COMPARATIVE STUDIES ON THE SOCIAL BEHAVIOUR OF NAUPHOETA CINEREA AND HENCHOUSTEDENIA FLEXIVITTA (DICTYOPTERA, BLATTARIA, BLABERIDAE, OXYHALOINAE).

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TO TONINHO, DANIEL AND CLARISSE

AND IN MEMORY OF RAMÓN ÂNGELO.

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ABSTRACT

The relationship between time of moulting and the formation of the adult male dominance hierarchy in Nauphoeta cinerea (O.) and Henchoustedenia flexivitta (W.) was described in detail.

Spacing-relationships of both cockroach species throughout nymphal instars and the first days after the final moult were examined and related to behavioural changes.

Several aspects of agonistic behaviour (qualitative and quantitative) were examined to investigate the ontogeny of agonistic behaviour leading to dominance hierarchy formation.

The influence of maturity and the role of isolation on the establishment of male hierarchies were discussed.

The relationship between homosexual and pseudofemale behaviour and its effect on the establishment of a dominance hierarchy in N. cinerea and H. flexivitta was investigated and discussed.

I. GENERAL INTRODUCTION

I. GENERAL INTRODUCTION

This study compares some aspects of the ontogeny of social behaviour in two species of cockroach, Nauphoeta cinerea (Olivier) and Henchoustedenia flexivitta (Walker).

The subject was chosen because the ontogeny of social interactions in cockroaches was not considered at all until 1976. There has been relatively little research carried out in the area, and even less on the effects of previous social experience. The results obtained from previous studies are not sufficient for a complete understanding of the subject.

Nauphoeta cinerea and Henchoustedenia flexivitta (Blaberidae-Oxyhaloinae) are closely related species, and thus possess suitable characteristics for comparative studies.

The agonistic behaviour of adult mature males of Nauphoeta cinerea was extensively studied by Ewing (1967, 1972, 1973). However, neither the behaviour of immature males, or the ontogeny of agonistic behaviour has been described. Henchoustedenia flexivitta has not previously been used for behavioural studies.

In general there has been little behavioural research done on either cockroach nymphs or immature adults (Lawson, 1965; Manning & Johnstone, 1970; Gautier, 1976; Olomon et al., 1976; Deleporte, 1978; Gorton & Gerhardt, 1979). Furthermore, cockroaches are very suitable material for such studies. They are easily maintained in the laboratory, are inexpensive and the nymphs have the same requirements and live in the same surroundings as the adults.

As cockroaches are long-lived Hemimetabola spending a long time in the nymphal stages, it is possible that the behaviour of the adult may be modified by experience and moreover that at least some of the non-sexual behaviour may develop, and be traced in its development through the nymphal instars to the adult (Lawson, 1965).

Some considerations about cockroaches.

Cockroaches comprise a very ancient group of insects. They are considered to be among the most primitive of the Pterygota, and fossils of their ancestors indicate that they have changed little since the period of their dominance (Mckittrick, 1964). Cockroaches were exceedingly abundant during the carboniferous period when they outnumbered all other insects (Scudder (1879) cited in Miall & Denny, 1886). Since that time they have slowly declined until the present.

Rehn (1951) reported that there are over 3,500 species of cockroaches. More recent estimates suggest that there are more than 4,000 species throughout the world, most of which live in the tropics.

A few cockroach species are pests to man but most are not. Because of their cosmopolitan abundance and the ease of culture these economically important species, especially Periplaneta americana (L.), often referred to as The Cockroach, are among the best known of all insects.

Some of the cockroach species have been extensively used for studies in biology, anatomy, physiology and ethology. Most of these studies were performed using tropical and sub-tropical species such as: Periplaneta americana (L.), Blaberus craniifer (Burm.), Blatta orientalis (L.), Blattella germanica (L.) and Nauphoeta cinerea (O.). However, very little is known concerning cockroach behaviour in natural habitats, and even less about the original habitat of most species of domicialiary cockroaches. Rehn (1945) determined the most likely origins of the various cockroaches with records of historical trade movements. The spread of cockroaches was greatly assisted by the early maritime Nations and man's commensal species now extend far outside their natural range. Natural distribution of cockroaches is largely influenced by climate.

Nauphoeta cinerea originated in East Africa and spread with shipping to the Orient and the New World (Rehn, 1945). Now it is a tropical domiciliary cockroach of the New and Old Worlds, occurring in Cuba, Mexico, Brazil and the Galapagos Islands. In the East, it is common in the Phillipines, Sumatra and Singapore and occurs in Australia, New Caledonia and the Hawaiian Islands. East African records extend from Egypt through the Sudan to eastern Tanzania, the Transvaal and Natal. It also occurs in Madagascar and Mauritius (Cornwell, 1968).

N. cinerea, originally named Blatta cinerea in 1789 from specimens taken in Mauritius, was not given its present name until 1922 by Olivier (Cornwell, 1968).

There are several proposed classifications of the cockroach and these differ markedly from one another. According to Mckittrick (1964) the Blattaria are considered to be a sub-order of the order Dictyoptera. He established a new classification of the Blattaria according to the morphology of the genitalia and the oviposition behaviour (Fig. I-1).

Nauphoeta cinerea and Henchoustedenia flexivitta (Blaberidae) are ovoviviparous Oxyhaloinae of the Panchloroid complex; Henchoustedenia was split off from the genus Nauphoeta by Princis (1954).

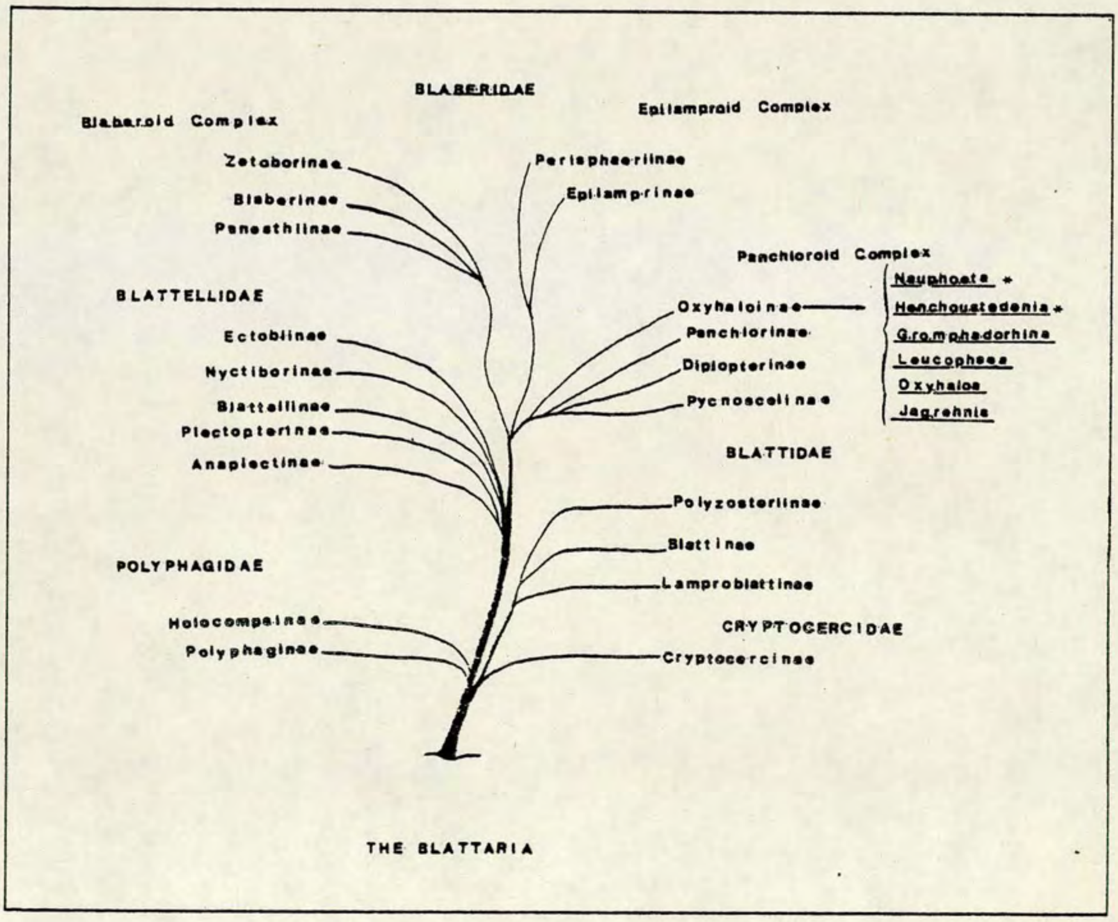

Fig. I.1 - Classification of Blattaria (after Mckittrick, 1964)

II. ANIMAL MAINTENANCE AND GENERAL METHODOLOGY

II. ANIMAL MAINTENANCE AND GENERAL METHODOLOGY

Colonies of Nauphoeta cinerea and Henchoustedenia flexivitta were maintained in the laboratory in large culture tanks at nearly constant temperatures (24-27°C) with a reversed light-dark cycle of 12:12 hr (photophase 9 pm - 9 am). They were fed with rat-nut and fresh food such as apples, carrots and cabbages. Water was provided regularly.

All the animals to be used in the behavioural study were taken at random from laboratory colonies and placed in clear plastic cages for observation. These containers were covered with clear plastic lids with net on top.

All observations were conducted between the end of the first and the beginning of the fifth hours of the dark phase of the cycle when the cockroaches were most active. Observations were made under red light (Fireglow 60W) to simulate dark conditions (Walther & Dodt, 1957; Goldsmith & Ruck, 1958; Barth, 1964; and many others).

Each cockroach was code-marked with fast-drying paint on its pronotum for individual recognition before being put in the observation tank. The method used in most of the behavioural observations was focal-animal sampling (Altmann, 1974).

Most of the observations were recorded using a key-punch apparatus with keys labelled for various behavioural activities and connected to an event recorder (by Esterline Angus Instrument Co. Inc., U.S.A.)

In each chapter of the thesis the detailed method used will be described when necessary.

Table II.1 summarizes all the experiments used in the present study, with their main objectives and in which section they were discussed.

Table II.1 - Summary of the experiments used in the present study.

Time of establishment	Characteristics of the experiments	Main objectives of the investigation	Section
Newly-hatched nymphs	Thirty nymphs of each species kept singly until final moult	Nymphal development in isolated individuals	III.3.1
	Thirty nymphs of each species reared together until final moult	Nymphal development in grouped individuals	III.3.1
	Three groups of five individuals of each species (1A, 1B, 1C) observed until some days after adult emergence	Time of moulting and its relation to dominance hierarchy formation	III.3.2 III.3.3
		Development of spacing-patterns in nymphs	IV.3.1
		Ontogeny of agonistic behaviour and measurement of aggressiveness with time	V.3.1 V.3.2 V.3.3
		Descriptive analysis of sexual behaviour among individuals already known to each other	VI.3.8
From the penultimate instar	Three groups of five individuals (1D, 1E, 1F) of *N cinerea* (replicates) One group of five individuals (1D) of *H. flexivitta* (replicate)	Time of moulting and its relation to dominance hierarchy and descriptive analysis of sexual behaviour among individuals already known to each other	III.3.3 VI.3.8

Table II.1 - (cont'd)

Time of establishment	Characteristics of the experiments	Main objectives of the investigation	Section
On the day of adult emergence	One group of five males of each species	Development of spacing patterns from day zero (day of emergency) to day ten	IV.3.2
	One group of three males and two females of _N_. _cinerea_	"	IV.3.2
	One group of two males and three females of _H_. _flexivitta_	"	IV.3.2
	Five pairs of males of each species	Onset of fighting and the establishment of a dominance-subordinate relationship	V.3.4
		Ontogeny of male sexual behaviour in the absence of a female and its relation to development of hierarchy	VI.3.4 VI.3.5
	Five groups of two males and one female of each species	Onset of fighting, courtship and the establishment of a dominance-subordinate relationship	V.3.4
		Ontogeny of male sexual behaviour in the presence of a female and its relation to development of hierarchy	VI.3.3
	Five paired males (one sexually mature and the other immature (zero-day old) of _N_. _cinerea_.	Influence of maturity on the establishment of male hierarchy	V.3.5
		Aspects of dominance related to maturity and its involvement to homosexual behaviour	VI.3.6

Table II.1 (cont'd)

Time of establishment	Characteristics of the experiments	Main objectives of the investigation	Section
After adult emergence	Four groups of five males of *N. cinerea* kept in isolation during the complete nymphal period and for various lengths of time after the final moult:	Influence of total isolation and time of moulting on dominance hierarchy formation	III.3.3
	1) 26-19-18-14 and 5-days-old 2) 16-11-10-10 and 9-days-old 3) 21-20-20-14 and 3-days-old 4) 36-26-20-18 and 1-day-old	Development of homosexual and pseudofemale behaviour in newly established groups and their relation to development of dominance	VI.3.7
	Two groups of five males of *N. cinerea* and *H. flexivitta* kept in isolation for various lengths of time after the final moult. *N. cinerea*: 1) 18-17-16-10 and 6-days-old 2) 15-12-10-10 and 5-days-old *H. flexivitta*: 1) 6-5-4-4 and 2-days-old 2) 11-10-7-4 and 1-day-old	Influence of isolation after the final moult and time of moulting on dominance hierarchy formation	III.3.3 V.3.7 V.3.8
	In each of these six groups of *N. cinerea* five females were introduced singly at three day intervals	Descriptive analyses of mating behaviour of *N. cinerea*	VI.3.1
	One group of four sexually mature males of *H. flexivitta* (three females were introduced singly at three day intervals	Descriptive analyses of mating behaviour of *H. flexivitta*	VI.3.2

III. THE RELATIONSHIP BETWEEN TIME OF MOULTING AND DOMINANCE HIERARCHY

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III. 1. - Introduction

III. 1.1 - Nymphal development

Cockroaches being Hemimetabolous show metamorphosis incomplete. The young (nymphs) which resemble the adult in appearance except for the absence of fully developed wings, external genitalia and adult colouring (Cornwell, 1968) also show the same adult habitat.

Nauphoeta cinerea and Henchoustedenia flexivitta are of a highly specialized false ovoviviparous type (terminology from Roth & Willis, 1958) in which the ootheca is oviposited into a brood sac or uterus and incubated within the female until hatching. The carrying of the eggs has no known direct detrimental effect on the female; it serves the function of protecting the eggs from predation or desiccation until hatching. However, the female is restricted from further egg laying and her fecundity per day of adult life is only approximately 25% of that of other cockroach species such as Periplaneta americana which are continuously forming eggs (Breed et al., 1980).

The nymphs are actively mobile from the moment they leave the ootheca. The post-embryonic growth consists of a series of nymphal instars separated by moults, producing increasingly larger nymphs and finally the adult. The number of moults and the duration of nymphal instars in different species of cockroaches varies considerably. Within each species the number of moults is more or less constant but may vary among individuals, between the sexes, and with season (Cornwell, 1968). The number of moults may increase if environmental conditions are unfavourable. Seamans & Woodruff (1939) found in Blattella germanica that loss of legs can induce an extra moult.

Moulting in cockroaches is controlled primarily by three hormones: juvenile hormone (JH) secreted by the corpora allata, ecdysone, secreted by the prothoracic glands, and brain hormone (BH) from neurosecretory cells in the brain. BH stimulates ecdysone secretion which in turn brings about moulting. Ecdysone and JH determine if the cockroach will moult into a nymph or an adult: if JH is present, a nymph will be produced; if it is absent the result will be an adult (Bell, 1981).

At the time of moulting the cockroach is highly susceptible to desiccation and to cannibalism.

The effect of population density on the development of cockroaches has been examined by Landowski (1938) for newly emerged nymphs of Periplaneta orientalis (H.) [correctly, Blatta orientalis (L.)] reared singly and in groups of two, four, six and 16 in standard size containers. Mortality increased with density, but the number of moults remained constant. All insects required the same developmental period for the first eight instars but from the ninth moult onwards this period shows a marked increase (Landowski, 1938).

In *Nauphoeta cinerea* the nymphs hatch as the female extrudes the ootheca from the brood sac; they shed their embryonic membrane and subsequently eat both membrane and ootheca. Newly hatched nymphs crawl beneath the female, even under her wings, and remain there for about an hour after hatching (Willis et al., 1958). From personal observations, the hatched nymphs stayed near, under and on top of the female's abdomen until cuticular tanning was completed (three-four hours). Willis et al. (1958) studied the nymphal development of *Nauphoeta cinerea* at 30°C. They found that in isolation males passed through seven moults in a period of 73 days while the females passed through eight moults in 94 days. There was no record of number of moults in nymphs reared in groups but the duration of nymphal instars was 72 days for males and 85 days for females.

In insects, moulting is commonly synchronized by external stimuli (Saunders, 1976). Leinaas (1981) found in *Hypogastrura* (collembola) that the moults are synchronized within aggregates. He suggested (1983) that this synchronization is co-ordinated by chemical communication through pheromones and is independent of age and visual stimuli. Pheromones have been shown to regulate aggregation and co-ordinated behaviour in some *Hypogastrura* species (Mertens & Bourgoignie, 1977).

Only a few examples are known where chemical communication directly affects development in insects: in Hymenoptera that have caste-forming colonies, pheromones are known to inhibit development of reproductive forms (Wilson, 1971). In some Orthoptera and Coleoptera reproductive maturity is synchronized by primer pheromones (Richards & Mangoury, 1968; Blum, 1974). A pheromone from adult Dermestes maculatus (Coleoptera), has been shown to inhibit larval development by delaying each moult. This aggregation pheromone affected the synchronization of development of different larval instars (Rakowski & Cymborowski, 1982).

III. 1.2 - Social hierarchies

The term social hierarchy is used in a wide variety of contexts (Gartlan, 1964, 1968; Rowell, 1974), with definitions about priority of access (competitive abilities) and traits that are related to an individual's status, and sometimes going as far as using the terms "aggressive" and "dominant" as synonyms.

The Norwegian naturalist, Shjelderup-Ebbe (1922), introduced the term social dominance in vertebrates when he published his work on the social psychology of domestic chickens in which he described the social organization, or pecking orders, of these birds, concluding that social dominance was one of the fundamental principles of biology (Shjelderup-Ebbe, 1931).

Carl Murchison and his colleagues (1935) published a series of papers that represent the earliest attempt to quantify and to analyse statistically the measurable and identifiable characteristics correlated with dominance.

Crawford (1939) reported that dominance had been found in all vertebrates except fishes and amphibia. Later (Braddock, 1945; McDonald et al., 1968) described dominance in fishes and Haubrich (1961) and Boice & Witter (1969) in amphibia.

Detailed analysis of dominance and some generalizations that accompany the idea were added by a number of investigators like Rowell, 1966, 1974; Brantas, 1968; Gartlan, 1968; Bernstein, 1970; van Kreveld, 1970; Watson & Moss, 1970; Drews, 1973; Kummer, 1973; Spigel & Fraser, 1974; Clutton-Brock et al., 1976; Hanby, 1976; Marler, 1976. The concept of social hierarchy or social dominance became generalized to all vertebrates and appears to be distributed throughout the animal kingdom (Gauthreaux, 1978).

The studies of social dominance in invertebrates started with Pierre Huber (1802) who first recognized dominance orders during his studies of bumble bees (Gauthreaux, 1978). Later the phenomenon of dominance in invertebrates was described for several animals. Among them: Polistes (Hymenoptera) (Heldmann, 1936; Pardi, 1948; Gervet, 1962; West, 1967); Orconectes virulis (crayfish) (Bovbjerg, 1953; Rubenstein & Hazlett, 1974); Procambarus alleni (crayfish) (Bovbjerg, 1956); Uca spp. (fiddler crabs) (Crane, 1958, 1967; Hyatt & Salmon, 1978, 1979); Microphrys bicornutus (spider crab) (Hazlett & Estabrook, 1974); Menippe mercenaria (stone crab) (Sinclair, 1977); Jasus lalandei (spiny lobster) (Fielder, 1965); Formica (ant) (Lange, 1967);

Gonodactylus bredini (mantis shrimp) (Dingle, 1969); Chortophaga viridifasciata (grasshopper) (Steinberg & Conant, 1974).

The first quantitative study of hierarchy establishment in Orthoptera was that of Alexander (1961) on crickets, Acheta sp. He observed that a hierarchy develops in a group of five males within six hours of being placed together. The hierarchy was found to be linear and fairly stable. This study stimulated several other studies on aggressive and territorial behaviour in Orthopteroid insects.

It is a fact that in a wide variety of animal societies, individuals comprising a group can often be ranked on a dominance-subordinate scale and specific behaviour patterns and physiological states can be associated with relative ranks among individuals. This is the case of the control of spatial relationship.

Dominance hierarchies may be independent or in conjunction with territoriality. For dominance hierarchy and territoriality to evolve, a cost/benefit ratio must exist which is small enough to make territorial and hierarchical interactions advantageous in terms of reproductive output (fitness) (Gorton et al., 1979).

Males of several species of cockroaches were described as territorial and having social hierarchies; Nauphoeta cinerea (Ewing, 1972, 1973; Bell & Gorton, 1978); Eublaberus posticus (Bell et al., 1978); Gromphadorhina brunnei (Zeigler, 1972); Cryptocercus punctulatus (Ritter, 1964); Blaberus spp. (Gautier, 1974, 1976).

Other cockroach species are less social and lack a fixed dominance hierarchy; *Periplaneta americana* (Bell & Sams, 1973; Olomon et al., 1976; Tourtellot & Breed, 1976; Deleporte, 1978); *Blattella germanica* (Breed et al., 1975); *Shavella couloniana* (Gorton, 1976) and *Byrsotria fumigata* (Breed & Byers, 1979).

There are three major types of social hierarchies (Bekoff, 1977):

1. One individual dominates all other members of his or her social group, with no rank distinctions among the subordinates (Wilson, 1975). This has been observed in iguanid lizards living under conditions of unnaturally high densities (Carpenter, 1971).
2. *Linear* - One individual (Alpha animal) dominates all other group members, another individual (Beta) dominates all other group members except Alpha, and so on. In this case dominance relations must be *transitive* (Harary et al., 1965; Moon, 1968), that is for any three individuals if \`1' dominates \`2' and \`2' dominates \`3', then \`1' also dominates \`3'.
3. *Non-linear* - Here the dominance relations has at least one or more *intransitive* triads (Chase, 1974), e.g. individual \`1' dominates \`3', \`3' dominates \`2', but \`2' dominates \`1'.

Bell & Gorton (1978) subdivided the *linear hierarchy* in three types using the following terms and definitions:

(1) *Toti-linear* = a dominance relationship among individuals in which there are no reversals, and a higher ranking individual is never defeated by a lower ranking individual.

Marler (1956), for example, illustrated a totally linear hierarchy resulting from agonistic encounters in captive chaffinches.

(2) Semi-linear = a dominance relationship among individuals in which reversals occur but the higher ranking individual defeats the lower ranking individual in more than 50% of encounters, e.g. Nauphoeta cinerea (Ewing, 1972).

(3) Linear = a dominance relationship among individuals in which reversals occur and higher ranking individuals do not always defeat lower ranking individuals in more than 50% of encounters, e.g. Periplaneta americana (Bell & Sams, 1973).

There is a general agreement that the dominance rank (dominance hierarchy or social hierarchy) is the set of sustained aggressive-submissive relations among a group of individuals (Bell & Sams, 1973). Although aggressive individuals are not necessarily the most dominant in a group, aggression does not necessarily lead to the establishment of dominance relations, and the formation of a dominance hierarchy does not necessarily lead to a reduction of aggression (Bekoff, 1977).

Rigid hierarchies and/or territoriality maintained by aggression are social designs important for the maintenance of some species and unimportant for others (Bell & Sams, 1973).

Flexible social systems have been found in a number of groups besides insects. It has generally been found that individuals of species that are territorial in nature or in uncrowded captive conditions tend to shift into dominance hierarchies when crowded. This has been shown in crayfish (Procambarus; Bovbjerg, 1956; Cambarellus; Lowe, 1956) and in many vertebrates, including fishes, reptiles, birds and mammals (Wilson, 1975, pp. 296-297).

In Eublaberus posticus dominance hierarchies were maintained in a variety of density and resource conditions, (Gorton et al. 1979). Observations on Blaberus colosseus and Blaberus atropos in a natural environment (caves of Trinidad) (Gautier, 1974, 1976, 1977) showed that the social structure varies according to the population density, from territorial structure, through intermediate structure to hierarchical structure. Previous work on Nauphoeta cinerea has shown that males kept in high density formed hierarchies while those males kept at low density were also territorial and usually the top-ranking males possessed territories (Ewing, 1972, 1973; Gorton et al., 1979).

