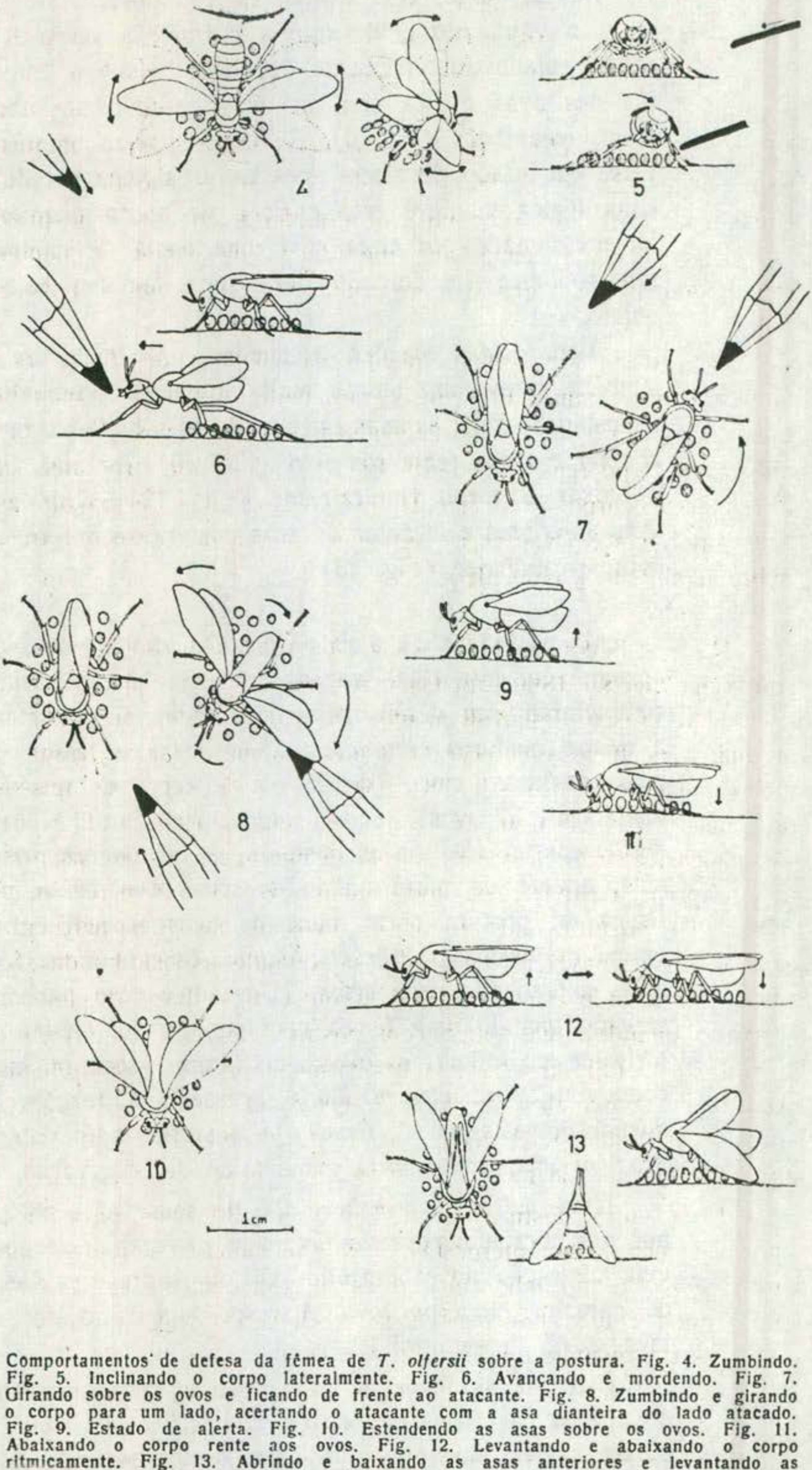
Muitas vezes, com a simples aproximação de uma pessoa ou uma batida no galho com a postura, a vespa-de-serra põe-se em estado aparentemente de alerta: eleva o corpo bem acima dos ovos e fica com as asas parcialmente abertas e um pouco levantadas (Fig. 9). A vespa-de-serra mantém-se muitas vezes em estado de alerta após exibir alguma reação de defesa. Uma fêmea manteve esta posição de alerta quando seu tórax foi pressionado por cima com uma hasta de capim e quando seu abdômen foi forçado para cima também com o mesmo objeto.

Além destas reações freqüentes, as fêmeas de *T. olfersii* também apresentam outras mais raramente observadas, quando molestadas: abrir as asas estendendo-as sobre os ovos (Fig. 11); abaixar o corpo rente aos ovos (Fig. 10); levantar, bruscamente, e baixar o corpo ritmicamente (Fig. 12); abrir e baixar as asas anteriores e levantar as asas posteriores até se encontrarem sobre o abdômen (Fig. 13).

Mortalidade dos ovos. Do total de ovos observados, aproximadamente 1890, apenas cerca de 134, ou seja, 7%, não completaram seu desenvolvimento. Destes, 67 ovos pertencentes a quatro posturas escureceram e murcharam, assim distribuídos pelas posturas: cinco (de 28 ovos), cerca de seis (de aproximadamente 27 ovos), todos e todos menos um (29 de 30 ovos). As fêmeas, de três destas posturas, se mantiveram sobre as mesmas, apesar de parte ou todos seus ovos terem perecido. A fêmea da postura onde todos os ovos menos um pereceram exibiu as mesmas reações de defesa, quando molestada, das fêmeas defendendo ovos vivos. (Um outro caso parecido foi observado quando uma fêmea com postura foi levada ao laboratório no seu folíolo: os ovos murcharam e secaram mas a fêmea continuou sobre eles e ainda apresentava reações de defesa quando molestada). A fêmea da postura onde morreram cinco ovos foi encontrada morta por ocasião da observação.

Uma outra postura teve 27 de seus 30 ovos parasitados por um microhimenóptero. Os ovos pareciam estar podres mas uma dissecção no laboratório revelou a presença de 12 larvas do parasito: uma por ovo. A vespa-de-serra desta postura estava morta quando foi localizada.

Cerca de 40 ovos de três posturas desapareceram, deixando apenas parte dos córions em contacto com o folíolo. Ao que parece haviam sido predados. Duas destas posturas estavam com



Comportamentos de defesa da fêmea de *T. olfersii* sobre a postura. Fig. 4. Zumbindo. Fig. 5. Inclinando o corpo lateralmente. Fig. 6. Avançando e mordendo. Fig. 7. Girando sobre os ovos e ficando de frente ao atacante. Fig. 8. Zumbindo e girando o corpo para um lado, acertando o atacante com a asa dianteira do lado atacado. Fig. 9. Estado de alerta. Fig. 10. Estendendo as asas sobre os ovos. Fig. 11. Abaixando o corpo rente aos ovos. Fig. 12. Levantando e abaixando o corpo ritmicamente. Fig. 13. Abrindo e baixando as asas anteriores e levantando as asas posteriores. Todas as figuras estão aprox. na mesma escala indicada. (original).

demorou exatamente 23 dias para eclodir e as outras pelo menos 23, 22 e 19 dias respectivamente.

A vespa-de-serra mantém suas patas fora do círculo de ovos de tal modo que eles fiquem todos sob seu corpo (Figs. 3a e 3b). As asas são mantidas fechadas e as antenas para trás. Durante esse período, enquanto a fêmea «choca» seus ovos, protege-os contra predadores e parasitas através de uma série de comportamentos de defesa, distintos. Estes diferentes comportamentos, de acordo com vários experimentos simples realizados no campo, são liberados por estímulos distintos e específicos.

Quando incomodada pela aproximação de uma pessoa ou por uma batida seca no galho com a postura, a vespa-de-serra levanta o abdômen, abre suas antenas e zumbe (agitando as asas rápida e energicamente) (Fig. 4). O ruído produzido é audível a vários metros de distância e dura cerca de um segundo. Esta é sem dúvida a reação de defesa mais comum da vespa-de-serra e pude provocá-la mais de 30 vezes. Este comportamento certamente é manifestado quando a fêmea é molestada por seus inimigos naturais. Assim, numa ocasião, uma vespa-de-serra reagiu zumbindo à aproximação de uma formiga. Outra reação comum apresentada pela vespa-de-serra é a de inclinar o corpo lateralmente sobre os ovos quando um objeto é aproximado destes pelos flancos (Fig. 5). Observei, uma vez, uma fêmea sobre os ovos reagir assim à aproximação de uma mosca.

Quando molestada, ou quando se aproxima um graveto ou uma haste de capim da vespa-de-serra pela frente, a fêmea tenta morder o objeto agressor e, quando consegue, o faz com força, puxando para baixo (Fig. 6). A vespa-de-serra de início levanta parcialmente as asas, abre as mandíbulas e avança um pouco sobre o agressor mordendo-o sem, no entanto, sair de cima dos ovos. À aproximação de uma mosca pela frente, uma fêmea com ovos reagiu procurando mordê-la. Por outro lado, quando atacada pelos flancos ou por trás, por um objeto ou inseto, a fêmea gira prontamente sobre a postura e põe-se de frente ao atacante e tenta mordê-lo (Fig. 7).

Outra reação muito característica que a fêmea exibe é a de zumbir e girar o corpo para um lado, sem, no entanto, retirar suas patas do lugar, afastando sua cabeça do atacante e acertando-o com a asa dianteira do lado atacado (Fig. 8). A vespa-de-serra assim procedeu toda vez em que se tocava um de seus tarsos anteriores com um graveto ou haste de capim.

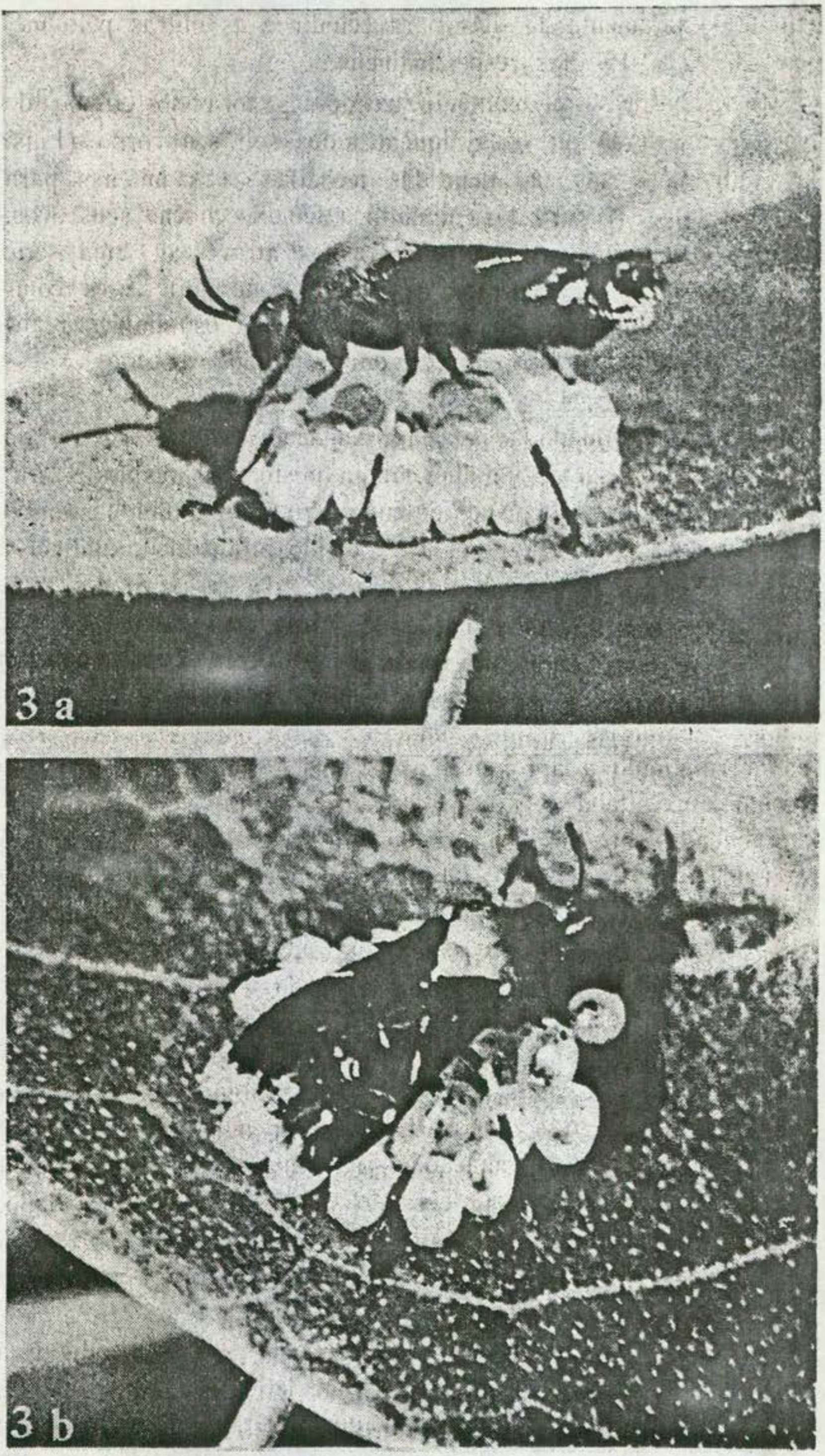


Fig. 3a e b. Fêmeas da vespa-de-serra quietas sobre seus ovos. Notar a disposição das patas fora dos circulos de ovos. Estes ovos estão bastante crescidos em relação aos ovos recém-colocados.

pa-de-serra abre com seu ovipositor serrilhado uma «tampa» triangular na epiderme da face dorsal do folíolo e põe o ovo em contato com o parênquima foliar. O ovo, no entanto, fica quase todo fora do folíolo com a epiderme foliar levantada aderida a um de seus lados. Os ovos ficam inclinados para o centro da postura. A postura é sempre feita na face dorsal do folíolo, aproximadamente eqüidistante entre a nervura central e a margem, preferencialmente próximo ao ápice do folíolo.

TABELA

Distribuição de ovos por posturas e ovos ovarianos em fêmeas recém-emergidas.

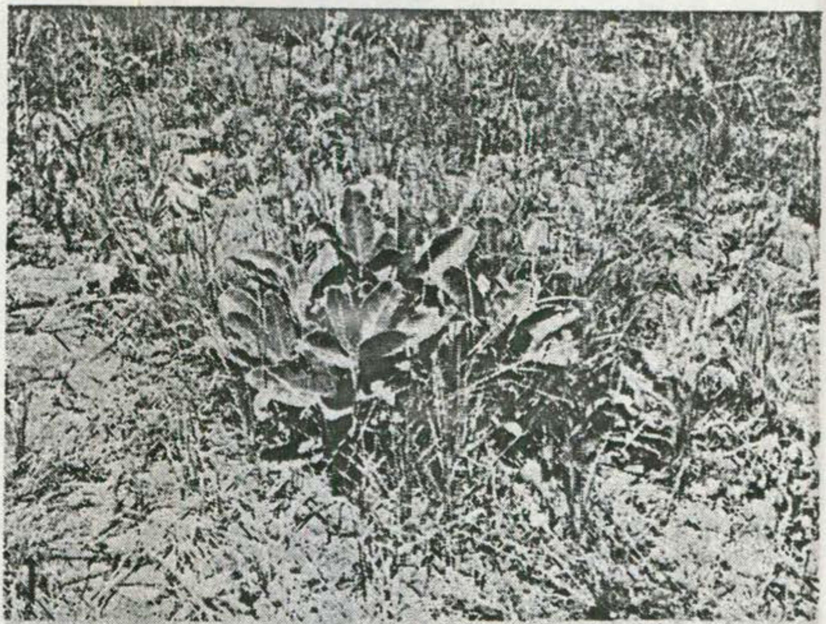
A distribuição para ovos por postura foi tratada como sendo unimodal. No entanto, a freqüência da distribuição parece indicar bimodalidade, sujeita a futura confirmação.

	Nº de casos observados	Média	Variação		Erro da média	Coeficiente de variação
			mín.	máx.		
Nº de ovos por postura	29	26,90	18	34	0,89	17,73
Nº de ovos nos ovários de fêmeas recém-emergidas	4	27,50	23	30	1,55	11,31

Cada fêmea põe apenas uma postura e tem em média 27,5 ovos nos ovários ao emergir (Tabela). Foram dissecadas 21 fêmeas que já haviam posto seus ovos, desde fêmeas jovens com posturas recentes até fêmeas com larvas e finalmente algumas recém-mortas. Todas as fêmeas dissecadas estavam com os ovários vazios ou mesmo já atrofiados, exceto uma que havia posto apenas 17 ovos, mas que, quando dissecada, revelou a presença de 9 ovos maduros nos ovários.

Comportamento maternal

Proteção aos ovos. Após concluir a postura, a fêmea permanece sobre os ovos cerca de 23 dias até a eclosão dos mesmos. Quatro posturas puderam ser acompanhadas durante quase todo o período entre a postura e a eclosão. Uma postura



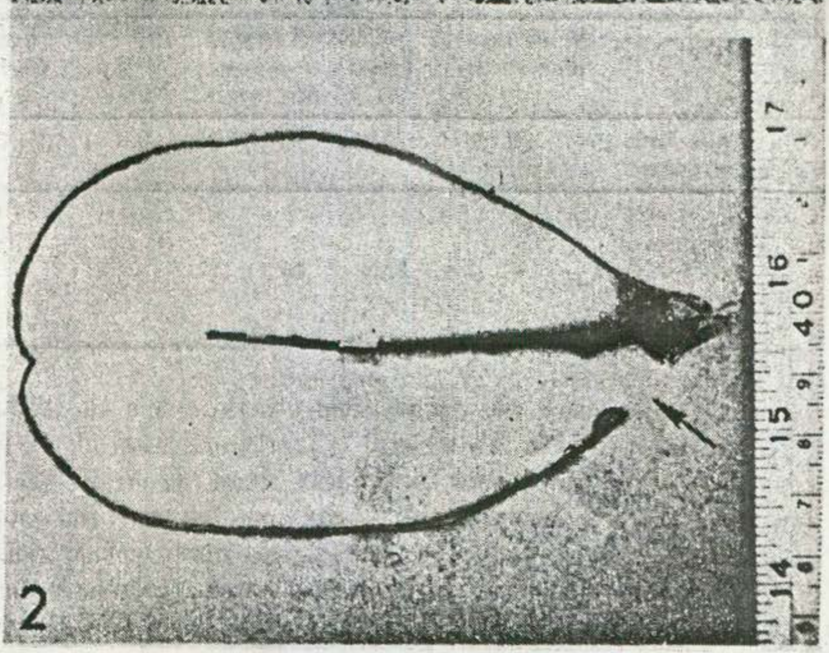


Fig. 1. Arbusto baixo de *Eriotheca pubescens* (Mart. & Zucc.), Bombacacea, planta hospedeira de *Themos olfersii*. Fig. 2. Resto de foliolo comido por larvas de 1º instar de *T. olfersii*. As larvas não comem a nervura central e nem a margem espessa e dura. A seta indica a porção de aprox. 10 mm da margem do foliolo, próxima à base deste, que as larvas comem para terem acesso à porção comestivel da lâmina foliar.

cinco folíolos muito coriáceos, medindo cerca de 15 cm de comprimento cada um. A vespa-de-serra tem preferência por arbustos baixos (Fig. 1).

O presente trabalho baseia-se em observações de campo realizadas entre outubro de 1973 e novembro de 1974 numa área de cerrado baixo de aproximadamente 10.000 m² no campus da Universidade de Brasília. Durante o período de observação foram realizadas um total de 40 visitas à área de estudo. Estas visitas ao campo, que duravam entre meia e três horas e totalizaram mais de 70 horas, foram feitas principalmente nos meses de outubro e novembro dos dois anos e sempre durante o dia, especialmente nas horas mais quentes e no final da tarde.

Foram marcados e examinados periodicamente 26 arbustos de *Eriotheca pubescens*. Nestes arbustos, foram marcadas e estudadas um total de 70 fêmeas com posturas. Destas, 26 foram examinadas apenas uma vez e 44 mais de duas vezes (muitas foram examinadas mais de dez vezes), num total de 200 observações sobre as 70 posturas. Foram feitas um total de 250 observações de fêmeas no campo, sendo que 178 das observações foram de fêmeas com ovos e 51 de fêmeas com larvas. Foram feitas um total de 109 observações sobre 38 grupos de larvas de diversas idades.

Em fins de junho de 1974 o cerrado da área de estudo pegou fogo, mas em agosto os arbustos já estavam com folhagem nova.

Além das observações sobre o comportamento natural das fêmeas e larvas, foram realizados vários experimentos simples para testar as reações de defesa das fêmeas e das larvas.

Observações

Oviposição. A fêmea escolhe um folíolo num arbusto para pôr seus ovos e, antes de colocá-los, passa algumas horas caminhando sobre o folíolo, principalmente na face dorsal deste. Durante o único ato de postura observado, o qual demorou pouco menos de três horas, a fêmea se manteve sobre a mesma. À medida em que cada ovo era posto, a fêmea mudava de posição, girando sobre os ovos já postos, porém sem sair um só momento de cima dos mesmos.

Os ovos, em número de 27 em média (Tabela), são postos todos próximos uns dos outros formando um pequeno círculo de aproximadamente 15 mm de diâmetro. Ao pôr o ovo, a ves-

«sawflies» do inglês e «mouches à scie» do francês, refere-se ao fato de as fêmeas de Sínfitas possuírem um ovipositor serrilhado. O termo mosca, no entanto, não é apropriado para designar himenópteros pois refere-se especialmente aos dípteros ciclorrafos e braquíceros. Portanto, na falta de um nome popular adequado, proponho o termo vespa-de-serra para os nossos representantes da subordem Sínfita.

A literatura sobre a biologia de Sínfitas neotropicais da família Argidae não é extensa e passo a resumi-la abaixo:

Curtis (1844) descreve pela primeira vez os aglomerados de casulos construídos pelas larvas de *Dielocerus formosus*, que denomina «ninhos». Sichel (1862) faz observações sobre a diapausa em *D. formosus.* Smith (1866) confirma as observações de Curtis através de informações de T. Peckolt, do Rio de Janeiro, que chamava *D. formosus* de «marumbouda seda». Ducke (1916) apresenta uma fotografia de um «ninho» de *Dielocerus* sp., que ele julga ser *D. formosus*, coletado por Alípio Miranda Ribeiro no noroeste de Mato Grosso. Segundo este, «os índios Nhambiquaras comem as larvas contidas nos aglomerados de casulos». Wheeler e Mann (1923) descrevem o comportamento gregário de larvas de Sínfita, provavelmente de Argidae segundo D. Smith (informação pessoal). Costa Lima (1927a) mostra fotografias de «ninhos» e larvas de *D. formosus* enviadas a ele por B. Pickel de Pernambuco e apresenta alguns dados sobre a diapausa desta espécie e revisa parcialmente a literatura. Costa Lima (1937) descreve um Icneumonídeo, *Lymeon dieloceri*, parasita das larvas de *Digelasinus diversipes.* Benson (1938) diz que *Dielocerus, Digelasinus* e *Pachytota* têm hábitos pré-sociais parecidos com os de *Perga* por tecerem seus casulos um ao lado do outro na forma de «ninhos». Monte (1941) descreve as larvas e adultos de *D. formosus* e diz que as larvas se alimentam de *Ingá* sp. em Minas Gerais. Monte e Silva (1946) dizem que as larvas de *Digelasinus diversipes* constroem seus casulos juntos formando «ninhos». Costa Lima (1960) revisa parcialmente a literatura sobre a família.

Material e métodos

Themos olfersii (Klug) é um Argídeo grande de coloração vistosa. A fêmea é preta e laranja enquanto que o macho, que é bem menor e tem antenas bifurcadas, tem coloração azul-metálica escura e amarela. É espécie comum nos cerrados do Distrito Federal. Os adultos surgem em meados de outubro, fim do período de seca, e são comuns até março, fim das chuvas. Os machos são raramente encontrados e são mais ágeis que as fêmeas.

A planta hospedeira desta vespa-de-serra é *Eriotheca pubescens* (Mart. & Zucc.), uma Bombacacea comum nos cerrados de Brasília. Esta planta tem folhas compostas, constituídas de

Já o comportamento gregário das larvas é bastante difundido entre os Sínfitas e ocorre também entre formas jovens de outros insetos, especialmente de lepidópteros (Long, 1955 e Wellington, 1957). Três são os grupos de Sínfitas que apresentam um gregarismo pronunciado e freqüente: as espécies de *Perga* e gêneros próximos (Pergidae), da Austrália, estudadas por Bennett e Scott (1859), Froggatt (1891, 1901, 1918 e 1923), Raff (1930 e 1934), Evans (1934) e Carne (1959, 1962, 1965, 1966 e 1969); as espécies holoárticas de Neodiprion (Diprionidae) estudadas principalmente por Ghent (1960) e as espécies neotropicais de *Dielocerus, Digelasinus* e *Pachytota* (Argidae) estudadas principalmente por Curtis (1844) e Costa Lima (1927 e 1960) e a espécie aqui estudada do gênero *Themos.*

O estudo de insetos pré-sociais justifica-se pelo fato de se constituírem em excelente material para o estudo da origem dos mecanismos de interação, atração e comunicação, presentes nas sociedades dos insetos eussociais (ver Wilson, 1972, para uma discussão sobre comportamentos pré-sociais). Certos componentes do comportamento eussocial já estão presentes nos insetos pré-sociais, onde podem ser mais facilmente observados e testados. Segundo Ghent (1960), o estudo do comportamento gregário das larvas de Sínfita ajudará bastante na compreensão da origem da divisão de trabalho entre os insetos sociais.

Sínfita é um grupo de himenópteros de distribuição principalmente holoártica e é pouco conhecido no Brasil, embora o Dr. David R. Smith, do U.S. Departament of Agriculture (informação pessoal), estime que existam pelo menos 700 espécies no Brasil. No entanto, o número de espécies brasileiras que foram estudadas biologicamente não vai além de dez, nada constando na literatura sobre a biologia de *Themos olfersii.* Outros trabalhos sobre comportamento gregário de larvas de Sínfitas brasileiros são os de Camargo (1955 e 1956) sobre *Paraperreyia dorsuaria* (Pergidae, Perreyiinae) e Pyenson (1940) sobre *Haplostegus epimelas* (Pergidae, Pergulinae).

As larvas de Tenthredinoidea são conhecidas popularmente no Brasil por falsas-lagartas (Marques, 1933, Monte e Silva, 1946 e Costa Lima, 1960) pela semelhança que apresentam com as verdadeiras lagartas, as lagartas de borboletas. Os adultos são as vezes chamados de vespas (Costa Lima, 1927) e outras vezes denominados de moscas-de-serra (Marques, 1933 e Costa Lima, 1960), ambos os termos não se tendo popularizado. O termo mosca-de-serra, uma tradução dos termos estrangeiros

Comportamento pré-social de Sínfitas do Brasil Central.
I. Themos olfersii (Klug) (Hymenoptera, Argidae)

Braulio F. de Souza Dias[1]

(Com 29 figuras)

Introdução

O presente trabalho tem dois objetivos: apresentar os resultados de um estudo inicial sobre o comportamento maternal das fêmeas do Sínfita *Themos olfersii* (Klug) e do comportamento gregário das larvas desta espécie. Sendo este o primeiro trabalho da série, será feita uma revisão da literatura sobre o comportamento pré-social em Sínfitas, com especial referência às espécies neotropicais.

Entre os Sínfitas encontramos duas formas de comportamento pré-social: o comportamento maternal ou subsocial, onde a mãe cuida da prole (contato entre gerações) e o comportamento gregário ou comunal das larvas (interação de indivíduos da mesma geração), «symphaedium» de Allee (1931).

Comportamento maternal é comum em vários grupos de insetos (Wilson, 1972), mas entre os Sínfitas, segundo Wheeler (1928), ocorre somente em certas espécies australianas de *Perga* (Pergidae). No entanto, Benson (1938) e Berland (1951) afirmam que as fêmeas de várias espécies neotropicais de *Dielocerus, Digelasinus* e *Pachylota* (Argidae) protegem os ovos e larvas novas. Infelizmente eles não citam os trabalhos nos quais basearam suas afirmações. Costa Lima (1960) cita *Perga lewisi* (Pergidae), da Austrália, e *Bergiana cyanocephala* (Cimbicidae), do Brasil, como tendo os mesmos hábitos. Os dois únicos trabalhos sobre o comportamento maternal em Pergídeos australianos, segundo Wheeler e Mann (1923), Evans (1934) e Carne (informação pessoal), são ainda os de Lewis (1837) e Froggatt (1901) sobre *Perga lewisi* da Tasmânia e sudeste da Austrália. *Bergiana cyanocephala,* por outro lado, foi estudada por Marques (1933) em Minas Gerais.

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[1] Estagiário no Laboratório de Zoologia da Universidade de Brasília, Brasília, DF.

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lide. After colliding, each of the two leading larvae abandon their positions and retreat to the end of one of the rows. This process continues for many hours. The rows usually meet together halfway between the midrib and the edge of the leaf so that the larvae on the posterior portion of one row lie on the midrib, and those on the posterior of the other row lie on the edge of the leaf. Therefore, these larvae at the end of the two rows cannot feed and have to wait altruistically their turn to eat.

The colonies readily amalgamate. The largest colonies, nevertheless, had only 40 to 50 larvae.

When disturbed, the larvae react simultaneously lifting their abdomen. When much disturbed they eject drops of a viscous liquid from the tip of their abdomen. When the weather is not favourable, they aggregate under the leaf in a massive ball.

The larvae cocoon in the soil under the host plant. It is not clear yet whether they cocoon togehter or not.

Agradecimentos

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displays the defensive and threatening reactions described above. However, when the feeding larvae move toward the leaf apex, the female stays behind at the leaf's base. Notwithstanding, she continues displaying the same defensive and threatening reactions which, possibly, still give some protection to the larvae.

Out of the females observed, 81% outlived the hatching of the eggs. Some of them brooded the eggs and young larvae for more than four weeks. Sometimes the female escorts the larvae when these move to another leaf. Some females abandoned their ovipositions and stood beside another female which brooded her youngs on a nearby leaf.

The female sawflies were never seen being preyed upon, despite the fact that they are big and conspicuous insects, that they stay over a month exposed to enemies on the foliage, and that they have no better weapon for defense than their powerful jaws. Nevertheless, three females, 4%, died apparently preyed upon. This low predation rate could be explained if the adultes were distasteful, which seems to be the case. In this case their conspicuous orange and black color could function as a warning coloration. If this is so, the brood would also benefit from the protection given to it by the warning coloration.

I observed the egg development of three ovipositions which accidentally lost their mothers. These eggs developed normally. It seems, therefore, that the only function of the maternal care in this species is to protect the eggs and young larvae against parasites and predators. It is likely, however, that this maternal care also protects the eggs and newly hatched larvae from destruction by heavy rains and desiccating.

In 98% of the cases observed (females with eggs), the females were found straddled over the eggs. Even when much disturbed, the female never flies or abandons her brood. It seems that the adults of this species never feed.

Gregarious Behaviour in Larvae

The larvae are gregarious from the time they hatch until they cocoon. The larval period lasts aprox. 30 days. The newly hatched larvae are big and have enormous heads and jaws when compared with newly hatched larvae of other sawflies with adults of similar size. Apparently these large jaws and the gregarious habits permit the larvae of *T. olfersii* to feed on the thick and hard leaves of *Eriotheca pubescens*, which have very thick edges.

This greater head development is possible due to a longer incubation period, during which the eggs grow in size, apparently at the expenses of the host leaf (Dias, not published). With an increase in the incubation period, the eggs would become too much exposed to parasites and predators, were it not for the evolution of a highly effective and prolonged maternal care.

It seems to me, then, that *T. olfersii* was able to occupy the ecological niche as feeders of thick leaves of «Cerrado» plants due to the evolution of large and gregarious first instar larvae capable of eating these leaves and also to the development of prolonged and efficient maternal care.

The young larvae gain access to the leaf blade by chewing their way through the thick edge of the leaf near its base. The larvae have a curious and unique feeding system. The larvae aline themselves one behind the other in two convergent rows. The leading larvae of each row are successively pushed forward toward each other until they colmitir que outras larvas possam comer. Este comportamento parece redundar em benefício para todo o grupo.

Como em geral as colônias são formadas por larvas nascidas de uma mesma postura, os membros de uma colônia têm carga genética parecida e, portanto, é muito vantajosa a proteção e «ajuda» mútua das larvas que garantiriam assim uma maior chance dos respectivos gens passarem para a geração seguinte.

É provável que as larvas também tenham gosto desagradável. Fisher (1930 segundo Hamilton, 1964b) apresentou evidências sugerindo que os caracteres de gosto ruim e coloração conspícua estão correlacionados com gregarismo em larvas de insetos.

Summary

The maternal care and gregarious behavior of the larvae of the sawfly *Themos olfersii* (Klug) are described. A revision of the literature on presocial behaviour in sawflies is presented, specially in neotropical species.

The larvae of *T. olfersii* feed on the leaves of *Eriotheca pubescens* (Mart. & Zucc.), a common Bombacacea in the «Cerrado» vegetation around Brasília.

Maternal Care

Each female lays an average of 27 eggs. The eggs are laid together, close to each other on the dorsal surface of the leaf, partially in contact with the leaf parenchyma, forming a circular mass of about 15 mm in diameter. When laying the eggs, the sawfly maintains herself over the eggs.

The period of incubation lasts an average of 23 days and the female stays straddled over the eggs until they hatch. The female, when disturbed by an approaching person, an insect, an object or when the leaf is struck, reacts displaying a series of defensive or threatening reactions. These supposedly protect her brood against potential enemies. I was able to distinguish 10 different types of displays: 1) buzzing; 2) bending her body to one side; 3) moving forward and biting; 4) turning around over the egg mass in order to face the offender; 5) buzzing while turning around her body, without moving her legs, and hitting the offender with the forewing of the threatened side; 6) raising her body and opening the wings, in what I called «state of alertness»; 7) spreading her wings over the eggs; 8) lowering her body close to the eggs; 9) raising and lowering her body rhythmically; 10) spreading and lowering her forewings while raising her hindwings until they meet above.

Maternal care in this species seems to be very effective since the egg mortality rate was only around 7%.

The young larvae stay at the hatching site and the female continues brooding them. When fully sclerotized, the larvae migrate together to the basal portion of the leaf where they start feeding together. The female escorts them and sits astride over them for many hours. She still

aumentam muito de tamanho, aparentemente às custas da folha hospedeira (Dias, não publicado).

Este aumento no período de incubação exporia demais os ovos aos possíveis predadores e parasitas, não fosse o cuidado maternal dispensado aos ovos. É provável, então, que este Sínfita só foi capaz de ocupar este nicho ecológico, de comedor de folhas coriáceas do cerrado, mediante a evolução de larvas de primeiro instar relativamente grandes e gregárias e cuidado maternal prolongado. Carne (1966) e Wilson (1972), aliás, admitem que muitos nichos ecológicos, desfavoráveis para espécies solitárias, puderam ser ocupados por espécies que desenvolveram comportamentos pré-sociais e sociais.

O modo de alimentar das larvas de *T. olfersii* alinhadas em duas fileiras convergentes parece ser único entre os Sínfitas. No entanto, o comportamento alimentar das lagartas de *Pieris brassicae* (Lepidoptera, Pieridae), segundo Long (1955), assemelha-se ao descrito aqui para *T. olfersii* num aspecto. A semelhança está que as larvas de ambas as espécies alternam períodos curtos de alimentação com períodos curtos de aparente inatividade. Long diz que as larvas de *P. brassicae* alternam entre períodos curtos de atividade, comendo numa área de alimentação comum, e inatividade aparente numa área próxima à área de alimentação. O período de inatividade aparente nesta espécie dura geralmente em torno de cinco minutos, às vezes até dez. As larvas de *T. olfersii*, de modo parecido, alternam entre um período de espera no final de uma das filas, com um período na faixa de alimentação, correspondente à porção anterior das duas filas. No entanto, em *P. brassicae* num dado momento todas as lagartas estão comendo ou estão inativas, enquanto que num grupo de larvas de *T. olfersii* num dado instante parte das larvas está comendo e parte está aparentemente inativa.

Long sugeriu que o tempo que as larvas ficam comendo ou «descansando» é provavelmente determinado fisiologicamente, dependendo do tempo necessário para ingerir e digerir uma certa quantidade de alimento tal que resultasse, por exemplo, no enchimento e esvaziamento da ingluvia. Embora seja provável que haja uma correlação entre o ritmo de alimentação e a fisiologia das larvas de *T. olfersii*, o que determina a saída das larvas da faixa de alimentação não são fatores internos mas sim a pressão do grupo.

O comportamento das larvas na fila de espera poderia ser taxado de altruísta pois estas larvas deixam de comer para percionar uma melhor proteção aos ovos e larvas contra possíveis predadores e parasitas. Estas reações de defesa ou agressão poderiam ser agrupadas nas seguintes categorias: 1) defesas de efeito principalmente visual (coloração de alarme; atitude de alerta; levantar e baixar o corpo ritmicamente; abrir e baixar as asas anteriores e levantar as asas posteriores); 2) defesas de efeito principalmente sonoro (zumbir); 3) defesas usando o corpo como barreira (girar sobre os ovos para ficar frente ao agressor; inclinar o corpo lateralmente sobre os ovos; estender as asas sobre os ovos; abaixar o corpo rente aos ovos); 4) reações de agressão (avançar e morder; zumbir girando o corpo e acertando o atacante com uma das asas anteriores). É provável, também, que o cuidado maternal ofereça alguma proteção aos ovos e larvas recém-nascidas contra a destruição por chuvas torrenciais e ressecamento.

Segundo parece, o fato das fêmeas de *T. olfersii* exibirem um cuidado maternal muito pronunciado e eficiente para com seus ovos e larvas novas permite que o número de ovos postos por fêmea seja baixo: média de 27 ovos. Este número está muito abaixo do número de ovos postos por fêmeas de outras espécies de Sínfita (Berland, 1951). Essa diminuição do número de ovos acompanhada de um maior cuidado maternal ocorre também entre algumas espécies sociais de aranhas (Kullmann, 1972). A propósito, Hamilton (1964a), diz que: «In certain circumstances an individual may leave more adult offspring by expending care and materials on its offsprings already born than by reserving them for its own survival and further fecundity».

Berland (1951) diz que uma das causas aparentes da raridade relativa dos Tenthredinoídeos nos países tropicais é a coriacidade das folhas. Ele cita que René Malaise verificou que 75% das falsas-lagartas na Birmânia se encontram sobre fetos (Pteridophyta, Filicales).

Parece-me que o fato das larvas recém-nascidas terem cabeças, e especialmente mandíbulas, bem desenvolvidas é que permite às larvas de *T. olfersii* comerem as folhas coriáceas de *Eriotheca pubescens*. O desenvolvimento de mandíbulas grandes e possantes, assim como de gregarismo, parece ser essencial para as larvas recém-nascidas poderem comer a margem espessa e dura destas folhas. No entanto, este maior desenvolvimento da cabeça das larvas de *T. olfersii* parece ser resultante do maior tempo de incubação dos ovos, durante o qual os ovos experimento para testar isto: ele trocou duas fêmeas que estavam sobre suas posturas e segundo suas palavras, «when first placed on each other's nests they seemed somewhat uneasy, as was to be expected from handling them, but on examining them the next day they appeared perfectly reconciled to the change». A este respeito, inclusive, as fêmeas de *T. olfersii*, como foi descrito acima, continuam a exibir as reações de defesa mesmo quando os ovos estão mortos.

Lewis acha que a principal função do cuidado maternal em *P. lewisi* é a proteção dos ovos e larvas contra os inimigos, pois ele nunca observou as fêmeas prestarem assistência às larvas, nem para ajudá-las a sair dos ovos ou na alimentação destas, e as colônias de larvas que ficaram acidentalmente sem a mãe sobreviveram satisfatoriamente.

É interessante notar que os adultos destas três espécies de vespa-de-serra nunca foram observados sendo predados, apesar de terem coloração vistosa e permanecerem várias semanas expostas sobre folhagens. Os adultos de outras espécies de Sínfita, por outro lado, são muito predados. Carne (1966), por exemplo, diz que os adultos de *Perga affinis* são muito predados por aves. É muito provável, então, que os adultos destas três espécies tenham gosto ruim. Portanto, é bem provável que a coloração vistosa das fêmeas destas vespas-de-serra funcione como uma coloração de alarme aos possíveis predadores, especialmente aves. Neste caso, a proteção, advinda desta coloração de alarme das fêmeas, deve estender-se aos ovos e larvas, visto que as fêmeas ficam próximas destes.

Hamilton (1964a) diz que o comportamento de um animal pós-reprodutivo deve ser inteiramente altruístico. De acordo com Blest (1963 segundo Hamilton, 1964a), em espécies aposemáticas (com coloração de alarme) a existência de vizinhos é uma vantagem, pois estes podem servir para ensinar a um predador inexperiente a coloração de alarme. Então, segundo ele, «with the warning-coloured moth it is altruistic to continue to live at least through the period during which other moths may not ~~the warning-coloured moth it is altruistic to continue to live at~~ have finished mating and egg-laying». Como a densidade da população de *T. olfersii* na área de estudo era grande e tendo em vista que as fêmeas vivem mais de um mês sobre as folhagens, a proteção conferida aos membros da população deve ser grande.

Assim, as fêmeas de *T. olfersii* utilizam-se de vários comportamentos altruísticos de natureza diversa que devem proporde *P. lewisi*, retiradas à força de cima de seus ovos, voltam para seus postos quando soltas. As fêmeas de *T. olfersii* também se comportam assim.

As fêmeas de *B. cyanocephala* e *P. lewisi* também apresentam reações de defesa enérgicas e elaboradas, algumas, inclusive, muito parecidas com as apresentadas por *T. olfersii*. As fêmeas das três espécies zumbem quando molestadas. A descrição que Froggatt dá deste comportamento para as fêmeas de *P. lewisi* é muito parecida com a acima descrita para *T. olfersii*: «she (the female) straddles the eggs with her wings half opened, the tip of her abdomen turned up, and with her jaws open, makes a slight buzzing sound if meddled with». Quanto às fêmeas de *B. cyanocephala*, Marques diz que quando certos microhimenópteros, parasitas de seus ovos, em «cadenciado e traiçoeiro vôo», procuram aproximar-se dos ovos, a fêmea agita as asas com certa energia, a fim de enxotá-los. Zumbir parece ser, então, uma reação de defesa muito comum nestas espécies de vespas-de-serra.

De acordo com Lewis, as fêmeas de *P. lewisi* mordem qualquer objeto que delas se aproxime, de maneira parecida como foi descrito acima para *T. olfersii*. Marques nada diz a este respeito sobre *B. cyanocephala*, mas nota que as fêmeas, quando «apoquentadas», têm o hábito de expelir, por via anal, certa quantidade de matéria semipastosa de cor pardacenta. Em *T. olfersii*, entretanto, isto nunca foi observado.

Assim como *T. olfersii*, as fêmeas de *P. lewisi* e *B. cyanocephala* dispensam atenta proteção às larvas novas. Estas últimas permanecem junto das larvas, protegendo-as, até morrer poucos dias depois da eclosão dos ovos. As fêmeas de *P. lewisi*, por outro lado, dispensam uma maior atenção às larvas, da mesma forma que *T. olfersii*. Segundo Lewis, «the mother insect follows them (the larvae), sitting with outstretched legs over her brood, preserving them from the heat of the sun, and protecting them from attacks of parasites and other enemies with admirable perseverance». Froggatt diz que as fêmeas desta vespa-de-serra quando estão sobre suas larvas «reminds one of an old hen protecting her chicks».

Lewis observou que algumas fêmeas de *P. lewisi* desertam seus ovos para juntarem-se a uma outra fêmea com postura, em folha próxima. Este fato também foi observado em *T. olfersii*. Parece, então, que as fêmeas destas duas espécies não distinguem sua prole da de outras fêmeas. Lewis chegou a fazer um

Encasulamento. Não pude observar as larvas se encasularem no campo. No entanto, encontrei uma vez uma larva madura morta, semi-enterrada no chão ao pé do arbusto onde se alimentara. Provavelmente não conseguiu perfurar o chão duro e seco e morreu ressecada.

Parece, então, que as larvas se enterram próximas de seu arbusto. Para verificar isto, levei para o laboratório, em duas ocasiões, algumas colônias de larvas maduras junto com galhos do arbusto hospedeiro e coloquei-as num terrário com terra homogênea e úmida. As larvas continuaram a comer os folíolos ainda por algumas horas mas depois desceram juntas ao chão do terrário. Parece, entretanto, que estranharam o ambiente artificial pois começaram a se dispersar tentando sair do terrário, o que muitas conseguiram. Infelizmente, a maioria morreu antes de se encasular.

Observei, todavia, que algumas larvas aproveitaram-se de um buraco aberto por outra larva para se enterrarem. Escavei os casulos de quatro larvas e verifiquei que duas haviam-se encasulado lado a lado.

Os casulos são finos, moles e revestidos de grãos de terra.

Discussão

Como foi exposto na introdução deste trabalho, o comportamento maternal de apenas duas outras espécies de Sínfitas está descrito na literatura: *Perga lewisi e Bergiana cyanocephala.* O que se sabe, no entanto, do comportamento maternal destas duas espécies é pouco. É interessante notar que em ambas as espécies referidas, assim como em *T. olfersii,* as larvas são bastante gregárias.