In Nauphoeta hierarchy stability is usually present nine days after the group is first set up, but the dominant male may often be identified as early as day three (Ewing, 1972). Although the highest-ranking and lowest-ranking male can be identified, there is not a complete linear hierarchy formed throughout the groups (Smith & Breed, 1982).

Nauphoeta males exhibit reversals in a subordinate/dominant relationship when paired with other individuals (Ewing & Ewing, 1973). Agonistic behaviour in groups of males is influenced by social status and only in Nauphoeta cinerea does the behaviour of the Alpha-male strongly determine the social pattern of interactions among individuals (Bell & Gorton, 1978).

These first sort of experiments in this chapter were designed to investigate any relationship between time of moulting and the formation of the adult male dominance hierarchy in Nauphoeta cinerea and Henchoustedenia flexivitta.

III. 2. - Materials and Methods

Pregnant females of Nauphoeta cinerea and Henchoustedenia flexivitta were removed from laboratory colonies and placed in individual jars (9 cm in diameter) until nymphal emergence. On hatching the nymphs were placed in three different experimental regimes. In all regimes shelter, food and water were provided.

(1) Thirty nymphs of each species were kept singly in jars (9 cm in diameter) until adult emergence. All moults were noted.

(2) Three groups (1A, 1B, 1C) of five individuals of each species were placed in 23 x 23 x 10 cm clear plastic cages for observation. In addition four other groups of five individuals were set up from the sixth-seventh instar; they were three groups of Nauphoeta cinerea (1D, 1E, 1F) and one group (1D) of Henchoustedenia flexivitta. In the last four groups the nymphs were reared with siblings of the same age in a plastic cage after hatching.

Each individual was code marked (individual; 1, 2, 3, 4 and 5). Shelters were placed in each corner and one at the centre of the cage. Observations on time of moulting and agonistic behaviour of adult males were made.

(3) One group of 30 individuals for each species was maintained with their mother in standard size cages until the final moult.

All moults were noted for each different regime. In the second regime each individual was re-marked as it moulted to aid individual recognition. As sex in these species can only be distinguished after the sixth moult, these groups had different proportions of males and females. These observations continued until the last individual to moult in the group was 15-days-old. Observations were made especially on agonistic behaviour in order to determine any relationship between time of moulting and the adult male dominance hierarchy. These observations on relationship of males after the final moult were carried out once a day for 15 days, starting on the day of emergence of another male in the group. How the observations of agonistic behaviour were made will be described in chapter five.

When Nauphoeta cinerea males of the first experimental regime, and the other individuals that were kept singly, reached adulthood they were set up in groups for agonistic behavioural observations. The individuals were kept singly even after the last moult until five males were ready (adults) for the setting up an experimental group. Four groups of five males were set up with different age-structures. As the time of final moulting (i.e. adult age) was known for each individual, this could be used for evaluating the relationship between it and the hierarchy formation in a particular group. The four groups of five males of N. cinerea had the following age-structure:

(1) 26-19-18-14 and 5-days-old

(2) 16-11-10-10 and 9-days-old

(3) 21-20-20-14 and 3-days-old, and

(4) 36-26-20-18 and 1-day-old

Unfortunately, very few males of Henchoustedenia flexivitta kept singly reached adulthood and no group of this species was set up for such observations.

After the male of both species in the third experimental regime had their final moult, they were kept singly for various lengths of time and then used in agonistic behavioural observations. Two groups of five males for each species were set up with the following age structure. Two groups of Nauphoeta cinerea:

(1) 18-17-16-10 and 6-days-old, and
(2) 15-12-10-10 and 5-days-old.

Two groups of Henchoustedenia flexivitta:

(1) 6-5-4-4 and 2-days-old, and
(2) 11-10-7-4-and 1-day-old.

In all groups the individuals were marked for individual recognition following the sequence of the final moult, i.e. individual `1' was the first male to moult in the group (the oldest male) and individual `5' was the youngest in the group.

In all groups of Nauphoeta cinerea in the first and third experimental regimes, females were introduced after the hierarchy became stable. In all groups the observation period was 30 minutes with six minutes of observation for each individual. Two observation periods were made per week. Ten observations were made for each group, five before the introduction of females and five afterwards. Five females were introduced in each group at three day intervals and removed after one hour, or after copulation occurred. Observations on agonistic behaviour were made always on the day following the introduction of female, since initially there was such a degree of disturbance that observations would have been atypical.

III. 3. - Results and Discussion

III. 3.1. - Some aspects of the biology of Nauphoeta cinerea and Henchoustedenia flexivitta

Some information on the biology of Nauphoeta cinerea and Henchoustedenia flexivitta was obtained during the study of behaviour.

The data were obtained from animals maintained in more or less constant temperature (24-27°C) and were found to vary quite considerably from that obtained for N. cinerea at 30°C) (Cornwell, 1968). Table III.1 shows the comparison between these two sets of data. Both show that young adult individuals do not mate. Further, the number of moults and the period of nymphal development in isolated individuals takes longer than those kept in groups.

The nymphal development of N. cinerea reared in the group of 30 individuals took 134 ± 10.52 days for males and 155 ± 11.63 days for females, while in isolation the duration of nymphal instars was 165 ± 7.72 days for males and 185 ± 10.88 days for females (Table III.1). The duration of nymphal instars of Henchoustedenia flexivitta reared in groups of 30 individuals was 135 ± 28.14 days for males and 161 ± 14.68 days for females, while in isolation it took 162 ± 19.25 days for males and 171 ± 18.34 for females. The variation between final moult was bigger in H. flexivitta in either groups isolated or grouped than in N. cinerea.

These results show that females take longer to mature than males and isolated nymphs take longer to mature than nymphs reared in groups. (Table III.1). Warton et al. (1967) found that isolated cockroaches of Periplaneta americana took longest to mature, while nymphs in groups from two to 25 matured increasingly early as the numbers were increased. Landowski (1938) found the same for Periplaneta orientalis [correctly, Blatta orientalis (L)] and Willis et al. (1958) for Blattella germanica.

Table III.1 - Some aspects of the biology of *N. cinerea* and *H. flexivitta*

Biological aspects	*N. cinerea* (Cornwell, 1968) Temp. 30°C	*N. cinerea* Temp. 24-27°C	*H. flexivitta* Temp. 24-27°C
Minimum period between moult to adult and copulation (days)	6 (both sexes)	3 M 4 F	more than 5
Interval between moult to adult and production of the first ootheca (days)	13	13 ± 1 (n=4)	15
Interval between moult to adult and hatch of the first brood (days)	44	56.56 ± 4.04 (n=23)	81 ± 1.4
Interval between hatch of successive broods (days)	1st-2nd: 40 7th-8th: 99	1st-2nd: 46	1st-2nd: 82 2nd-3rd: 68 3rd-4th: 66
Hatched eggs per ootheca	31	30.68 ± 5.9 (n=29)	30 (n=4)
Number of moults	7 MM 8 FF	8-9 MM 8-10 FF	8-9 M&F
Period of nymphal development (days)			
-in isolation MM	73	165 ± 7.7	162 ± 19.2
FF	94	185 ± 10.9	171 ± 18.3
		groups of 30 individuals	
-in groups MM	72	134 ± 10.5	135 ± 28.1
FF	85	155 ± 11.6	161 ± 14.7
		groups of 5 individuals	
-in groups MM		146 ± 27.4	131 ± 32.0
FF		146 ± 55.4	137 ± 53.1

III. 3.2. - Nymphal development of Nauphoeta cinerea and Henchoustedenia flexivitta in groups of five individuals

Tables III.2, III.3 and III.4 show the number of moults and the time of moulting in days for each individual of each instar in groups 1A, 1B and 1C of Nauphoeta cinerea. Figure III.1 shows the nymphal development of 15 individuals of this species (groups 1A + 1B + 1C). Tables III.5, III.6 and III.7 provide similar information for Henchoustedenia flexivitta (groups 1A, 1B and 1C). Figure III.2 shows the nymphal development of 12 individuals of the latter species (groups 1A + 1B + 1C).

Even though the nymphs in each group came from one family and were all the same age, there was a considerable variation in moulting dates. The smallest variation was two days for the first instar of H. flexivitta (group 1A - Table III.5) and the biggest was 32 days for the eighth instar of N. cinerea (group 1A - Table III.2). This wide variation may suggest some kind of social pressure on the nymphal development.

The variation (gap) in the moulting date increased from the first to the last instar with very few exceptions (Tables III.2, III.3, III.4, III.5, III.6 and III.7) (Fig. III.1 and III.2).

The number of moults varies among the individuals in both species. The results shown in Figures III.1 and III.2 are very similar for both species. The means of moulting date for each instar are very close and both species presented great variability in relation to nymphal development among individuals.

The nymphal development of N. cinerea reared in groups of five individuals took 146 ± 27.4 days for males and 146 ± 55.4 for females. However, with the exception of one male which took 206 days to reach adulthood, the duration of nymphal development for males decreased to 134.6 ± 7.3 days.

The duration of nymphal instars of H. flexivitta following the same experimental conditions took 131.5 ± 32 days for males and 137.5 ± 53 days for females. In both species the females had a larger variation in moulting dates than males.

The first individual to moult in the first instar continues to be the first in all the following instars and generally is a male. It becomes the top ranking in the group when it reaches adulthood. Dominance hierarchy could not be determined for nymphs of either species. However, some nymphs of Nauphoeta cinerea showed overt aggression under special situations such as when they attempt to eat the skin of another individual during the ecdysis processes.

Table III.2 - Nymphal development in N. cinerea (group 1A)

Moults Indiv.	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	Sex
1	17	33	49	65	79	97	119	147	193*	-	F
2	18	39	58	77	95	115	136	154	171	197*	F
3	14	28	46	64	81	99	119	144	176	186*	F
4	20	40	59	78	100	117	134	153	206*	-	M
5	13	26	41	57	72	88	106	132*	-	-	M
Range (days)	7	14	18	21	28	29	30	32			
x̄:	16.4	33.2	50.6	68.2	85.4	103.2	122.8	146	186.5	191.5	
s:	±2.9	±6.3	±7.76	±9.0	±11.7	±12.4	±12.3	±8.9	±16.0	±7.8	

*=adult emergence x̄=mean s=standard deviation

Table III.3 - Nymphal development in N. cinerea (group 1B)

Moults Indiv.	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	Sex
1	15	26	40	56	70	87	107	130*	-	-	M
2	18	32	48	64	82	100	122	148*	-	-	F
3	14	26	37	51	66	82	103	125*	-	-	M
4	17	32	47	69	87	103	119	141*	-	-	M
5	16	30	44	59	77	95	117	138	159	184*	F
Range (days)	4	6	10	18	21	21	19	23			
x̄:	16	29.2	43.2	59.8	76.4	93.4	113.6	136.4			
s:	±1.6	±3.0	±4.6	±7.0	±8.6	±8.8	±8.2	±9.1			

*=adult emergence x̄=mean s=standard deviation

Table III.4 - Nymphal development in N. cinerea (group 1C)

Moults Indiv.	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	Sex
1	26	40	56	75	96	114	133	158*	-	-	F
2	21	35	50	67	84	101	121	147*	-	-	F
3	24	38	55	77	96	113	132	160*	-	-	F
4	24	37	51	66	82	100	120	145*	-	-	M
5	21	38	52	70	88	103	122	147*	-	-	F
Range (days)	5	5	6	11	14	14	13	15			
x̄:	23.2	37.6	52.8	71.0	89.2	106.2	125.6	151.4			
s:	±2.2	±1.8	±2.6	±4.8	±6.6	±6.8	±6.3	±7.0			

Total Groups 1A,B,C:

x̄:	18.5	33.3	48.9	66.3	83.7	100.9	120.7	144.6	181	189
s:	±4.0	±5.2	±6.6	±8.3	±10.1	±10.5	±10.1	±10.1	±18.6	±7.0

*=adult emergence x̄=mean s=standard deviation

The following tables show the number of moults and days in which each moult occurred in groups of five initial individuals of <u>Henchoustedenia</u> <u>flexivitta</u>.

Table III.5 - Nymphal development in <u>H</u>. <u>flexivitta</u> (group 1A).

Moult Indiv.	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	Sex
1	13	26	43	57	78	93	111	139*	-	M
2	13	31	46	69	84	98	112	130	159*	M
3	13	26	46	64	81	99	119	147*	-	M
4	13	28	46	63	80	98	113	132	162*	M
5	15	32	48	68	91	107	124	143	174*	F
Range (days)	2	6	5	11	13	14	13	17	15	
$\bar{x}$:	13.4	28.6	45.8	64.2	82.8	99	115.8	138.2	165	
s:	±0.9	±2.8	±1.8	±4.8	±5.1	±5.0	±5.5	±7.2	±7.9	

*=adult emergence $\bar{x}$=mean s=standard deviation

Table III.6 - Nymphal development in <u>H</u>. <u>flexivitta</u> (group 1B)

Moult Indiv.	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	Sex
1	15	32	48	63	79	96	116	147*	-	M
2	13	30	43	58	73	89	107	135*	-	M
3	18	38	62	(died)	-	-	-	-	-	-
4	18	41	57	79	95	112	128	149	179*	F
5	20	44	(died)	-	-	-	-	-	-	-
Range (days)	7	14	19	21	22	23	21	14		
$\bar{x}$:	16.8	37.0	52.5	66.6	82.3	99.0	117.0	143.6		
s:	±2.8	±5.9	±8.6	±11.0	±11.4	±11.8	±10.5	±7.6		

*=adult emergence $\bar{x}$=mean s=standard deviation

Table III.7 - Nymphal development in <u>H</u>. <u>flexivitta</u> (group 1C)

Moult Indiv.	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	Sex
1	16	33	49	66	82	101	124	154*	-	F
2	18	35	50	66	83	101	124	153*	-	F
3	17	38	55	71	91	118	140	160	189*	F
4	19	37	54	70	88	107	126	146	176*	F
5	19	38	(died)	-	-	-	-	-	-	-
Range (days)	3	5	6	5	9	17	16	14	13	
$\bar{x}$:	17.8	36.2	52.0	68.2	86.0	106.7	128.5	153.2	182.5	
s:	±1.3	±2.2	±2.9	±2.6	±4.2	±8.0	±7.7	±5.7	±9.2	
Total Groups 1A,B,C:										
$\bar{x}$:	16.0	33.9	49.8	66.2	83.7	101.6	120.3	144.6	173.2	
s:	±2.6	±5.4	±5.7	±5.9	±6.4	±8.2	±9.2	±9.2	±11.1	

*=adult emergence $\bar{x}$=mean s=standard deviation

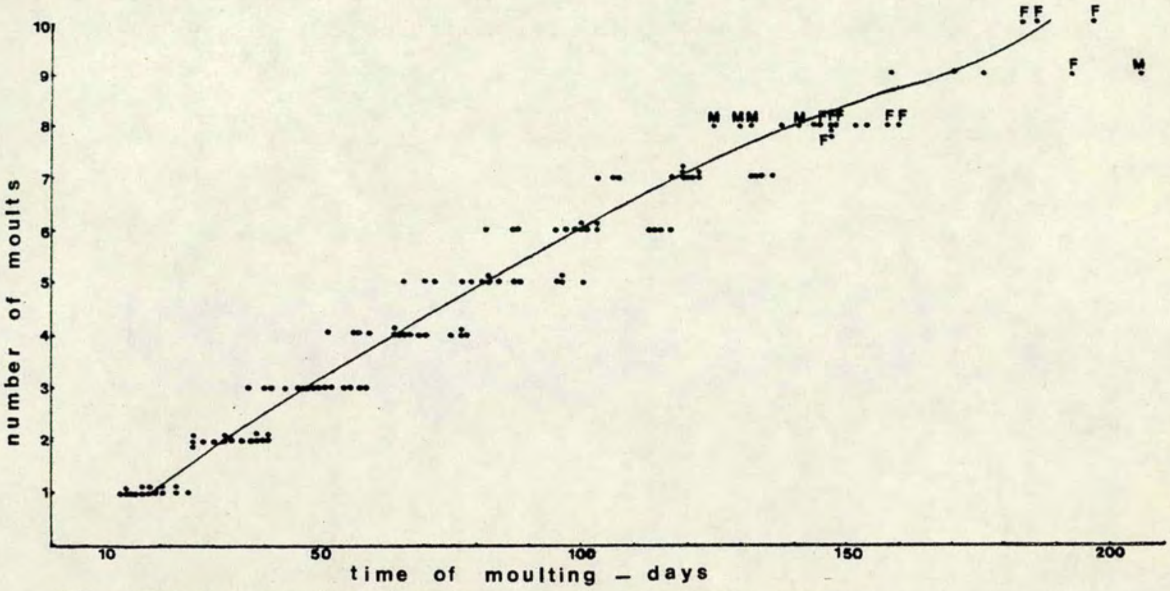

Fig. III.1 - Nymphal development in <u>Nauphoeta</u> <u>cinerea</u>
(n=15)

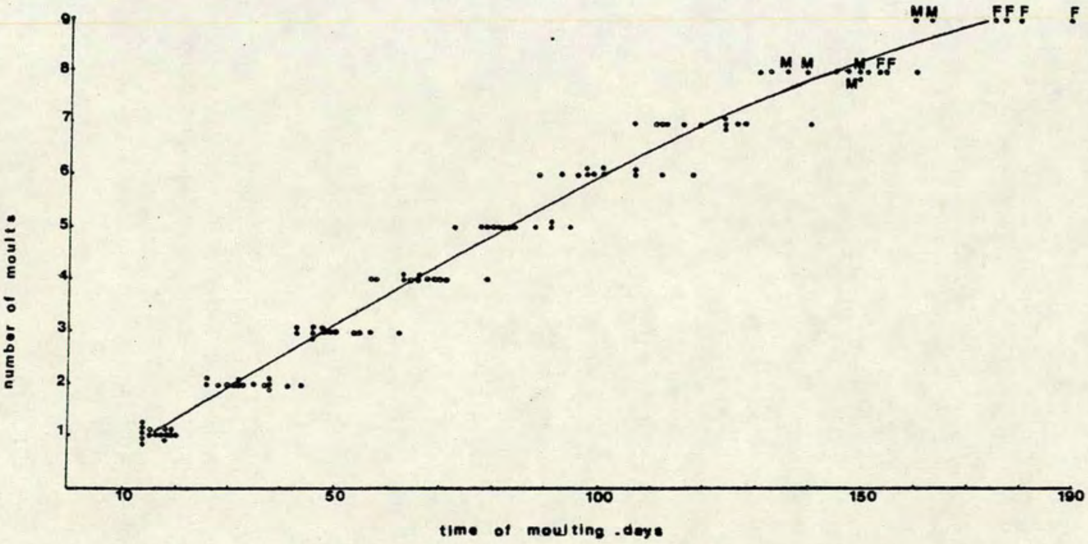

Fig. III.2 - Nymphal development in <u>Henchoustedenia</u> <u>flexivitta</u>
(n-initial=15; n-final=12)

Figure III.3 shows the variation in moulting date for each instar between isolated and grouped individuals (five individuals - groups 1A, 1B, 1C) of Nauphoeta cinerea and Henchoustedenia flexivitta. In N. cinerea the variation increased throughout the successive instars (Fig. III.3). In H. flexivitta there was an increase until sixth instar and then a slight decrease. Both species showed after the third instar smaller variation between moults in isolation than in groups, except in the seventh instar (Fig. III.3). The biggest variation of moulting date for either species in isolation was on the sixth instar.

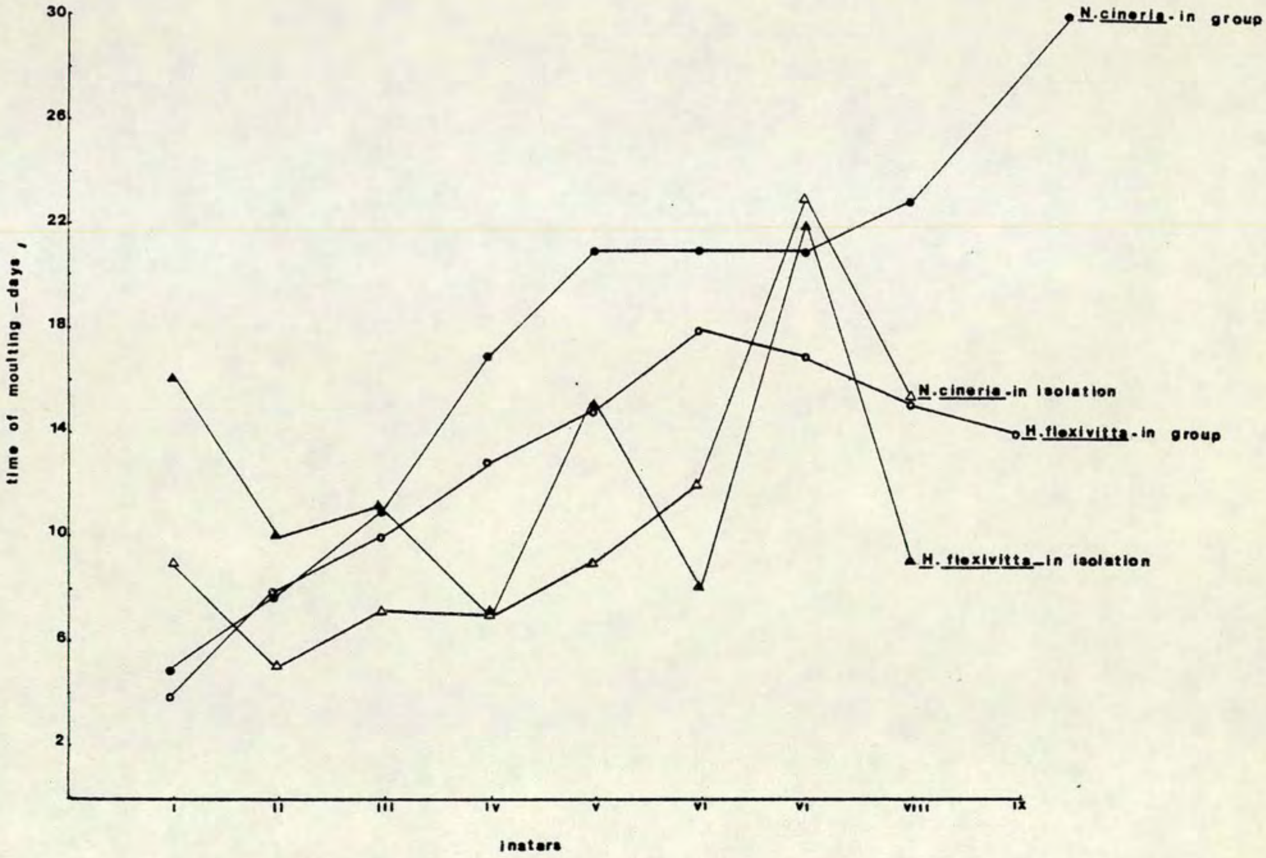

Fig. III.3 - Variation of time of moulting ($\bar{x}$) for each instar between isolated and grouped (n=5) individuals

III. 3.3 - Dominance hierarchy formation

For each group the data were analysed separately. The number of agonistic encounters were counted and the dominance relationships determined from the results of the overt and submissive encounters. One individual was assumed to be dominant over another individual if it engaged in more interactions and won more encounters than its opponents in which there was a clear outcome. Among these cockroach species: Nauphoeta cinerea and Henchoustedenia flexivitta, it is not difficult to determine "winners" and "losers".

III. 3.3.1 - Dominance hierarchy formation in N. cinerea

In group 1A of N. cinerea (Table III.8 and Fig. III.4) there were only two males (individuals 4 and 5); when male 4 had its final moult, the male 5 was 74-days-old and was already established in the group with three females. Even though very few agonistic encounters were observed (Table III.8), male 4 showed submissive behaviour most of the time. Male 5, the first male to moult, was also the dominant in the group (Table III.8 and Fig. III.4). This very low level of aggression probably is due to the age of the oldest male and perhaps because it had already mated with the three females in the group, competition for mating was less.

When there is a big gap in age between the mature male and the younger one, it seems that the onset of fighting in the latter is delayed.

In the following tables (Table III.8 to III.23) the winners of the agonistic encounters are compared in rows, losers in columns. Numbers of encounters occurred are shown in parentheses (W = wins, L = losses).

Table III.8 - Agonistic encounters (2) in *Nauphoeta cinerea* (group 1A)

	M5	M4	W	L
M5		2	2	0
M4			0	2

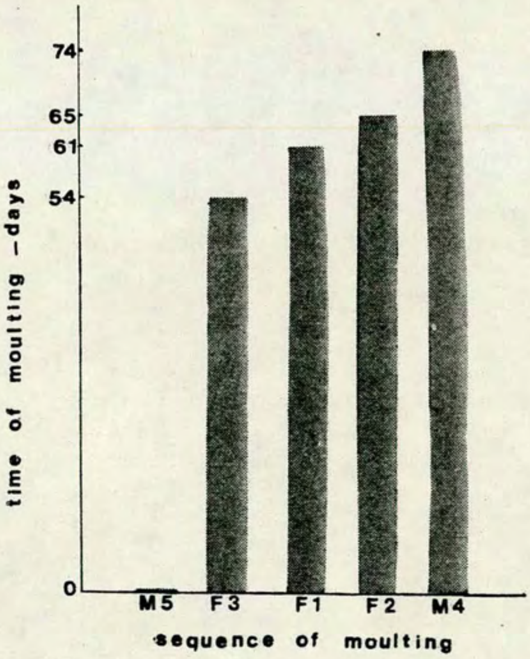

Fig. III.4 - Sequence of the final moults in *Nauphoeta cinerea* (group 1A)

The agonistic encounters in N. cinerea (group 1B) were more numerous than in other groups probably because the final moult variation in days (five days between male `3' and male `1' and 11 days between male `1' and male `4') was not as great as in group 1A (74 days) (Table III.8).

Male `3', the first male to have its final moult in group 1B, was the top-ranking male (Table III.9 and Fig. III.5). The dominance hierarchy which developed among males had the same sequence as adult moulting (Table III.9 and Fig. III.5). Table III.9 (a) shows the agonistic encounters between male `3' and male `1'. Male `3' was clearly dominant over male `1', winning 100% of the encounters. After male `4''s final moult (Table III.9 (b)), the hierarchy did not change and male `1' was dominant over male `4'. The dominance hierarchy repeated the same sequence as adult moulting (Fig. III.5) : male `3' → male `1' → male `4'. Hence, the first individual to moult seems to have great advantages over the others.

Table III.9 - Agonistic encounters in <u>Nauphoeta</u> <u>cinerea</u> (group 1B)

(a) Agonistic encounters (35) before male 4 had its final moult (observations during nine days)

	M3	M1	W	L
M3		35	35	0
M1	-		0	35

(b) Agonistic encounters (22) after male 4 had its final moult (observations during 15 days)

	M3	M1	M4	W	L
M3		9	1	10	2
M1	2		10	12	9
M4	-	-		0	11

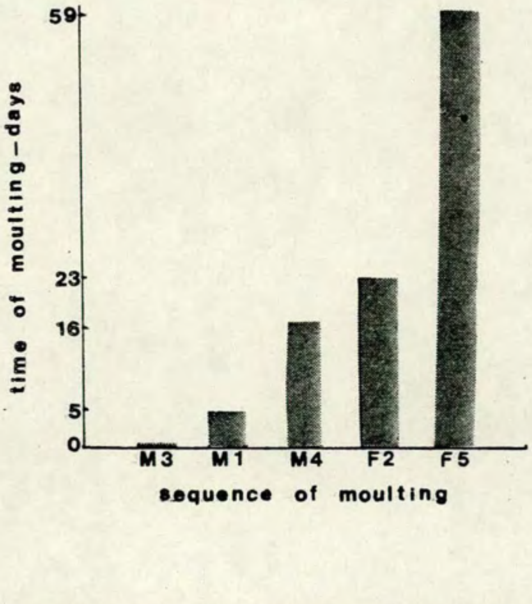

Fig. III.5 - Sequence of the final moults in <u>Nauphoeta</u> <u>cinerea</u> (group 1B)

In group 1C, there were four females and only one male and because of this the group could not be used.

Groups of N. cinerea (1D, 1E and 1F) were set up from sixth - seventh instar, but all individuals in the same group came from one family and were the same age. In all three groups the order of male dominance hierarchy was the same as the sequence of moulting as shown in Tables III.10, III.11, III.12 and Figures III.6, III.7 and III.8.

Ewing (unpublished data) noticed that in a group of eight male nymphs of N. cinerea there was a variation of 15 days between the first animal to have its final moult and the last. She found that the first male to moult became the top-ranking one.

Table III.10 - Agonistic encounters (18) in Nauphoeta cinerea (group 1D)

	M4	M2	W	L
M4		16	16	2
M2	2		2	16

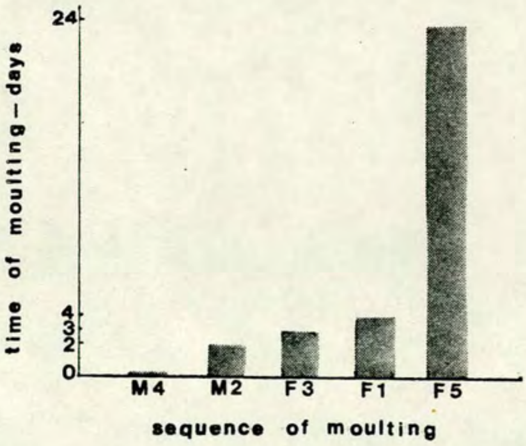

Fig. III.6 - Sequence of the final moults in Nauphoeta cinerea (group 1D)

Table III.11 - Agonistic encounters (19) in <u>Nauphoeta</u> <u>cinerea</u> (group 1E)

	M2	M1	W	L
M2		9	9	0
M1	-		0	9

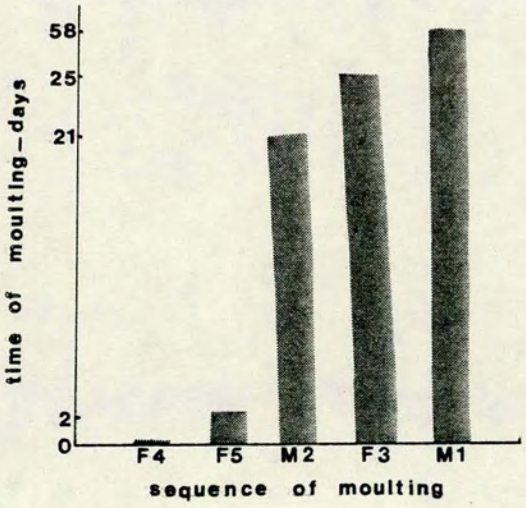

Fig. III.7 - Sequence of the final moults in <u>Nauphoeta</u> <u>cinerea</u> (group 1E)

Table III.12 - Agonistic encounters (22) in Nauphoeta cinerea (group 1F)

	M5	M2	M1	W	L
M5		9	6	15	2
M2	2		5	7	9
M1	-	-		0	11

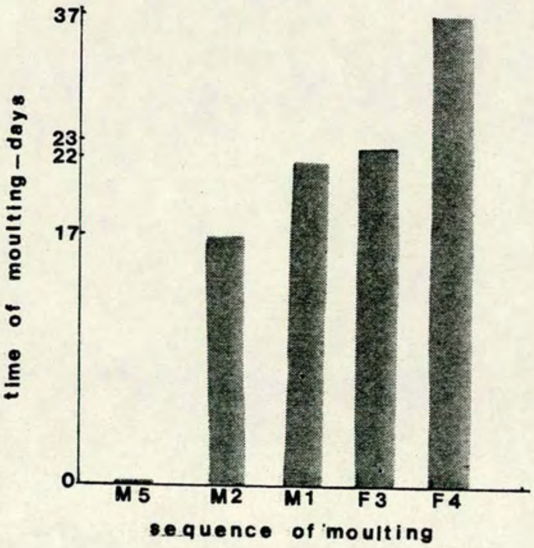

Fig. III.8 - Sequence of the final moults in Nauphoeta cinerea (group 1F)

III. 3.3.2 - Dominance hierarchy formation in Henchoustedenia flexivitta

In Henchoustedenia flexivitta the data suggest a result similar to that obtained for Nauphoeta cinerea. The sequence of males in the adult hierarchy follows the order of adult moulting. In group 1A of H. flexivitta (Table III.13 and Fig. III.9) the group was composed of four males and one female. In group 1B of H. flexivitta (Table III.14 and Fig. III.10) there were two males and one female because one nymph died soon after the second moult and another soon after the third. Both were the last individuals to moult of that instar. The moulted skins (exuviae) were found in the observation cage, but not the bodies of the nymphs.

This suggests that both were eaten by the other nymphs. On the following day the moulted skins had also disappeared. Group 1C of Henchoustedenia flexivitta was not considered because it was composed of four females. One individual died soon after the second moult and the same event occurred as in group 1B.

Group 1D of H. flexivitta (Table III.15 and Fig. III.11) was formed by two males and three females. In all groups the first male to have its final moult became the top-ranking one in the group.

Table III.13 - Agonistic encounters in <u>Henchoustedenia</u> <u>flexivitta</u> (group 1A)

(a) Agonistic encounters (6) before males 2 and 4 had their final moults (observations during 12 days)

	M1	M3	W	L
M1		6	6	0
M3	-		0	6

(b) Agonistic encounters (60) after males 2 and 4 had their final moults (observations during 15 days)

	M1	M3	M2	M4	W	L
M1		22	11	5	38	12
M3	12		6	2	20	22
M2	-	-		2	2	17
M4	-	-	-		0	9

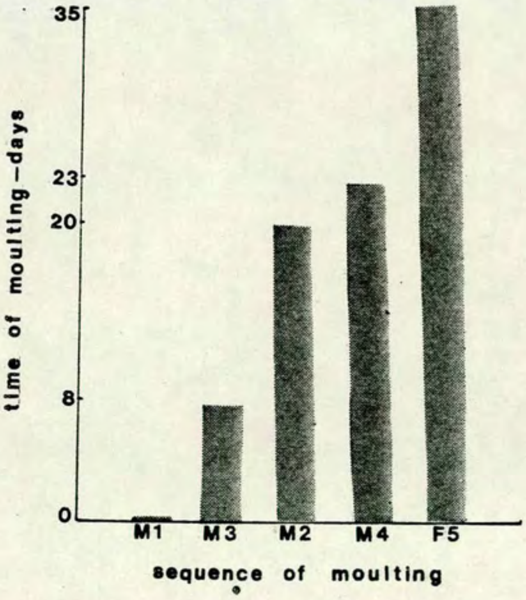

Fig. III.9 - Sequence of the final moults in <u>Henchoustedenia</u> <u>flexivitta</u> (group 1A)

Table III.14 - Agonistic encounters (16) in <u>Henchoustedenia</u> <u>flexivitta</u> (group 1B)

	M2	M1	W	L
M2		16	16	0
M1	-		0	16

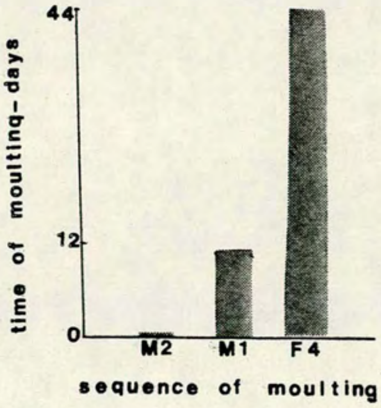

Fig. III.10 - Sequence of the final moults in <u>Henchoustedenia</u> <u>flexivitta</u> (group 1B)

Table III.15 - Agonistic encounters (12) in <u>Henchoustedenia</u> <u>flexivitta</u> (group 1D)

	M2	M5	W	L
M2		12	12	0
M5	-		0	12

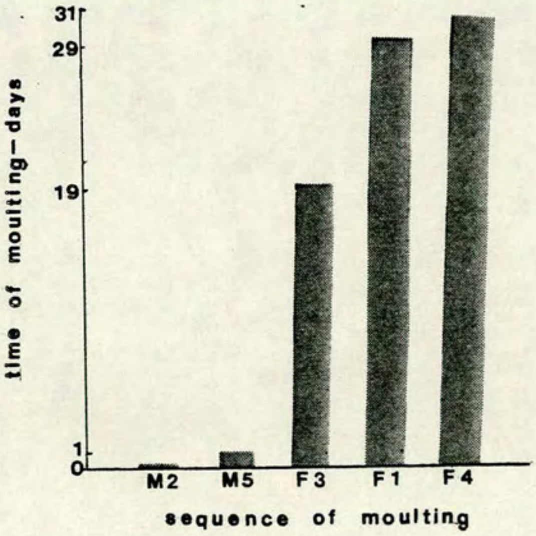

Fig. III.11 - Sequence of the final moults in <u>Henchoustedenia</u> <u>flexivitta</u> (group 1D)

Generally the first male to become adult become top-ranking and the sequence of male moulting is repeated in the male adult dominance hierarchy. When a mature male is paired with an immature male, the former becomes dominant. The same result was found by Gautier (1976, 1979) in Blaberus craniifer males: generally the mature male is dominant over the immature one. He suggested that physiological changes occurring around the imaginal moult period play a role not only on the behaviour of these cockroaches, but also in the behaviour of the partner. The data obtained for Nauphoeta cinerea and Henchoustedenia flexivitta support this.

Immature males seem to sexually attract mature males (first to moult and dominant) because homosexual behaviour is involved during the first days of the interactions. Four to five days later the sexual behaviour of the dominant male decreases and aggresiveness increases. The presence of homosexual behaviour may delay the onset of aggressiveness and alters the spacing patterns.

All groups observed were different in relation to the number of males and females and in the sequence of moulting.

In group 1E of N. cinerea (Table III.11 and Fig. III.7) when the first male moulted there were already two females (19- and 21-days-old) in the group. However, the presence of females did not change the fact that the first male to moult became dominant in the group.

I have not observed groups composed entirely of males which were set up before the final moult, but Ewing (unpublished data) showed the same dominance relationship for groups of N. cinerea males, set up on the sixth instar.

III. 3.3.3 - Dominance hierarchy formation in groups kept in isolation throughout the nymphal instars and/or after the final moult.

Groups of five males which were isolated during the nymphal instars were set up for agonistic behavioural observations. Tables III.16, III.17, III.18 and III.19 show the results obtained for Nauphoeta cinerea. The agonistic encounters were counted and according to the number of winners and losers the dominance relationships were established. Although the top-ranking and the most submissive male in the group could be easily determined the intermediate individuals sometimes did not show a purely linear hierarchy. In group 1 of N. cinerea (Table III.16) all the individuals were mature males, but the youngest individual (male 5) was five-days-old. The dominance hierarchy did not repeat the sequence of the final moult. The youngest individual was the most submissive, but was not the most attacked (Table III.16 (a)). After the introduction of females the original hierarchy was disrupted (Table III.16 (b)). Ewing (1972) showed that introduction of females raised the general level of aggression and disrupted the hierarchy completely. In my results the number of agonistic encounters varies either increasing (groups 2,3) or decreasing (groups 1,4) after the introduction of females. These differences were not significant using X^2 ($p \leq .05$, df=1) for independent groups. It was observed that male aggression was significantly increased directly after the introduction of females. The presence of females stimulated male aggression with a no lasting effect on the following day (observation period).

Table III.16 - Agonistic encounters of adult males of *Nauphoeta cinerea* isolated throughout the nymphal instars (group 1)

(a) before introduction of females (116)

	4	2	3	1	5	W	L
4	-	10	19	12	11	52	10
2	4	-	11	9	7	31	21
3	2	6	-	6	1	15	35
1	3	4	3	-	1	11	30
5	1	1	2	3	-	7	20

(b) after introduction of females (104)

	3	1	2	5	4	W	L
3	-	11	8	8	11	38	21
1	12	-	6	7	10	35	19
2	6	3	-	5	1	15	15
5	2	5	1	-	4	12	23
4	1	0	0	3	-	4	26

Table III.17 shows a similar result for group 2 of *N. cinerea*. In this group all individuals were mature males and the youngest (male 5) was nine-days-old. However, he was still the most submissive and also was not the most attacked. The dominance hierarchy did not show the same sequence as final moulting (Table III.17 (a)). Besides, the dominance hierarchy changed completely after the introduction of females and the number of agonistic encounters increased, but these differences were not significant (Table III.17 (b)).

Table III.17 - Agonistic encounters of adult males of Nauphoeta cinerea isolated throughout the nymphal instars (group 2)

(a) before introduction of females (125)

	1	3	4	2	5	W	L
1	-	25	16	21	13	75	8
3	7	-	6	9	5	27	27
4	0	1	-	5	6	12	26
2	0	1	2	-	4	7	36
5	1	0	2	1	-	4	28

(b) after introduction of females (149)

	3	5	2	1	4	W	L
3	-	16	7	9	19	51	21
5	6	-	11	10	16	43	33
2	11	7	-	5	10	33	22
1	3	6	4	-	3	16	25
4	1	4	0	1	-	6	48

In group 3 of N. cinerea (Table III.18) there were four mature males and one immature male (three-days-old). At the beginning, the three-days-old male was not attacked by any of the other males. It was extremely submissive and never started any agonistic encounters until the introduction of females (Table III.18 (a)). The introduction of females disrupted the hierarchy (Tables III.18 (b)) and increased the number of agonistic encounters. Nothing can be said about general level of aggression because these differences were not significant (Table III.18).

Table III.18 - Agonistic encounters of adult males of Nauphoeta cinerea isolated throughout the nymphal instars (group 3).

(a) before introduction of females (110)

	4	1	2	3	5	W	L
4	-	11	8	12	8	39	18
1	11	-	11	11	6	39	24
2	5	11	-	6	2	24	31
3	2	2	2	-	2	8	29
5	0	0	0	0	-	0	18

(b) after introduction of females (143)

	3	2	5	4	1	W	L
3	-	10	13	9	18	50	17
2	6	-	12	6	13	37	24
5	8	7	-	3	9	27	32
4	3	3	2	-	9	17	21
1	0	4	5	3	-	12	49

Table III.19 shows the results for group 4 of *N*. *cinerea*. In this group there were four mature males and one very immature male (one-day-old). Individual `5' (the youngest) was attacked only twice and showed submission all the time (Table III.19 (a)). Here also the sequence of the dominance hierarchy was not the same as adult moulting. Interestingly, male `5' was the most aggressive one after the introduction of females. The hierarchy was also disrupted after the introduction of females (Table III.19 (b)). The decrease in the number of agonistic encounters after the introduction of females were not significant.

Table III.19 - Agonistic encounters of adult males of *Nauphoeta* *cinerea* isolated throughout the nymphal instars (group 4)

(a) before introduction of females (99)

	2	1	3	4	5	W	L
2	-	11	25	20	2	58	4
1	2	-	6	10	0	18	22
3	2	5	-	10	0	17	31
4	0	6	0	-	0	6	40
5	0	0	0	0	-	0	2

(b) after introduction of females (73)

	5	4	2	3	1	W	L
5	-	12	6	6	11	35	5
4	0	-	3	3	4	10	19
2	3	3	-	2	2	10	18
3	0	2	6	-	1	9	13
1	2	2	3	2	-	9	18

In all groups where nymphs and immature adults were isolated from each other, the dominance hierarchy of the adult males did not repeat the same sequence of the final moulting as happened when groups were set up while they were nymphs. However, in all groups the youngest male was the most submissive and in three cases it was immature.

Perhaps isolation can cause delayed adult maturity as well as retarded nymphal development and in this case nine-days-old could be considered as an immature male. Izutsu et al. (1970) suggested that mutual stimulation accelerates the growth and development of nymphs of Blattella germanica. May be the development of dominance hierarchy occurs while the males are still immature, i.e. in the first days of adult life. Perhaps isolation delays maturity through lack of social contact. To attempt to answer these suggestions the following experiments were set up using nymphs that were reared in groups and with their mother, but isolated singly for different lengths of time after the final moult.

Tables III.20 and III.21 show the results obtained for groups 1 and 2 of N. cinerea. Here the findings are very similar to those already described. In group 1 (Table III.20 (a)) the youngest male (six-days-old) was the most submissive. The hierarchy did not show exactly the same sequence as that of the final moult although it was similar. Here also the introduction of females into the group disrupted the hierarchy and increased the number of agonistic encounters, but the difference was not significant (Table III.20 (b)). Here social deprivation by isolation occurred only after the final moult since the nymphs were reared in groups. Manning & Johnstone (1970) suggested the possibility that the onset of aggressiveness in Nauphoeta cinerea is associated with the activation of the corpus allatum, which is in turn stimulated by activity in the brain, initiated neurally and neuro-humoraly by social contact. They considered contact with another individual as an important factor in the normal development of aggressive behaviour on Nauphoeta cinerea.

Table III.20 - Agonistic encounters of adult males of Nauphoeta cinerea isolated after the final moult (group 1)

(a) before introduction of females (94)

	1	2	4	3	5	W	L
1	-	12	9	8	8	37	8
2	3	-	9	7	8	27	18
4	3	2	-	4	5	14	23
3	1	3	2	-	3	9	21
5	1	1	3	2	-	7	24

(b) after introduction of females (107)

	2	5	4	1	3	W	L
2	-	7	14	12	8	41	18
5	6	-	3	8	10	27	14
4	8	2	-	3	2	15	24
1	3	3	5	-	3	14	28
3	1	2	2	5	-	10	23

In the second group of N. cinerea (Table III.21) the youngest male was five-days-old and again he was the most submissive and least attacked by others (Table III.21 (a)). Individuals `3' and `4' were of the same age (10-days-old) and had very similar numbers of encounters. After the introduction of females (Table III.21(b)) the hierarchy was totally disrupted and the number of agonistic encounters was more or less the same.

Table III.21 - Agonistic encounters of adult males of Nauphoeta cinerea isolated after the final moult (group 2)

(a) before introduction of females (123)

	2	1	3	4	5	W	L
2	-	18	16	10	3	47	15
1	5	-	8	13	8	34	20
3	6	0	-	9	3	18	33
4	2	2	6	-	3	13	38
5	2	0	3	6	-	11	17

(b) after introduction of females (125)

	5	4	1	2	3	W	L
5	-	10	9	6	13	38	19
4	7	-	3	8	9	17	26
1	4	11	-	3	3	21	23
2	4	4	6	-	6	20	26
3	4	1	5	9	-	19	31

Tables III.22 and III.23 show the results for Henchoustedenia flexivitta reared in groups while nymphs and isolated singly soon after the final moult for various lengths of time. In group 1 (Table III.22) all individuals were very young with ages ranging from six to two-days-old. Only male `1' could be considered as mature. He attacked most and won more encounters than any other male.

Individuals 2, 3 and 4 were five and four-days-old. They did not show great differences in the number of encounters won and lost. Individual `5', the youngest (two-days-old) was, again as in Nauphoeta cinerea, the most submissive (Table III.22). The low number of encounters may be explained by the youth age of the participants.

In group 2 of H. flexivitta there were three mature males and two immature (four and one-day-old). Both suffered few attacks (Table III.23) and were submissive all the time. Once again the sequence of hierarchy did not repeat the same sequence as final moult (Table III.23).

Table III.22 - Agonistic encounters of adult males of Henchoustedenia flexivitta isolated after the final moult (group 1)

Encounters (38)

	1	4	3	2	5	W	L
1	-	9	2	3	2	16	9
4	3	-	3	4	0	10	10
3	3	1	-	1	1	6	7
2	2	0	2	-	1	5	8
5	1	0	0	0	-	1	4

Table III.23 - Agonistic encounters of adult males of Henchoustedenia flexivitta isolated after the final moult (group 2)

Encounters (60)

	2	1	3	4	5	W	L
2	-	22	4	2	3	31	19
1	17	-	5	0	0	22	27
3	2	5	-	0	0	7	9
4	0	0	0	-	0	0	2
5	0	0	0	0	-	0	3

The overall results suggest that dominance hierarchy develops from the third day after the final moult. Indirectly, time of moulting determines hierarchy formation in a group as the latter follows the same sequence.

In groups where the individuals were kept in isolation singly during nymphal instars and/or after the final moult dominance hierarchy did not follow the sequence of the final moult. This suggests that social contact among males may play a role in the dominance hierarchy formation by delaying maturity and the onset of aggressiveness. This stimulation (social contact) is more important during the first days after the final moult than during the nymphal instars.