De modo parecido com o descrito aqui para *T. olfersii,* as fêmeas de *P. lewisi* (Froggatt, 1901) após a postura colocam-se sobre os ovos com as patas afastadas, em volta da massa de ovos e aí ficam até a eclosão dos mesmos. As fêmeas de *B. cyanocephala* (todas as observações aqui feitas sobre este Sínfita baseiam-se em Marques, 1933) também ficam sobre os ovos ou na proximidade destes até a eclosão dos mesmos. Tanto as fêmeas de *B. cyanocephala* como as de *P. lewisi,* segundo Lewis e Froggatt, não saem de cima de seus ovos quando molestadas e aderem firmemente à folha com suas garras poderosas, exatamente como *T. olfersii.* Lewis verificou que as fêmeas

Não tive oportunidade de observar estas larvas no ato de migração. As larvas, no entanto, devem migrar todas juntas pois as colônias não se desfazem após a migração de uma folha para outra. A regra geral parece ser a de mudar sempre para o folíolo vizinho, na mesma folha, após terminar de comer o anterior. Após comerem todos os folíolos da primeira folha, as larvas migram para uma folha vizinha onde repetem o procedimento.

Defesa. Muitas vezes, quando o dia estava nublado e ventando, ou então, quando chovia, observei que as larvas param de comer e ficam amontoadas na face ventral do folíolo onde comiam, próximas à sua margem. Pude observar, em duas ocasiões, que as larvas menores estavam no centro do agrupamento de larvas. Neste amontoado, as larvas dispõem-se com as cabeças voltadas para fora do círculo e os abdômens, curvos e pendurados, para o centro. A massa de larvas é bem compacta e nem todas as cabeças das larvas atingem a periferia do círculo (Fig. 29). Em certas ocasiões verifiquei que algumas larvas do amontoado se alimentavam.

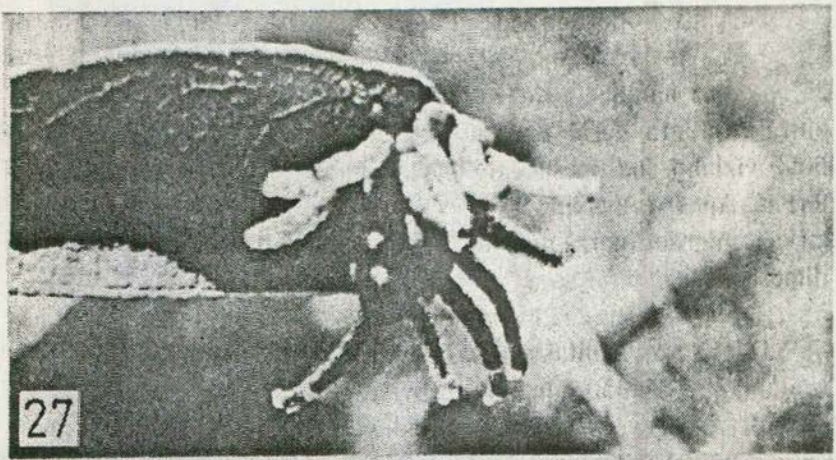
As larvas assumem esta atitude, às vezes, mesmo quando o dia é claro e o sol é forte.

Quando incomodadas, estando comendo ou amontoadas na face ventral do folíolo, as larvas respondem elevando seus abdômens. Elas mantêm os abdômens levantados por alguns instantes e, não sendo mais incomodadas, baixam-no lentamente até voltarem à posição normal. Mas, se são novamente molestadas, elas voltam a levantar o abdômen tantas vezes quantas forem perturbadas. Nesses casos, quando são bastante molestadas, elas excretam gotas de um líquido muito viscoso pela extremidade do abdômen, através de dois tubos da região anal (Figs. 27 e 28).

As larvas sempre reagem assim a uma batida seca no galho onde estão. Neste caso, todas as larvas reagem juntas.

Quando experimentei tocar na cabeça de algumas larvas com um graveto, elas responderam elevando o abdômen e projetando-o por cima de sua cabeça de tal modo que o abdômen ficou na forma de uma ferradura. Então, elas excretaram gotas do líquido viscoso sobre o graveto (Fig. 19). É interessante notar que as larvas têm uma mancha negra na extremidade do abdômen, a qual deve ter função na defesa.

Larvas maduras, quando retiradas à força das folhas com a mão, enrolam-se.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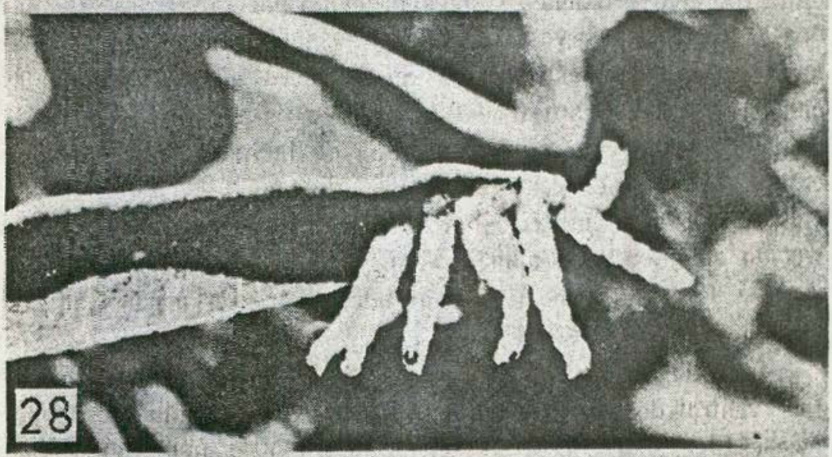
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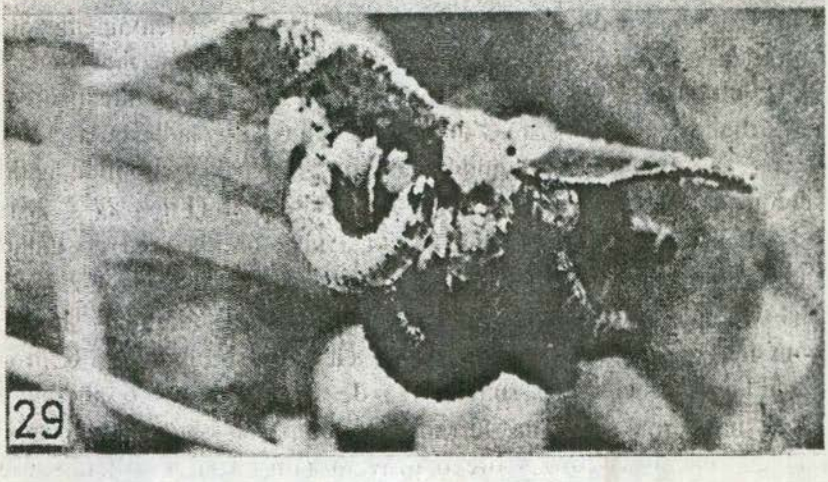
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Fig. 27. Larvas em atitude de defesa elevando seus abdômens. Note que as larvas expelem gotículas de um líquido viscoso pela extremidade do abdômen. Fig. 28. Idem, note a presença de uma mancha negra na extremidade dorsal do abdômen das larvas. Fig. 29. Larvas amontoadas na face ventral do folíolo. As cabeças estão voltadas para a periferia do círculo e os abdômens estão no centro. As larvas adotam esta atitude quando o tempo está desfavorável.

campo, mas pude observar algumas vezes que elas continuavam a se alimentar mesmo depois das 19 horas, quando já era escuro.

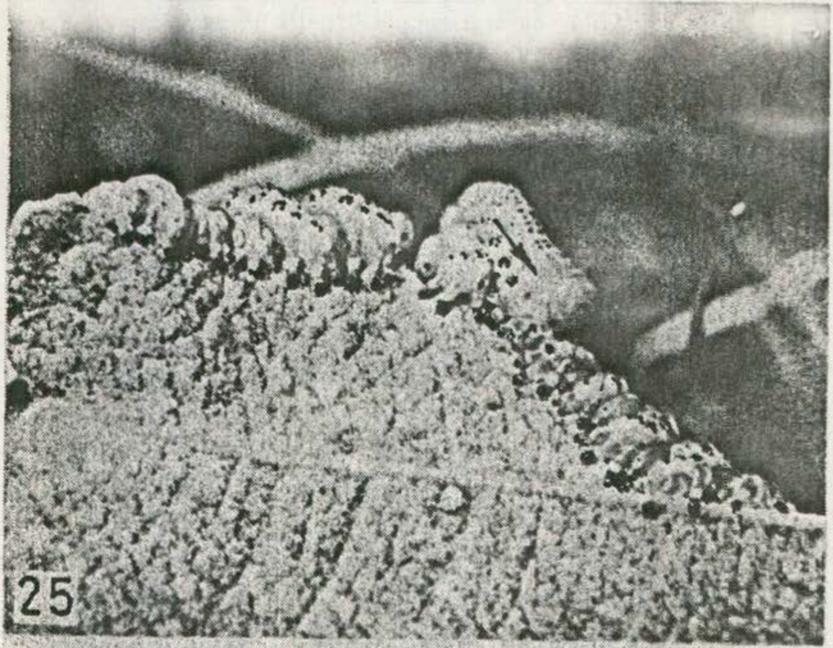
Manutenção da colônia. Durante todo seu desenvolvimento, as larvas originadas de uma mesma postura permanecem quase sempre juntas. Em apenas cinco das colônias observadas houve dissociação do grupo. Em dois desses casos, uma larvinha havia se desgarrado do resto da colônia, que permanecia unida, provavelmente durante alguma migração do grupo. Numa outra ocasião, parte de uma colônia jovem migrou para o folíolo vizinho mas algumas larvas permaneceram no folíolo original, protegidas ainda pela fêmea-mãe. Os outros dois casos observados foram de colônias jovens que entraram em contato com uma ou mais colônias velhas e se desmembraram em dois ou três grupos: alguns dos subgrupos da colônia desmembrada foram se unir às outras colônias enquanto que outros ficaram só.

O gregarismo destas larvas é muito pronunciado. Assim, várias colônias em observação, quando próximas umas das outras, acabaram por se unir, especialmente colônias jovens. Foram observadas, também, muitas colônias mistas no campo, isto é, colônias com larvas de diferentes instares. Aliás, é muito comum a associação de larvas maduras com larvas ainda no primeiro instar.

Mas, apesar desta tendência que as colônias têm de se unirem, nunca vi colônias muito grandes. Este fato certamente é devido à circunstância de que os arbustos da planta hospedeira são pequenos. O número médio de folíolos por planta é de 97,5 (mín. = 20; máx. = 250; para 13 plantas examinadas) segundo contagem feita em agosto de 1974, no final do período de seca, nos arbustos de *Eriotheca pubescens* com posturas.

Assim, cada arbusto suporta apenas algumas colônias de larvas. O maior número de colônias observadas num único arbusto foi de sete.

Em geral as colônias são formadas apenas por larvas nascidas de uma mesma postura, daí terem geralmente de 20 a 30 larvas. As colônias mais velhas ficam menores porque sempre algumas larvas morrem. Esta perda, no entanto, é contrabalanceada muitas vezes pela fusão de duas ou mais colônias. As maiores colônias observadas tinham de 40 a 50 larvas e eram constituídas de larvas jovens. Por estranho que pareça, nunca encontrei colônias de larvas maduras com mais de 30 larvas.



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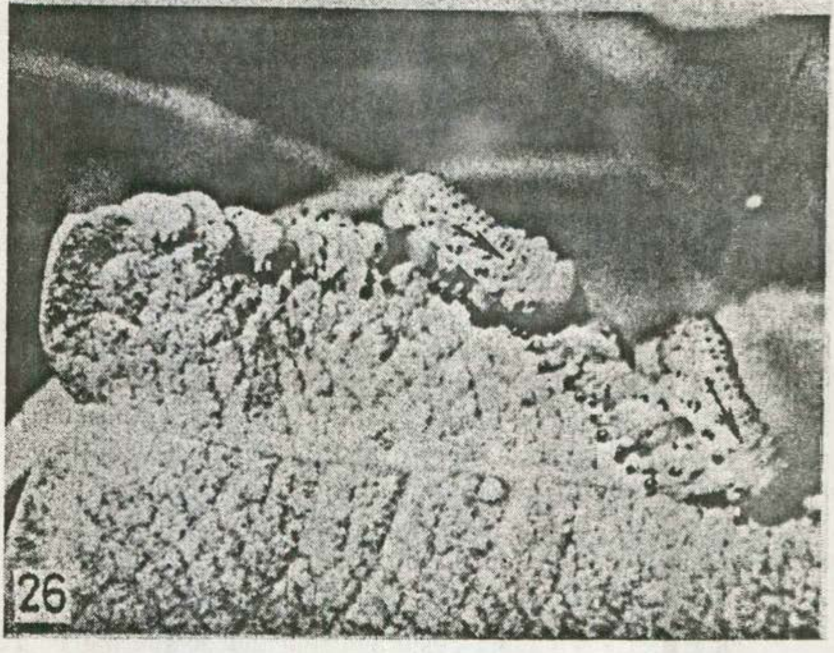

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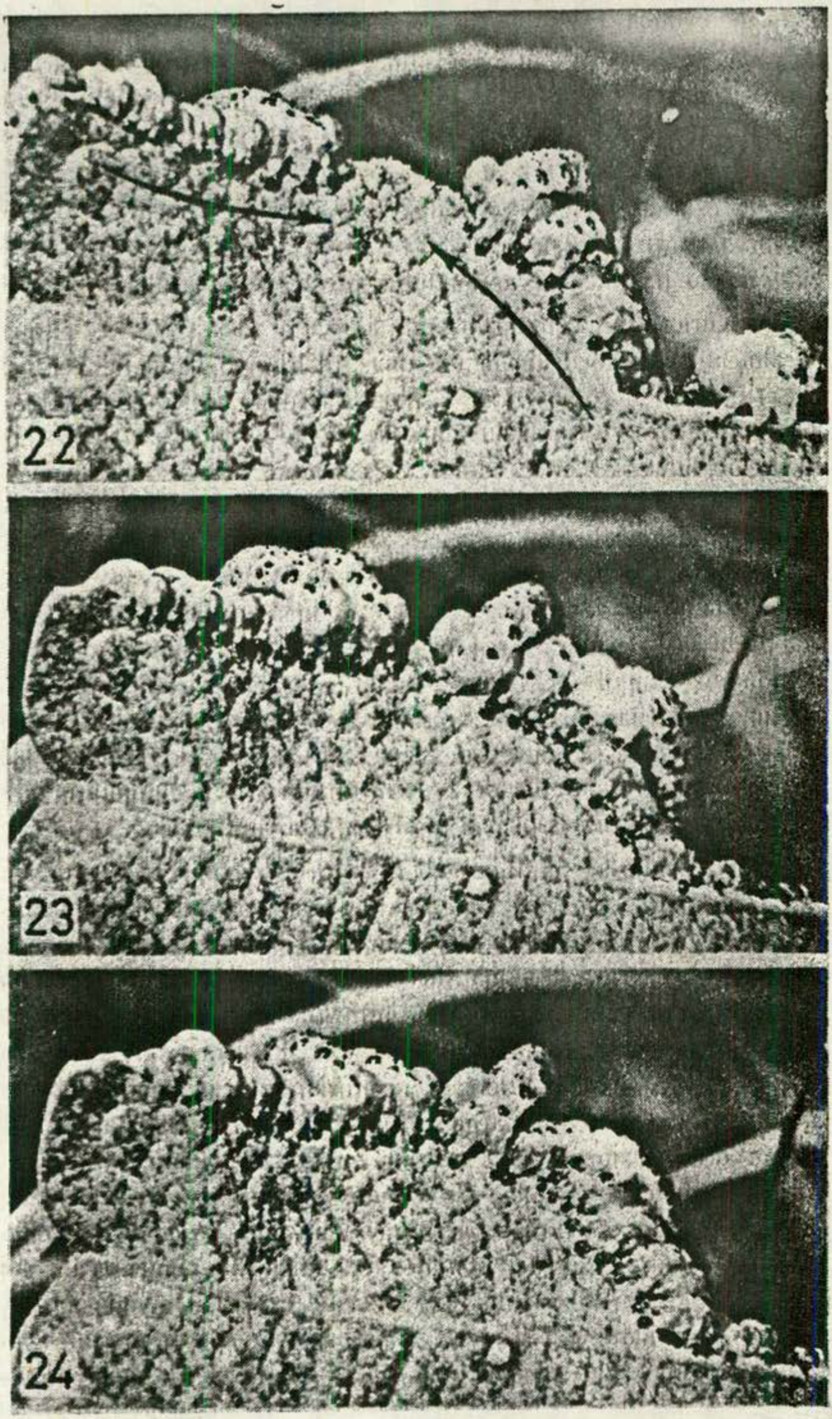
Figs. 25 e 26. (continuação das figs. 22 a 24). A larva que fica comprimida pelo choque das duas filas retira-se e vai para o fim de uma das filas (Fig. 25, seta). O processo continua e logo outra larva fica comprimida e retira-se, por sua vez, para o fim de uma das filas (Fig. 26, setas). As fotos 22 e 26 foram tiradas em seqüência, com intervalos de poucos segundos entre uma e outra.



Figs. 22 a 24. Comportamento alimentar das larvas de *T. olfersii*. Larvas alinhadas em duas fileiras convergentes. As setas indicam a direção em que as larvas caminham. À medida em que comem, as larvas caminham para a frente de modo que as duas fileiras se chocam. Uma das larvas que encabeçam as fileiras fica, então, comprimida pelas companheiras (segue nas figs. 25 e 26).

comem. O abdômen fica todo solto e curvo para um dos lados: geralmente de forma que não fique exposto ao sol. As larvas ficam coladas umas às outras, comprimindo-se mutuamente, mesmo sendo o folíolo bem espaçoso e o número de larvas pequeno. Elas sempre ficam uma atrás da outra enfileiradas: a cabeça da larva que está atrás encosta e aperta o último segmento torácico da larva da frente. Isto é assim tanto para as larvas recém-nascidas como para as larvas maduras prestes a encasularem-se.

O curioso do comportamento alimentar destas larvas é que geralmente elas se dispõem em duas fileiras convergentes (Figs. 17, 18 e 22 a 26). O que acontece é que à medida que comem, as larvas caminham para a frente e portanto as duas fileiras colidem. Ocorre, então, que as duas larvas que encabeçam as filas ficam comprimidas até que uma delas sai da fila e, caminhando sobre as cabeças e tórax das companheiras, vai para o fim de uma das duas filas. As demais larvas, no entanto, continuam a caminhar e logo duas outras larvas ficam comprimidas, repetindo-se o processo. Este ciclo repete-se assim por muito tempo. Às vezes, encontrando uma brecha no meio de uma das filas, a larva retirante aí se introduz. Muitas vezes a larva retirante, ao invés de acomodar-se no fim da fila, empurra a última larva e força sua entrada em penúltimo lugar: a última larva, para isso, tem que se afastar um pouco.

Observando-se as figuras 17 e 18, percebe-se a vantagem desse sistema: como as fileiras de larvas são mais compridas que a largura do folíolo entre a nervura central e sua margem, a porção posterior de uma das filas fica sobre a margem do folíolo e a porção terminal da outra fila fica sobre a nervura central. Acontece que as larvas não comem estas partes do folíolo. Ora, as duas fileiras se encontram a meio caminho entre a nervura central e a margem e, então, como todas larvas revezam ordenadamente de posição, todas têm chance de comer na parte boa do folíolo. Cronometrei, uma vez, a velocidade das larvas nestas fileiras e verifiquei que uma larva de tamanho médio chega a ficar dez minutos na faixa de alimentação. As larvas que estão no fim da fila, faixa de espera, têm que aguardar pacientemente sua vez de comer. Às vezes esta organização se desfaz, havendo apenas uma fileira ou duas ou mais orientadas em sentidos divergentes. Mas em pouco tempo as larvas voltam à organização original.

As larvas se alimentam durante todo o dia, mesmo nas horas mais quentes. Não fiz observação de larvas à noite no estava quieta sobre seus ovos e assim continuou até a eclosão dos mesmos, como foi verificado posteriormente.

As fêmeas de *T. olfersii* aderem-se firmemente às folhas através de suas fortes garras e nunca abandonam os seus ovos mesmo quando muito molestadas. Observou-se algumas vezes que retirando-se as fêmeas à força de cima dos ovos, elas prontamente voltam a colocar-se sobre eles, quando soltas.

Esta vespa-de-serra nunca foi vista alimentando-se no campo. Além disso, os adultos desse Sínfita nunca foram coletados em flor em cinco anos de coleta de insetos nos cerrados do Distrito Federal. Parece, então, que os adultos não se alimentam.

Comportamento gregário das larvas

As larvas de *T. olfersii* são gregárias desde que nascem até se encasularem. Elas gastam aproximadamente 30 dias entre o nascimento e o encasulamento. Estas larvas têm um colorido verde com manchas negras e ficam razoavelmente bem camufladas sobre as folhas.

Comparadas às larvas recém-nascidas de outros Sínfitas com adultos de tamanho comparável, as larvas recém-nascidas de *T. olfersii* além de serem maiores, impressionam pelo enorme tamanho das cabeças e mandíbulas.

Alimentação. As larvas sempre iniciam a comer pelo próprio folíolo onde a fêmea fez a postura e geralmente começam pela sua base. De 33 casos observados, em apenas duas ocasiões as larvas iniciaram a comer em outra parte do folíolo: na margem lateral mediana. Primeiramente elas comem um trecho de aproximadamente 10 mm da margem do folíolo, o suficiente para terem acesso à região do folíolo entre a margem e a nervura central que lhes servirá de alimento. A destruição desta porção da margem do folíolo parece ser feita sempre por várias larvas: foi de seis o menor número de larvas observadas que conseguiu comer esta porção da margem.

As larvas de primeiro, segundo e algumas vezes de terceiro instar não comem a nervura central e nem a margem do folíolo (Fig. 2). Isto deve-se ao fato de ser a margem do folíolo muito espessa e dura. Já as larvas grandes comem a margem do folíolo mas não sua nervura central.

As larvas sempre comem abraçando as duas superfícies do folíolo com suas patas e caminham para a frente à medida que aparentemente predadas: uma foi encontrada em pedaços, asas e patas apenas, ao lado dos ovos sobre o folíolo; os restos de outra fêmea foram encontrados no chão abaixo do folíolo com suas larvas: estava sem cabeça, tinha uma perfuração no lado ventral do abdome e todo o interior de seu corpo estava vazio; uma outra fêmea foi encontrada em pedaços no chão sob o folíolo com suas larvas.

Foi acompanhado o desenvolvimento de três posturas que perderam suas fêmeas-mães no início do desenvolvimento dos ovos. Os ovos se desenvolveram normalmente e não parece ter demorado mais nem menos que as posturas com fêmeas para eclodir. Os ovos centrais destas posturas desenvolveram mais rapidamente que os periféricos, o que aliás também ocorre nas posturas com fêmeas.

Constância do comportamento maternal. Durante todo o período de cuidado maternal a vespa-de-serra praticamente não se afasta nunca de seu posto. Em 98% das observações feitas de fêmeas com ovos, a vespa-de-serra estava quieta sobre seus ovos. As quatro ocasiões em que a fêmea foi observada separada de seus ovos são descritas a seguir. Uma fêmea estava quieta fora da postura no final da tarde, e como não foram feitas outras observações desta vespa-de-serra não se sabe se ela voltou para cima dos ovos ou não. Outra fêmea estava quieta sobre uma haste de capim próxima à sua postura quando localizada por volta do meio-dia, mas quando me aproximei, a vespa-de-serra foi para cima de seus ovos espontaneamente e lá ficou quieta.

Esta fêmea continuou sobre seus ovos até a eclosão destes, segundo foi observado nas cinco observações seguintes. Uma fêmea foi vista, também por volta do meio-dia, caminhando sobre as folhas de um galho vizinho ao da sua oviposição. Transportada, por intermédio de uma haste de capim, para o folíolo com seus ovos a vespa-de-serra logo os encontrou e colocou-se sobre eles. E aí continuou até a eclosão dos ovos, conforme foi verificado nas sete observações posteriores. A quarta fêmea estava longe dos ovos, andando sobre algumas folhas do galho vizinho, quando foi vista às 11 horas. Com o auxílio de uma haste de capim, ela foi transportada para o seu folíolo e pareceu reconhecer prontamente sua oviposição pois colocou-se sobre esta. Logo em seguida, no entanto, abandonou os ovos. À tarde desse mesmo dia, quando a postura foi inspecionada, a vespa-de-serra

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Comportamento Pré-social de Sínfitas do Brasil Central. II. Dielocerus diasi Smith, 1975 (Hymenoptera, Argidae)

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Trabalho dedicado à memória de Frei Thomaz Borgmeier.

Abstract

Presocial behavior in sawflies of Central Brazil. II. *Dielocerus diasi* Smith, 1975 (Hym., Argidae) — *Dielocerus diasi* belongs to a group of Neotropical Argid sawflies where social organization and behavior have reached the highest degree in Symphyta. Females insert their eggs into the leaf tissues of *Sclerolobium aureum* (Tul.) (Leg., Caesalpinae), and stay over the leaf for three to four weeks guarding the eggs, and young larvae against predators and parasites. The adult sawfly is conspicuously colored and distasteful, which might explain why females guarding their youngs are almost left undisturbed by predators. Apparently the females also defend a «leaf territory» against other females through buzzing advertising signals. The larvae are highly gregarious, feeding day and night in an ordered way in tight groups. Individual colonies readily fuse forming groups of sometimes more than 500 larvae. The larvae present a remarkable groupal defense display against enemies. Larvae spin their cocoons together forming big mass cocoons attached to the tree trunks. The larvae before spinning their individual cocoons, spin an elaborated and bulky communal cover, involving division of labor of an elementary type.

Life cicle is completed by most individuals in 90 days, but a significant proportion of the larvae spend an aditional year or two in diapause as prepupae. Especial attention has been given to the study, in the field and in laboratory, of adult emergence, copulation, location and choice of leaves for egg laying, «territory» defense before and after egg laying, egg laying, maternal care, group feeding and defense, migration of larvae ,interactions between adults and larvae, communal spinning of cocoons and parasitism. Eggs and young larvae are almost free from parasites, but older larvae are parasitised by the Tachinid fly *Spathimeigenia dieloceri* (Townsend), and the Chalcidid wasps *Spilochalcis* sp. and *Brachymeria* sp. The larvae and prepupae inside the mass cocoons are heavily parasitised by the Ichneumonid wasp *Lymeon ?dieloceri* (Costa Lima).

The literature on the ecological significance of maternal care and larval gregarism is summarized.

Introdução

O primeiro trabalho desta série, que trata do comportamento de *Themos olfersii* (Klug, 1834) (Argidae), saiu no volume 18 desta revista (Dias, 1975). Neste primeiro trabalho foi feita uma

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revisão bibliográfica sobre o comportamento pré-social em sínfita em geral, além de uma análise comparativa dos comportamentos maternais que ocorrem neste grupo.

No presente trabalho apresento os resultados de um estudo sobre o ciclo vital, parasitismo e comportamento pré-social (comportamento maternal e gregarismo larval) de *Dielocerus diasi* Smith, 1975. Na discussão faço uma comparação entre os comportamentos pré-sociais das duas espécies, além de uma avaliação sobre os possíveis significados destes comportamentos.

Dielocerus Curtis compõe juntamente com *Digelasinus* Malaise, *Mallerina* Malaise e *Topotrita* Kirby a subfamília Dielocerinae, restrita à região neotropical (Smith, 1975). O gênero *Dielocerus,* segundo Smith (1975), tem dez espécies descritas, sendo sete do Brasil, das quais apenas uma teve sua biologia estudada: *D. formosus* (Klug) (ver Dias, 1975). Segundo Smith (1975), *D. diasi* é muito próxima de *D. formosus* morfologicamente e, como será discutido no final deste trabalho, as duas espécies são também muito próximas etologicamente.

Ao resumo da literatura sobre a biologia de Argídeos neotropicais que apresentei no trabalho anterior, deve-se acrescentar mais um trabalho: Townsend (1942), que descreve uma mosca parasita de larvas de *Dielocerus formosus, Spathimeigenia dieloceri* (Tachinidae), criada por Oscar Monte em Pará de Minas, MG, e dá alguns dados sobre sua biologia.

Material e Métodos

A espécie de vespa-de-serra aqui estudada foi descrita pelo Dr. David R. Smith do U. S. Department of Agriculture a partir de material que lhe enviei (Smith, 1975). *Dielocerus diasi* é um sínfita grande: as fêmeas chegam a medir mais de 15 mm de comprimento. Os machos são bem menores que as fêmeas. Tanto a fêmea como o macho têm uma coloração laranja e preto vistosa e muito conspícua. É espécie muito comum nos cerrados do Distrito Federal, chegando em alguns lugares a atingir densidade considerável. Esta espécie também já foi coletada em Vianópolis, GO, no mês de novembro, e em Chapada (Chapada dos Guimarães?), MT, em setembro (Smith, informação pessoal).

A planta hospedeira das larvas deste sínfita é *Sclerolobium aureum* (Tul.) (Leguminosae, Caesalpinae), uma árvore comum nos cerrados de Brasília. Esta árvore atinge 15 metros de altura, é semidecídua e tem folhas não muito coriáceas cobertas de densa pelugem, especialmente na face inferior. A sua distribuição não é contínua e uniforme nos cerrados do Distrito Federal, pois ela tende a aparecer em grandes concentrações em certos lugares.

Este trabalho baseia-se em observações de campo e de laboratório realizadas a partir de setembro de 1970. Os estudos concentraram-se em cinco áreas de cerrado do Distrito Federal onde havia grande densidade da planta hospedeira, que chegava a ser a árvore dominante nestas áreas, assim como uma grande população da vespa-de-serra. Estas cinco áreas são: 1) cerrado próximo ao Biotério no campus da Universidade de Brasília; 2) cerrado próximo ao setor de Embaixadas Sul de Brasília; 3) cerrado próximo ao Aeroporto Internacional de Brasília; 4) cerrado do bairro Lago Sul de Brasília; e 5) cerrado na altura do km 47 da estrada Brasília-Formosa (GO), próximo a Planaltina. Foram realizadas cerca de 70 excursões ao campo, maioria com duração de uma a três horas, sendo que algumas prolongaram-se por todo o dia.

Cerca de 300 árvores de *S. aureum foram examinadas periodicamente.* Quarenta oviposições com suas fêmeas mães foram estudadas detalhadamente. Cerca de 50 colônias de larvas foram observadas e mais de 800 aglomerados de casulos foram inspecionados. Noventa destes foram levados para o laboratório para estudos e observações. Perto de 2000 adultos do sínfita e cerca de 250 parasitas emergiram no laboratório. Os comportamentos de muitos destes foram observados nas primeiras horas após a emergência.

Foram realizados alguns experimentos simples no campo com fêmeas cuidando da prole e com colônias de larvas se alimentando e fiando casulos comunalmente. Testou-se no laboratório o possível gosto e cheiro desagradáveis dos adultos de *D. diasi* com diversos predadores terrestres.

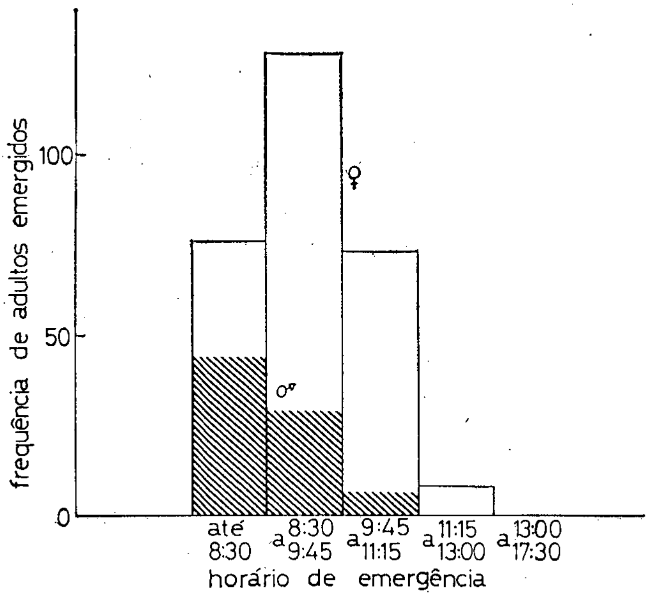
Exemplares das espécies estudadas, incluindo o tipo e parátipos de *D. diasi* Smith, foram depositados na Coleção Entomológica do Laboratório de Zoologia, Departamento de Biologia Animal da Universidade de Brasília, 70000 Brasília, DF e no U. S. National Museum, Washington, DC, E.U.A.

OBSERVAÇÕES

Emergência

Os adultos de *D. diasi* são encontrados durante todo o ano nos cerrados do Distrito Federal, visto que os ciclos de diferentes populações não estão sincronizados. A duração média para um ciclo vital é de 90 dias (excetuando-se os casos de diapausa), assim distribuídos: 14 dias para o período de incubação do ovo; cerca de 45 dias para o período larval; 20 a 40 dias para o período de casulo; e um a dois dias para o período entre a emergência e a postura (maturação?). Deste modo poderiam ocorrer até quatro ciclos por ano.

Dos 90 aglomerados de casulos (cada um com 50 a 600 casulos) coletados no campo e levados ao laboratório, cerca de dez prestaram-se para o cálculo da razão sexual, de onde emergiram 922 adultos (mínimo 29, máximo 499) na proporção de um macho para três fêmeas: razão sexual média para dez aglomerados (macho/fêmea) foi de 0,31 ± 0,19, variando de 0,18 a 0,61. Os adultos emergem nas primeiras horas da manhã até as dez horas, sendo que os machos emergem um pouco antes que as fêmeas: o pico de emergência dos machos é em torno



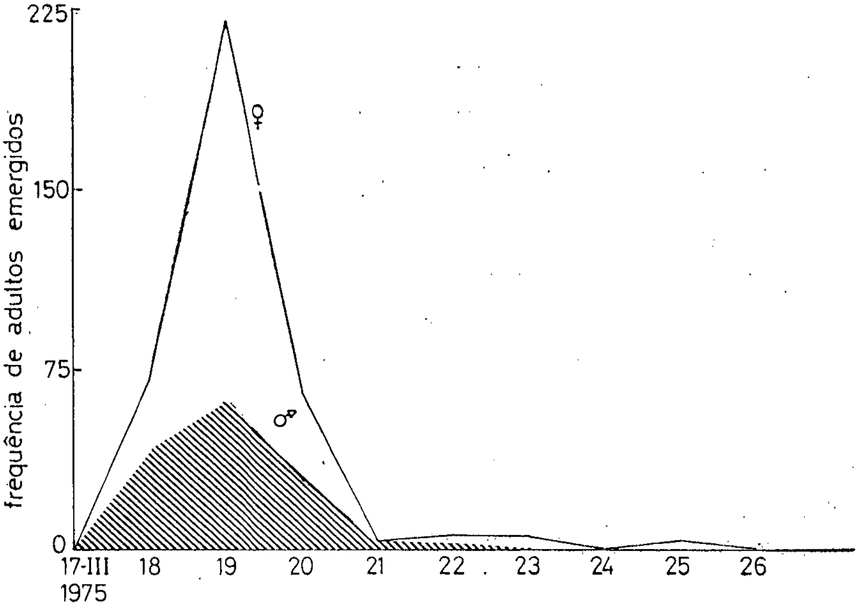


Figura 1 (superior). Gráfico de emergência dos adultos de um aglomerado de 500 casulos em intervalos aproximados de 90 minutos durante o dia. Os dados representam a soma dos adultos emergidos em dois dias consecutivos. — Figura 2 (inferior). Curva de emergência dos adultos do mesmo aglomerado de casulos. Todos os adultos emergiram entre 18 e 25 de março de 1975.

das oito horas e o pico das fêmeas é em torno das nove horas (Figura 1). Em muitos dos aglomerados de casulos observados a emergência dos adultos prolongou-se por muitas semanas, até um ou dois meses. Em outros, onde a umidade foi mantida alta, o período de emergência de adultos limitou-se a poucos dias (três a quatro dias) (Figura 2). Assim, acredito que os períodos prolongados de emergência (diapausa forçada) observados em laboratório foram devidos à baixa umidade do ambiente onde foram mantidos. A emergência dos adultos de um determinado aglomerado no campo deve ocorrer dentro de poucos dias. É interessante notar que aparentemente os primeiros indivíduos a emergir são dos casulos periféricos (Figura 3).

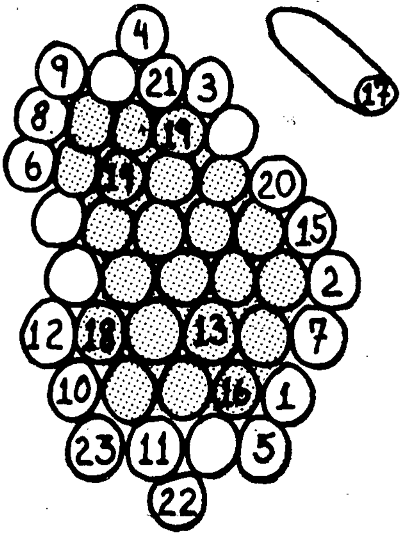


Figura 3. Seqüência de emergência dos adultos de um aglomerado de 45 casulos. Os números indicam a ordem de emergência dos adultos da geração sem diapausa que emergiram entre o 19º e o 64º dia depois da data de encasulamento. Os adultos dos casulos sem número emergiram após um ano de diapausa entre o 332º e o 410º dia depois da data de encasulamento. Os casulos centrais (não periféricos) aparecem sombreados.

No laboratório, freqüentemente este sínfita entra em diapausa na fase de prepupa. Algumas prepupas ficaram em diapausa por mais de dois anos. Assim, de nove aglomerados de casulos mantidos no laboratório, emergiram 93 adultos na época normal (20 a 30 dias após encasularem), 62 emergiram após um ano de diapausa e 20 emergiram após dois anos de diapausa. A razão sexual varia às vezes consideravelmente entre as gerações sem e com diapausa de um mesmo aglomerado de casulos. Num aglomerado, por exemplo, emergiram 23 adultos na geração sem diapausa com uma razão sexual de 0.05, e 22 adultos emergiram após um ano de diapausa com um razão sexual de 0,29.

Para emergir, os adultos cortam uma tampa circular de 4 a 5 mm de diâmetro na extremidade livre dos casulos com suas finas e pontiagudas mandíbulas. Após atravessarem a cobertura protetora que reveste o aglomerado de casulos, os adultos ficam alguns instantes quietos secando-se. Logo após emergirem, as vespas-de-serra excretam uma quantidade grande de um líquido viscoso pardacento e mal cheiroso, que seca em pouco tempo. Por vezes, ao serem pegos, os adultos recém-emergidos soltam este líquido fétido num pequeno jato. Outro comportamento de defesa exibido por adultos recém-emergidos é o de fingir de mortos quando pegos: as vespas-de-serra dobram as patas, curvam-se um pouco e ficam imóveis por vários segundos e até minutos: média de 30,8 ± 31 segundos para 25 observações, variando de zero até 135 segundos. Uma fêmea chegou a ficar 16 minutos imóvel ao ser manuseada.

Cópula

Os machos após emergirem permanecem sobre o aglomerado de casulos e copulam com as fêmeas assim que estas emergem (inbreeding). Não observei nenhum comportamento de cortejo. São os machos que iniciam a cópula. Eles tentam copular com todo adulto da vespa-de-serra que passe perto deles, seja fêmea ou macho. Alguns machos tentaram, inclusive, copular com meu dedo, talvez porque este estivesse com forte cheiro da fêmea pelo manuseio. O macho para copular, aproxima-se rapidamente da fêmea por trás, com seu abdômen curvado sob si, e monta parcialmente sobre a fêmea procurando encaixar as peças genitais. Conseguido isto, ele gira para um lado e torce seu corpo de forma a ficar voltado para o lado oposto da fêmea.

Durante a cópula o casal fica imóvel, mas se perturbado, a fêmea começa a andar arrastando o macho, sem porém desfazer a união. A cópula é bastante demorada, prolongando-se por muitos minutos, as vezes por mais de dez minutos. Por vezes, um segundo e até um terceiro macho sobe numa fêmea que já está copulando com outro, tentando copular na altura do torax da fêmea. Marquei cerca de 60 vespas-de-serra para verificar se uma fêmea copula com mais de um macho no espaço de uma hora após sua emergência e observei que, com exceção de uma única que copulou com dois, aquelas que copularam uma vez não deram mais atenção aos machos. Os machos, apesar disso, continuaram tentando copular, porém, logo desistiram e afastaram-se.

As fêmeas após copularem mostram-se muito ativas, procurando subir qualquer obstáculo, zumbindo muito até voar. Algumas conseguem voar poucos minutos depois de emergirem. Os adultos apresentam um geotropismo negativo muito pronunciado assim como um fototropismo positivo forte. Logo após emergirem, os adultos são capazes de voar curtas distâncias mas, após algum tempo já conseguem atingir distâncias consideráveis, embora com um vôo pesado e ruidoso.

Escolha da Folha de Postura

Cada fêmea após copular e localizar uma árvore de sua planta hospedeira, *Sclerolobium aureum* (Tul.), escolhe uma folha para fazer a postura. A fêmea voa em círculos ao redor da copa desta árvore, pousando por breves instantes em várias de suas folhas. Após pousar numa folha, geralmente uma das mais apicais de um galho do alto da copa, a vespa-de-serra caminha silenciosamente, com suas asas dobradas, em passos rápidos explorando suas duas superfícies.

Desta primeira folha ela passa caminhando pelo galho para outras folhas vizinhas deste galho, que também são exploradas. Logo ela alça vôo e vai pousar noutra folha apical de outro galho distante, onde repete o mesmo comportamento exploratório. Após pousar e explorar um certo número de folhas de vários galhos, a fêmea tende a voltar repetidamente para uma certa folha, onde fica cada vez mais tempo. Depois de cerca de meia hora de escolha, a vespa-de-serra não sai mais de sua folha favorita.

Procurei verificar se algumas das seguintes características da folha influenciam na sua escolha pela vespa-de-serra: tamanho (comprimeito), estado de conservação (se comida ou não), posição no galho, altura acima do chão e idade. Tamanho, idade e posição no galho são dependentes um do outro. A vespa-de-serra nunca põe ovos nas folhas novas e pequenas do ápice dos galhos. Excetuando-se, contudo, estas folhas novas, as fêmeas põem ovos em folhas de tamanhos e idades bastante variáveis. Efetivamente as posturas não são distribuídas ao acaso nos galhos: há uma nítida preferência por folhas segundo seu posicionamento no galho. Cada galho-não-ramificado possui de cinco a sete pares de folhas. Nos galhos mais velhos todas as folhas são aproximadamente do mesmo tamanho, mas nos galhos jovens existe desde brotos apicais minúsculos até folhas maduras, grandes, basais. Nunca observei posturas no primeiro par de folhas (esta numeração é feita a partir do ápice do galho em direção à base), mesmo em galhos mais velhos. Do mesmo modo, as fêmeas não põem ovos nas folhas mais basais. Todas as posturas observadas localizavam-se em folhas do segundo, terceiro ou quarto pares de folhas, sendo que nos galhos mais novos a preferência é por folhas mais basais (4º par) e nos mais velhos a preferência vai para folhas mais apicais (2º par). As vespas-de-serra preferem folhas intactas, porém, em árvores muito infestadas e com poucas folhas intactas disponíveis, não é raro encontrar posturas em folhas parcialmente comidas. Apesar de fazerem postura em árvores grandes e arbustos, as fêmeas sempre escolhem folhas do alto da copa, isto é, de galhos mais jovens.

Estabelecimento do «Território» Foliar

Após escolher sua folha, a vespa-de-serra passa cerca de 24 horas sobre esta antes de começar a pôr os ovos. Durante esta fase, a fêmea exibe alguns comportamentos característicos cuja função não está bem clara ainda. Durante o dia alterna entre períodos curtos de imobilidade com períodos de movimentação. Durante a fase de imobilidade, a vespa-de-serra fica geralmente no centro da superfície inferior da folha, numa região onde serão postos os ovos (área principal), com as asas parcialmente estendidas.

Durante os períodos de movimentação ela caminha em semicírculos sobre a superfície inferior da sua folha, especialmente sobre a área principal, com as asas parcialmente estendidas. Enquanto caminha, alterna períodos de silêncio, com períodos de zumbido, provocado pela agitação das asas. O zumbido é muito forte e audível a alguns metros de distância e pode durar mais de dez segundos. À noite a fêmea fica imóvel, com as asas dobradas, na superfície inferior da folha, especificamente na área principal. Enquanto caminha sobre a folha, a fêmea aproxima bastante suas peças bucais e extremidade do abdômen da superfície foliar.

Aparentemente estes comportamentos da fêmea visam fazer uma marcação visual e sonora da folha onde fará sua postura, isto é, marcação e defesa de um «território» de criação da prole: que será chamado de território foliar. Outra observação que evidencia isto é o fato de que as fêmeas são muito sensíveis aos zumbidos de outras fêmeas próximas. Geralmente cada galho-não-ramificado, com dez a 14 folhas, comporta apenas uma postura. Apenas uma vez observei uma fêmea nova escolher uma folha de um galho-não-ramificado que já continha outra fêmea, com ovos, estabelecida. Cada vez que a fêmea nova zumbia, a outra ficava agitada, saía de seu posto usual na base da folha e colocava-se sobre seus ovos, junto à margem da folha, com a cabeça voltada para a direção da fêmea nova. Raramente a fêmea com postura zumbia quando a outra zumbia.

Postura

A postura dos ovos é feita sempre no período entre 11 e 15 horas do dia. Assim, as fêmeas emergem cedo, copulam e geralmente conseguem encontrar uma folha adequada antes do meio-dia, e fazem sua postura no meio do dia seguinte.

As fêmeas de *D. diasi* ao emergirem já estão com todos seus óvulos prontos para serem postos. Cada fêmea tem em média 76 óvulos, que ocupam quase tôdo o abdômen (Tabela I). A fêmea tem 16 ovaríolos em cada ovário (32 no total), cada um com dois ou três óvulos. Em geral, portanto, o número de ovos colocados deve se situar entre o mínimo de 64 e o máximo de 96, com uma média teórica de 80.