IV. DEVELOPMENT OF SPACING PATTERNS

IV. - DEVELOPMENT OF SPACING PATTERNS

IV. 1. - Introduction

The spatial relationships of individuals in the experimental cages in the laboratory can be observed by considering the position of individuals as points in space. The distribution is random when the presence of one individual has no effect on the spatial position of any other individual and the probability of finding an individual is equal for all points assuming no environmental features more or less attractive. When the individuals are gregarious they are clumped near one another and there will be a higher frequency of areas with no individuals. The distribution is regular when the individuals tend to arrange themselves as far apart as possible. This condition can be expected when individuals are territorial or otherwise actively avoid each other, i.e. require some type of social interaction (Gorton et al, 1979). Clark & Evans (1954)described the spatial-dispersion of animals in nature as regular, random or clumped (i.e. aggregated).

The spatio-temporal dispersion of animals results to a large extent from the direct, and directed, response of individuals to environmental features and to the presence or absence of conspecifics (Brown & Orians, 1970).

According to King (1973) aggregations of animals result from the attraction of individuals to favourable conditions in physically and biotically heterogenous environments, from restricted processes of dispersal, or from social interactions among individuals.

Gregariousness is commonly observed in many species of insects and may be a general phenomenon for Blattaria (Roth & Willis, 1957, 1960), although not many species of this group have been studied. Early observations by Pettit, (1940) and Ledoux (1945) showed gregarious behaviour in *Blattella germanica* and *Blatta orientalis*. Roth & Willis (1960) reviewed all early observations and experiments on cockroach aggregation.

Aggregation pheromone has been demonstrated for many species of cockroaches. The behavioural response of an insect stimulated by the aggregation pheromone is movement toward the pheromone source and/or cessation of locomotion, at least temporarily once the insect has arrived at the source (Shorey, 1973). In *Periplaneta americana* nymphs the faecal-aggregation pheromone acts as an attractant and inhibits locomotion, but tactile stimuli and perhaps other social factors may be involved in this aggregation (Burk & Bell, 1973).

Raisbeck (1976) reported an aggression-dispersal pheromone in *P. americana*. She observed that both males and females produce a substance that stimulates aggression when the cockroaches are prevented from coming into oral contact with their faeces.

In *Blaberus craniifer* and *Eublaberus distanti* the aggregation pheromone is produced by the mandibular glands of all individuals (nymphs and adults) except at moulting time (Brossut, 1970, 1979; Brossut et al., 1974). On the other hand, in several cockroach species the aggregation pheromone is secreted by rectal pad cells into the rectal lumen and then excreted with the faeces without relation to sex or nymphal instar (Ishii & Kuwahara, 1967, 1968; Ishii, 1970; Izutsu et al., 1970; Bell et al., 1972, 1973 and Burk & Bell, 1973).

In some Blaberidae and Blattidae nymphs these faecal-aggregation pheromones are not strictly species-specific, since cross-reactions do occur between closely related species and some species do not aggregate even to their own faeces pheromone (Ishii, 1970; Bell et al., 1972; Roth & Cohen, 1973).

It was suggested that all cockroach species secrete a potential aggregation pheromone, i.e. this function is a primitive characteristic (Bell & al., 1972). They also suggested that perhaps in the evolution of cockroaches some species such as Parcoblatta pennsylvanicus lost their need for an aggregation pheromone.

The spacing-patterns in some cockroach species are related to social organization and vary according to the age, status and sex of the individual (nymphs or adult), e.g. Periplaneta americana (Silverman & Bell, 1979; Rivault, 1982), Blattella germanica (Sommer, 1975) and Periplaneta fuliginosa (Fleet et al., 1978). In migratory locusts, animals reared in crowded situations were much more aggregative than animals reared in isolation which tend to disperse themselves evenly in the environment (Gillet, 1973).

In adult Byrsotria fumigata the animals tend to remain somewhat clumped in one-ninth of the available area, regardless of the size of that area (Breed & Byers, 1979). This work also concluded that this clumping was usually near the dominant male. This type of clumping around a dominant male has also been observed in Nauphoeta cinerea (Smith & Breed, 1982).

Nauphoeta cinerea females and subordinate males are attracted to dominant males. If so, "the subordinate males may be able to exploit the females that are attracted to the dominant". It was suggested that maintenance of an approximate minimum distance from the dominant male rather than complete avoidance of him is an important outcome of this behaviour (Breed et al., 1980).

There are a number of examples of male pheromones that cause females to approach from a distance; such pheromones presumably have the primary behavioural role of bringing the two sexes together for mating (Shorey, 1973). They are found in various species including Nauphoeta cinerea, Leucophaea maderae and Byrsotria fumigata (Roth & Barth, 1964; Roth, 1965; Roth & Dateo, 1966).

Gregarious behaviour has been reported for Nauphoeta cinerea (Roth & Cohen, 1973; Farine et al., 1981; Sreng, 1982). Farine et al. (1981) showed an aggregation pheromone in nymphs and adults of N. cinerea. According to them, two phenomena may explain the lack of gregariousness among adults: the sexual behaviour and the agonistic behaviour among males. They suggested that the establishment of dominance hierarchy and territoriality by agonistic behaviour is linked with the chemical release by the sternal and tergal glands. In their view the gregarious behaviour in Nauphoeta cinerea evolves during nymphal development, increasing from the third instar, reaching the maximum at the fourth to seventh instar and decreasing considerably among the adults.

Although the role of the gregarious pheromone was not studied in the present work, it was suggested by Bell et al. (1972) that all cockroach species secrete an aggregation pheromone and has been demonstrated for many species. Therefore, some discussion about this may be made.

The role of the gregarious pheromone among Blattaria is very difficult to determine. The spacing-relationships are complex and several different factors can be involved. In Cryptocercus (Cleveland & Nutting, 1955) the gregariousness is of vital importance for the transmission of protozoan symbionts. In several other Blattaria gregariousness accelerates the growth and development of nymphs (Landowski, 1938; Pettit 1940; Chauvin, 1946; Willis et al., 1958; Ishii & Kuwahara, 1967; Wharton et al., 1967, 1968; Izutsu et al., 1970). Izutsu et al. (1970) suggested that the growth acceleration in Blattella germanica is caused by mutual stimulation and not by any chemical substances produced by the cockroaches themselves.

In Periplaneta americana the pheromone seems to induce trail-following in other males of the species (Brousse-Gaury, 1975). Generally, the patterns of gregariousness in Blattaria varies with the species, the growth stage and with physiological conditions.

The aim of the set of experiments to be described was to observe spacing-relationships in _Nauphoeta cinerea_ and _Henchoustedenia flexivitta_ throughout nymphal instars and the first days after the final moult, and to relate these, if possible, to behavioural changes.

IV. 2 - Materials and methods

Pregnant females of N. cinerea and H. flexivitta were removed from stock colonies and placed in individual jars (9 cm diameter) until the nymphs hatched.

On the day of hatching five nymphs from the same female were placed in 23x23x10 cm plastic cages for observation. Each cage was provided with five shelters, water-bottle and food. There were three groups of five individuals for each species. (These same groups were used for observations on nymphal development and ontogeny of agonistic behaviour.)

Each animal was code-marked for individual recognition and re-marked as it moulted.

The containers were covered with plastic-net lids and placed over a 2.5x2.5 cm grid with designations of A-I on the x-axis and 1-9 on the y-axis.

The position of each animal in space at any time was recorded in reference to this co-ordinate system (Gorton et al., 1979; Breed & Byers, 1979).

When one cockroach positioned itself in more than one square, it was considered to be in the square containing the greater proportion of its body.

The position of each cockroach in the cage and the distance between it and the others was noted at the beginning and end of each observation period using the co-ordinate system.

The observation period was 30 minutes and observations were made twice a week, throughout the nymphal instars. The observations continued until the last individual to become an adult was 10 days-old. As these groups were set up without previously knowing the sex of the individuals, the sexual composition of the groups differed from each other. In addition, two other replicates of five individuals for each species were used for observations on spacing relationships on adults from "Day 0" until "Day 10".

The adults (males and females) were taken from stock colonies for experimental use on the day of adult emergence (considered as "day 0"), while they were teneral, thus ensuring that they were at the same age.*

The observations on spacing-patterns of adults followed the same method described for nymphs. The individuals were marked and their sexes were known.

The groups differed markedly in relation to sex composition since they were set up according to the availability of teneral animals in the stock-colonies. They were made up as follows:

(1) Nauphoeta cinerea. One group of five males and another with three males and two females.

(2) Henchoustedenia flexivitta. One group of five males and another with two males and three females.

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* When Nauphoeta cinerea adult (n=5) emerges from the final nymphal skin, the wings are totally unexpanded, but after about 15 minutes, they completely cover the abdomen. The process of tanning takes about four to four and a half hours to complete. These two phenomena allow teneral animals to be aged fairly acurately.

In order to analyse the data obtained, the following method was used (Farine et al., 1981). In the nymphs, if all five individuals stayed clumped in adjacent grids and in the same shelter aggregation was considered 100%; the figure decreased according to dispersal of individuals into different shelters until the maximum dispersion (0%) when each individual occupied different shelters and distant grids.

The same system was used for adults, but sex differences were also taken into account.

Three observations on nymphal-spacing patterns were made for each instar in each group. The means were taken and considered in the results.

The observations on adult-spacing patterns for each group were made every other day from "Day 0" until "Day 10". As the differences in time of final moulting among the individuals in groups set up from hatching made the analysis very difficult to do, most of the results of adult-spacing patterns were confined to the replicates.

IV. 3 - Results and discussion

IV. 3.1 - Spacing-patterns in N. cinerea and H. flexivitta nymphs

Figure IV.1 shows the spacing-pattern of Nauphoeta cinerea nymphs in three groups (1A, 1B, 1C). The nymphs show a gregariousness throughout the nymphal instars with a peak at the sixth instar and decreasing afterwards (Fig. IV.1). Comparing the results obtained in this experiment with those obtained by Farine et al., (1981) for the same species (Fig. IV.2) similarities can be seen. However, on Figure IV.2 there is a great increase of gregariousness in the third instar decreasing only after the eighth instar. In the experiments of both the present study and Farine et al. the groups were set up in the same way, i.e. the individuals in the groups were maintained together from the hatching until adulthood. However, Farine et al. (1981) used 40 nymphs in the group and in the present study only five nymphs were observed in each group. In their study Farine et al. did only one observation for each instar and because time of moulting is not synchronized in Nauphoeta cinerea, I supposed that different instars could be mixed, mainly in the last instars because of the large number of nymphs used in that experiment.

Figure IV.3 shows a similar result for the gregarious behaviour of Henchoustedenia flexivitta. The nymphs exhibited gregarious behaviour during the nymphal instars with peaks in some instars, but showed a decrease in the last instars as in Nauphoeta cinerea (Fig. IV.1 and IV.2).

The points in graphs (Fig. IV.1 and IV.3) represent the means of three observation periods for each instar while those of Farine et al. (Fig. IV.2) represent a single observation, perhaps the curve of Fig. IV.2 as opposed to the many peaks of Fig. IV.1 might be explained by the difference on the observational technique.

It was noticed that nymphs of both species frequently moved away from the main group before moulting and stayed separated for many hours, sometimes even for one or two days. In Blaberus craniifer in all instars and in both sexes the gregariousness decreased during the time of moulting, from 72 hours before to 24 hours after. In this species the moulting alters the production of gregarious pheromone (Brossut et al., 1974). The observations described above for N. cinerea and H. flexivitta seem to agree with those for Blaberus craniifer.

Gregariousness has been demonstrated in nymphs of several cockroach species. In Gromphadorhina brunneri (seven instars) the nymphs show a low level of gregariousness during the first three instars, but at the fourth instar, 82% of the nymphs live aggregated, and 100% at the fifth instar and became less gregarious in the last instars (Gerhardt, 1972; Gohovanlou, 1974). On the other hand in Blaberus craniifer the gregariousness increases progressively during the nymphal development and is at its maximum among adults (Brossut, 1970). In Eublaberus distanti the gregariousness is weak during the first three instars and is very strong from the fourth instar onwards (Brossut, 1979). In *Nauphoeta cinerea* and *Henchoustedenia flexivitta* the nymphs show a high level of gregariousness until the sixth instar decreasing in the last instars. (Fig. IV.1 and IV.3).

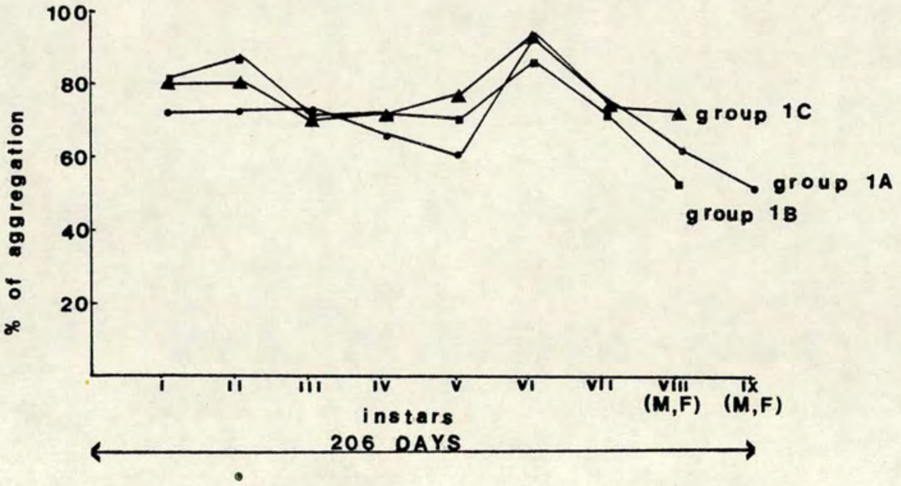

Fig. IV.1 - Gregariousness in *N. cinerea* nymphs

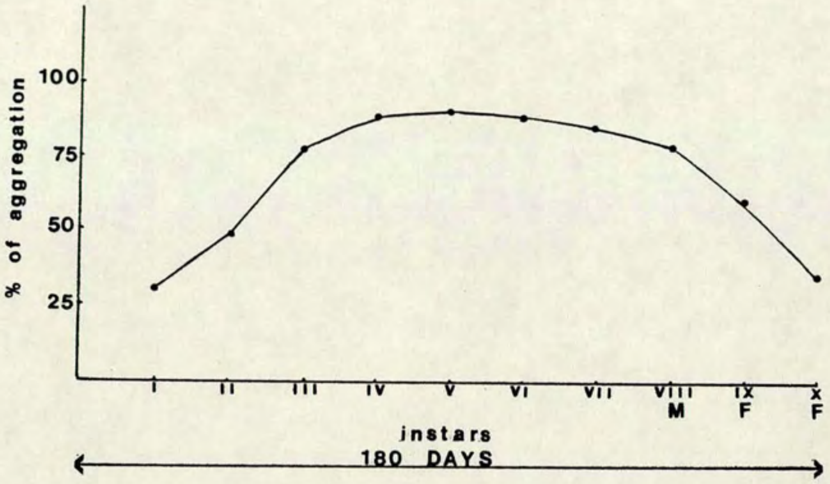

Fig. IV.2 - Gregariousness in N. cinerea nymphs
(After Farine et al, 1981)

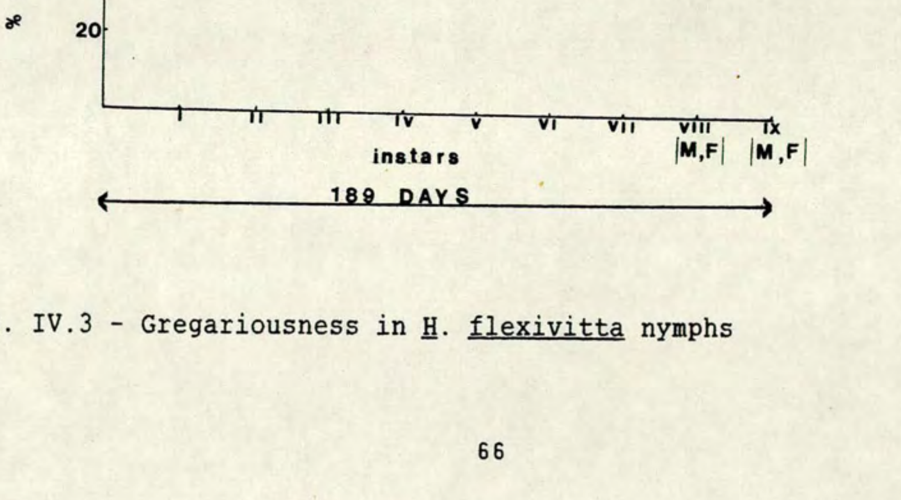

Fig. IV.3 - Gregariousness in H. flexivitta nymphs

IV. 3.2. - Spacing-patterns in Nauphoeta cinerea and Henchoustedenia flexivitta adults

It is well known from laboratory and field experiments in Blaberidae that social status of adult males can be influenced by population size: when the density is low, males own territories which they defend against other males; at intermediate densities there is a hierarchy with dominant and subordinate males; while the males are gregarious when density is high (Ewing, 1972; Ziegler, 1972; Ghovanlou, 1974; Gautier, 1976). However, the spacing-patterns in adult males are much more complex as several factors such as status of the males, agonistic behaviour and homosexual behaviour may interfere in its development.

The spacing-patterns for adults of both sexes of Nauphoeta cinerea (Fig. IV.4) and Henchoustedenia flexivitta (Fig. IV.5) were observed and analysed.

The first intention was to use the same groups which had been observed as nymphs, but this proved impossible since several days elapsed between the final moult of the first and last individual. Therefore, the replicate groups were analysed.

The females of both species were still gregarious (Fig. IV.4 and IV.5) until at least 10 days after emergence. They do not expend energy on agonistic behaviour, as was also shown for Eublaberus posticus by Gorton et al. (1979).

Frequently dominant males and even the submissive individual were observed around the females in both species

Nauphoeta cinerea and *Henchoustedenia flexivitta*.

In some species females can modify the spacing-patterns throughout adult life. In *Blaberus craniifer* the gregariousness decreases notably, during the gestation period, but the females continue to produce the gregarious pheromone (Brossut et al., 1974). One analogous phenomenon is observed in *Byrsotria fumigata* where the pregnant females continue to produce the sexual pheromone but are not receptive (Barth, 1961).

The tendency for *Nauphoeta cinerea* males to space themselves increases after the third day following the final moulting (Fig. IV.4) while in *Henchoustedenia flexivitta* this behaviour increases only after the fourth day (Fig. IV.5). In both species increased spacing coincides with the onset of fighting which does not occur between young immature males less than three-days-old. Thus, young immature males are still sociable. Other groups studied confirmed these results in both species but discussion is reserved until consideration of agonistic behaviour in Chapter five.

In *Nauphoeta cinerea* sometimes sexual behaviour (homosexual) among males modifies the male spacing-patterns as occurred on fifth and sixth days (Fig. IV.4). Homosexual behaviour among *Henchoustedenia flexivitta* males also accurs, but not so frequently as in *N. cinerea*.

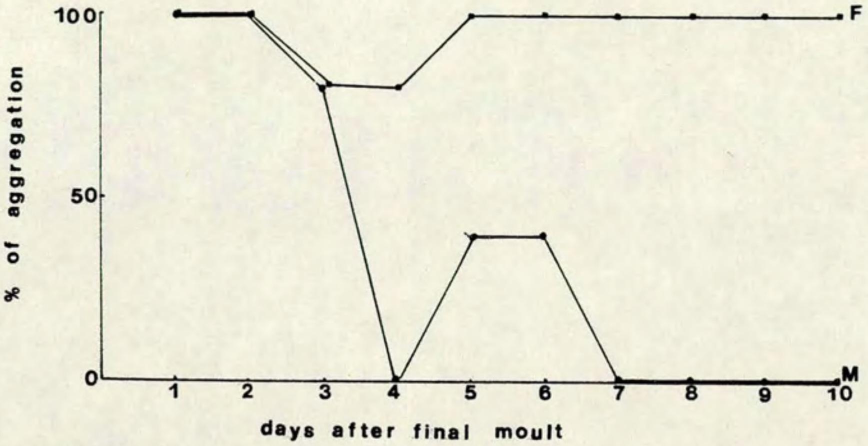

Fig. IV.4 - Spacing-patterns in adults (<u>N</u>. <u>cinerea</u>)

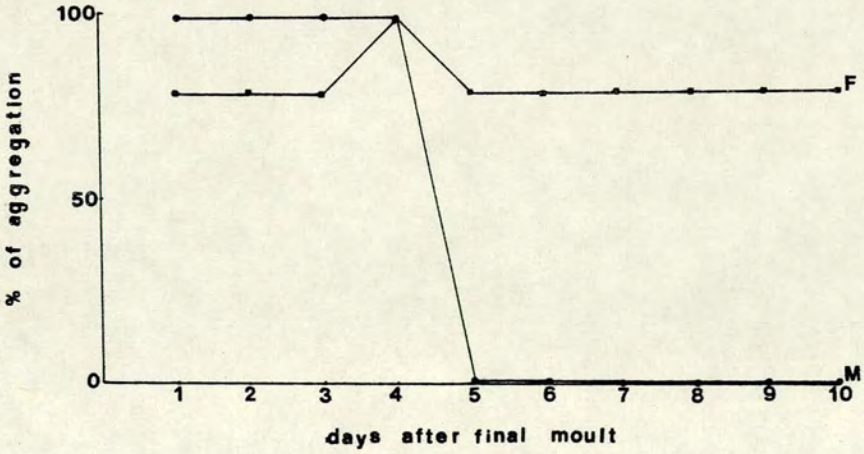

Fig. IV.5 - Spacing-patterns in adults (<u>H</u>. <u>flexivitta</u>)

V. AGONISTIC BEHAVIOUR

V. AGONISTIC BEHAVIOUR

V. 1 - Introduction

Animals may fight members of their own species for a variety of reasons such as competition for food, water, territory or a mate. Individual differences in fighting ability determine who will have priority of access to such resources.

Some species may fight to the death, but in the majority after a brief display, one retreats or shows submissive behaviour. The winner is thus generally determined without great risk of injury.

Dominance-subordinate relationships are found throughout the animal kingdom and occur in many cockroach species. However, a paucity of field work on cockroaches hampers our ability to understand how and why agonistic behaviour operates in nature.

V. 1.1 - Concepts concerning agonistic behaviour

There are several proposed definitions concerning agonistic behaviour and some of them are presented here.

According to Hinde (1970 p.333) it includes all behaviour associated with a struggle among individuals of the same species, i.e. the initial attack, the retaliatory strike, the flight, the pursuit, the threat and the retreat. He also mentions that the term `aggression' refers to the initiation and attack phases of the agonistic behaviour. King (1973) gave the same definition as Hinde (1970) adding that agonistic behaviour is the means by which an animal can most readily alter its social environment. He discussed the role of external environment inducing some of the internal changes varying the expression of agonistic behaviour in different individuals and species. He put aggression into an ecological framework, grouping the effects of aggression as:

1. Reduction of population by mortality and dispersion,
2. Spacing of individuals within the population, and
3. Groupment of individuals in case of female aggression during maternal behaviour.

The intensity of aggression may determine such factors as dispersal patterns and individual breeding success, both of which are often functions of access to limiting resources, including mates (Gorton et al., 1979).

Moyer (1968) had already distinguished six types of aggression: (1) inter-male, (2) territorial, (3) maternal, (4) fear-induced, (5) irritable, and (6) instrumental. Of these, inter-male, territorial and maternal are most easily distinguished in cockroaches. Of the others, fear-induced usually induces fleeing response, while the two other types recognized by Moyer involve a complexity of motivation which is probably beyond the capabilities of a cockroach (Breed et al. 1975).

For the purpose of this chapter, agonistic behaviour is defined as any combative behaviour involving a struggle or contest among individuals of the same species.

V. 1.2. - Agonistic behaviour in cockroaches

Agonistic behaviour has been studied in the Arthropoda with regard to the sequence of acts which characterize encounters, and information theory has been applied to evaluate the quantity of information transferred during interactions (Hazlett & Brossert, 1965; Dingle, 1969; Hazlett & Estabrook, 1974; Steinberg & Conant, 1974; Hyatt & Salmon, 1979).

Agonistic behaviour is widespread among cockroaches and has been investigated since 1964.

Species of cockroaches in which agonistic behaviour has been studied fall into three general categories (Table V.1).