Tabela I

Tipo de ovos	*N*	*Amplitude*	*Média* ($\bar{X}$)	*Desvio Padrão (S)*
nº de ovos: ovarianos	30	45 — 95	75,67	11,18
por postura	33	39 — 92	75,33	12,60
não colocados	11	0 — 4	1,09	1,58

Número de ovos ovarianos, número de ovos por postura e número de ovos não colocados por fêmea. Dados cumulativos de 1972 a 1975 para várias populações.

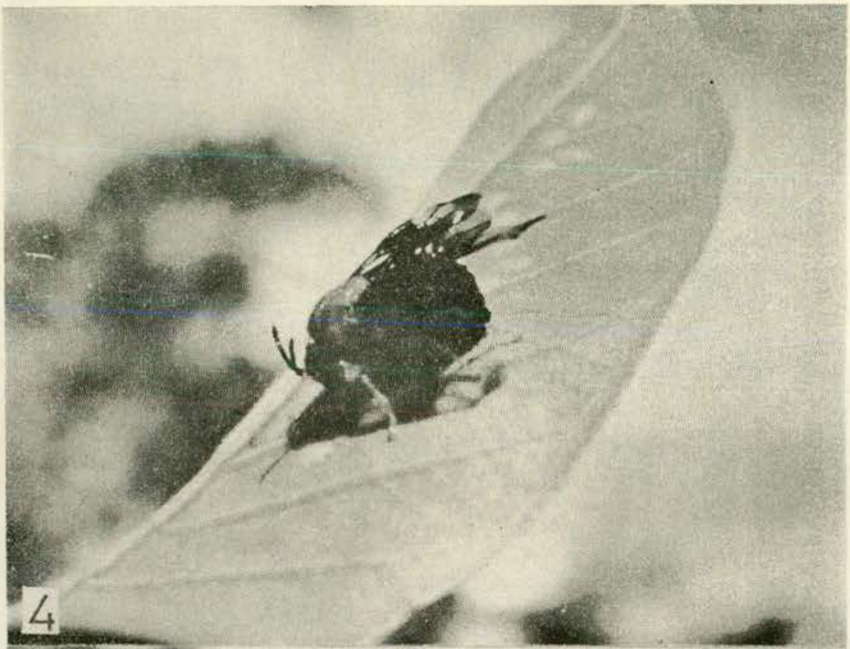
A vespa-de-serra coloca todos os ovos numa mesma folha, no lado inferior, inserindo-os espaçadamente no interior desta, entre o parênquima e a epiderme inferior. A fêmea abre uma nova cavidade para cada ovo. Os ovos são postos na área principal, isto é, na região da folha onde a fêmea concentrou sua movimentação e displays (zumbidos).

Para pôr um ovo ,a vespa-de-serra escolhe um lugar conveniente na lâmina foliar, entre as nervuras, colocando-se sobre o local com a cabeça voltada para a nervura central e a base da folha (pecíolo) (Figura 4).

A fêmea prende-se firmemente à folha com suas garras e curva um pouco o abdômen para baixo. Introduz o ovipositor na epiderme foliar e aprofunda-o devagar, balançando o corpo de um lado para o outro continuamente, porém sempre caindo cada vez mais para o lado oposto àquele onde o ovipositor penetra na folha e com as asas parcialmente estendidas. Com o ovipositor, a vespa-de-serra abre uma câmara semicircular sob a epiderme inferior da folha, em seguida empurra seu abdômen mais para baixo e retira o ovopositor deixando um ovo na cavidade. Retirado o ovipositor, a vespa-de-serra afasta-se sem prestar nenhuma atenção ao ovo que pôs. No ponto de inserção do ovipositor na folha estravasa um pouco de líquido foliar verde escuro. Esta marca verde continua evidente por alguns dias. O ovo colocado sob a epiderme foliar forma uma dilatação — «bolha» — que denuncia sua presença (Figuras 6 e 7).

A vespa-de-serra demora em média de 80 a 85 segundos para por um ovo. Não sei ao certo quanto tempo a fêmea leva para por todos os ovos, mas não demora mais que duas a três horas. No caso de uma vespa-de-serra que foi observada atentamente, colocou 33 de seus 61 ovos em menos de uma hora e 50 minutos. Enquanto põe os ovos e logo após completar a postura, a vespa-de-serra caminha agitadamente sobre os ovos já postos silenciosamente e vez por outra zumbindo (Fig. 5).

Os ovos não são distribuídos uniformemente pela folha, mas concentrados em uma das metades longitudinais, entre a margem e nervura central. De um total de 14 oviposições, 7 estavam totalmente colocadas de um único lado da nervura central, 4 tinham 90 a 99% dos ovos em um único lado, 2 tinham 80 a 89% dos ovos em um único lado e uma tinha 60 a 69% dos ovos em um único lado da nervura central da folha. Não há nenhuma correlação entre o tamanho da folha e o número de ovos postos. Cada fêmea põe em média 75 ovos, todos na mesma folha (semelparidade), e sobra em média um ovo no seu ovário (Tabela I).



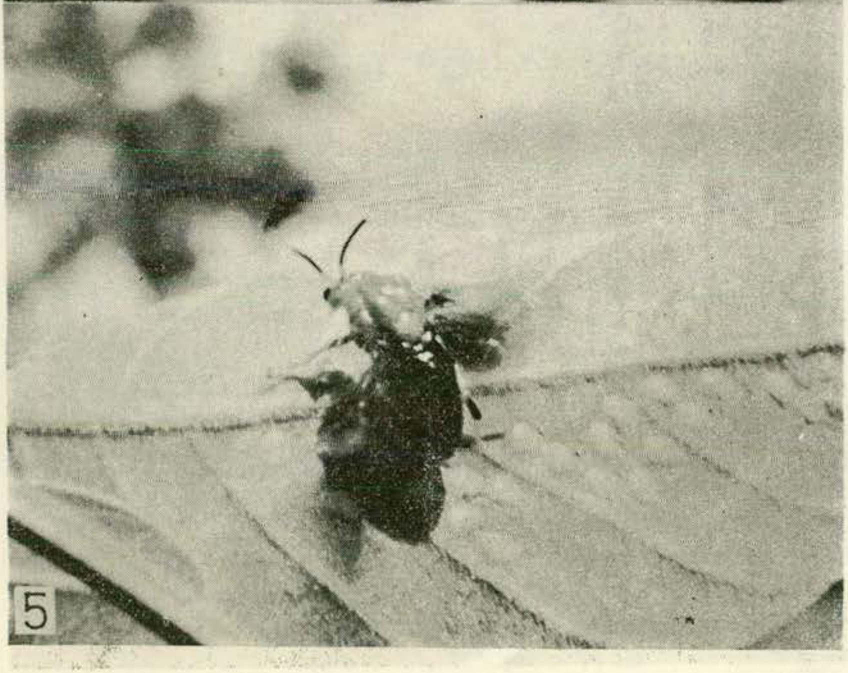
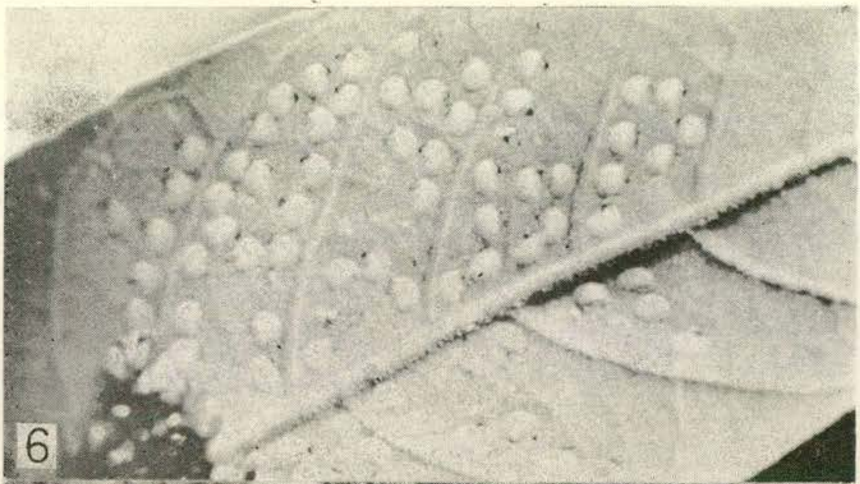


Figura 4. Fêmea pondo ovos dentro da lâmina de uma folha da árvore hospedeira, *Sclerolobium aureum* (Tul.) (Leg., Caesalpinae). — Figura 5. Fêmea zumbindo durante a fase de oviposição. A fêmea eleva a parte anterior do corpo ao zumbir.



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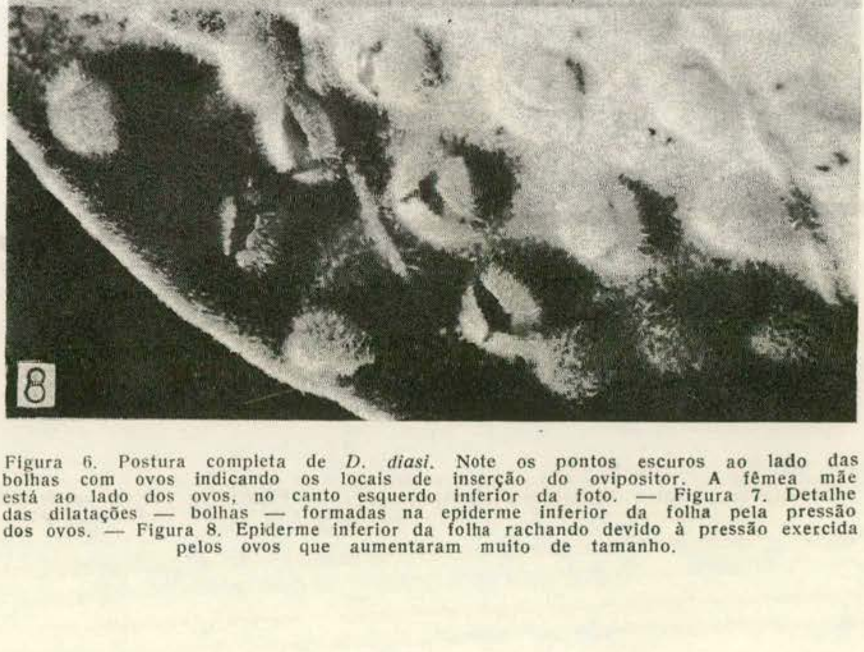

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Figura 6. Postura completa de *D. diasi*. Note os pontos escuros ao lado das bolhas com ovos indicando os locais de inserção do ovipositor. A fêmea mãe está ao lado dos ovos, no canto esquerdo inferior da foto. — Figura 7. Detalhe das dilatações — bolhas — formadas na epiderme inferior da folha pela pressão dos ovos. — Figura 8. Epiderme inferior da folha rachando devido à pressão exercida pelos ovos que aumentaram muito de tamanho.

Comportamento Maternal

Após completar a postura, a fêmea coloca-se na base da folha, na sua superfície inferior, junto ao pecíolo, com a cabeça voltada para ele e com as asas parcialmente estendidas. Freqüentemente a fêmea deixa este seu «posto» e caminha silenciosamente sobre a postura, demorando-se por vezes sobre esta. No seu «posto» na base da folha a vespa-de-serra está estrategicamente colocada para defender seus ovos do ataque de qualquer predador ou parasita que tentar se aproximar da folha pelo pecíolo.

Quando molestada, a vespa-de-serra exibe uma série de comportamentos de advertência e defesa: 1) zumbir; 2) andar em círculos sobre a postura; 3) elevar bruscamente e abrir um pouco mais as asas; 4) elevar a cabeça e abrir as mandíbulas ao máximo; 5) avançar e morder; 6) zumbir girando o corpo para um lado, sem se mover do lugar, e acertando o atacante com a asa dianteira do lado atacado; 7) caminhar sobre a postura zumbido; 8) ficar quieta imóvel sobre a postura. A fêmea de *D. diasi,* no entanto, se comparada à fêmea de *Themos olfersii* responde menos aos estímulos, isto é, ela é menos excitável (ver Dias, 1975). Suas reações mais freqüentes são: caminhar por cima da postura, e zumbir. Ao zumbir, a fêmea levanta a parte anterior do corpo e, quando muito molestada, ela abre as mandíbulas enquanto zumbe (Figura 5). A reação de morder é liberada apenas por estímulos fortes. Ao morder um objeto ela puxa-o com força para baixo, acertando-o com uma das asas anteriores enquanto zumbe, girando o corpo para um lado.

Aproximei várias vezes um inseto ou pequeno animal (vespas *Polistes* sp., moscas domésticas e lagartos *Anolis* sp.) de folhas com posturas e as fêmeas mães sempre reagiram caminhando em círculos sobre os ovos, zumbindo repetidamente. A aproximação de uma pessoa é suficiente para liberar o comportamento de zumbir girando o corpo. Uma batida seca na folha com postura, ou no galho onde a folha está, pode liberar pelo menos três destes displays: zumbir; caminhar sobre os ovos; e elevar bruscamente um pouco as asas parcialmente estendidas, abaixando-as em seguida. Por mais molestada que seja, a vespa-de-serra nunca abandona sua folha. Uma fêmea com postura ficou muito agitada quando, durante a noite, incidi o facho de luz de uma lanterna sobre ela: movimentou-se e zumbiu fracamente.

Presenciei duas vezes um acontecimento raro e interessante: uma folha com postura e fêmea mãe ser invadida por larvas novas de outra postura. No primeiro caso, larvinhas do primeiro ínstar invadiram a folha de uma postura nova e a fêmea mãe desta saiu de sua folha e ficou caminhando inquieta sobre o galho e a folha vizinha do mesmo par. Depois ela ficou quieta no galho a poucos centímetros abaixo de sua folha, com suas asas parcialmente estendidas e cabeça voltada para baixo. Certamente a presença das larvinhas confundiu a fêmea! As larvinhas invasoras caminharam sobre a postura e estabeleceram-se na margem basal da folha, muito próximo da postura, para comer. No dia seguinte as larvinhas continuavam na folha da postura, agora comendo junto ao ápice da folha, e a fêmea da postura voltara para seu posto da base da sua folha, com as asas parcialmente estendidas e a cabeça voltada para o pecíolo. Nos dois dias subseqüentes as larvinhas continuaram a comer na mesma folha e a fêmea mãe continuou no seu posto. Vez por outra, no entanto, ela caminhava sobre sua postura e aproximava-se das larvas invasoras. Estas prontamente elevavam seus abdômens defensivamente. Posteriormente, após comerem metade da folha mas respeitando a porção com a postura, as larvinhas abandonaram a folha. A fêmea mãe, contudo permaneceu na sua folha de postura não se deixando «enganar» novamente pela passagem das larvinhas invasoras. No segundo caso, larvas de 2º ou 3º ínstar, com a idade de dez dias, invadiram a folha de outra postura nova. A fêmea desta, no entanto, não abandonou sua folha com postura. Ficou parada ou caminhando sobre sua postura, aproximando-se muito das larvas invasoras que comiam no ápice da folha. Não observei qualquer atitude de defesa das larvas frente a proximidade da vespa-de-serra. Um ou dois dias depois as larvas invasoras abandonaram a folha da postura, deixando intacta a porção da folha com a postura. A fêmea mãe não abandonou sua folha: continuou sobre os ovos, com a cabeça voltada para a base da folha.

Durante o período de incubação, que dura 14 dias, os ovos aumentam cerca de três vezes em volume devido à absorção de água e provavelmente substâncias nutritivas da folha (Dias, não publicado). No final ,os ovos estão tão grandes que a epiderme inferior da folha, não resistindo à pressão dos ovos, arrebenta deixando os ovos expostos (Figura 8).

Observações de campo indicam que a mortalidade dos ovos é muito baixa, os únicos ovos mortos observados estavam secos e murchos. Não observei nenhum caso de parasitismo ou predação de ovos.

Os ovos eclodem todos no mesmo dia. À medida que nascem, as larvas permanecem juntas à postura, formando pequenos grupos compactos. Depois que a maioria das larvas nasceu, elas migram para fora da folha de postura induzindo a fêmea mãe, ao passarem pela base da folha ,a sair de seu posto e descer pelo galho uns 4 a 8 cm. As larvinhas migram para uma das folhas apicais do galho-não-ramificado da postura. Portanto, enquanto as larvinhas migram para comer nas folhas apicais, a fêmea mãe desloca-se para uma porção mais basal no galho da postura, geralmente entre o 1º e 2º pares de folhas abaixo da folha de postura. Aí ela fica com suas asas parcialmente estendidas e com a cabeça voltada para baixo, isto é, para a base do galho (Figura 9a).

Nos locais onde os ovos foram inseridos, o tecido foliar, após a eclosão dos ovos, escurece e morre deixando marcas circulares de cor marrom.

A fêmea após a eclosão dos ovos continua viva por muitos dias, quieta, agarrada ao galho da folha da postura. Cinco fêmeas observadas viveram entre 11 e 12 dias após a eclosão de seus ovos. Durante esta fase pós-eclosão, a vespa-de-serra quando molestada ainda exibe o display de zumbir. O interessante é que mesmo depois de morta, ela continua agarrada ao galho, aí ficando por várias semanas sem ser comida por nenhum animal.

Geralmente antes da fêmea morrer, as larvinhas terminam as folhas apicais do galho-não-ramificado da postura e migram pelo galho abaixo para mudarem-se para um galho-não-ramificado vizinho. Logo as larvas migrantes encontram a fêmea mãe na sua frente. Quando as primeiras larvas encostam na fêmea, ela caminha silenciosamente e, sem mostrar agitação, uns 2 cm mais para baixo ao longo do galho em direção à base. As larvas continuam a caminhar e novamente se encontram com a fêmea. Esta novamente caminha mais uns 2 cm para a base do galho, e assim por diante até que a fêmea mãe alcança a base do galho: a bifurcação com o galho principal. Aí ela fica no lado inferior, com as asas parcialmente estendidas e a cabeça volta para baixo (Figura 9b, c, d). As larvas caminhando pelo lado superior do galho alcançam a bifurcação e galgam o galho principal. As larvas nesta fase estão no final do 1º instar ou no 2º instar, portanto ainda pequenas (8 a 10 mm). A fêmea não sai mais desta posição. Uma das migrações de larvas que observei, aconteceu um fato interessante. Quando a fêmea mãe, coagida pelas larvas, já estava quase chegando à base do galho, ela repentinamente deu meia-volta e começou a voltar por onde viera, para o ápice do galho, caminhando por cima das larvas migrantes. Surpreendentemente, as larvas que estavam na frente imediatamente deram meia-volta e seguiram a fêmea mãe por uns 4 a 5 cm. A fêmea caminhou uns 5 cm para cima e parou junto a uma concentração de larvas. Algumas larvas reiniciaram a caminhada para baixo, e a fêmea continuou a caminhar galho acima mais uns 3 cm e parou. Já então todas as larvas estavam migrando para baixo. A fêmea, então, deu meia-volta novamente e caminhou rapidamente para baixo, alcançando as larvas da dianteira antes que estas alcançassem a base do galho. A fêmea ficou na base do galho quieta enquanto as larvas subiam pelo galho principal. Em apenas um caso observei uma fêmea deixar sua posição na base do galho-não-ramificado da sua postura: ela caminhou pelo galho principal até a base do 1º galho-não-ramificado acima do seu, a uns 10 cm de distância.

As fêmeas adultas não se alimentam.

Coloração Aposemática e Cheiro Ruim

Apesar da coloração conspícua e do grande tamanho, não observei nenhum caso de predação de adultos de *D. diasi* no campo.

Para verificar a possibilidade deste inseto ser repugnante aos predadores (gosto ou cheiro ruins), ofereci vários espécimens para diversos predadores de insetos conservados em viveiros no laboratório. Todos eles estavam se alimentando normalmente, principalmente de ortópteros e isópteros. Os animais usados para estes testes foram: três sapos grandes, *Bufo* sp., vários adultos e jovens do escorpião *Tityus trivittatus* e um adulto de *Tityus mattogrossensis,* dois adultos da lacraia *Scolopendra viridicornis,* dois adultos aranha caranguejeira *Acanthoscurria atrox,* quatro adultos da aranha viúva negra, *Latrodectus curacaviensis* e uma colônia experimental da formiga tocandira, *Dinoponera gigantea* da região Amazônica. O resultado foi um só: nenhum destes temíveis predadores comeu a vespa-de-serra, e muitos mantiveram distância. Apenas as Tocandiras e as Lacraias chegaram a atacar o sínfita. As tocandiras com muito custo conseguiram paralisar a vespa-de-serra e arrastá-la para o ninho, mas uma

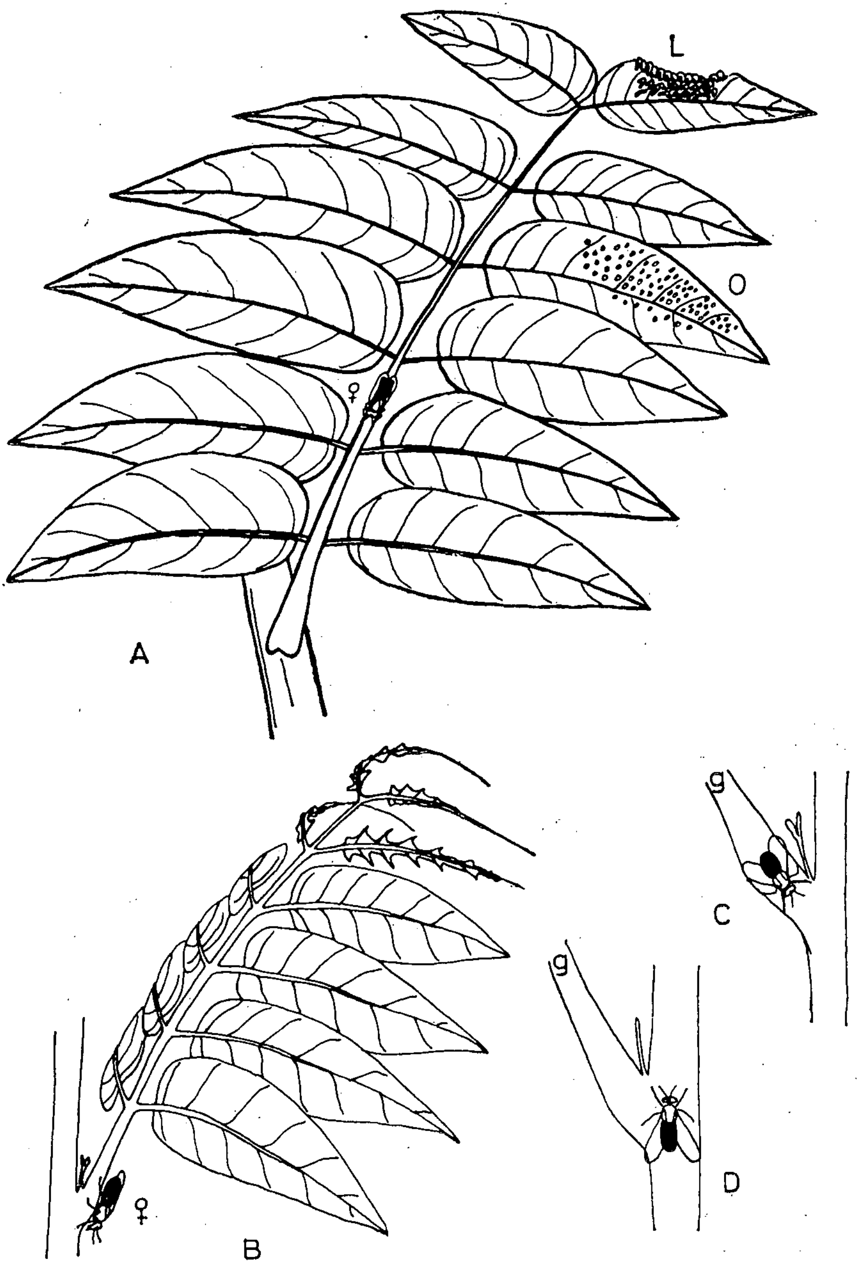


Figura 9. Comportamento maternal após a eclosão dos ovos. — Figura 9a. Fêmea no meio do galho-não-ramificado da sua postura: O = ovos e L = larvas recém-nascidas comendo numa das folhas apicais do galho. — Figura 9b. Fêmea na base do galho-não-ramificado de sua postura, depois que suas larvas migraram para outro galho. As folhas apicais foram comidas por suas larvas. — Figuras 9c e 9d. Idem, fêmeas com outras orientações na base de seus galhos-não-ramificados: g = galhos-não-ramificados de suas posturas.

vez dentro do ninho, jogaram a vespa-de-serra intacta no lixo. As lacraias abandonaram as vespas-de-serra intactas após matá-las. Deve-se levar em conta que os predadores utilizados para os testes não ocorrem juntos com o sínfita na natureza.