Table V.1. - Categories of social organization in some cockroach species (based in Bell et al., 1979)

Categories of social organization	Species	Author
1. Species with fairly stable dominance hierarchies among males through ritualized dominance and submissive behaviour, some of which are territorial.	Nauphoeta cinerea Eublaberus posticus Blaberus craniifer B. atropos B. colosseus	Ewing (1972) Bell & Gorton(1978) Bell et al. (1978) Gautier & Morvan(1971) Gautier (1976) Gautier, 1974; 1977 Gautier, 1974; 1977
2. Species which are aggressive, but do not form stable dominance hierarchies and are weakly territorial or not territorial.	Periplaneta americana Shavella couloniana	Bell & Sams (1973) Zanforlin et al.(1973) Tourtellot & Breed (1976) Deleporte (1978) Gorton (1976)
3. Species in which agonistic behaviour is not commonly observed or occurs only at low intensity.	Blattella germanica	Breed et al. (1975)

The repertoire of fighting techniques employed by cockroaches is not large, but does include a series from warnings to combat tactics.

Body-jerking and stilt-walking are threat or intention-movements. These appear to be sterotyped agonistic patterns in Periplaneta americana (Roth & Willis, 1952; Barth, 1970) P. brunneae, P. australasiae (Barth, 1970), and Nauphoeta cinerea (Ewing, 1967, 1972). Body-jerking has been observed in Cryptocercus punctulatus (Ritter, 1964); Leucophaea maderae and Byrsotria fumigata (Barth, 1961). Non-aggressive agonistic actions are withdraw and antennation.

The pattern of fighting in Nauphoeta cinerea has been described by Kramer (1964) and in more detail by Ewing

(1967, 1972) and Bell & Gorton, 1978).

The full description and definitions of behaviour patterns in adult males of Nauphoeta cinerea will be given in Materials and Methods of this chapter (Table V.2).

The displays of agonistic action patterns in Blattaria species are very similar. However, there is a wide diversity in the characteristics and intensity of agonism.

Nauphoeta cinerea and Periplaneta americana with similar behaviour patterns are quite distantly related (McKittrick, 1964). Breed et al. (1975) reached the tentative conclusion that agonistic behaviour in Blattaria is probably more related to the ecology of each species than to a phylogenetic progression in the order. This is substantiated by the fact that primitive Blattaria, represented by Cryptocercus display the full repertoire of agonistic behaviour.

While agonistic behaviour patterns are relatively constant throughout the Blattaria species so far studied, there is a high degree of variability in the function of the agonistic encounters. Nauphoeta cinerea establishes dominance and territoriality through agonistic encounters (Ewing, 1972; Bell & Gorton, 1978) but also like Periplaneta americana (Bell & Sams, 1973) uses fighting as a dispersive mechanism increasing spacing-out among males. Blattella germanica uses fighting as a maternal protective and dispersive mechanism. Levels of agonism are higher in B. germanica females carrying oothecae than those that are not (Breed et al., 1975). In Shav'ella couloniana females with oothecae are often targets of biting and cannibalism (Gorton, 1979). Agonistic behaviour may function in defence of territory in Eublaberus posticus (Bell et al., 1978), Blaberus craniifer, B. atropos and B. colosseus (Gautier, 1974, 1976, 1977). Blaberus spp. males defend rock platforms in caves in Trinidad (approximately 3x1m.) for up to several weeks against other males. Gautier suggested that factors such as the number of males, the number of "attractive sites" and entry of females into the area influence territoriality.

Breed et al. (1975) hypothesized that the aggressive interactions in a population constituted communication among members of the population concerning various factors affecting the population, and that the population will respond to this communication.

Theories of animal communication have attempted to explain several facets of inter-individual interactions. Dingle (1973) explored how information is transferred from individual to individual. The use of game theory to show the potential for physical damage in combat is limited were proposed by Maynard-Smith (1974) and Maynard-Smith & Price (1973).

Parker (1974) studied different ways in which individuals might assess the strategy or capability of their opponent.

These theoretical treatments have been quite useful in helping to define ways in which agonistic interactions should be analysed and in focusing study on critical points of theoretical interpretation (Breed & Rasmussen, 1980).

Caryl (1979) points out, as did Maynard-Smith (1974), that there is no advantage to an individual in an interaction in signalling its intentions. However, an exception to this is that many animals obviously signal their fighting abilities by displays. This fact was observed for many species of animals in the laboratory and in the field.

Among cockroach species in which agonistic interactions have been described, the signalling system of Periplaneta americana is relatively unsophisticated (Breed & Rasmussen, 1980).

Many species including Byrsotria fumigata (Breed & Byers, 1979; Bell et al., 1979); Nauphoeta cinerea (Ewing, 1972; Bell & Gorton, 1978) Eublaberus posticus (Bell et al., 1978) and Blaberus craniifer (Gautier, 1979) have well-developed signalling systems that include the capacity for subordinate behaviour and for forming dominance relationships between individuals.

Species of cockroaches, which may be territorial, have rigid hierarchies and strong dominance-subordinate relationships typically have "ritualized" submissive behaviour in which individuals recognize the status of others, and where the subordinates either retreat or submit when they encounter a dominant individual (Ewing, 1967, 1972; Bell et al., 1978; Gautier, 1974; Bell & Gorton, 1978).

In Nauphoeta cinerea the dominant males depend primarily on lunging[*] to maintain their dominant status (Bell & Gorton 1978). The dominant individual in a group could be recognized by the fact that it engaged in and won more interactions than other individuals (Breed et al., 1980).

In Leucophaea submissive behaviour is a small part of the repertoire, and agonistic acts are mainly aggressive. In Periplaneta submissive behaviour is not observed, and a variety of aggressive acts comprised its agonistic behaviour (Bell et al., 1979).

During agonistic interactions in Nauphoeta cinerea, the dominant male assumes positions comparable to those in sexual behaviour; for instance abdominal extension which exposes the glandular surfaces. Sreng (1982) suggested that the chemical signal secreted by the sternal and tergal glands are utilized by the dominant males for maintaining the other males in submission. Submission, as a terminal act, is a behavioural pattern in which the subordinate individual crouches with its antennae drawn posteriorly under the pronotum and wings (Bell et al., 1978). This act is identical to crouching exhibited by unreceptive females of all species of the Blaberus complex in response to male courtship attempts (Barth, 1968a).

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[*] Dominant male N. cinerea accurately turn the body towards a tactile stimulus and then lunge in that direction (Bell, 1978).

Ewing (1972) found that the rank of the Nauphoeta cinerea male (at low population density) did not confer any special mating status. However, Breed et al. (1980) demonstrated that dominant males of N. cinerea mate more often than would be expected by random mating and that females are able to discriminate, by odour, between a dominant and submissive male.

Patterns of agonistic behaviour based on ethometric analyses depend largely on four factors according to Bell et al. (1979).

1. characteristics and frequency of agonistic acts,
2. dominance-submissive interactions resulting in submissive behaviour
3. presence of territoriality and/or dominance hierarchies, and
4. intensity of aggressiveness in acts of a species.

V.1.3. - Ontogeny of social interactions

The ontogeny of social interactions is of interest because it is a system upon which selection can act in different ways at different times in the life of an animal (Gorton & Gerhardt, 1979).

Since agonistic behaviour is important in many species of animals for communicative purposes, it is of interest to study the ontogenetic sequence by which agonistic behaviour patterns develop in an animal which grows through a continuum rather than highly differentiated life cycle stages (Olomon et al., 1976).

Previous studies on the ontogeny of behaviour in insects have dealt with temporal changes in worker function in highly eusocial species (Michener, 1974). Cammaerts-Tricot (1975) has found that young worker ants participate more in recruitment for display in response to a predatory threat, while older workers participate more in direct attack.

One of the first studies on the effect of previous social experience on the development of social interactions in cockroaches was made by Manning & Johnstone (1970). They investigated the effects of early adult experience on the development of aggressiveness in males of the cockroach Nauphoeta cinerea and reached the following conclusions: The development of aggressiveness in male N. cinerea is greatly dependent on experience following the final moult. Contact with another individiual who behaves aggressively leads to delay in development or even to suppression of the response; non-aggressive contact or courtship leads to rapid development of aggressiveness. As these authors pointed out, more behaviour experiment is still required to clarify this situation.

Olomon et al. (1976) studied ontogenetic and temporal aspects of agonistic behaviour in nymphs of Periplaneta americana and concluded that the intensity of agonistic behaviour increases as the animal grows older either through physiological changes or social experience, but they did not separate the ontogenetic changes which were dependent on social experience from those regulated by physiological changes associated with growth. Besides, they did not know the age and precise instar of the cockroaches and so grouped and designated them by approximate size into five observational groups. They observed that very small (young) nymphs seemed to have low levels of aggression, but that aggression increases with age; no sex difference was observed in the intensity of aggression in nymphs. The entire agonistic behaviour pattern is displayed by the nymphs, but actions of high aggressive intensity are observed less frequently than in adults. These results were obtained from 10 minute observations for each of the five groups of Periplaneta americana nymphs.

Deleporte also (1978) investigated the ontogenetic development of interindividual relations in nymphs of Periplaneta americana. Only males were used in these experiments. The animals were raised either in communities of five individuals ("grouped") or completely isolated ("isolated") and he made 15 minute observations on three groups of five individuals in each condition. He concluded that the increase in frequency of aggressive behaviour from hatching to adult was very similar in the "grouped" and "isolated" samples with two main discontinuities (at second to third instar and eighth to ninth instar) where the frequency showed a sudden increase. In the grouped males social contacts caused a delay and a lower frequency in the expression of some aggressive patterns. He also disagreed with the technique used by Olomon et al. (1976) in their study of behaviour ontogeny in which they age animals by size.

The ontogeny of social interactions in Shavella couloniana (asocial, lacking dominance hierarchies or territoriality) and Eublaberus posticus (dominance and at least transient site specificity in males) was investigated by Gorton & Gerhardt, (1979) following the same methodology as Olomon et al. (1976). Their conclusions were that the behavioural repertoire of both species increased with age. Shavella couloniana become more intensely agonistic with age whereas in Eublaberus posticus agonism decreased with age. Encounters tended to become longer with increasing age in Shavella and shorter in Eublaberus.

Cockroaches make an ideal model system for studying aggression because, (a) they display many of the same aggression-related phenomena as other species such as mammalian, herding animals or birds, (b) it is easy to manipulate colonies in the laboratory.

The following experiments were designed to investigate both qualitatively and quantitatively the ontogeny of agonistic hierarchy formation among individuals.

For this: (a) Groups of five newly-hatched individuals of both Nauphoeta cinerea and Henchoustedenia flexivitta were observed until the final moult in order to measure the aggressiveness over time. (b) Pairs of young adult males and groups of two males and one female of both species were established on the day of final moult and observed over a 10-day period in order to determine the onset of fighting, courtship and the establishment of a dominance-subordinate relationship. (c) Pairs of mature and immature males of _N_. _cinerea_ were observed for determining the influence of maturity on the establishment of male hierarchy and on the development of fighting on the younger male. (d) Groups of males of _N_. _cinerea_ and _H_. _flexivitta_ whether isolated before moulting or not, were established some days after the final moult. The main objectives of these observations were to discuss the role of isolation and the influence of male age on the establishment of male hierarchy and on the development of fighting in other males in the group.

V. 2 - Materials and methods

Most of the experimental groups described here had already been used in earlier observations (Table II.1).

The following experimental regimes were chosen to investigate the ontogeny of agonistic behaviour and to measure the aggressiveness throughout the nymphal period (regime 1); to determine the onset of fighting and courtship (regimes 2 and 3); to discuss the influence of maturity on the establishment of male hierarchy (regime 4) and to determine the influence of isolation during nymphal instars and/or after the final moult on the establishment of male hierarchy (regimes 5 and 6).

(1) Three groups of five nymphs of Nauphoeta cinerea and Henchoustedenia flexivitta (groups 1A, 1B, 1C) were set up on the day of hatching.

The observation periods were of 30 minutes duration and the "Focal- animal-sampling" method of Altmann (1974) was used. Observations lasted until 10 days after the last individual reached adulthood. Behavioural acts directed by any individual to any other in the group were considered as potentially reciprocal. Overall and reciprocal activity rates may vary independently. In each group three observation periods were devoted to each individual at each nymphal instar. Each focal individual was sampled at the same time of the day and was observed for six minutes during each observation period. Thus, the total observation period for each individual in each instar was 18 minutes.

(2) Five groups of two males of the same age of each species (N. cinerea and H. flexivitta).

(3) Five groups of two males and one female of the same age of each of N. cinerea and H. flexivitta.

Individuals used in the experimental regimes (2) and (3) were taken from the culture stock on the day of adult emergence and placed in a observation tank (23x23x10cm). They were observed for 36 minutes (18 minutes for each male) when possible for 10 consecutive days.

(4) Five groups of two males (one sexually mature and the other immature) of N. cinerea.

The sexually mature individuals (more than seven days after adult emergency) were taken from a colony in which the nymphs had been reared together since hatching. The immature individuals were removed from the culture stock on the day of adult emergence. The two males were housed in the observation tank (23x23x10cm) on the same day. The observation method followed was the same as in regimes (2) and (3).

(5) Four groups each consisting of five males of N. cinerea were also used for observations of agonistic behaviour. These males had been kept in isolation during the complete nymphal period and for various lengths of time after the final moult. These groups were described in detail in chapter III.

(6) Two groups of five males of each species (N. cinerea and H. flexivitta) which were reared with nymphs of the

same age but kept singly from the day of adult emergence for various lengths of time were also used for observations.

These groups were also described in detail in chapter III. The observational method followed those used in the regimes cited previously.

Using the key punch apparatus connected to an event recorder the following records were made for each age class: number of agonistic encounters, initiator and responder of each encounter, winner and loser of each encounter, number of acts in each encounter, sequence of acts and time of each encounter.

As each key of the apparatus was labelled as one behavioural act, all this information could be gathered together in a paper roll (Esterline Angus, Indianapolis, Ind., U.S.A.) and after that the information were decoded and transcribed in a behavioural observation sheet.

It is appropriate at this point to define the repertoire of agonistic acts which was employed during the study. <u>Nauphoeta cinerea</u> males have the largest and most complex repertoire of agonistic acts of cockroach males of any species (Kramer, 1964; Ewing, 1967, 1972; Bell & Gorton, 1978); these are listed and defined in Table V.2 which is modified from Bell & Gorton (1978) who in turn based his work on the descriptions of Ewing (1967, 1972, 1973).

Table V.2 - Definitions of agonistic acts encountered in adult males of <u>Nauphoeta cinerea</u>

1. <u>Approach</u> (Ap) - One individual moves decisively and directly toward another. Some encounters can be initiated by an immediately preceding act such as antennate or lunge.

2. <u>Antennate</u> (An) - One individual antennates another.

3. <u>Step on</u> (S.o.) - One individual puts its forelegs over the abdomen of another. This act can last for several minutes and is described for the first time from this study.

4. <u>Butt</u> (Bu) - One individual executes a quick thrust with the pronotum against the body of another.

5. <u>Kick</u> (K) - Execution of a quick leg extension.

6. <u>Lunge</u> (L) - Quick forward running of one individual toward another, terminating in contact.

6.1. <u>Grapple</u> (G) - One individual lunges at another and the executor may attempt to grip the other dorsally with its legs.

6.2. <u>Bite</u> (Bi) - Use of mandibles by one individual against another.

7. <u>Stilt</u>-posture (S.p.) - An individual elevates its body off the substratum, especially with its forelegs. While in stilt posture the animal may jerk, extend its abdomen with tip directed upwards, or stridulate.

7.1. <u>Jerk</u> (J) - Forward, backward or sideways vibration of low amplitude and high frequence.

7.2. <u>Abdominal extension</u> (A.e.) - The abdomen is extended exposing the intersegmental membranes; the abdomen tip is arched upward (referred to as threat posture by Ewing, 1967).

7.3. <u>Stridulation</u> (S) - Sounds produced by rubbing the lateral ventral margins of the pronotum against the anterior costal vein (Hartman & Roth, 1967).

8. <u>Crouch</u> (C) - Submissive act executed by lowering the body against the substratum with legs tucked beneath the wing margins; antennae are usually positioned laterally at about 60° to the longitudinal body-axis.

8.1. <u>Climb</u> (Cl) - Dominant individuals climb on to the abdomen of other individuals.

9. <u>Does Nothing</u> (D.n.) - An individual appears not to perform any behavioural acts. This category includes, however, short-distance movements and turning of individuals.

This category was not considered during the analysis of the results.

10. Withdraw (W) - When an individual leaves the site of an encounter after the other individual involved has submitted or done nothing.

11. Retreat (R) - One individual decamps at the termination of an encounter which does not involve submission or truce.

12. Truce (T) - Termination of an encounter which ends with both individuals spaced within antennal contact of each other and with no further agonistic acts by either antagonists.

All the agonistic acts listed in Table V.2 above were recorded during interactions among males of *Nauphoeta cinerea*, while males of *Henchoustedenia flexivitta* showed almost the same repertoire.

To facilitate analysis five levels of apparent intensity of agonistic interactions were distinguished (Table V.3). The levels recognized were modified from Bell & Sams (1973), Olomon et al. (1976), Gorton (1979) and Gorton & Gerhardt (1979).

Table V.3 - Ordinal scale of levels of apparent intensity of agonistic interaction

1. Encounters in which the major elements are antennation, step-on, truce, withdraw or retreat.
2. Encounters in which the major elements are threat or intention movements (stilt posture, jerk or climb).
3. Encounters in which the major elements are lunging, grappling, kicking or biting demonstrated by one animal.
4. Encounters in which the major elements are biting, grappling or kicking demonstrated by both animals.
5. Encounters in which the major elements are biting, grappling or kicking demonstrated by both animals as they turn in a tight circle

V. 3 - Results and Discussion

V. 3.1 - Ontogeny of agonistic acts in nymphs of *Nauphoeta cinerea*

The first analysis investigated the agonistic acts frequencies in each instar for each individual for the three groups (1A, 1B, 1C) of *Nauphoeta cinerea*. Eight individual tables were made for each group (one for each instar). Frequencies of acts in these tables were very small. In spite of grouping some acts together, and some animals (e.g. two females), or dropping an animal if it did almost nothing, the frequencies were still very low in these individual tables. Thus, the Friedman two-way analysis of variance by ranks was used to compare behavioural patterns of different individuals within groups after lumping some acts together or dropping the "category" if it did not occur for any individual.

In group 1A, only in the fourth instar did the Friedman-test ($X_r^2=10.5$; n=5; k=4) show significant ($p \leq .05$) differences in the behaviour patterns among individuals while in group 1B a significant result was obtained in the first instar ($X_r^2=9.42$; $P \leq .05$) and in group 1C, in the first and eighth instars ($X_r^2=9.78$ and 10.62 respectively, $P \leq .05$). These differences show that there was not a consistent variability pattern among individuals within groups. Considering the three groups in group 1A (three females and two males) nymphs showed differences in the fourth instar, in group 1B (two females and three males) the differences were in the first instar while in group 1C (four females and one male) the nymphs were found to be different in the first and in the last instars. Twenty-four individual tables were analysed and significant differences were found in only four in a variable pattern. Moreover as the groups had different sex compositions analysis was very difficult.

As the differences showed no consistent pattern, I considered it justifiable to lump together the individuals as one group for latter analysis.

In the three groups (1A, 1B, 1C) of N. cinerea there were six males and nine females. The two categories were lumped together and the frequencies of agonistic acts in each instar were analysed using X^2 from the third instar (see Appendix V.2). The results showed significance ($P \leq .05$) only in the sixth instar (X^2=17.84; df=4). This result may be explained due to increase in proportion of aggressive acts when one male nymph (group 1A) attempted to eat the skin of another during ecdysis and this was perhaps only part of feeding behaviour. Based on that, the results suggest that male and female nymphs in N. cinerea have similar behaviour patterns. Olomon et al. (1976) observed that there was no sex difference in the intensity of aggression in the nymphs of Periplaneta americana.

The three groups (1A, 1B, 1C) of N. cinerea were lumped together to give a total of 15 nymphs (six males and nine females) in Table V.4. The Friedman-test was used [n=3 (groups); k=5 (agonistic acts)] to compare the three groups. The test was made for each instar separately. Aggressive acts occurring at very low frequencies throughout the nymphal instars were lumped together and labelled as "aggressive acts". These lumped acts were: butt, bite, kick, jerk, climb and stilt posture. The terminating acts such as truce and retreat also were lumped together for analysis. Non-aggressive acts such as approach, antennate and step-on were analysed separately as their frequencies were very high in all instars. The results for each separate group and for the Friedman-test are given in Appendix V.3. The results were significantly different ($P \leq .05$) in the first [($X_r^2=10.74$; n=3 (groups); k=5 (acts)] in the seventh ($X_r^2=9.05$, n=3; k=5) and in the eighth instar ($X_r^2=8.72$; n=3; k=5). The differences were not significant from the second to the sixth instar. So, it may be assumed that in most instars the behaviour of nymphs is similar.

Nymphs of N. cinerea in the first three instars had 10 acts in their behavioural repertoire: approach, antennation, step-on, butt, kick, stilt-posture, jerking, climb, truce and retreat. Of these acts, butt, kick, jerk, climb and retreat were rare, occurring with a very low proportion.

Nymphs from the fourth instar added only one act to the repertoire: bite which occurs at low frequencies or is absent in some later instars. The only exception occurred in the sixth instar where bite had a sudden increase in proportion. This act was not common and the increased proportion was due to one nymph attempting to eat the skin of another during ecdysis. I could not decide if these acts were aggression behaviour or if they were only part of feeding; however, I have concluded that it was perhaps the latter since the proportion decreased in later instars. Interestingly, the biting nymph was a male and the first to moult; it later became the dominant individual in this group. No new acts were added after the fourth instar and the proportions of most acts were approximately the same throughout the nymphal instars (Table V.4).

Individual acts demonstrated differing patterns. The frequency of antennation was very high in the first five instars, decreasing subsequently.

This may be due in part to social experience. Approach frequency decreased in the eighth instar compared to the seventh (Table V.4), but because the proportion remained the same, this could be explained as due to increase in encounter length, since in the seventh instar the mean of encounter length was 20 seconds and in the eighth the mean was 60 seconds. Means of encounter lengths were extremely variable throughout the nymphal instars of N. cinerea.

Step-on increased in frequency throughout the nymphal instars reaching peaks in the seventh and eighth instars. From the sixth instar step-on supplanted antennation in frequency and proportions (Table V.4).

Each instar of N. cinerea (Table V.4) was compared to the next older instar using X^2 ($P \leq .05$). Significant differences were found only when fifth instar was compared to sixth instar ($(X^2)=13.82$; df=4). Although agonistic acts frequencies varied between the fifth and sixth instars, in general little variation was noted between instars.

Table V.4 - Frequencies and (proportion) of agonistic acts in each instar of Nauphoeta cinerea nymphs

Instars:	I	II	III	IV	V	VI	VII	VIII	Total
Acts:									
Approach	37 (.287)	20 (.290)	24 (.264)	31 (.287)	30 (.294)	44 (.333)	66 (.340)	40 (.330)	292 (.309)
Antennate	53 (.411)	24 (.348)	30 (.330)	34 (.315)	32 (.314)	20 (.151)	21 (.108)	19 (.157)	233 (.246)
Step-on	11 (.085)	6 (.087)	12 (.132)	15 (.139)	15 (.147)	25 (.189)	45 (.232)	34 (.281)	163 (.172)
Aggressive	5 (.040)	6 (.086)	10 (.110)	12 (.110)	8 (.078)	26 (.198)	32 (.164)	11 (.090)	110 (.117)
Terminating	23 (.178)	13 (.188)	15 (.165)	16 (.153)	17 (.167)	17 (.129)	30 (.155)	17 (.141)	148 (.156)
Total	129	69	91	108	102	132	194	121	946

V.3.2 - Ontogeny of agonistic acts in nymphs of Henchoustedenia flexivitta

Frequencies of acts for individuals and instars of the three groups (1A, 1B, 1C) of Henchoustedenia flexivitta were analysed. The Friedman two-way analysis of variance by ranks was used after lumping some acts together (see Appendix V.4). The results showed significant differences ($P \leq .05$) in group 1A (n=5: four males and one female; k=5) for the third ($X_r^2=14.4$), fifth ($X_r^2=9.44$), sixth ($X_r^2=14.2$) seventh ($X_r^2=9.48$) and eighth instars ($x_r^2=13.2$). In group 1B (n=3: two males and one female; k=4) the differences were not significant for any instar whilst in group 1C (n=4 females; k=4) the results showed significance only for the fifth instar ($x_r^2=9.9$). These results did now show any consistency with specific behaviour patterns. For group 1A, it may be suggested that there were differences in behaviour patterns among individual nymphs from the third instar. However, this cannot be said for groups 1B and 1C. Perhaps the number of males in the group could influence the variability of behaviour pattern among individual nymphs. As the differences showed no consistent pattern, individuals were lumped together for later analysis.