Embora estes testes sejam apenas preliminares, a conclusão a que se chega é que os adultos deste sínfita têm cheiro e provavelmente gosto muito ruins que repelem os predadores.

Comportamento Gregário das Larvas

As larvas são gregárias desde o nascimento até o encasulamento, período este que demora em média cerca de 45 dias.

Comportamento de alimentação em grupo. — As larvas recém-nascidas sempre iniciam a comer pela folha mais apical imediatamente vizinha à folha da postura. A folha da postura nunca é comida pelas larvas novas! As larvas alimentam-se sempre coletivamente, alinhando-se em compacta fila indiana onde a cabeça de cada larva encosta e comprime o tórax da larva e os abdômens ficam soltos e curvos para um lado. Neste arranjo ocorre amplo contato corporal cabeça-tórax, tórax-abdômen e abdômen-abdômen entre os indivíduos que se comprimem mutuamente. As larvas abraçam as duas superfícies da folha na margem, com os corpos orientados paralelamente ao comprimento da folha. Elas sempre se orientam numa mesma direção, quase sempre com as cabeças voltadas para o ápice da folha, e caminham para a frente enquanto comem (Figura 10a).

No entanto, nem todos os membros da colônia comem ao mesmo tempo, pois a qualquer momento 30 a 50% das larvas não estão comendo: estão quietas agrupadas na face inferior da folha junto ao grupo ativo que está comendo (Figura 10b). A colônia como um todo alimenta-se ininterruptamente dia e noite mas, as larvas, tomadas individualmente, aparentemente alternam num ciclo de atividade e inatividade cuja duração não foi determinada. Apenas durante os períodos de chuva a colônia toda fica inativa. Este comportamento cíclico de atividade e inatividade, no entanto, só ocorre nas colônias com larvas novas ou médias pois, nas colônias de larvas grandes todas comem ininterruptamente.

Geralmente as larvas iniciam o ataque a uma folha comendo sua margem a aproximadamente meia distância entre a base e o ápice da folha. As larvas não iniciam a comer isoladamente mas sim gregariamente.

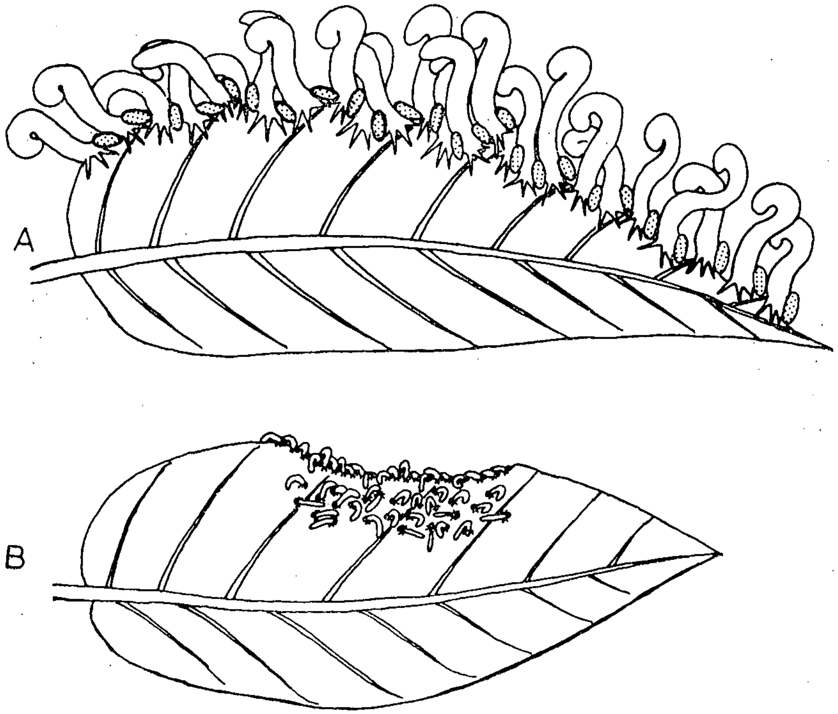


Figura 10. Comportamento de alimentação em grupo das larvas. — Figura 10a. Larvas comendo na margem da folha alinhadas em compacta fila indiana com as cabeças orientadas para o ápice da folha. — Figura 10b. Grupo de larvas jovens típico: enquanto parte das larvas comem alinhadas na margem da folha, parte das larvas ficam quietas agrupadas mais para o centro da folha, na face inferior desta, em abstinência.

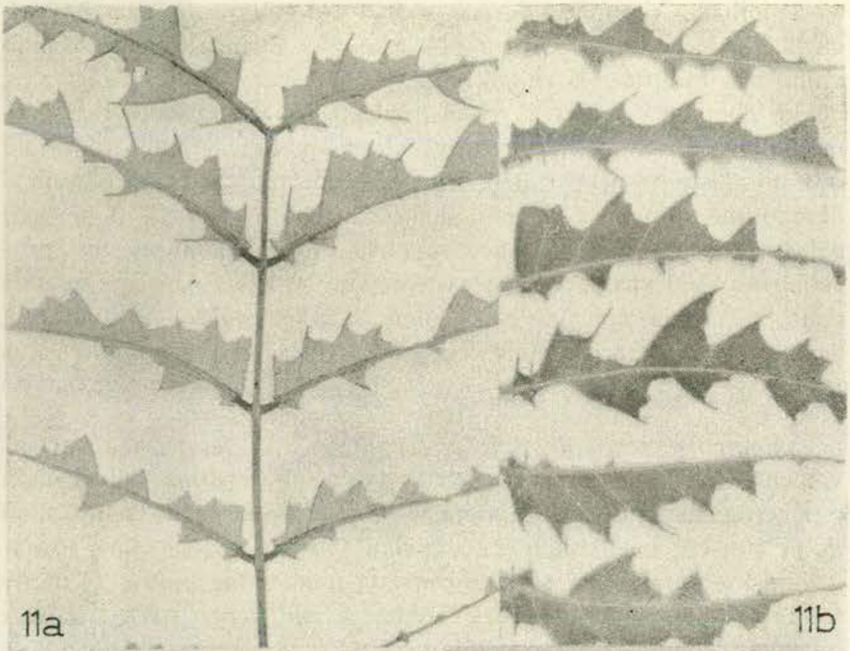
As larvas evitam comer as nervuras laterais maiores, preferindo comer a lâmina foliar entre estas nervuras. O resultado disto é um padrão de destruição da folha bem característico (Figura 11). Quando uma larva alcança uma nervura lateral ela pára de comer e acompanha-a até seu ápice, onde come uma pequena porção da nervura para prosseguir comendo na área interneural seguinte. A próxima larva que vem a seguir, come mais um pequeno pedaço do ápice da nervura e uma porção grande da área interneural. Em conseqüência deste hábito, quando as áreas interneurais já estão quase totalmente comidas as nervuras laterais maiores ainda estão praticamente intactas. Portanto, as larvas de *D. diasi* poderiam ser definidas como «esqueletonizadoras» parciais. Algumas vezes quando muitas larvas comem uma mesma folha, as nervuras laterais são totalmente comidas. A nervura central, entretanto, nunca é comida. Freqüentemente as larvas abandonam as folhas semicomidas para iniciarem a comer em outra. Muitas vezes as larvas voltam mais tarde para terminarem de comer as folhas abandonadas semicomidas. A ação das larvas provoca sério desfolhamento da copa das árvores mais infestadas (Figura 12).

Manutenção da colônia. — As larvas originadas de uma mesma postura permanecem juntas até se encasularem. O gregarismo é tão pronunciado que quando duas colônias se encontram, coalescem imediata e permanentemente. Como as larvas migram muito de um galho para outro, a chance de várias colônias que estão na copa de uma mesma árvore se encontrarem é grande. O resultado é a formação de colônias gigantescas com mais de 500 larvas nas árvores muito infestadas. É comum encontrar-se colônias mistas de larvas maduras e novas.

Durante as freqüentes migrações as larvas permanecem próximas mas não necessariamente em contato. Uma colônia em marcha não tem líderes e não se desloca em bloco orientada constantemente para a frente como fazem as lagartas processionárias («armyworms», dos autores ingleses). Ao contrário, os deslocamentos das larvas de *D. diasi* lembram a movimentação confusa de formigas no início da formação de um carreiro: algumas larvas deixam a folha onde comem e iniciam a caminhar pelo galho em direção à sua base, mas logo param e começam a voltar; outras larvas, então, saem da folha e caminhando pelo galho avançam mais um pouco antes de voltarem e assim sucessivamente. Desse modo, examinando-se um grupo de larvas migrando, vê-se larvas caminhando nos dois sentidos opostos: indo e vindo. Algumas larvas que estavam na dianteira chegam a voltar à folha inicial onde comiam.

No entanto, a colônia como um todo progride incessantemente numa mesma direção. Aparentemente as larvas fazem uma marcação química por onde caminham deixando um rastro. Se não, de que forma larvas bastante retardatárias conseguem alcançar o resto do grupo percorrendo grandes distâncias exatamente pelo mesmo caminho seguido pelas primeiras?

As migrações não são feitas ao acaso mas seguem algumas regras. As larvas geralmente só abandonam um galho-não-ramificado após terem comido total ou parcialmente todas as



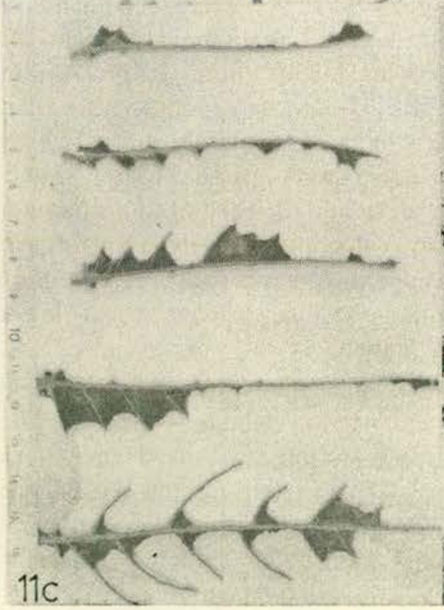


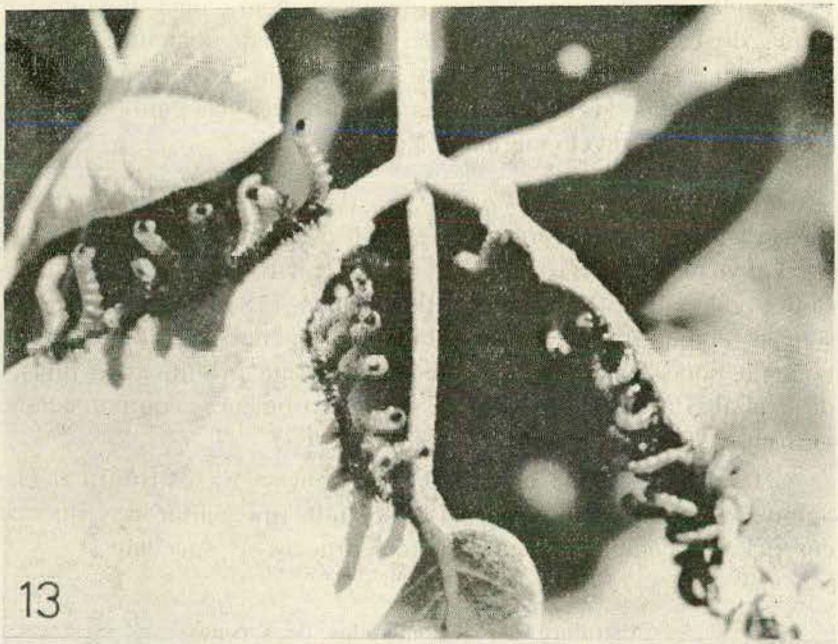
Figura 11. Padrão de destruição das folhas de *Sclerolobium aureum* pelas larvas de *D. diasi*. — Figura 11a. Galho-não-ramificado parcialmente comido por larvas do último instar. Note o aspecto espinhoso das folhas devido ao hábito das larvas de comerem principalmente as regiões interneurais das folhas deixando as nervuras laterais quase intactas. — Figura 11b. Idem, folhas apenas parcialmente comidas. — Figura 11c. Idem, folhas quase totalmente comidas. Muitas vezes as larvas comem até as nervuras laterais mas deixam a nervura central intacta. — Figura 12. Árvore hospedeira quase totalmente desfolhada pelas larvas do sínfita. O lado esquerdo desta árvore ficou prejudicado pela presença de outra árvore atrás.

suas folhas. Aí então, descem por este galho até sua base e encontrando o tronco sobem por este até alcançarem o próximo galho-não-ramificado, cujas folhas a começar pelas apicais são, então, comidas. As larvas comem, desta maneira, sucessivamente os galhos-não-ramificados cada vez mais apicais até atingirem o topo deste tronco. Então, elas descem migrando pelo tronco abaixo até atingirem a bifurcação com outro tronco, pelo qual sobem. Neste segundo tronco repetem novamente o mesmo procedimento, devastando sucessivamente galhos-não-ramificados cada vez mais apicais. Nas colônias mais velhas, no entanto, as migrações parecem mais confusas, nem sempre seguindo estas regras.

Comportamento de defesa grupal. — As larvas reagem vivamente a estímulos mecânicos e visuais: levantam coordenada e sincronicamente seus abdômens jogando-os para frente num golpe brusco; imediatamente abaixam seus abdômens para tornar a jogá-los para frente sincronicamente num golpe busco. O efeito total é espetacular e surpreendente, e suficiente para assustar qualquer inimigo potencial (Figura 13). As larvas pequenas e médias mantêm seus abdômens eretos, abaixam até tocar na folha e tornam a levantá-los verticalmente num golpe rápido. Já as larvas grandes mantêm os abdômens, quando elevados, um pouco inclinado para trás e com a extremidade curva. Outro fato que distingue as larvas pequenas das grandes é que aquelas têm uma mancha negra na extremidade dorsal do abdômen que fica muito conspícua durante o display defensivo. É provável que esta mancha negra tenha por função assustar ou confundir os inimigos fazendo-os «acreditar» que é a cabeça da larva. As larvas grandes não têm esta mancha.

Entre os estímulos visuais e mecânicos que liberaram os displays defensivos das larvas estão: 1) visuais — movimentos bruscos de uma pessoa, uma mão ou um graveto a menos de um metro da colônia de larvas; a passagem de um inseto, inclusive uma fêmea adulta da própria espécie, voando próximo da colônia; e até mesmo a proximidade de uma fêmea da vespa-de-serra na mesma folha onde as larvas comem, como foi descrito acima no capítulo de comportamento maternal; 2) mecânicos — batidas na folha ou galho onde as larvas comem.

Ao contrário das larvas de *Themos olfersii* (ver Dias, 1975), as larvas de *D. diasi* não excretam líquido viscoso repelente pela extremidade do abdômen.



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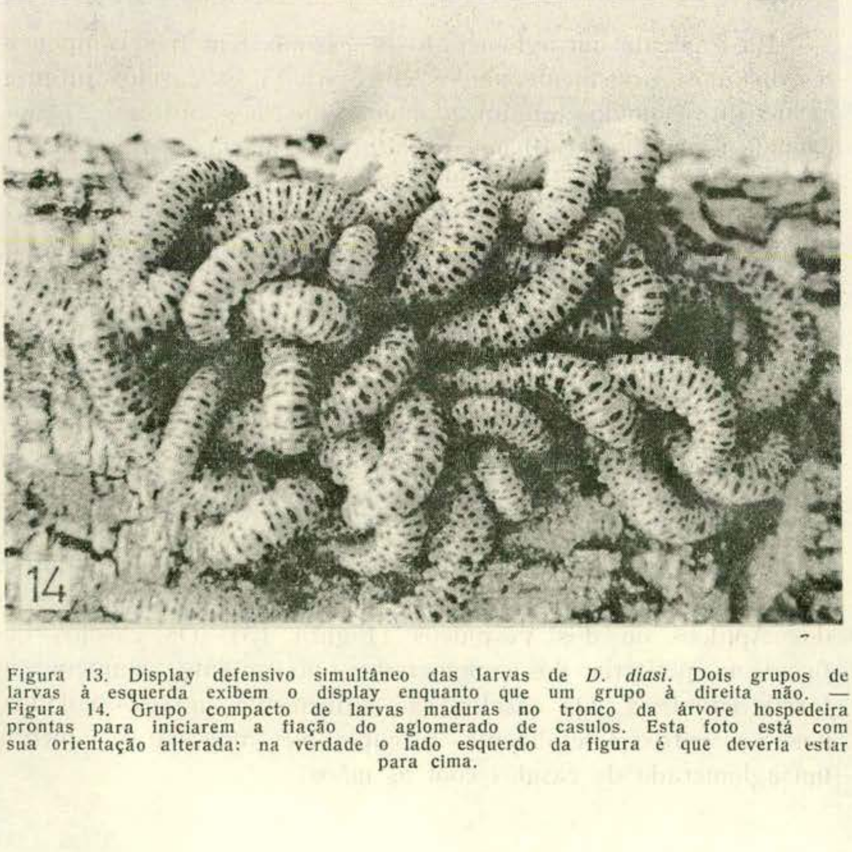

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Figura 13. Display defensivo simultâneo das larvas de *D. diasi*. Dois grupos de larvas à esquerda exibem o display enquanto que um grupo à direita não. — Figura 14. Grupo compacto de larvas maduras no tronco da árvore hospedeira prontas para iniciarem a fiação do aglomerado de casulos. Esta foto está com sua orientação alterada: na verdade o lado esquerdo da figura é que deveria estar para cima.

As larvas maduras adotam freqüentemente uma postura em forma de esse (S). Experimentei tocar insistentemente com um graveto na cabeça de uma larva grande: ela contorceu todo seu abdômen várias vezes em todas as direções chegando a bater com força no graveto algumas vezes.

Fiação comunal dos casulos. — As larvas de *D. diasi* tecem seus casulos juntos formando grandes aglomerados de casulos grudados nas cascas das árvores. Na construção destes aglomerados, chamados de «ninhos» por Curtis (1844), as larvas desenvolvem um trabalho coordenado e seqüenciado. Este comportamento pode ser entendido como uma forma primitiva de divisão de trabalho: «o efeito aditivo de contribuições equipotenciais» (Carne, 1966).

Darei em seguida uma descrição concisa da estrutura destes aglomerados de casulos para em seguida apresentar a seqüência em que os comportamentos de construção se sucedem.

Estrutura dos Aglomerados de Casulos

Basicamente um aglomerado de casulos tem três componentes distintos, firmemente unidos entre si: 1) os casulos propriamente ditos, unidos organizadamente uns aos outros; 2) uma camada espessa (até 10 mm de altura) e macia de fios de seda longos e entrelaçados formando uma trama intrincada como uma esponja ou bucha — a «esponja»— que reveste os casulos»; 3) finalmente revestindo os casulos e a esponja há uma camada fina e contínua de seda branca — a «capa» (Figura 15). A capa e a esponja (cobertura) devem servir como uma boa proteção aos casulos contra chuva, fogo (comum nos cerrados) e ataque de predadores e parasitas (efeito isolante).

Os casulos são muito espessos e duríssimos: suas paredes têm entre 0,1 e 0,2 mm de espessura. Os casulos medem internamente entre 15 e 17 mm de comprimento e de 5 a 8 mm de largura máxima. São cilíndricos quando construídos isoladamente, o que é raro, mas nos aglomerados os casulos adquirem uma forma poligonal, hexagonal ou pentagonal, como num favo dos Apídeos ou dos Vespídeos (Figura 15). Os casulos que ficam na periferia dos aglomerados, no entanto, mantêm sua forma cilíndrica. Os casulos são firmemente unidos (colados) uns aos outros lateralmente. É impossível amassar ou quebrar um aglomerado de casulos com as mãos.