In the three groups (1A, 1B. 1C) of Henchoustedenia flexivitta there were six males and six females. The sexes were lumped together and the frequencies and proportions of acts performed were analysed. The data were analysed after grouping all the aggressive and terminating acts (X^2) and Wilcoxon Matched Pairs - sign ranked in the eighth instar). The differences were not signficant ($P \leq .05$, df=4). Throughout the nymphal instars male and female did not show marked differences in the behaviour pattern (for the raw data and tests see Appendix V.5).

The most frequent acts for both sexes were: approach, antennate, step-on and retreat. In relation to the aggressive acts the most frequent were climb followed by stilt-posture. Biting and jerking were not observed in either sex after the sixth instar.

The results in Table V.5 represent three groups consisting of five, four and three individuals of Henchoustedenia flexivitta, (for the raw data and tests see Appendix V.6.). All three groups had the same behaviour pattern as the differences between them were not significant (X^2, df=6 and Friedman-test; $P \leq .05$). Tests were carried out for each instar separately following the same technique as for Nauphoeta cinerea. The three groups (1A, 1B, 1C) of H. flexivitta were lumped together and considered in Table V.5 as only one consisting of a total of 12 individuals (six males and six females).

H. flexivitta had 11 acts (see Appendix V.3) in their behavioural repertoire throughout the nymphal instars, some of which occurred at very low frequencies or were absent in specific instars. Only four acts occurred at considerable frequencies: approach, antennate, step-on and retreat (Table V.5). Individual acts also demonstrated differing frequency patterns as in N. cinerea. Some clear agonistic acts like bite and jerk which had occurred at very low frequency in the first six instars did not appear in the seventh and eighth.

As nymphs of both species were always clumped, observation of some acts such as antennate and step-on could be missed. Therefore these acts could possibly have a higher frequency than recorded particularly in the early instars.

Most of the nymphs of both species in different instars used simple, usually non-aggressive acts in their encounters such as approach, antennate, step-on and retreat/withdraw (Tables V.4 and V.5).

The higher activity frequency peaks (Table V.5) were in the fourth, fifth and sixth instars decreasing markedly in the seventh and eighth. The mean durations of the encounters were very variable increasing from nine seconds in the first four instars to 105 seconds in the eighth instar. This fact may suggest that interactions among individuals did not decrease, but the encounters tended to be longer. A similar phenomenon occurred in the of Nauphoeta cinerea nymphs.

Each instar of H. flexivitta (Table V.5) was compared to the next older instar (X^2, $P \leq .05$; df=4) and no differences were found. Thus, these differences in activity frequency were not significant.

Table V.5 - Frequencies and (proportions) of agonistic acts in each instar of Henchoustedenia flexivitta nymphs

Instars:	I	II	III	IV	V	VI	VII	VIII	Total
Acts: Approach	35 (.265)	41 (.299)	53 (.310)	84 (.316)	79 (.307)	77 (.333)	47 (.345)	19 (.333)	435 (.314)
Antennate	34 (.257)	28 (.204)	31 (.181)	33 (.124)	38 (.148)	30 (.130)	13 (.095)	7 (.123)	214 (.154)
Step-on	24 (.182)	27 (.197)	41 (.240)	69 (.259)	51 (.198)	65 (.281)	42 (.309)	13 (.228)	332 (.239)
Aggressive	17 (.127)	23 (.167)	25 (.147)	32 (.119)	33 (.127)	21 (.092)	17 (.125)	8 (.140)	176 (.127)
Terminating	22 (.166)	18 (.131)	21 (.123)	48 (.180)	56 (.217)	38 (.164)	17 (.125)	10 (.176)	230 (.166)
Total	132	137	171	266	257	231	136	57	1387

The behavioural repertoire of Nauphoeta cinerea and Henchoustedenia flexivitta remains more or less the same throughout the nymphal stages, and this contrasts strongly with the results obtained for Shavella couloniana and Eublaberus posticus where the repertoire increased with age (Gorton & Gerhardt, 1979). However, in Periplaneta americana (Olomon et al., 1976) the entire repertoire is displayed by the nymphs which is similar to the results obtained for N. cinerea and H. flexivitta, but actions of high aggressive intensity in nymphs are not observed or less frequently than in adults.

In N. cinerea and H. flexivitta the nymphs still clumped throughout the nymphal instars which might increase tolerance to conspecific contact and mediate the very low level of aggression among nymphs.

There is no dominance hierarchy among nymphs of either species and each individual without regard to sex or instar has an equal a priori access to resources.

Agonistic behaviour may be part of the repertoire of socially inexperienced, newly emerged individuals. I fully agree with Olomon et al., (1976) when he suggests that the ontogenetic development of agonistic behaviour in cockroaches may simply be preparation of motor patterns used by adults, analogous to play behaviour observed in mammals.

V. 3.3 - Agonistic behaviour in Nauphoeta cinerea and Henchoustedenia flexivitta nymphs

The ordinal scale for agonism was used to quantify agonistic encounters based on the description of Table V.3 (Section V.2). No agonistic encounters on levels 4 and 5 were observed (Table V.3) in nymphs of either species.

Table V.6 shows the frequency and percentage distribution of intensity of level of aggressiveness and the mean level of aggressiveness for each instar of N. cinerea. It was found that in every instar encounters were of a very simple nature (level 1), with more than 60% comprising acts such as approach, antennation, step-on and terminating acts. In the first instar 92% of the encounters were at level 1. Proportions of the encounters varies in each instar. Nymphs in the sixth and seventh instars presented a mean level of agonism greater than any other instars (Table V.6 and Fig. V.1). The standard deviation was used to show high variability (Table V.6). Proportions of encounters in each level on the fifth instar were compared with those of the sixth instar ($X^2=7.29$, df=2) the differences were found to be statistically significant ($P \leq 05$) (Fig. V.1).

Another method* was used for measuring the increase of aggressiveness over time for each of the 15 individuals. Then these measures of aggressiveness were tested using Wilcoxon-signed-rank; individuals were used instead of matched pairs. The results for N. cinerea (N=15 individuals; T=8.5) show that in fact there was an increase of aggressiveness over time. According to this method, N. cinerea nymphs increase the level of aggressiveness over time (first to eight instar). In Periplaneta americana (Olomon et al., 1976; Deleporte, 1978) and Shavella couloniana (Gorton & Gerhardt, 1979) the nymphs also became more intensely agonistic with age, but in Eublaberus posticus (Gorton & Gerhardt, 1979) agonism decreased with age. Analysis of increase of aggressiveness over time for each separate individual seems to be a good measure to detect the real development of agonism.

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* The aggressiveness (Xij) for each animal (j) at time i (=instars I-VIII) was determined (=no. of encounters of level 1 at time i x 1 + no. of encounters of level 2 at time i x 2 + no. of encounters of level 3 at time i x 3).

The measure of increase of aggressiveness over time for animal j is: $mj=(X_1j \times -7 + X_{2j} \times -5 + X_3j \times -3 + X_4j \times -1 + X_5j \times 1 + X_6j \times 3 + X_7j \times 5 + X_8j \times 7)$

Table V.6 - Frequencies and (percentage) levels of agonism for each instar of Nauphoeta cinerea

Instars:	I	II	III	IV	V	VI	VII	VIII	Total
Levels:									
1	49 (92.5)	28 (84.8)	37 (82.3)	42 (82.3)	40 (85.1)	43 (66.1)	52 (62.7)	38 (79.2)	329 (77.4)
2	3 (5.6)	3 (9.1)	6 (13.3)	1 (2.0)	4 (8.5)	5 (7.7)	10 (12.0)	3 (6.2)	35 (8.2)
3	1 (1.9)	2 (6.1)	2 (4.4)	8 (15.7)	3 (6.4)	17 (26.2)	21 (25.3)	7 (14.6)	61 (14.4)
Total (N)	53	33	45	51	47	65	83	48	425
Mean level	1.09± 0.35	1.21± 0.54	1.22± 0.52	1.33± 0.73	1.21± 0.54	1.60± 0.87	1.62± 0.86	1.35± 0.72	

Table V.7 shows the result obtained for Henchoustedenia flexivitta using the same method of analysis.

In H. flexivitta in each istar the encounters at level 1 represented more than 50% of the total and reached 79% on the sixth instar (Table V.7).

In H. flexivitta the lowest mean level of agonism was in the sixth instar (Table V.7 and Fig. V.1) in contrast to Nauphoeta cinerea where mean levels were greatest in the sixth and seventh instar (Table V.6 and Fig. V.1).

H. flexivitta (Table V.7) performed 22% more encounters than N. cinerea (Table V.6). The frequencies of encounters on level 3 were very similar 61 (14.4%) in N. cinerea and 62 (11.4%) in H. flexivitta.

Comparisons of frequency of encounters at level 2 in N. cinerea (35-8.2%) and H. flexivitta (106-19.4%) shows that they were more frequent in the latter species.

In N. cinerea the highest percentage of encounters at level 2 occurred at the third instar (13%) and the lowest

(2%) in the fourth instar (Table V.6). In H. flexivitta the lowest percentage of encounters at this level was also at the fourth instar (12.5%) but the highest was at the eighth instar (40%) (Table V.7).

In H. flexivitta performance of acts such as stilt-posture, jerk, and climb was more frequent than in N. cinerea, and this was responsible for such variation in frequency of encounters at level 2.

Measures of increase of aggressiveness over time were made for H. flexivitta following the same method used for N. cinerea. The result (T=16; N=12) shows that there is no increase of aggressiveness over time in this species. The variation seen on Fig. V.1 is not significant. This result suggests that H. flexivitta maintains approximately the same level of agonism throughout the nymphal instars or at least the aggressiveness is not increasing with age as in N. cinerea.

Comparing the mean level of aggressiveness for both species (Tables V.6, V.7 and Fig. V.1) by using Wilcoxon matched-pairs signed-ranks test (N=8 [no. of instars]; T=8.5), the differences did not show any significance. However, when the proportions of different levels of agonism were tested (X^2) (Totals of Tables V.6 and V.7) the result showed significant differences between them ($X^2=23.82$, df=2, $P \leq .05$).

It appears that a measure of agonism based on mean level of aggressiveness may not be reliable. The use of different methods to measure agonism and its increase over time would yield better results. According to the analysis of total number of encounters during nymphal instars and the proportions of encounters at three different levels of agonism, H. flexivitta apparently is more agonistic than N. cinerea.

Probably this difference is not due to the mean level of agonism but to the differences in frequencies of encounters, especially at level 2 (Tables V.6 and V.7).

Table V.7 - Frequencies and (percentage) of levels of agonism for each instar of Henchoustedenia flexivitta

Instars:	I	II	III	IV	V	VI	VII	VIII	Total
Levels: 1	35 (66.1)	40 (67.8)	45 (66.2)	77 (74.0)	56 (64.4)	79 (79.0)	32 (65.3)	13 (52.0)	377 (69.2)
2	13 (24.5)	12 (20.3)	20 (29.4)	13 (12.5)	16 (18.4)	14 (14.0)	8 (16.3)	10 (40.0)	106 (19.4)
3	5 (9.4)	7 (11.9)	3 (4.4)	14 (13.5)	15 (17.2)	7 (7.0)	9 (18.4)	2 (8.0)	62 (11.4)
Total (n)	53	59	68	104	87	100	49	25	545
Mean level	1.43± 0.66	1.44± 0.69	1.38± 0.57	1.39± 0.71	1.53± 0.77	1.28± 0.58	1.53± 0.78	1.56± 0.64	

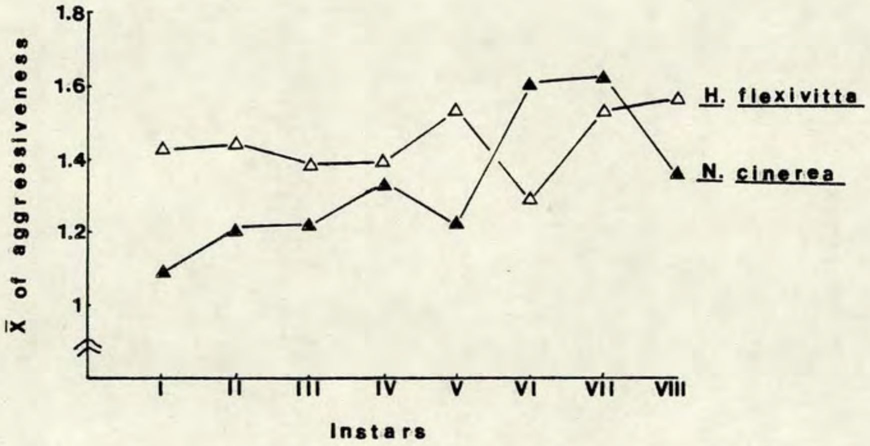

Fig. V.1 - X̄ level of aggressiveness in each nymphal instar of Nauphoeta cinerea

V. 3.4. - Agonistic behaviour in young male adults of *Nauphoeta cinerea* and *Henchoustedenia flexivitta*

In both species pairs of young male adults of the same age were observed in detail over a 10-day period.

The results (see Appendices V.7 and V.8) indicate a consistent pattern of events in *Nauphoeta cinerea* leading to the start of fighting on the fourth day after adult emergence and to the establishment of a dominance-subordinate relationship. Table V.8 shows the results for five groups of two males and Table V.9 for five groups composed by two males and one female. The differences observed between dominant and subordinate males were analysed, lumping the data into three ages sets: (0-3 days), (4-6 days), and (7-10 days), and lumping agonistic acts into the following three sets: non-aggressive, aggressive and terminating acts. Truce was not considered in this analysis as the individual terminating the encounter could not be determined.

Dominance cannot be determined in *N. cinerea* before "day three" (i.e. before the onset of fighting) as differences between the performance of dominant and submissive males in both groups were not significant ($P \leq .05$) when ages "0-3" were analysed $(X^2)=2.29$; df=2).

Some agonistic acts such as lunge, bite, butt and grapple were not observed until "day 3" in the adult stage (Appendices V.7 and V.8). In both groups mutual antennation, step-on, climb and truce were the most common acts performed by both male, dominant and subordinate during the first three days of adult life (Tables V.8 and V.9 and Appendices V.7 and V.8).

The period of highest activity in the groups of two males alone was during the first four days (0-3), decreasing onwards apart from a single peak on the sixth day (Table V.8 and Appendix V.7). However, in the first three days they were proportionally less agonistic than in subsequent days.

In groups composed of two males and one female the peak activity was significantly greater on the fourth day than any other (Appendix V.8). This was due to the males engaging in more interactions - perhaps competing for mating success.

9 ?

Table V.8 - Frequencies of agonistic acts in five groups of two males of *Nauphoeta cinerea*
(D = dominant; S = subordinate)

Age (days)	(0-3)		(4-6)		(7-10)	
Male status:	D	S	D	S	D	S
Acts: Non-aggressive	30	32	28	4	17	1
Aggressive	14	7	13	0	6	1
Terminating	5	5	0	7	0	0
Total	49	44	41	11	23	2

Table V.9 - Frequencies of acts in five groups of two males and one female of Nauphoeta cinerea
(D = dominant; S = subordinate)

Age (days)	(0-3)		(4-6)		(7-10)	
Male status:	D	S	D	S	D	S
Acts: Non-aggressive	16	27	43	9	12	0
Aggressive	3	7	35	0	7	1
Terminating	0	0	0	21	0	10
Total	19	34	78	30	19	11

Tables V.10 and V.11 show the frequency of three sets of acts performed by dominant and subordinate males of Henchoustedenia flexivitta. Table V.10 shows the results obtained for five groups composed of two males and Table V.11 for five groups composed of two males and one female. The results show that in both groups the onset of fighting occurred only on the sixth day of adult life (Appendices V.9 and V.10). Onset of fighting in this species was later than in Nauphoeta cinerea where it occurred on the third and fourth days after adult emergence (Appendices V.7 and V.8).

Some acts observed in N. cinerea (Apendices V.7 and V.8) were not observed in H. flexivitta, (Appendices V.9 and V.10) for example butt, jerk, climb, abdominal extension and crouch.

Aggressive acts such as bite, lunge and grapple were observed in both sets of groups only after the fifth day following emergence.

Analysis of these data was made following the same technique as in N. cinerea.

In groups composed of only males (Table V.10) individuals stayed very inactive on the days "0" and "2" and "3". The activity peak was on the seventh day and from the fourth until the tenth day the activity of the dominant individual was greater than that of the subordinate (Appendix V.9). However, no significant differences were observed in the performance of dominant and subordinate individuals during the first seven days of adult life (Table V.10).

In groups of two males and one female (Table V.11) all interactions between males observed during the first four days were initiated and performed by the dominant individuals. The dominant males were far more active and this continued from the very beginning (with exception of terminating acts) until the end of the observation period. The peak activity was on the sixth and seventh days: at this time the subordinate individual terminated most of the encounters (retreating) and this was responsible for the increase in the number of acts performed by him (Table V.11 and Appendix V.10).

The differences between dominant and subordinate males showed significance at age four to six (X^2)=12.24, df=2, $P \leq .01$) and at age seven to ten (X^2=8.06, df=2, $P \leq .05$). The results for both species indicate that the presence of female may induce the earlier development of the formation of the hierarchy and anticipate the onset of fighting in at least one male; perhaps, accelerating the maturation.

Table V.10 - Frequencies of agonistic acts in five groups of two males of Henchoustedenia flexivitta (D = dominant; S = subordinate)

Age (days)	(0-3)		(4-6)		(7-10)	
Male status:	D	S	D	S	D	S
Acts: Non-aggressive	12	16	40	7	133	23
Aggressive	0	0	15	6	112	7
Terminating	0	0	0	0	7	77
Total	12	16	55	13	252	107

Table V.11 - Frequencies of agonistic acts in five groups of two males and one female of Henchoustedenia flexivitta (D = dominant; S = submissive)

Age (days)	(0-3)		(4-6)		(7-10)	
Male status:	D	S	D	S	D	S
Acts: Non-aggressive	10	0	23	14	44	15
Aggressive	0	0	8	12	29	13
Terminating	0	0	5	22	7	11
Total	10	0	36	48	80	39

Encounters between young adult males of N. cinerea and H. flexivitta were counted and grouped in levels of agonism following the same techniques used in the study of nymphs. In groups composed of two males of N. cinerea the mean level of agonism increased progressively as the individuals became older (Table V.12 and Fig. V.2). In the presence of a female the mean level of agonism increased rapidly reaching a peak at age four to six days and decreasing slightly afterwards (Table V.13 and Fig. V.2). The frequencies of encounters were very low at age seven to 10-days and this fact made the comparative analysis very difficult. It seems that this slight decrease on agonism is not significant. However, it is well known that in several species of cockroaches the presence of females increases the general level of aggression in males. The slight decrease of agonism after the sixth day in N. cinerea (Table V.13) may be explained by copulation having already occurred and this motivation for aggression therefore having ceased for a short period.

The same pattern of behaviour occurred in H. flexivitta. In the absence of a female in the group the mean level of male agonism increased from the beginning to the end of the observation period (Table V.14 and Fig. V.3). Comparisons between the two sets of age four to six and seven to ten days using X^2(=10.54, df=2) show that the increase of agonism is significant ($P \leq .05$). In the presence of a female the highest mean level of agonism was at age four to six days and decreased afterwards (Table V.15 and Fig. V.3).

The analysis of these differences showed that they are statistically significant ($P \leq .05$; $X^2=7.61$; df=2) (Fig. V.3).

Table V.12 - Levels of agonism in five groups of two males of <u>Nauphoeta</u> <u>cinerea</u>

Age/Days:	(0-3)	(4-6)	(7-10)
Level			
1	19	9	4
2	10	5	8
3	1	2	0
Total	30	16	12
Mean level	1.4±0.55	1.56±0.70	1.67±0.47

Table V.13 - Levels of agonism in five groups of two males and one female of <u>Nauphoeta</u> <u>cinerea</u>

Age/Days	(0-3)	(4-6)	(7-10)
Level			
1	17	12	5
2	2	17	2
3	1	7	3
Total	20	36	10
Mean level	1.2±0.51	1.86±0.71	1.80±0.87

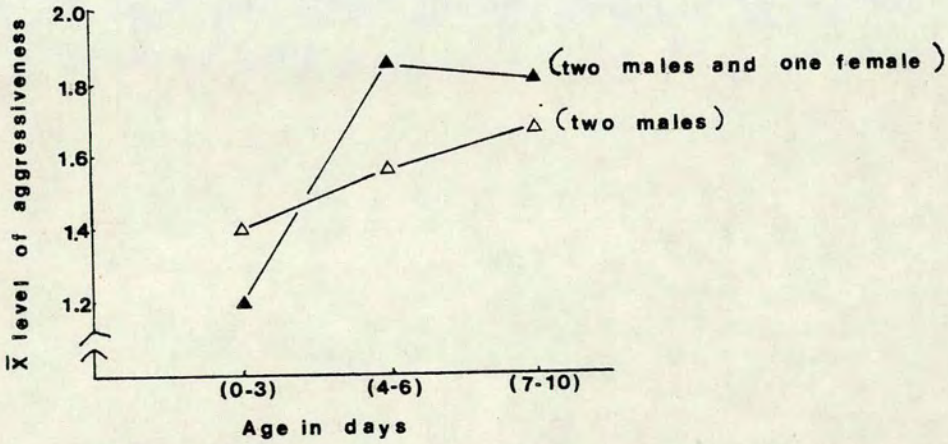

Fig. V.2 - Mean level of agonism at three different ages in two sets of five groups of <u>Nauphoeta</u> <u>cinerea</u>

Table V.14 - Levels of agonism in five groups of two males of <u>Henchoustedenia</u> <u>flexivitta</u>

Age/Days	(0-3)	(4-6)	(7-10)
Level			
1	14	14	40
2	0	15	25
3	0	6	53
Total	14	35	118
Mean level	1.0±0.0	1.77±0.72	2.11±0.88

Table V.15 - Levels of agonism in five groups of two males and one female of <u>Henchoustedenia</u> <u>flexivitta</u>

Age/Days	(0-3)	(4-6)	(7-10)
Level			
1	4	9	19
2	1	12	4
3	0	11	14
Total	5	32	37
Mean level	1.2±0.4	2.06±0.79	1.86±0.93

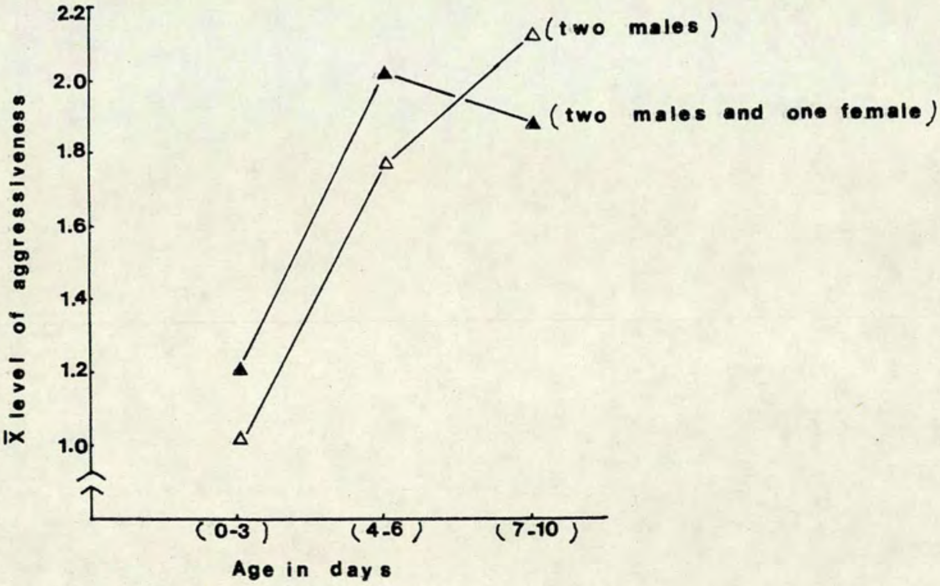

Fig. V.3 - Mean level of agonism at three different ages in two sets of five groups of <u>H</u>. <u>flexivitta</u>.

Males of Nauphoeta cinerea begin to fight on day three to four. This onset of fighting coincides with the maximum level of production of seducin (day three to six according to Roth & Dateo, 1966). However, aggressiveness at this time appears in only one of each pair of males. Perhaps the onset of fighting in one male delays onset in his partner. Acceleration of maturation in the dominant male may explain why the appearance of fighting is restricted to only one of the males. Various hypotheses can be made based on changes in the physiology after the final moult. After the third day of the final moult, if homosexual behaviour does not occur, males space-out. It seems possible that mutual contact could influence which male becomes dominant and such contact probably occurs during the first three days of adult life.

In both Nauphoeta cinerea and Henchoustedenia flexivitta the establishment and maintenance of the dominance-subordinate relationship is correlated with aggressiveness.

V. 3.5. - Behaviour in pairs of mature and immature males of Nauphoeta cinerea

In Nauphoeta cinerea five separate groups were set up, each consisting of a mature and an immature male. Very few aggressive encounters were observed before the immature male was four-days-old. However, most of the encounters which did occur were on the first and second days after being put together. This might be because of stress in the new environment and/or failure of the mature male to recognize the immaturity of the other. Table V.16 summarizes the results of agonism obtained in all five groups. In all groups the older male (mature) was dominant and did not attack the immature from day two to six (i.e. age of the immature male). From day one homosexual behaviour was observed but discussion of this will be reserved until the next chapter. However, for now it can be said that the results suggest that sexual behaviour is involved in the establishment of dominance-subordinate relationship. Gautier (1976) found similar results for <u>Blaberus</u> <u>craniifer</u> males.

After day seven, both individuals could be considered as mature males. By this time the aggressive behaviour reappeared (Table V.16) and homosexual behaviour decreased.

In all groups aggressive behaviour in the younger male appeared for the first time at day seven (Table V.16). Its onset might be considered delayed when compared to normal conditions. Manning & Johnstone (1970) found that in <u>Nauphoeta</u> <u>cinerea</u> contact with mature males and females delayed the onset of fighting in young males, whereas contact with other young males tended to accelerate it.

The results confirm that contact with a mature individual who behaves aggressively leads to a delay in the development or even to suppression of the aggressive response.

More than 90% of the agonistic encounters performed by the older (dominant) male on level 1 was composed of acts such as: approach → antennate → step-on → withdraw. In level 3 of all agonistic encounters included: approach → lunge, followed by/or biting → grappling.

The younger individual (subordinate) terminates most of the aggressive encounters by retreating (35%) and by showing submissive posture (10%). He initiated 6.8% of the non-aggressive encounters composed of approach → antennate → withdraw, and after the seventh day he behaved aggressively in only 4.5% of the encounters. In the overall results the mature individual initiated 89% of the total encounters performed in all the groups.

At this point it can be suggested that young males not producing the maximum level of sexual hormone "seducin" are not attacked but treated as females and very often courted by other males.

In groups of paired mature and immature males fighting was not very frequent and it seems that the immature male was an inadequate stimulus for eliciting aggression in the older one. Fighting reappeared only on the seventh day after the initial introduction (Table V.16).

Aggressive encounters at level 2 were not observed in these groups (Table V.16).

Unfortunately no comparable observations could be made on <u>Henchoustedenia</u> <u>flexivitta</u> because of cultural difficulties.

Table V.16 - Levels of agonism of N. cinerea in paired mature and immature males

Age in days of the immature male:	0		1		2		3		4		5		6		7		8		9	
I : immature M : mature Levels of agonism:	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M
1		2		2		4		16		16		18		11		10			12	19
2																				
3		16		5											2	10	6	19		28
Mean level		2.78 ±0.63		2.43 ±0.90		1.0		1.0		1.0		1.0		1.0	3.0	2.0 ±1.0	3.0	3.0	1.0	2.19 ±0.98
No. of retreats	13		5				2						8		5		12		16	
No. of submissive posture			2				6						5				5			

V. 3.6 - Agonism in males of Nauphoeta cinerea kept in isolation throughout the nymphal instars and for some days after the final moult

Observations were made of four groups each consisting of five males of N. cinerea which had been kept in isolation for the whole of their lives prior to the setting-up of the groups. (i.e. during entire nymphal period and also for various lengths of time after the final moult).

Table V.17 shows the results obtained for agonistic behaviour in these groups. Individuals were designated from "1" to "5" following the sequence of final moulting. Thus, individual "1" was the oldest in its group and "5" was the youngest, i.e. the last to moult.

The individuals started to show aggressive behaviour (fighting) immediately the groups were set up.

In group 1 (Table V.17) the age structure was 26-19-18-14-and 5-days old (i.e. after the final moult) when behavioural observations started. The dominant individual was "male 4" kept in isolation for 14 days after the final moult. Individual "5" (youngest) suffered attacks, but was the most subordinate male in the group. He was kept in isolation for five days after the final moult. The highest mean level of agonism (Table V.17) belonged to male "2". However, he lost more aggressive encounters than male "4".

In group 2 (Table V.17) the age structure was 16-11-10-10-and 9-days-old respectively. The dominant male was individual "1" kept in isolation for 16 days after the final moult. He had also the highest mean level of agonism in the group. Individual "5", the youngest, kept in isolation nine days after the final moult was much attacked, but he retreated or showed submissive behaviour in all encounters in which he participated. Only once did he attack another male which was at level "3" of aggressiveness (Table V.17, group 2).

In group 3 (Table V.17) the age structure was 21-20-20-14-and 3-days-old. The dominant individual was male "4" kept in isolation 14 days after the final moult. Individual "5" kept in isolation for only three days after the final moult was attacked very seldom. He did not initiate any encounters with other males. He terminated all encounters in which he participated by retreating or showing submissive behaviour (Table V.17, group 3).

In group 4 (Table V.17) the age structure was 36-26-20-28-and 1-day-old. The dominant individual - "male 2" - was kept in isolation for 26 days after the final moult. Individual "5" kept in isolation for one day after the final moult was attacked only twice in all the observation period and did not initiate any encounters with other males in the group (Table V.17, group 4).

During the observation period the individuals became two weeks older. However, this increased age did not change the hierarchy in the groups and the agonistic behaviour of each individual remained the same. These results indicate that although isolation can delay onset of fighting in males of N. cinerea, fighting has already appeared by the age of 14 days (age of the youngest dominant male when the groups were established). The suggestion that isolation may delay the onset of fighting is supported by the subordinate behaviour of the youngest individuals in all groups. In all four groups the youngest males were the most subordinate individuals and showed a very low level of agonism. The results also support the idea that aggressive behaviour of young immature males can be delayed or suppressed by interactions with mature males who behave aggressively. Even at the end of the 14 days of observations the youngest individual in each group was still not fighting properly.

Table V.17 - Levels of male agonism of N. cinerea kept in isolation throughout the nymphal instars and after the final moult

groups	Individuals from oldest to youngest:	1	2	3	4	5
1	Levels of agonism:					
	1	4	3	7	4	2
	2	3	6	3	18	1
	3	3	22	5	30	4
	Mean Level	1.9±0.83	2.62±0.66	1.86±0.88	2.5±0.63	2.28±0.88
	No. of retreats	26	18	30	10	12
	No. of sub-posture	4	3	5	-	8
2	1	18	4	7	5	3
	2	14	-	7	2	-
	3	43	3	13	5	1
	Mean Level	2.33±0.84	1.86±0.99	2.22±0.83	2.0±0.91	1.5±0.87
	No. of retreats	9	30	24	24	24
	No. of sub-posture	-	6	3	2	4
3	1	10	9	2	10	-
	2	11	5	3	8	-
	3	18	10	3	21	-
	Mean Level	2.20±0.82	2.04±0.89	2.12±0.78	2.28±0.84	-
	No. of retreats	24	30	26	18	16
	No. of sub-posture	-	1	3	-	2
4	1	5	13	5	4	-
	2	3	13	5	2	-
	3	10	32	7	-	-
	Mean Level	2.28±0.87	2.33±0.82	2.12±0.83	1.33±0.47	-
	No. of retreats	18	4	30	36	2
	No. of sub-posture	4	-	1	4	-

V. 3.7 - Agonism in males of N. cinerea and H. flexivitta kept in isolation only after the final moult

Two groups of five males of each species kept in isolation for various lengths of time after the final moult were used for agonistic observations. Tables V.18 and V.19 show the results obtained from N. cinerea and H. flexivitta respectively. Only encounters which had a clear outcome were counted and used in this analysis. Interactions terminated by truce were not considered.

Male individuals started to fight immediately after the groups were set up even though in group 1 of H. flexivitta the oldest male in the group was only six-days-old. In all groups of both species the dominant individuals were males "1" or "2", the oldest or next to oldest in the group (Table V.18 and V.19).

V. 3.7.2 - Agonism in groups of Nauphoeta cinerea

In group 1 of N. cinerea (Table V.18) the age structure was 18-17-16-10-and 6-days-old. The dominant individual was "male 1", the oldest in the group kept in isolation for 18 days after the final moult. There was much fighting among individuals "1", "2" and "3", which were of similar ages and kept in isolation for similar lengths of time. Male "5" (six-days-old) was attacked more than male "4" (10-days-old). One explanation for this could be the effect of "seducin" which was at a maximum level of male "5" according to the results of Roth & Dateo (1966). It is well known that this sexual hormone can arouse the level of aggressiveness amongst males in addition to attracting females.

In group 2 (Table V.18) the age structure was 15-12-10-10-and 5-days-old. The dominant individual was "male 2" kept in isolation for 12 days after the final moult. Male "5" was again the most subordinate individual in this group. There was much fighting between males "1" and "2" for top-ranking status in the hierarchy in this group.

In both groups of *N. cinerea* the youngest male was the most subordinate individual and by the age of 10 days the fighting behaviour was still not fully developed. These observations support the hypothesis that both isolation and interaction with mature aggressive males may delay the onset of aggressiveness. No great difference can be seen when these two groups are compared with the four which were kept in isolation during the complete nymphal period as well as for varying periods after adult emergence (Table V.17). This possibly indicates that interactions after the final moult have more effect on the establishment of the male hierarchy than interactions during nymphal stages.

Table V.18 - Levels of agonism in males of *N. cinerea* kept in isolation after the final moult

Group	Individuals:	1	2	3	4	5
1	Level of Agonism					
	1	12	7	5	6	2
	2	7	5	2	4	2
	3	18	15	2	4	3
	Mean Level	2.16±0.88	2.30±0.85	1.67±0.82	1.86±0.83	2.14±0.83
	No. of retreats	8	18	21	23	24
2	1	8	3	3	7	8
	2	4	9	3	4	1
	3	22	34	12	2	3
	Mean Level	2.41±0.84	2.67±0.59	2.5±0.76	1.61±0.74	1.58±0.86
	No. of retreats	22	15	33	38	17

V. 3.7.2 - Agonism in groups of Henchoustedenia flexivitta

In group 1 of H. flexivitta there was a very low level of aggression (Table V.19). This was due to two possible reasons: (a) the youth of the members of the group, and (b) the small gap between ages. The dominant individual was "male 1", the oldest male in the group (six-days-old). Male "5", the youngest individual was the least attacked and initiated fewest encounters in the group (Table V.19).

In group 2 the dominant individual was male "2". Most aggressive encounters were observed between male "2" and "1", age 10 and 11 days respectively. Males "4" and "5" followed similar patterns of behaviour and were the most subordinate in the group. They did not attack any other male in the group (Table V.19). Their ages at the beginning of the observational period were four- and one-day-old respectively.

There is a critical age for the onset of fighting and this can be delayed by suppressing mutual interaction among males after the final moult. Individuals with similar ages fight more than individuals with a wide gap between ages. The most immature individual in a group was always the most subordinate male.

In both species the male hierarchy in groups set up from hatching follows the same sequence as the age after the final moult. But isolation after final moulting also has an effect on the hierarchy in that groups set up from isolated individuals determining a dominance order different from the sequence of final moult.

Table V.19 - Levels of agonism in males of H. flexivitta kept in isolation after the final moult.

	Individuals:	1	2	3	4	5
Group 1	Level of Agonism:					
	1	1	2	-	-	-
	2	1	-	4	5	-
	3	16	3	2	5	1
	Mean level	2.83±0.5	2.2±0.98	2.33±0.47	2.5±0.5	3.0
	No. of retreats	9	8	7	10	4
2	1	4	6	3	-	-
	2	4	12	2	-	-
	3	14	13	2	-	-
	Mean level	2.45±0.78	2.22±0.75	1.86±0.83	-	-
	No. of retreats	27	-	9	2	3

In summary, almost the entire agonistic repertoire is displayed by nymphs of N. cinerea and H. flexivitta although actions of high aggressive intensity are observed at a very low frequency compared with those of adult males. Usually the nymphs of both species use simple non-aggressive acts in their encounters. A hierarchy based on overt aggression is not formed during nymphal development. There is an increase of aggressiveness over time in N. cinerea nymphs. However, this fact was not confirmed for H. flexivitta nymphs.

After the final moult the dominance hierarchy is gradually established following the same sequence as adult moulting. During the first days of adult life the individuals are still sociable. It seemed possible that some kind of mutual contact among males during this period could influence which male becomes dominant and moreover is a crucial factor for the normal onset of fighting at day three or four.

In the first four days of adult life in both species the most common acts performed by individuals were: approach, antennation and step-on. Thereafter, antennation decreased and step-on was suppressed from the repertoire unless homosexual behaviour had occurred.

In *N. cinerea* after day four of adult life aggressive encounters primarily consisted of lunging by one individual and retreating by another. Lunge followed by biting or grappling are important acts to maintain the dominant position of males in this species.

In *H. flexivitta* "intention" movements such as stilt-posture, stilt-walk and jerk play an important role in maintenance of male dominance.

Social deprivation by isolation after the final moult can affect the hierarchy formation as after isolation the dominance hierarchy does not follow the sequence of adult moulting. Isolation also can delay the onset of aggressiveness. It is suggested that some kind of social contact is required for aggressive behaviour to appear between day three-four after the final moult. However, contact with mature males who behave aggressively also delays the onset of fighting in the younger.

VI. RELATIONSHIP BETWEEN HOMOSEXUAL, PSEUDOFEMALE BEHAVIOUR AND DOMINANCE

VI. RELATIONSHIP BETWEEN HOMOSEXUAL, PSEUDOFEMALE BEHAVIOUR AND DOMINANCE

VI. 1 - Introduction

In cockroaches adult behaviour appears gradually in the first days after the final moult. In addition to behavioural acts which are clearly agonistic, homosexual and pseudofemale behaviour also occurs among males of Nauphoeta cinerea and Henchoustedenia flexivitta. Because of the relationship between courtship, homosexual behaviour and the development of the male dominant hierarchy some aspects of sexual behaviour will be described in this chapter.

The concepts and definitions used here were taken from Barth (1964): Mating behaviour is all behaviour associated with and including copulation, while courtship is the sequence of interactions between sexes preceding and frequently resulting in copulation. Homosexual behaviour (widest description sensu - Morris, 1952) is any mutual sexual behaviour involving two individuals of the same sex. In this account, the term refers particularly to the behaviour of males which actively court other males. In this context the term "homosexual courtship" was used, as the term courtship is defined as interactions between sexes preceding copulation. Males which respond to such homosexual courtship showing motor-patterns characteristic of the female's sexual behaviour are said to be showing pseudofemale behaviour (Morris, 1952).

The mating behaviour of many species of cockroach is known in some detail. Except for a few species, mating behaviour exhibits remarkable uniformity in the overall sequence of events. The majority of studies on mating behaviour on Blattaria are those of Barth (1961, 1964, 1968a, b, c, 1970), Roth & Willis (1952, 1954) and Roth & Barth (1967).

In Nauphoeta cinerea particularly, mating behaviour has been the subject of intensive studies by Roth & Willis (1954), Barth (1961), Roth (1962, 1964a, b), Roth & Barth (1964, 1967), Roth & Dateo (1966), Dimeo et al. (1978), Fukui & Takahashi (1980) and Takahashi & Fukui (1980).

On the other hand to my knowledge the mating behaviour of Henchoustedenia flexivitta has not previously ben described. However, the two species, N. cinerea and H. flexivitta, are phyletically very close.

The information available in the literature on cockroach mating behaviour shows different patterns based largely on the nature of the releaser of the preliminary courting responses. Table VI.1 summarizes the information available.

Table VI.1 - Releasers of the preliminary courtship behaviour in cockroaches

Characteristics	Species	Authors
Females produce a *volatile* sex attractant (pheromone) which attracts males from a distance and acts as the principal releaser of their courting behaviour	*Periplaneta americana* (Periplanone a and b)	Persoons & Ritter (1979)
	P. australasiae and *P. brunnaea*	Simon & Barth (1977b)
	P. fuliginosa	Barth (1961, 1964)
	Blaberus craniifer	
	B. giganteus and *B. discoidales*	Bell et al. (1974)
	Blatta orientalis	Simon & Barth (1977b)
	Pycnoscellus indicus and *P. surinamensis*	Roth & Barth (1964)
	Eublaberus positicus	Barth (1968a)
	Hyporhicnoda litomorpha	Barth (1968a)
Males produce a *volatile* sex pheromone which releases the mounting and feeding behaviour of receptive females	*Nauphoeta cinerea* (tergal and sternal glands)	Roth & Dateo (1966) and Persoons & Ritter (1979)
	Leucophaea maderae (tergal glands)	Engelmann (1965) Roth & Dateo (1966), Barth (1968a), Roth (1969)
	Eurycotis floridana	Barth (1961, 1968a)
	Supella longipalpa (tergal glands)	Roth & Willis (1952)
Males and *females* produce sex pheromones	*Byrsotria fumigata*	Roth & Barth (1964)
	(female sex pheromone is volatile)	Barth (1968a) and Bell et al. (1974)
	Latiblattella angustifrons *L*. azteca *L*. vitrea (tergal glands) (male and female sex pheromone are volatile)	Willis (1970)
	Parcoblatta fulvescens	Wendelken & Barth (1971)
	Blattella germanica Females produce a non-volatile sex pheromone	Roth & Willis (1952)

Hence, Nauphoeta cinerea is one of the species of Blattaria in which the sexual pheromone is released by the male. Roth & Dateo (1966) called this pheromone "seducin", they showed that it is attractive to receptive females over a short distance and may be responsible for the female's choice. Sreng (1982) described this distance as 10 cm.

Sex recognition in N. cinerea is accomplished by several factors: (a) chemical stimulus (pheromones); (b) tactile stimulus; and (c) auditory stimuli (Roth & Barth, 1964; Hartman & Roth, 1967a, b; and Barth, 1968b).

(a) Chemical Stimulus

In N. cinerea the sex pheromone produced by the courting male releases the female's "mounting and feeding" behaviour (Roth & Willis, 1952; 1954; Engelmann, 1960; Barth, 1961; Roth & Barth, 1964; Roth & Dateo, 1966; Hartman & Roth, 1967b; Hartman & Suda, 1973).

Roth & Dateo (1966) observed that extractable levels of pheromone are low at adult emergence and increase as males grow to six days of age, and then level off. This fact was confirmed by Dimeo et al. (1978) whose study also located the site of production of "seducin". In males one day after adult emergence this was confined to the posterior part of the abdomen from the fifth sternite, but by the third to fifth day it had spread to the first four abdominal sternites.

Females of Periplaneta americana begin to secrete sex pheromone about eight days after adult ecdysis (Hawkins & Rust, 1977) while behavioural responses of males to sex pheromone develop sequentially beginning at adult ecdysis. However, wing-raising and abdominal extension were not released until days eight and 10 respectively (Silverman, 1977).

In Nauphoeta cinerea the importance of chemical stimuli in the release of mating behaviour is very complex. According to Sreng (1982) there are two successive chemical signals in N. cinerea:

(1) the pheromone secreted by the sternal glands which attracts the female from a distance, and

(2) an aphrodisiac secreted by the tergal glands.

Chemical analyses showed that the secretion of the sternal glands is formed essentially of volatile products, while the secretion of tergal glands is composed of proteins, fatty acids and a small quantity of volatile products (Sreng, 1982).

Prior to mating, the male of Nauphoeta cinerea adopts a calling posture, the obdomen is flexed upwards and the sternal glands release the sexual pheromone. After a quick antennal contact (tactile stimulus), the male pulls down its abdomen, raises its wings exposing its tergal glands which secrete an aphrodisiac (Sreng, 1982). In various cockroach species the receptive female then mounts the male's abdomen and "feeds" upon glandular secretions (Roth & Dateo, 1966; Barth, 1970; Simon & Barth, 1977a). Following this the male extends his abdomen and thrusts the hooked phallomere to engage the genitalia of the receptive female (Hartman & Roth, 1967b). After genital connnection is made, the pair pivot 180°, achieving an apposed position which is retained during copulation (Roth & Willis, 1954). Usually virgin females that feed on the male's tergal surface will mate and this feeding behaviour may be used as an indicator of female receptivity (Roth & Barth, 1964). However, from personal observations females on the day of emergence were seen showing "mounting and feeding" behaviour which does not imply that they were receptive. The duration of copulation averages about 20 minutes (Roth & Stay, 1962), but this will vary with the age of the male and the time interval between matings.

After mating, _N_. _cinerea_ females are unreceptive until after parturition, at which time they may or may not mate again (Roth, 1962).

(b) **Tactile Stimulus**

In addition to chemical stimuli, tactile estimuli are important releasers of various parts of the sequence of mating behaviour in both male and female cockroaches, and both play a role in the sex discrimination which occurs during the initial antennation of the female by the male (Roth & Willis, 1952; Simon & Barth, 1977a).

Recognition of the female by the male of Blattella germanica is brought about by contact chemoreceptive through antennal contact between the two sexes (Roth & Willis, 1952).

The releaser of the wing-raising display in cockroaches is very complex, although in Periplaneta spp full wing-raising is released after antennal contact (Simon & Barth, 1977a).

Fukui & Takahashi (1980) observed that in Nauphoeta cinerea antennal contact plays an important role in recognition of the female by the male. They concluded that the display of wing-raising by males is elicited by their recognition of mature females through antennal contact with the female body surface.

Several authors have isolated and identified from the female body of N. cinerea chemical substances responsible for causing wing-raising in males (Nishida et al., 1974, 1975, 1976a, b; Sato et al., 1976).

The cuticular wax of N. cinerea functions as a contact chemical in sex discrimination. The surface extract of females has higher activity than that of males (Takahashi & Fukui, 1980).

Although the importance of antennal contact in recognition of the female by the N. cinerea males has been mentioned several times, antennal fencing between sexes is not necessary to cause wing-raising. Males were found to raise their wings not only to intact females, but also to antennectomized females. Even after removal of antennae, palps and cerci, males of N. cinerea and other species are still able to identify and copulate successfully with females.

In several species removal of an increasing number of sense organs from the males increases the average length of time required for mating to occur, as well as reducing the percentage of males which ultimately mate (Roth & Willis, 1952; Roth & Barth, 1967).

In N. cinerea contact with other individuals, regardless of sex, may elicit wing-raising (Barth, 1961a; Roth, 1962). Indeed, homosexual courtship behaviour in N. cinerea is not uncommon in the absence of females (Roth & Barth, 1967). Homosexual behaviour is widespread in cockroaches. For several species of cockroaches homosexual courtship is observed under natural conditions as well as in mating chambers. The possible roles of male-aggregation and homosexual interaction in the prevention of interspecific hybridization and the prolongation of sexual behaviour have been pointed out by Simon & Barth (1977b). In several species of Periplaneta homosexual interactions seem to promote the formation of conspecific groups of courting males (Simon & Barth, 1977c).

(c) Auditory Stimulus

Stridulating structures have been found in several genera of the ovoviviparous Oxyhaloinae (Nauphoeta, Henchoustedenia, Leucophaea, Oxyhaloa, Jagrehnia, Gromphadorhina) and one genus (Panchlora) of Panchlorinae of the Blaberidae (Roth & Hartman, 1967a; Nelson & Fraser, 1980). In Nauphoeta cinerea the sound is produced by posterior, anterior, and side to side displacement of the pronotum rubbing against the costal veins (Hartman & Roth, 1967a).