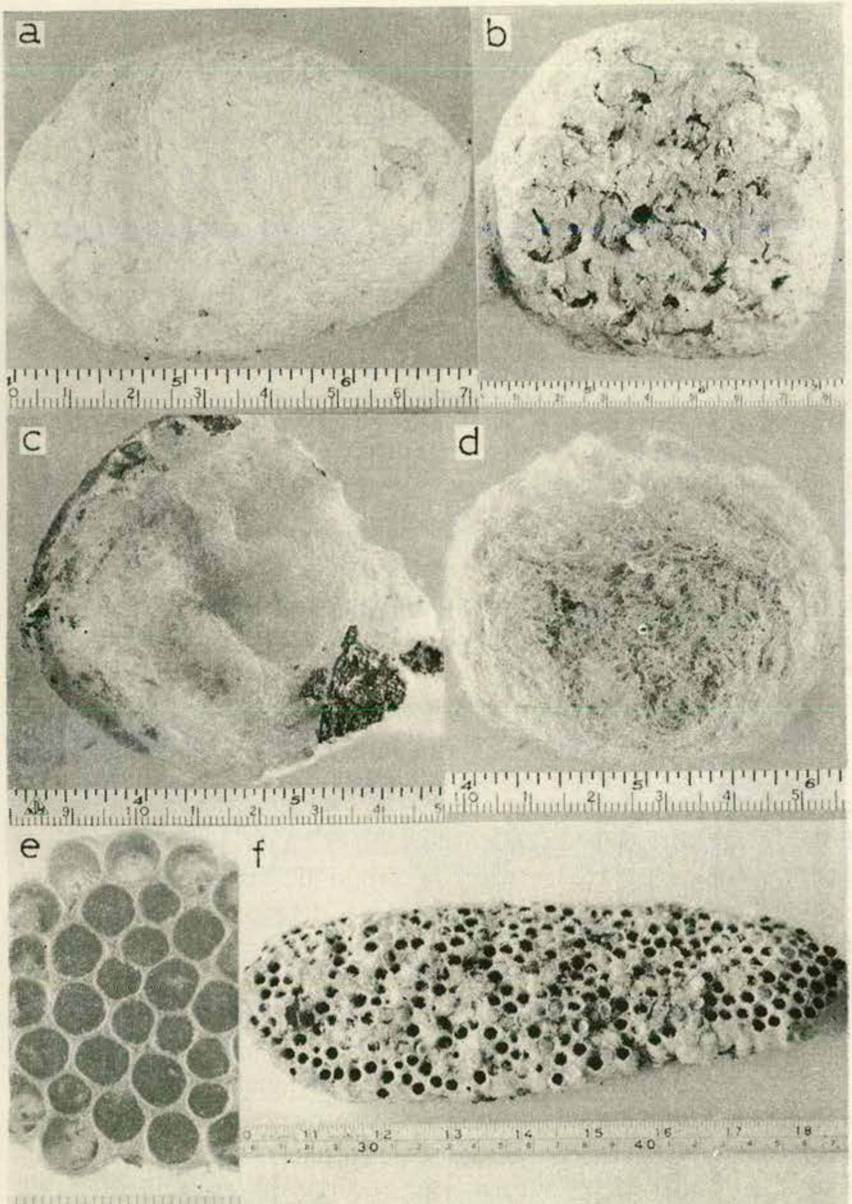


Figura 15. Estrutura dos aglomerados de casulos. — Figura 15a. Capa externa intacta. — Figura 15b. Capa externa após a emergência dos adultos, mostrando as marcas semicirculares feitas pelos adultos para saírem. — Figura 15c. Cobertura de um aglomerado destacada dos casulos vista por dentro mostrando a camada da esponja. — Figura 15d. Esponja fiada por um grupo de larvas experimental no laboratório. — Figura 15e. Corte transversal de um "favo" de casulos de *D. diasi* mostrando a grande compactação entre os casulos. — Figura 15f. Aglomerado de casulos grande cuja cobertura foi retirada. Os casulos estão todos abertos pois os adultos já emergiram. Em todas as figuras, menos Fig. e, a escala superior é em polegadas e a inferior é em centímetros. A escala da Figura e é em milímetros.

Os casulos geralmente alinham-se paralelos uns aos outros, perpendicularmente à superfície do tronco ou galho da árvore, colando-se firmemente à casca da árvore por uma de suas extremidades. As larvas sempre ficam orientadas com as cabeças voltadas para a extremidade livre do casulo, ou seja, aquela afastada da casca da árvore. No entanto, nos aglomerados com poucos casulos (menos de 20 casulos), os casulos ou estão grudados à casca da árvore pelos seus lados, orientados paralelamente à superfície do tronco e horizontalmente ou então estão agrupados desordenadamente sem nenhuma orientação geral (raros casos observados). Observei aglomerados com mais de 500 casulos medindo mais de 300 cm^2 de área.

Construção dos Aglomerados de Casulos: Seqüência dos Comportamentos

1. Larvas maduras que comiam juntas nas folhas, migram juntas através dos galhos para baixo procurando um galho grosso ou tronco conveniente para fiar os casulos (os casulos são fiados em alturas que vão desde próximas do chão até mais de quatro metros acima do solo, mas preferem construir os casulos na faixa entre meio e dois metros acima do chão, e especialmente em torno de forquilhas).
2. As larvas permanecem muito unidas, compactando-se e abraçando com as mandíbulas a casca da árvore por várias horas e até dias (observei até dois dias). As cabeças das larvas ficam voltadas para o interior do grupo de larvas (Figura 14).
3. As larvas fiam a capa externa delgada, aderindo-a firmemente à casca da árvore (não sei se todas as larvas participam desta tarefa).
4. As larvas fiam a camada da esponja, inicialmente contra a capa externa e depois em torno de si mesmas.
5. As larvas tecem seus casulos individualmente mas ordenadamente e procurando compactar-se ao máximo. Provavelmente existe uma ordem na fiação dos casulos: os centrais seriam fiados primeiro e os outros em redor progressivamente (Figura 16).

Experiências no laboratório indicam que as larvas não tecem seus casulos se a capa externa e a esponja forem retiradas na etapa cinco (acima). Mas quando experimentei recobri-las com gaze e algodão ou papel simulando a capa externa e esponja, elas retomaram a atividade e teceram seus casulos normalmente (Figura 18).

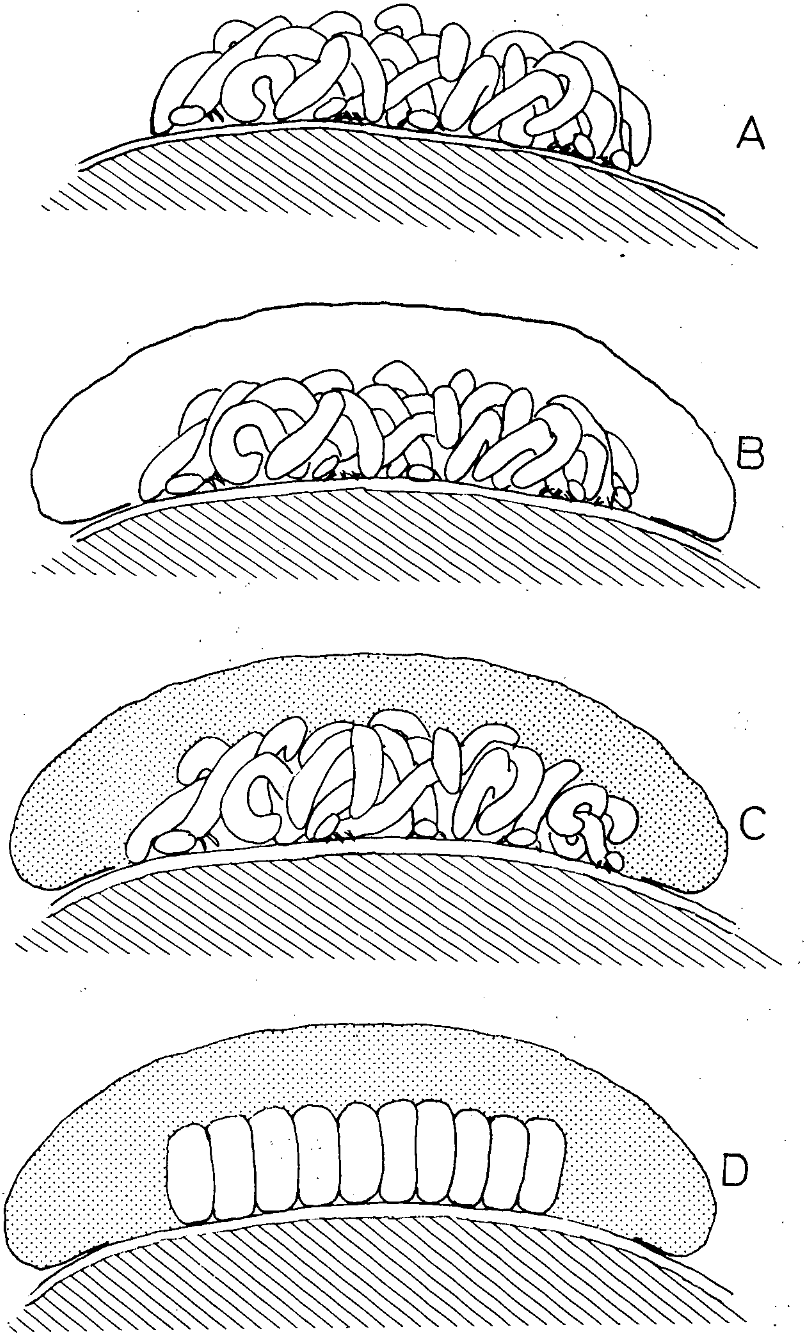
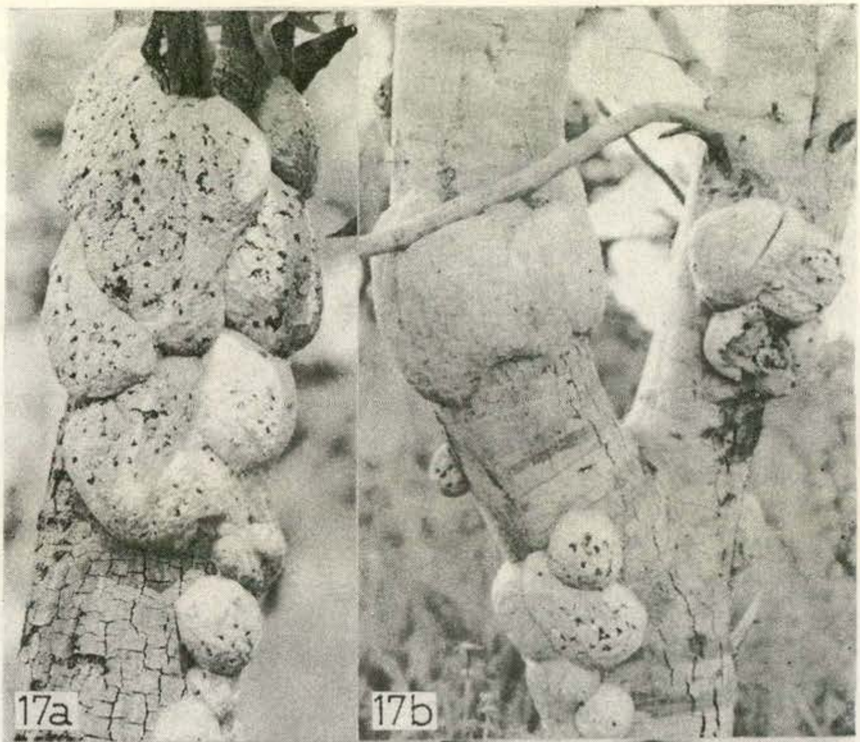
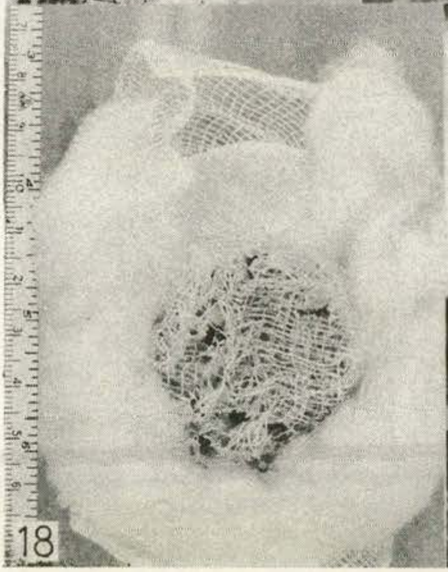
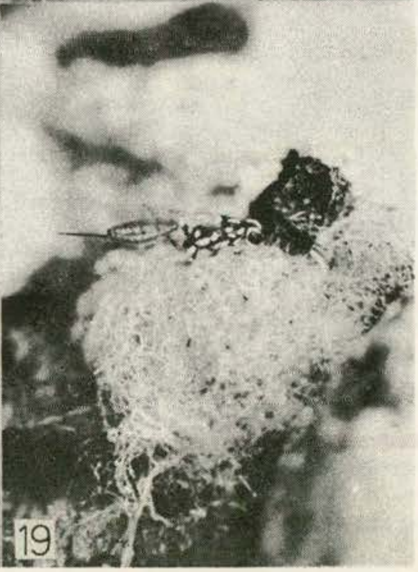


Figura 16. Seqüência de construção de um aglomerado de casulos. — Figura 16a. Larvas amontoadas sobre a casca do tronco da árvore hospedeira. — Figura 16b. A capa externa é fiada, e fixada no tronco. — Figura 16c. A esponja é fiada contra a capa externa. — Figura 16d. Os casulos individuais são fiados ordenada e compactamente. A área sombreada representa a esponja e a área hachuriada representa o tronco da árvore hospedeira em corte transversal.







Figuras 17a e 17b. Troncos de duas árvores hospedeiras cheios de aglomerados de casulos da vespa-de-serra. Note a tendência dos aglomerados serem fiados um ao lado do outro. — Figura 18. Aglomerado de casulos tecido em condições experimentais: a cobertura havia sido removida antes das larvas fiarem seus casulos e estes só foram fiados depois que uma nova cobertura de gase e algodão foi simulada. — Figura 19. Fêmea do Icneumonídeo *Lymeon ?dieloceri* sobre aglomerado de casulos de *D. diasi*.

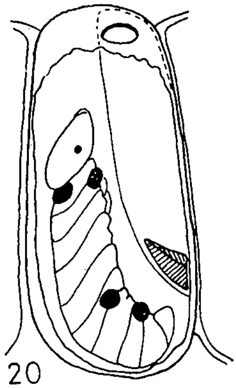
Uma questão importante surgiu durante estas observações: já que a confecção do aglomerado de casulos resulta de um trabalho feito em conjunto, em cooperação por um grupo de larvas e tendo em vista que as poucas larvas que ocasionalmente encasulam-se separadamente não tecem capa nem esponja, qual é o número mínimo de larvas capaz de tecer um aglomemerado de casulos completo com capa e esponja? Não tenho até o momento resposta para esta questão, mas apenas algumas evidências: de 18 pequenos aglomerados de casulos que observei (variando entre um e 23 casulos por aglomerado), apenas dois (um com três casulos e o outro com apenas um) não tinham a capa externa, embora tivessem a esponja. Os outros 16 aglomerados (com quatro a 23 casulos) tinham capa e esponja. Vários casulos isolados que observei na natureza não tinham capa nem esponja! É provável, portanto, que o número mínimo de larvas para tecer o aglomerado completo seja de três a quatro.

Outro fato interessante é que há uma tendência das árvores atacadas serem crescente e continuamente infestadas ano após ano enquanto que muitas árvores hospedeiras vizinhas não são sequer tocadas! Encontrei algumas árvores superinfestadas com mais de 140 aglomerados de casulos de todos os tamanhos nos seus galhos e tronco (Figura 17). Ao procurar um local para tecerem seus casulos, as larvas geralmente escolhem áreas vizinhas a outro aglomerado de casulos preexistente.

Parasitismo

Não foi observado nenhum caso de parasitismo do ovo ou adulto de *D. diasi*. Já as larvas, especialmente quando encasuladas, são muito parasitadas. Dos 90 aglomerados de casulos levados ao laboratório 28 estavam total ou parcialmente parasitados. Foram identificadas quatro espécies de parasitóides: um Tachinidae, um Ichneumonidae e dois Chalcididae. As espécies mais comuns são o Icneumonídeo e o Taquinídeo.

O Icneumonídeo foi determinado pelo Dr. R. W. Carlson do U. S. Department of Agriculture como sendo *Lymeon* sp. (Cryptinae). Comparando com a descrição de Costa Lima (1937) de *Lymeon dieloceri* (Costa Lima) acredito que se trata da mesma espécie. Segundo Costa Lima (1937), *L. dieloceri* é parasita de *Digelasinus diversipes*, um Argídeo muito próximo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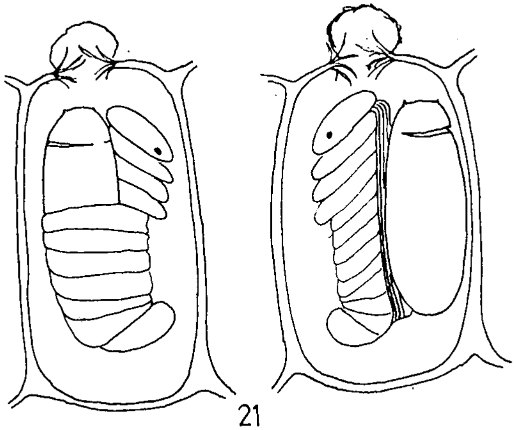
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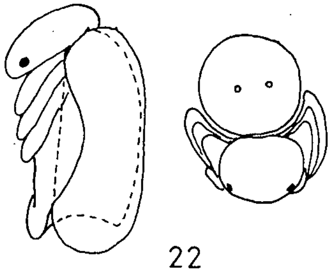
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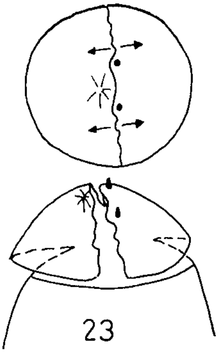
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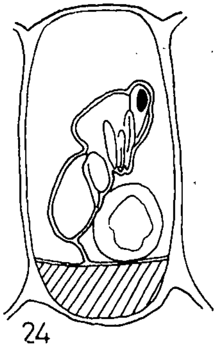
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Figura 20. Casulo do sínfita atacado pelo parasitóide *Lymeon ?dieloceri*. A larva do sínfita fica toda furada e o icneumonídeo tece seu casulo afunilado ao lado, contra a parede do casulo do hospedeiro. Para emergir, o parasitóide abre uma pequena tampa na extremidade livre do casulo hospedeiro. — Figura 21. Dois casulos do sínfita atacados por *Spathimeigenia dieloceri* mostrando duas disposições típicas do pupário do parasitóide: parcialmente dentro dos restos da larva hospedeira ou totalmente fora desta. Nos dois casos o taquinídeo adulto já emergiu e as aberturas de saída estão indicadas: a maior parte do serviço é feito pela larva que antes de pupar desfia quase que totalmente uma pequena região da parede do casulo hospedeiro, pois ao adulto só resta empurrar uma fina tampa externa para sair do casulo do sínfita. — Figura 22. Detalhe do encaixe do pupário do taquinídeo com os restos da larva hospedeira, vista lateral e superior. — Figura 23. Detalhe da abertura feita no pupário pelo taquinídeo ao emergir. — Figura 24. Casulo do sínfita atacado pelo parasitóide *Spilochalcis* sp., mostrando pupa do calcidídeo, a pelota amorfa do que restou da larva do hospedeiro e a grande quantidade de dejetos do parasitóide (hachuriado).

de *D. diasi,* que também contrói aglomerados de casulos com cobertura comunal.

As fêmeas do Icneumonídeo não se interessam pelas larvas, mesmo maduras, do Sínfita, parasitando-as apenas quando estas já se acham encasuladas. A fêmea de *Lymeon dieloceri* ao caminhar sobre os aglomerados de casulos da vespa-de-serra movimenta rápida e energicamente suas antenas apalpando a cobertura dos casulos (Figura 19). Provavelmente uma cobertura espessa deve dificultar o trabalho deste parasitóide pois seu ovipositor não é longo. Ao menos 19 dos 90 aglomerados de casulos criados em laboratório estavam parasitados pelo Icneumonídeo.

A larva do parasitoide consome a larva ou prepupa do Sínfita por dentro e após completar seu desenvolvimento abandona seu hospedeiro para tecer seu casulo ao lado dos restos do hospedeiro dentro do casulo deste. A larva do hospedeiro parasitada apresenta-se menor, um pouco murcha e com algumas perfurações. O parasitóide tece seu casulo de fina seda branca junto a parede interna do casulo do Argídeo na forma de um longo funil com a parte mais larga voltada para a extremidade livre do casulo do hospedeiro (Figura 20). Dentro de seu casulo o parasitóide defeca e pupa. Para emergir, o adulto abre uma pequena tampa circular com suas finas mandíbulas. O diâmetro desta «tampa» é de 1,5 mm para a fêmea e 1,1 mm para o macho. Vencida esta barreira é necessário que o parasitóide abra seu caminho através do emaranhado de fios da esponja e da capa de aglomerado de casulos. Muitos Icneumonídeos foram encontrados mortos na camada da esponja — aparentemente não foram capazes de vencer aquela barreira!

O Taquinídeo é *Spathimeigenia dieloceri* (Townsend, 1942), determinado pelo Dr. C. W. Sabrosky do U. S. Department of Agriculture. As fêmeas desta mosca injetam suas larvas nas larvas maduras de *Dielocerus formosus* segundo Townsend (1942) citando observações de Oscar Monte em Minas Gerais, porém nunca tive oportunidade de presenciar o comportamento desta mosca relativo a *D. diasi.* De qualquer forma o parasitismo não impede as larvas de *D. diasi* de construírem seus casulos normalmente. Dos 90 aglomerados de casulos criados em laboratório, pelo menos 12 foram parasitados pelo Taquinídeo. De 8 aglomerados emergiram 59 adultos da mosca. Em um aglomerado de casulos pequeno, 17 dos 24 casulos foram parasitados por este parasitóide. Em outro, 85 dos 122 casulos foram por ele parasitados.

A larva deste parasitóide consome totalmente a larva ou prepupa de Argídeo por dentro, saindo total ou parcialmente do hospedeiro para formar o pupário, dentro do casulo hospedeiro (Figuras 21 e 22). Porém, antes de pupar, a larva com suas mandíbulas aparentemente rasga e desfia uma pequena porção na extremidade livre do casulo hospedeiro, deixando apenas uma fina camada por atravessar (Figura 21). O pupário da mosca ocupa grande parte do casulo e comprime a pele flácida e vazia de que restou do hospedeiro. O pupário mede em média 9 a 9,5 mm de comprimento por 3,5 a 4 mm de largura máxima e tem uma forma cilíndrica.

Ao emergir a mosca expande o ptilino, triplicando o volume da cabeça, arrebentando a parte superior do pupário e depois a «tampa» formada racha-se ao meio (Figura 23). A mosca adulta, então, força a passagem para fora do casulo através da região que fora desfiada quando larva e escapa abrindo passagem, ou preferencialmente aproveitando-se de passagens abertas por outros, através da esponja e capa do aglomerado de casulos. Num aglomerado de casulos onze moscas saíram por uma única abertura na capa! Algumas moscas morrem sem conseguir atravessar a cobertura dos aglomerados de casulos.

Os dois Calcídideos parasitas de *D. diasi* são *Spilochalcis* sp. e *Brachymeria* sp., determinados pelo Dr. G. Gordh de U. S. Department of Agriculture. Apenas três dos 90 aglomerados de casulos estavam parasitados por *Spilochalcis* sp. e somente dois por *Brachymeria* sp. Num aglomerado de casulos, 34 dos 57 casulos foram parasitados por *Spilochalcis* sp. Apenas dois adultos de *Brachymeria* sp. emergiram no laboratório, cada um de um aglomerado de casulos diferentes.

As larvas do parasitóide *Spilochalcis* sp., uma por hospedeiro, reduzem a larva hospedeira dentro do casulo desta a uma pelota irreconhecível, escura e pastosa medindo aproximadamente 3 mm de diâmetro. Antes de pupar, o parasitóide defeca abundantemente preechendo aproximadamente 1/4 do casulo, recobrindo este resíduo líquido marrom com uma fina película (Figura 24). O parasitóide adulto para emergir abre uma tampa circular com suas mandíbulas na extremidade livre do casulo hospedeiro. O diâmetro desta abertura é de 2,5 a 3,1 mm. Cada adulto abre sua própria passagem através da esponja e capa de aglomerado de casulos. Provavelmente os Calcidídeos parasitam o hospedeiro na fase de larva livre, o que não impede-as de tecerem seus casulos normalmente.

Os aglomerados mais velhos de *D. diasi* são também muito atacados por lagartas de um micro-lepidóptero, *Ectomyelois decolor* (Zeller) (Pyralidae, Phycitinae), comensal-predador que parece comer principalmente os resíduos e enxúvias de sínfita e parasitas, mas que nos casos de grande infestação ataca também as larvas e pupas do sínfita e dos parasitas. Quinze dos 90 aglomerados de casulos mantidos no laboratório estavam atacados por este microlepidóptero. De um aglomerado bastante infestado emergiram mais de 45 mariposas.

Discussão

Coloração Aposemática e Mimetismo:

Os testes de laboratório indicam que as fêmeas adultas de *D. diasi* possuem gosto e/ou cheiro desagradáveis aos predadores. Certamente a grande conspicuidade das fêmeas devido à sua coloração vistosa laranja e preto e aos displays defensivos e de advertência, deve auxiliar muitos predadores potenciais, especialmente aves, a evitarem estes insetos.

Segundo Blest (1963), no caso de insetos aposemáticos é altruístico e vantajoso para a espécie que os adultos tenham vida longa mesmo após completarem a reprodução pois isto aumenta a densidade de insetos aposemáticos, acarretando um conseqüente aumento na proteção contra predadores. Portanto, uma das vantagens das fêmeas pós-reprodutivas de *D. diasi* continuarem vivas, além de oferecer uma proteção direta à sua prole, deve ser a de aumentar a proteção das fêmeas vizinhas, algumas das quais poderão ainda não ter depositado seus ovos. Este comportamento altruístico tende a aumentar o «inclusive fitness» das fêmeas vizinhas, fêmeas estas que podem não ter nenhum parentesco entre si. O fato das fêmeas depois de mortas continuarem agarradas às folhas pelo pecíolo por muitas semanas deve ser mais uma adaptação para aumentar o número visível de fêmeas nas folhas.

É interessante observar que grande número de sínfitas Sul-americanos das famílias Argidae, Cimbicidae ,Pergidae e Tenthredinidae têm coloração laranja e preto. Parece existir um grande complexo mimético que abrangeria insetos de outras ordens também. Várias espécies de *Dielocerus* e *Themos,* entre elas *T. olfersii* (Dias, 1975), têm este padrão de coloração. Superficialmente a semelhança de coloração entre *D. diasi* e *T. olfersii* é impressionante.

«Território Foliar»:

A existência de um «território» explicaria porque freqüentemente as fêmeas zumbem sem nenhum estímulo externo a não ser a presença próxima de outras fêmeas. Estes zumbidos poderiam servir de sinais de advertência contra outros animais e especialmente contra outras fêmeas da mesma espécie. A análise do comportamento de cuidado maternal das larvas novas sugere que o «território» de cada fêmea abrangeria todo um galho-não-ramificado constituído por um grupo de 10 a 14 folhas incluindo a folha da postura. Se assim for, cada fêmea estará defendendo o suprimento inicial de alimento (folhas) para suas larvas, posto que as larvas recém-nascidas sempre iniciam a comer pelas folhas apicais do galho-não-ramificado de sua postura. Se mais de uma fêmea pusesse seus ovos em folhas de um mesmo galho-não-ramificado próximo, esta grande migração precoce poderia causar uma mortalidade considerável. De fato, entre as centenas de posturas observadas apenas um caso de duas posturas num mesmo galho-não-ramificado foi constatado.

A existência de um «território» não é a única explicação possível para justificar os fatos verificados e será necessário realizar uma série de experimentos para comprová-la. O período de 24 horas que a fêmea demora entre a escolha da folha e a postura poderia ser devido a uma regulação interna ou ainda à necessidade de estímulos externos para ativar o comportamento de postura.

Comportamento de Cuidado Maternal:

Embora faltem evidências mais conclusivas, a baixa mortalidade de ovos e larvas jovens e o fato de estímulos mecânicos e visuais (especialmente a aproximação de qualquer animal) liberaram diversos comportamentos defensivos e agressivos por parte da fêmea, indicam que estes displays teriam como função proteger a prole contra predadores e parasitas. Lewis estudando o comportamento maternal de *Perga lewisi* na Tasmânia e Marques estudando o mesmo comportamento em *Bergiana cyanocephala* em Minas Gerais chegaram à mesma conclusão (ver Dias, 1975 para uma discussão detalhada sobre comportamento maternal nestas espécies e em *Themos olfersii*). Marques, inclusive ,observou fêmeas de *B. cyanocephala* repelirem micro-himenópteros parasitas de seus ovos através do comportamento de zumbir. A mesma conclusão é também válida para os comportamentos de cuidado maternal em *T. olfersii* (Dias, 1975). Odhiambo (1959, segundo Wilson, 1971) forneceu evidências de que o principal inimigo que causa a evolução de comportamentos de cuidado maternal em Hemíptera (os quais apresentam um paralelismo muito grande com os sínfitas pressociais) são os insetos parasitas, particularmente aqueles que atacam os ovos.

Eberhard (1975), no primeiro estudo sério sobre os efeitos ecológicos de comportamento de cuidado maternal em inseto pressocial, verificou que no Pentatomídeo *Antiteuchus tripterus* o efeito líquido do comportamento de cuidado maternal dos ovos e ninfas de primeiro instar contra predadores de ovos e ninfas é altamente positivo, isto é, aumenta a sobrevivência dos ovos e ninfas jovens. No entanto, contra duas vespas parasíticas (Scelionidae) o efeito do comportamento de cuidado maternal é negativo, pois diminui a taxa de sobrevivência dos ovos. Isto porque a presença do hemíptero indica a localização dos ovos para as vespas. Eberhard verificou também que os detalhes do comportamento de defesa do hemíptero e do ataque das vespas influenciam fortemente as taxas de sobrevivência dos ovos em diferentes posições da postura.

Entre todos os fatores ambientais que, segundo Wilson (1975), levam à evolução de cuidado maternal, apenas dois poderiam explicar a origem de comportamento de cuidado maternal nos Argídeos: 1. Pressão de predadores e parasitas; 2. especialização para fontes alimentares difíceis de serem exploradas. Em trabalho anterior (Dias, 1975), reuni evidências para mostrar que no caso de *T. olfersii* provavelmente estes dois fatores foram decisivos.

Quanto ao provável efeito dos displays das fêmeas de *D. diasi* e *T. olfersii* sobre predadores e parasitas existem duas possibilidades (seguindo o raciocínio de Prop, 1960):

1. Os displays proporcionariam uma defesa ativa.

a) Eles poderiam simplesmente, assustar os predadores e parasitas, sem no entanto serem realmente perigosos para o inimigo;

b) os displays seriam perigosos para os inimigos podendo causar dano para pequenos atacantes.

2. Os displays poderiam fazer parte de uma advertência aposemática, baseada na associação de conspicuidade e ausência de atratividade ou repugnância (gosto e cheiro ruins etc.).

Provavelmente contra predadores grandes (especialmente aves) haveria um efeito conjugado das hipóteses 1a e 2. Quanto aos parasitas, devido ao seu pequeno tamanho, o efeito deve ser segundo as hipóteses 1a ou 1b.

É possível que a simples presença, mesmo um pouco afastada, da fêmea viva ou morta sirva para dar alguma proteção às larvas contra predadores grandes devido à sua coloração aposemática.

Vantagens do Gregarismo Larval:

Autores antigos, estudando insetos com larvas gregárias, só viam inconvenientes e prejuízos causados às larvas por permanecerem juntas. Allee (1931), por exemplo, dizia que «no obvious benefit accrues to the individuals. They are more conspicuous as a result of the grouping and cannot defend themselves better than if alone». Outros diziam que as larvas gregárias seriam mais suscetíveis a ataques de doenças infecciosas, predação e parasitismo além de sofrerem uma competição entre si pelo alimento disponível. Apenas recentemente é que os estudos experimentais e observações detalhadas de Ghent (1960) e Prop (1960) com larvas de *Neodiprion* e *Diprion* (Diprionidae), e Carne (1962, 1966) e Seymour (1974) com *Perga* (Pergidae), demonstraram que o gregarismo larval traz uma série de vantagens ecológicas. Carne (1966) lembra que pode ser significativo o fato de que os insetos, pragas de florestas mais prejudiciais e mais vastamente distribuídas, são gregários naquelas fases de crescimento mais suscetíveis a pressões (stresses) do meio ambiente.

Uma vantagem do gregarismo é a maior eficiência dos displays defensivos conjugados contra predadores e parasitas, segundo demonstrou Prop (1960) e já anunciado por Evans (1934). Nas larvas de *D. diasi* o efeito total dos displays defensivos coordenados e sincronizados é espetacular e surpreendente o suficiente para assustar qualquer inimigo em potencial. Tostowaryk (1972), estudando a predação de larvas de *Neodiprion* pelo hemíptero *Podisus modestus,* observou que o comportamento gregário incluindo os displays larvais tenderia a atrair os predadores reduzindo, portanto, o tempo de procura de presa. No entanto, as reações de defesa através de «group effort» (densidades $\geq$ 10) das larvas ativas sobrepujava sua atratividade. Concluiu que «*Neodiprion* sawflies are successful in reducing predation pressure by feeding aggregately, producing a more effective defence against predators through group effort». Prop (1960) observou que o gregarismo resulta também em maior vigilância, pois muitas vezes uma larva que não foi diretamente aproximada ou ameaçada pelo inimigo responde primeiro.

Outra vantagem do gregarismo é que este possibilita o aparecimento de diversas formas de cooperação entre as larvas. Entre os sínfitas pressociais esta cooperação aparece na forma de tipos primitivos de divisão de trabalho. O mais elementar deles é exemplificado pelo comportamento das larvas de primeiro instar de *Neodiprion pratti* de dividirem a tarefa de encontar locais propícios para alimentação nas duas folhas de pinheiro (Ghent, 1960). Carne (1966) observou que este tipo primitivo de divisão de trabalho está presente em duas fases do desenvolvimento larval em *Perga affinis:* nas larvas recém-nascidas que encontram dificuldade para sair do interior da lâmina foliar onde os ovos são postos, e nas larvas maduras que têm dificuldade em encontrar locais propícios para cavar e penetrar no solo para encasular. Em ambos os casos as larvas dividem entre si o trabalho de localizar um ponto onde perfurar a dura epiderme foliar ou solo duro seja possível. A dependência na integração cooperativa neste nível elementar de divisão de trabalho é antes no sentido estatístico do que no sentido obrigatório (Ghent, 1960). Carne (1966) diz que uma forma elementar de divisão de trabalho, não muito afastada da anterior no continuum da sociabilidade, porém visivelmente mais avançada, é o «efeito aditivo de contribuições equipotenciais de um número de indivíduos». Este comportamento é comumente exemplificado pelas situações onde duas ou mais formigas combinam seus esforços para transportar uma presa cujo peso é maior do que uma sozinha poderia suportar. A construção de aglomerados de casulos cooperativamente por larvas de *Dielocerus*, *Digelasinus* e *Pachylota* é mais um exemplo desta forma elementar de divisão de trabalho, talvez o mais alto nível atingido por larvas do sínfita. As larvas de *Perga* também constroem seus casulos junto em grandes aglomerados organizadamente na forma de favos de abelha, mas não tecem uma cobertura comum (Evans, 1934 e Carne, 1962). Não há portanto cooperativismo entre as larvas de *Perga* para realizarem algo que sozinhas não poderiam fazer. Em várias espécies de microhimenópteros (Chalcididae e Icheumonidae) as larvas também constroem seus casulos junto e organizadamente sem contudo tecerem uma cobertura comum a todos (Curtis, 1844, e Goidanich, 1956). Talvez o caso mais parecido com os aglomerados de casulos dos Argídeos seja o das larvas do gênero *Apanteles* (Braconidae) que tecem grande quantidade de fios de seda que formam uma conspícua massa cotonosa branca de alguns centímetros de comprimento, no meio da qual tecem os casulos individuais «que assim ficam mais protegidos» (Costa Lima, 1962 — ver Figura 38). O valor adaptativo dos aglomerados de casulos ainda não está claro. É provável que a espessa cobertura surgiu como proteção contra o ataque de parasitas, hipótese esta já aventada por Curtis (1844) que raciocinava que «the slightly gummy outside covering of the nest would resist a long flexible aculeus, and a short one could not reach the cells through the woolly wall which encloses them, and even if it did, the cell itself at that distance from the Icneumon could not be penetrated by the delicate ovipositor». Apesar disso, no entanto, o Icneumonídeo *Lymeon ?dieloceri* parasita com muito sucesso os aglomerados de casulos de *D. diasi.*

Outras vantagens do gregarismo larval são: diminuição da perda de calor por convecção, aumentando a temperatura das larvas no sol e conseqüentemente aumentando o ritmo de digestão e desenvolvimento larval (Seymour, 1974) e diminuição da competição intra-específica (De Vita, 1975).

Comportamento Pré-social em Argidae, Resumo e Comentários

Conhece-se atualmente quatro gêneros de Argídeos neotropicais que têm espécies pré-sociais, apresentando comportamento maternal e gregarismo larval: *Dielocerus* Curtis, *Digelasinus* Malaise, *Pachylota* Curtis e *Themos* Norton. No entanto apenas as seguintes espécies tiveram parte de suas biologias estudadas: *Dielocerus formosus* (Klug) (ver Dias, 1975), *D. diasi, Digelasinus diversipes* (Monte e Silva, 1946) e *Themos olfersii* (Dias, 1975). Segundo Benson (1938) estes gêneros pertencem a três subfamílias distintas: Dielocerinae *(Dielocerus* e *Digelasinus),* Pachylotinae *(Pachylota)* e Theminae *(Themos).* Nada se conhece sobre a biologia dos outros Argídeos neotropicais. É provável, entretanto, que grande parte deles tenham comportamento pré-social.

A biologia de *Dielocerus diasi* e *D. formosus* parece ser muito parecida: ambas espécies apresentam comportamento maternal e gregarismo larval. Os aglomerados de casulos construídos pelas duas espécies são idênticos (ver figuras de aglomerados de casulos de *D. formosus* em Costa Lima, 1927). As duas espécies são [illegible] parasitadas por *Spathimeigenia dieloceri* (Tachinidae) e *Lymeon dieloceri* (Ichneumonidae). No entanto como os comportamentos de *D. formosus* não foram estudados não posso fazer uma comparação mais detalhada das duas espécies. *Dielocerus diasi* parece restringir-se à área do Planalto Central brasileiro coberta de Cerrado (onde ocorre sua planta hospedeira, *Sclerolobium aureum*), enquanto que *D. formosus* parece ocorrer ao longo da costa leste brasileira na área da mata atlântica onde ocorre sua planta hospedeira, *Inga* sp. (Leguminosae, Mimosacea) (Monte, 1941).

Os comportamentos pré-sociais de *D. diasi* e *Themos olfersii* (Dias, 1975) são basicamente muito semelhantes. As fêmeas das duas espécies são relativamente grandes (15 mm de comprimento), conspícuas pela coloração laranja e preto, têm longa vida (máximo observado de 27 a 38 dias) e são provavelmente repelentes aos predadores. As fêmeas emergem com todos os óvulos completamente desenvolvidos, e põem todos eles de uma só vez (semelparidade) em uma só folha. Cada espécie tem apenas uma planta hospedeira: árvores do cerrado. Os ovos são postos em contato com o parênquima foliar e o período de incubação é demorado (14 a 23 dias). Os ovos crescem muito, aumentando três a quatro vezes de volume absorvendo água e talvez nutrientes da folha. As fêmeas exibem um cuidado maternal prolongado e elaborado, não se afastando nunca de perto da postura, e apresentam displays defensivos, de advertência e agressão variados, muitos deles iguais ou muito parecidos: zumbir, zumbir girando o corpo, avançar e morder, elevar e abrir bruscamente as asas. Estes displays são liberados em ambas as fêmeas por estímulos mecânicos e visuais. As fêmeas também cuidam das larvas novas por muitos dias (máximo observado de 12 a 15 dias), mudando sua posição em conseqüência dos deslocamentos das larvas (interação entre gerações distintas). As larvas são altamenta gregárias durante todo o período larval (30 a 45 dias de duração) e alimentam-se juntas na margem da folha alinhadas uma atrás da outra em filas indianas compactas, voltadas todas para uma mesma direção e caminham para a frente à medida que comem. As larvas individualmente alternam entre períodos de abstinência e períodos de alimentação, apesar da colônia como um todo comer incessantemente. As larvas migram juntas e colônias de larvas distintas quando se encontram fundem-se. Todas as larvas da colônia elevam seus abdômens bruscamente e simultaneamente como defesa contra inimigos. As larvas têm uma mancha negra dorsal na extremidade do abdômen, que teria papel na intimidação dos inimigos. Adultos, ovos e larvas pequenas são relativamente pouco predados e parasitados.

O comportamento maternal em *T. olfersii* parece ser bem mais especializado do que em *D. diasi* pois enquanto fêmeas desta espécie põem em média 75 ovos, as de *T. olfersii* põem apenas 27 ovos em média; o período de incubação dos ovos de *T. olfersii* é maior (23 dias contra 14 dias em *D. diasi*); as fêmeas de *T. olfersii* ficam sempre sobre suas posturas enquanto que as de *D. diasi* em geral ficam apenas próximas de suas posturas; as fêmeas de *T. olfersii* apresentam um maior número de displays defensivos e respondem mais aos estímulos, isto é, são mais excitáveis que as de *D. diasi;* as larvas recém-nascidas de *T. olfersii* são bem maiores, quase o dobro do tamanho das de *D. diasi*. Outra diferença entre as duas espécies é que enquanto os ovos de *D. diasi* são postos dentro da lâmina foliar entre o parênquima e a epiderme inferior, os de *T. olfersii* são encaixados na epiderme superior da folha em contato com o parênquima. Além disso, os ovos de *D. diasi* são espalhados por grande extensão da lâmina foliar enquanto que os de *T. olfersii* são colocados muito próximos uns dos outros, formando um circulo de aproximadamente 15 mm de diâmetro. As fêmeas de *T. olfersii* apresentam vários displays não apresentados pelas fêmeas de *D. diasi:* girar sobre a postura sem sair de cima dela; inclinar o corpo lateralmente sobre a postura; estender as asas sobre os ovos; abaixar o corpo rente aos ovos; elevar e abaixar o corpo ritmicamente; e abrir e abaixar as asas anteriores sobre os ovos e levantar as asas posteriores. As fêmeas de *D. diasi* também apresentam alguns displays particulares: andar em círculos sobre a postura; elevar a cabeça e abrir as mandíbulas; e caminhar sobre a postura zumbindo. Mesmo no caso dos displays exibidos pelas duas fêmeas existem algumas diferenças: por exemplo, no display de zumbir, enquanto as fêmeas de *T. olfersii* elevam a parte posterior do corpo, as de *D. diasi* elevam a parte anterior do corpo e abrem as mandíbulas. As fêmeas de *D. diasi* depois de mortas continuam agarradas ao galho da postura por muitas semanas, enquanto que as de *T. olfersii* imediatamente caem ao chão.

Quanto ao gregarismo larval, as larvas de *T. olfersii* parecem mais especializadas no comportamento de alimentação grupal pois desenvolveram o elaborado mecanismo de comerem em duas filas convergentes que se chocam, onde as larvas revesam continuamente de posição. Enquanto em *T. olfersii* as larvas que não estão comendo estão no fim das duas filas convergentes, as larvas abstinentes de *D. diasi* saem da formação em fila indiana e agrupam-se ali perto. Enquanto as larvas recém-nascidas de *T. olfersii* sempre iniciam a comer pela própria folha da postura, as de *D. diasi* sempre iniciam a comer por uma das folhas apicais do galho-não-ramificado da postura e nunca pela folha da postura.. Em relação aos displays defensivos das larvas, os de *D. diasi* chamam mais a atenção pois as larvas após levantarem seus abdômens, abaixam-nos imediatamente e tornam a levantá-los brusca e simultaneamente tantas vezes quanto forem estimuladas, ao passo que as larvas de *T. olfersii* mantém seus abdômens elevados até cessarem os estímulos. A mancha negra dorsal da extremidade do abdômen está presente em todos os estágios das larvas de *T. olfersii* mas aparece apenas nos estágios iniciais das larvas de *D. diasi*. As larvas de *T. olfersii* excretam um líquido viscoso repelente, enquanto que as de *D. diasi* não o fazem. A principal diferença, no entanto, entre os gregarismos larvais das duas espécies está na fiação dos casulos: enquanto as larvas de *T. olfersii* tecem seus casulos aparentemente isolados e certamente sem uma cobertura comum enterrados no solo, as de *D. diasi* são muito mais especializadas pois tecem aglomerados de casulos elaborados, com cobertura protetora comum, nas cascas dos galhos e troncos da árvore hospedeira. Portanto, enquanto as larvas de *D. diasi* apresentam uma forma primitiva de divisão de trabalho na construção de seus aglomerados de casulos, as de *T. olfersii* tecem seus casulos individualmente sem cooperação.

Schmidt (1974) cita *Dielocerus*, numa tabela comparativa sobre comportamentos pré-sociais em insetos, como possuindo comportamento de cuidado maternal dispensável (Brutvorsorge e Brutfürsorge), isto é, onde a retirada da mãe não prejudica o desenvolvimento dos ovos e larvas, e associação Adulto-larvas (Larven-Adult-Familie). Na mesma tabela cita alguns Tenthredinídeos como possuindo cuidado maternal elementar (Brutvorsorge) e associação de irmãos na fase larval (Geschwisterverband) na forma de grupos de alimentação (Fressgemeinschaft, feeding group). É evidende que *Dielocerus* deveria ter sido citado como possuindo também associação de irmãos na fase larval não só para alimentação como também para defesa e fiação dos casulos. Serão necessários estudos mais cuidadosos sobre o comportamento maternal de *D. diasi* e *T. olfersii* para verificar se a retirada da fêmea mãe realmente não prejudica o desenvolvimento e sobrevivência da prole.

Wilson (1971) diz que «the difficult theoretical problem of why some of these (presocial insects) groups have not taken the final step to eusociality remains. That they have not done so is an absorbing mistery...». Knerer e Atwood (1973) e Knerer (1974) analisando as manifestações sociais entre os Symphyta concluem que *Perga* e *Dielocerus* alcançaram sob a presente relação com o alimento, o máximo de sua possibilidade social, pois o transporte de tecido vegetal para o ninho resulta apenas custoso, e sua conservação para as larvas que vão eclodir não é possível para a vespa-de-serra. Segundo os mesmos autores, um provisionamento contínuo com matéria vegetal mastigada parece pouco racional por causa da pobreza energética do material. O alimento (folhas grandes), portanto, segundo esses autores, é impróprio para transporte e consumo posterior em um ninho, a existência do qual é necessária em qualquer sociedade evoluída de insetos (Knerer e Atwood, 1973). Eles concluíram que o socialismo em Symphyta é um beco sem saída!

Certamente estudos detalhados dos efeitos ecológicos dos comportamentos pré-sociais nos argídeos neotropicais e outros sínfitas esclarecerão muitas questões ainda hoje sem solução.

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