The situation regarding the possible role of auditory stimuli in mating behaviour is not clear. In most cases the sounds are incidental to the movements which produce them and there is no evidence that they have any effect on the behaviour of the partners (Roth & Hartman, 1967a, b). Stridulation sometimes occurs in courtship behaviour, but more frequently is associated with defensive behaviour (Hartman & Roth, 1967b). However, Nelson & Fraser (1980) demonstrated a communicative function for the sounds in Gromphadorhina portentosa and stated that they are important in courtship. G. portentosa are wingless so wing-raising and wing-fluttering are necessarily absent, but lateral oscillation and tergal feeding behaviour, noted frequently in other cockroaches are absent as well (Fraser & Nelson, 1984). Thus, they suggested that hissing in G. portentosa is analogous to tergal feeding in other cockroaches, which probably functions to hold the female in position for the male to attach.

Both sexes of Nauphoeta cinerea stridulate when alarmed, but the pattern of sounds produced differs from that produced by males during courtship (Hartman & Roth, 1967b). The males stridulate during courtship only if the female is unreceptive; and an unreceptive female apparently is not induced to mate by male stridulation (Hartman & Roth, 1967a, b). The sound is audible for only a short distance and it is uncertain whether the female receives any stimulus (Barth, 1968a).

There is no evidence that visual stimuli have any function in mating behaviour. Roth & Willis (1952) found that vision plays no role in sex recognition and subsequent mating behaviour in Blattella germanica. This is also true for Periplaneta americana and Byrsotria fumigata (Barth, 1961) and is probably true for most species which have been studied.

Physiological bases of mating behaviour

Various studies in Nauphoeta cinerea and other insects have indicated that maturation of components of the adult endocrine system occurs during the two or three days after the final moult (Manning & Johnstone, 1970).

N. cinerea males begin to mate and produce spermatophores when two to three-days-old, and when seven days or more old, a male is capable of producing two or three complete or partially complete spermatophores in a 24-hour period (Roth, 1964a).

Females less than three-days-old do not mate although courted by males. This may be interpreted as a period during which neuroscretory material is accumulating prior to its release, the latter event presumably stimulating the receptive centre of the brain. Onset of receptivity can usually be correlated with yolk deposition in, and growth of, the oocytes (Roth & Barth, 1964).

The corpora allata are inactive in newly emerged adult females of *N. cinerea*, but become active during the sexual maturation period and are normally inactive throughout the pregnancy period (Barth, 1968a).

The endoplasmic reticulum of neurosecretory cells of the pars intercerebralis of *Blaberus* is not fully developed until day three after the adult emergence, and this probably limits the functioning of the corpus cardiacum/corpus allatum complex (Willey & Chapman, 1962).

Roth (1962) believed that the corpus allatum hormone controlled mating in virgin females of *N. cinerea* by inducing the sexual feeding behaviour on the courting male's tergum. However, Roth & Barth (1964) found that allatectomy in *N. cinerea* and *Leucophoea maderae* has little effect on the mating behaviour, showing that female receptivity is not intrinsically controlled by the corpus allatum hormone. It seems that the activation of corpus allatum coincides with the sexual maturation period, but has no effect on the mating behaviour.

Dominance hierarchy and mating success

Ewing (1972) found no correlation in *N. cinerea* between dominance and mating success. However, she found correlations between rank and territorial possession and territorial possession and mating success. She also showed that the introduction of a receptive female disrupted the hierarchy and induced more aggression between males. Moreover, Breed et al. (1980) found that dominant males seem to gain certain advantages because they are found to mate more frequently than males of low status. They also demonstrated the importance of olfactory cues in the recognition of potential mates and virgin females indeed show preference for the dominant odour.

The previous discussion concerned normal mating behaviour between males and females and "homosexual courtship" behaviour. However, the main objective of the following observations was to investigate any relationship between homosexual and pseudofemale behaviour and the establishment of a dominance hierarchy in N. cinerea and H. flexivitta.

VI. 2. Material and Methods

Observations on mating, homosexual and pseudofemale behaviour were conducted in groups of Nauphoeta cinerea and Henchoustedenia flexivitta already described in detail for earlier observations (Table II.1).

Most of the experiments were performed on N. cinerea as observations on H. flexivitta were limited due to cultural difficulties. In order to make a descriptive analysis of mating behaviour the following experiments were conducted.

The successful mating behaviour of H. flexivitta was observed (n=3) only in one group of four males set up after the final moult. In N. cinerea it was observed (n=29):

(a) in four groups of five males kept in isolation during the nymphal instars and set up after the final moult (n=20), and

(b) in two groups of five males reared in groups while they were nymphs but kept singly for different lengths of time after the final moult (n=9).

In each of these groups five females were introduced singly at three day intervals. The introduction of females started after the male hierarchy was formed and had become stable. These females were taken from the stock culture on the day of adult emergence and were kept in isolation in a jar of 9 cm diameter for at least five days. This procedure assured that the females were virgins and probably physiologically receptive. Each female was kept in the male group either until the end of copulation or for a one hour period if copulation did not occur.

(a) Nauphoeta cinerea

Observations on courtship and/or homosexual and pseudofemale behaviour were conducted in groups 1 and 2 (mixed groups), in an attempt to make a descriptive analysis of sexual behaviour among individuals already known to each other, as follows:

(1) groups of five adult individuals set up on the day of the nymphs hatching (1A, 1B, 1C);

(2) groups of five adult individuals set up in the penultimate nymphal instar (1D, 1E, 1F).

The purpose of experiments 3 and 4 was to investigate qualitatively the development of homosexual and pseudofemale behaviour and relate it to the development of dominance hierarchy.

(3) groups of five adult males which had been kept in isolation throughout the nymphal instars,

(4) groups of five adult males which had been kept in isolation for various lengths of time after the final moult.

Group 5 was set up to examine certain aspects of dominance related to maturity and the involvement of homosexual behaviour in the setting up of status, and also to examine aspects of subordinate male responses.

(5) pairs of individuals composed of one mature male and another immature.

Groups 6 and 7 were established to investigate the ontogeny of male sexual behaviour in the presence and absence of a female and relate it to the development of the dominance hierarchy.

(6) pairs of males of the same age set up on the day of adult emergence, and

(7) groups composed of two males and one female of the same age and set up on the day of adult emergence.

For comparative purposes, similar experiments were performed on H. flexivitta, but as stated earlier, these experiments were limited by availability of insects.

(b) **Henchoustedenia flexivitta**

1. groups of five adult individuals set up on the day of nymphs hatching (1A,1B),
2. a group of five adult individuals set up in the penultimate nymphal instar (1D),
3. groups of five adult males which had been kept in isolation for various lengths of time after the final moult,
4. pairs of males of the same age set up on the day of adult emergence, and
5. groups of two males and one female of the same age set up on the day of adult emergence.

Observations were carried out on each group for one hour periods. Interactions between males and females and occurrence of courtship, homosexual courtship or copulation were recorded. The number of male-male interactions and the number of approaches to the females were scored. Interactions between two males ending in wing-raising by one of them were considered to be a homosexual courtship. The pseudofemale response was constituted by the act of "mounting-feeding" by one male generally preceded by wing-raising by the other.

VI. 3. - Results and Discussion

VI. 3.1 - Mating behaviour in Nauphoeta cinerea

Twenty-nine examples of successful mating behaviour were observed. In most cases after the introduction of the female into a group of five males the general level of aggression was increased. During copulation the pair was much disturbed by other males and the female in seeking a refuge led and dragged the male behind her. Such female behaviour was observed in other cockroach species (Roth & Barth, 1967). After the female was removed from the group the general level of aggression remained high and the level of homosexual and pseudofemale behaviour increased.

Mating failed only once when a female was introduced into a group. In this case the female was courted by all the males, but did not show any receptivity although she was virgin and 12-days-old.

The sequence of acts during courtship behaviour in most of the cases included: approach → antennate → wing-raising, sometimes added by jerking movements and abdominal extension. In 29 of the successful matings observed, the female response of "mounting and dorsal feeding" occurred within seven minutes of her introduction. Copulation normally started within a short period of the introduction of the female (Fig. VI. 1).

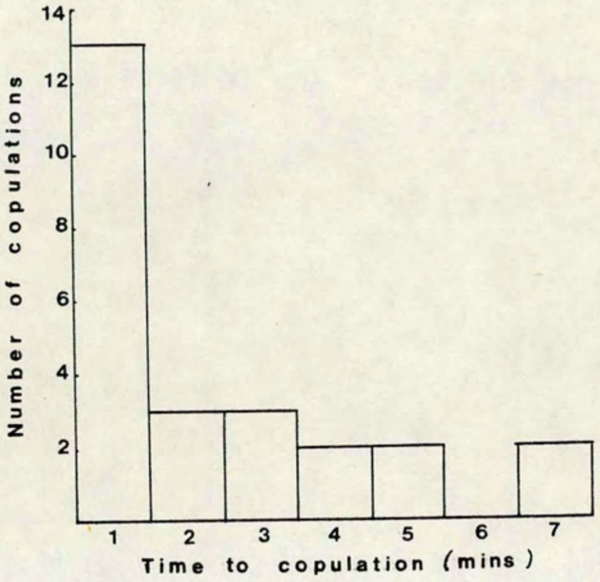

Fig. VI.1 - Time to copulation in N. cinerea

The duration of copulation was fairly constant (10-14 minutes) and was shorter than that observed by Roth & Stay (1962) who recorded averages of 20 minutes. The results are shown on Fig. VI. 2. Perhaps the shorter duration of copulations was due to the heavy attacks on the copulating pair by the other males and the absence of suitable shelter for protection against these attacks.

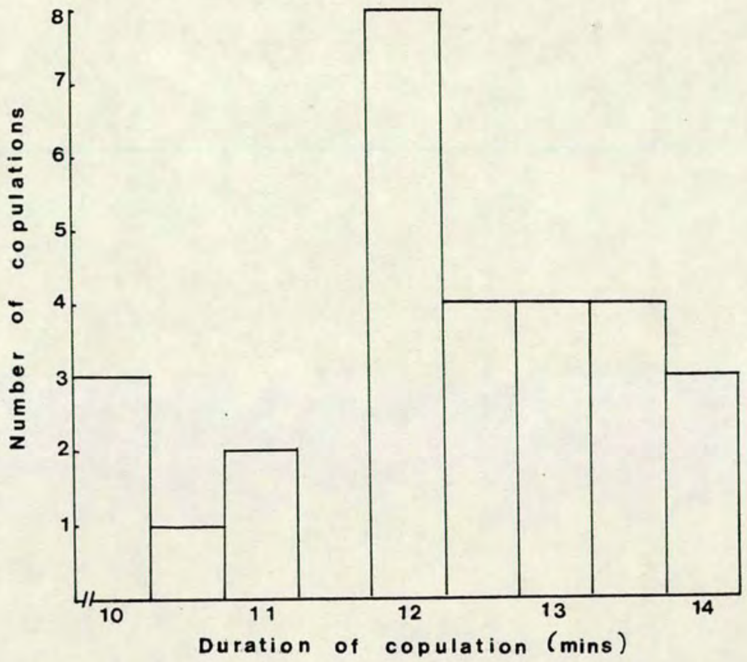

Fig. VI.2 - Duration of copulations in *N. cinerea*

In the six groups of *N. cinerea* there were 30 males, and 30 females (five in each group) were presented to them. One female did not show receptivity and was removed from the group after one hour of observation. Thirteen males did not engage in any copulation so only 16 were responsible for the 29 copulations. The six top-ranking males, one in each group, managed to perform 15 copulations ($\bar{x}$=2.5) while the other 14 copulations were made by 11 subordinate individuals ($\bar{x}$=1.3). It seems probable that dominant males have better access to females and this is shown by the experiments of Breed et al. (1980) in which a virgin female of *Nauphoeta cinerea* did indeed show preference for the male dominant odour.

VI. 3.2 - Mating behaviour in Henchoustedenia flexivitta

Mating behaviour of H. flexivitta is very similar to that described for Nauphoeta cinerea. Preliminary courtship by males includes approach → antennation → jerking → wing-raising and sometimes stridulation. After an antennal contact between a male and female, the male carries out wing-raising. The female then mounts and palpates the surface of his abdomen which is exposed to her. The assumption of the opposed copulatory position occurs rapidly (within a few seconds) and the female seems to be responsible for most of the pivoting. The pairs were observed to remain in copulation for an average of 27 minutes (n=3).

Fig. VI.3 shows the time spent in sexual behaviour which occurred until copulation involving the four males of only one group and three introduced females at three day intervals. In this group of four males (set up after the final moult), the sequence of hierarchy before introduction of the first female was: male 4 → male 3 → male 1 → male 2. Timing started with the introduction of the female to the male's cage.

Five minutes after the introduction of females, male courtship started. Females displayed mounting and feeding behaviour 15 minutes after their introduction. Copulation began after 25-40 minutes and lasted for 25-28 minutes. The copulating pair were attacked by other males. The displays of homosexual and pseudofemale behaviour coincided with the beginning of the copulation period (Fig. VI.3).

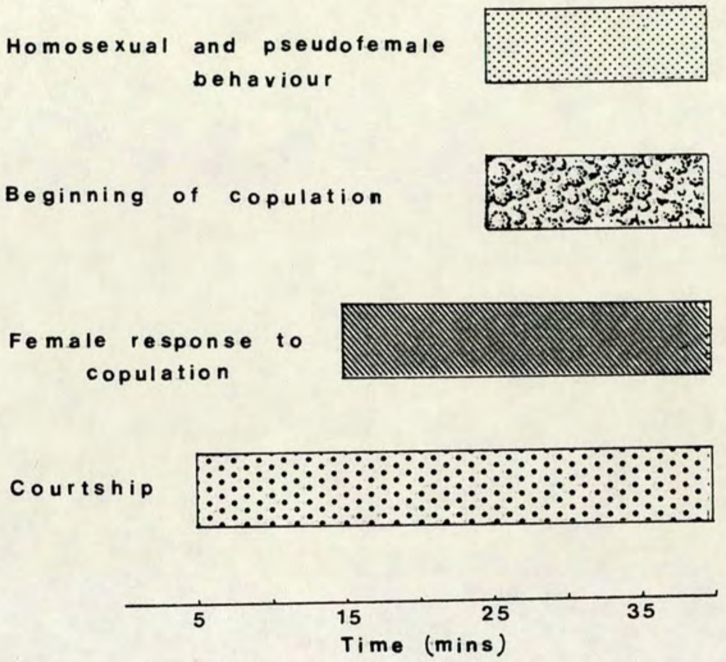

Fig. VI.3 - Time spent in sexual behaviour from their first occurrence to copulation

It was noticed that introduction of a female may disrupt the male hierarchy in H. flexivitta. The general level of homosexual and pseudofemale behaviour increased with the introduction of a female. When homosexual behaviour is observed generally the dominant male shows homosexual behaviour and the subordinates show pseudofemale behaviour performing "mounting and dorsal feeding".

In this group of H. flexivitta male 3 mated more frequently than the other males and indeed he was the dominant individual after the introduction of the first female in the group. However, the low number of cases observed does not allow any definitive conclusions about the better access to female by the dominant male in this species, although it has been demonstrated in Nauphoeta cinerea by Breed et al. (1980).

Although the number of successful copulations observed in H. flexivitta were so low that no conclusive results could be reached, it is interesting to note some differences between N. cinerea and H. flexivitta. In N. cinerea time to copulation is immediate (Fig. VI.1) and within seven minutes all copulations had occurred, while in H. flexivitta time to copulation took 15 to 40 minutes (Fig. VI.3). The duration of copulation was fairly constant in both species, but was shorter in N. cinerea (10-14 minutes) (Fig. VI.2) than in H. flexivitta (25-28 minutes).

VI. 3.3 - Ontogeny of sexual behaviour

The ontogeny of sexual behaviour in both species was determined by observations in five grups composed of two males and one female of the same age.

In _Nauphoeta cinerea_ there were no behavioural differences between the two males in each group on days "0" and "1" after the final moult. Both males showed exploration and mutual contact, performing very few activities. However, the first male to initiate a courtship always became the dominant in the group. The onset of courtship occurred slightly before the onset of fighting in all groups observed.

The results observed in five groups of _N. cinerea_ are given in Fig. VI.4.

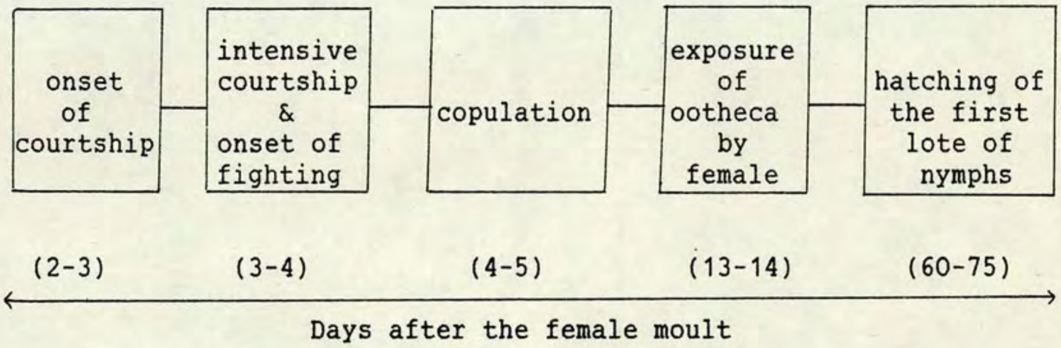

Fig. VI.4 - Ontogeny of sexual behaviour in _Nauphoeta cinerea_

In two of these groups homosexual and pseudofemale behaviour was observed between day six and ten. The dominant individual always showed male behaviour such as jerking, wing-raising and abdominal extension and the subordinate individual always showed pseudofemale behaviour like mounting and dorsal feeding. by day 14 both males were often observed courting the unreceptive female. On such occasions males often stridulate during courtship.

The results shown in Fig. VI.4 can be discussed in the light of physiological and hormonal changes occurring after the final moult. On the day of adult emergence in this species the corpora allata became active and began the development of accessory glands (Barth, 1968a). Males can form complete spermatophores from day three and the maximum levels of seducin are not found before day four (Roth & Dateo, 1966). The onset of courtship and fighting coincides with the maximum production of seducin. Several authors have suggested, and the results presented here, support the view that the pheromone "seducin" has two effects: it attracts females and arouses aggression in mature males. This is also supported by the fact that females are not normally attacked and this is also the case with immature males before day three (i.e. when not producing maximum levels of seducin).

In <u>Henchoustedenia</u> <u>flexivitta</u> the males showed very few activities during the first four days after the final moult. There were no significant differences between acts performed by the two males in the groups. Here also the first male to court the female became the dominant one. The onset of courtship and fithting in all groups occurred nearly at the same time between days five and seven, a little later than in <u>Nauphoeta</u> <u>cinerea</u>. Copulation seems to have occurred in all groups between day six and seven because courtship behaviour decreased heavily on the following days.

In one group homosexual behaviour was observed on day eight after the final moult. This behaviour was shown by the dominant male who had actively courted the female on day six.

The development of the components of male sexual behaviour in _Nauphoeta_ _cinerea_ and _Henchoustedenia_ _flexivitta_ appears to be related to the increase of age. Table VI.2 shows when different components of male sexual behaviour in _N_. _cinerea_ were first observed after the final moult (days). The results showed in Tables VI.2 and VI.3 were confined to mixed groups established during nymphal instars.

Table VI.2 - Development of the components of male sexual behaviour in N. cinerea

Component of male sexual behaviour	Age in days after the final moult
Antennation	0
Stilt-posture	2
Jerking	3
Wing-raising	3
Abdominal extension	3
Pseudofemale behaviour	3
Homosexual behaviour	3
Stridulation	4
Phallomere extrusion	4

Rust (1976) found a specific sequence of behavioural components of male sexual behaviour in Periplaneta americana as the concentration of sex pheromone was increased. Silverman (1977) showed the same sequence exposing inexperienced young males to pheromone. Thus, he concluded that the behavioural components develop separately in a sequential pattern. Perhaps the same conclusion might be applied to Nauphoeta cinerea and Henchoustedenia flexivitta (Tables VI.2, VI.3).

Table VI.3 - Development of the components of male behaviour in H. flexivitta.

Component of male sexual behaviour	Age in days after the final moult
Antennation	0
Stilt-posture	3
Jerking	3
Wing-raising	6
Phallomere extrusion	6
Homosexual behaviour	12 (8*)
Pseudofemale behaviour	14

* represents observations in other groups.

It appears that during the establishment of male hierarchy in both species elements of sexual behaviour were frequent. The sexual behaviour developed among males had a particular effect on the agonistic system. This was more clearly observed in *Nauphoeta cinerea* than in *Henchoustedenia flexivitta*. According to Bell & Gorton (1978) *N. cinerea* is the only cockroach species studied where the dominant male strongly determine the social pattern of interactions among individuals. Basing their study on quantitative data, they demonstrated a distinct difference in the role played by the dominant male of *Nauphoeta* in comparison to the dominant males in other species.

VI. 3.4 - Homosexual and pseudofemale behaviour in groups composed of two males of the same age in *Nauphoeta cinerea*

Nauphoeta cinerea males show homosexual courtship by day five of adult life even in the absence of females. The homosexual courtship was observed in four of the five groups of two males commencing on the fourth day after the final moult and continuing with intensity on days five and six. On day seven aggressiveness was seen for the first time and thereafter homosexual behaviour was seldom seen.

In these groups composed of two males a dominance-subordinate relationship was established after the eighth day of adult life. Males who showed homosexual behaviour on day five later became the dominant in the group while the male which showed pseudofemale behaviour was always the subordinate individual. However, pseudofemale behaviour such as mounting and feeding was only seen in two of the five groups. In the other groups the submissive posture was often seen.

It seems that such pseudofemale responses or submissive postures often seen in subordinate males of Nauphoeta cinerea helps to reduce attacks from the dominant individuals.

In these groups the males were fairly inactive in the first four days of adult life. Particularly on day zero the subordinate male usually initiated the encounters by antennation. During these first days the males kept very close together, spending most of the time within antennal contact range or stepping-on. Abdominal extension was first observed on day three and was performed by the dominant male. Once the dominant male had begun to court high scores for anntennal contact, abdominal extension and aggressive posture were observed and this could be related to stress caused by unsuccessful mating.

The hypothesis of earlier maturation of the dominant male is supported by the fact that the first male to show courtship always became dominant in the group.

VI. 3.5 - Homosexual and pseudofemale behaviour in groups composed of two males of the same age in Henchoustedenia flexivitta

Five pairs of H. flexivitta males of the same age were observed in detail for 15 days for homosexual and pseudofemale behaviour. Thereafter observations were made sporadically for 40 days.

In two of these five groups homosexual behaviour was shown by the dominant male from day 11 onwards. Although accurate records of activity of males were not made, in one group by day 15 the dominant male seemed to be very active and stressed, running about most of the time with his phallomere extruded. In the other the dominant male showed similar behaviour from day six onwards. By the age of 30 days both of the males originally dominant in these groups died. This also occurred in other groups of _H_. _flexivitta_ and _Nauphoeta_ _cinerea_ in which the originally dominant male died early. However, as detailed observations were performed for only 15 days, it cannot be confirmed that these males were still dominant by the age of 30 days. In this context Ewing (1972) found in _N_. _cinerea_ that after a few weeks males changed rank, probably because they had less time to eat and drink. However, the males in the present study seemed very stressed and such stress can cause fatality. The stress syndrome is generally accompanied by internal changes which lead to death as has been demonstrated for many animals including cockroaches.

Ewing (1967) suggested that in _N_. _cinerea_ subordinate males die from stress as a result of fighting. She also suggested that older adults are less susceptible to death under these conditions. Perhaps the subordinate males in the present study do not show such stress due to the rate of pseudofemale behaviour and submissive posture observed which may reduce the aggressiveness of the top-ranking males at least during the first days after emergence.

Pseudofemale behaviour of H. flexivittta occurred in only one group and was shown for the first time on day 14 by a subordinate male.

In these groups, as in N. cinerea groups homosexual behaviour was confined to the dominant male and pseudofemale behaviour to the subordinate.

It was noticed that pseudofemale behaviour generally appeared later than homosexual behaviour and was less frequent than the latter.

As in N. cinerea, males in these groups showed low activity during the first four days of adult life, performing much mutual antennation. They kept very close together spending most of the time in the same shelter within antennal contact range. According to Bell (1978) dominant males of N. cinerea respond vigorously to tactile stimulation with directional turns toward the stimulus and then executes the next act. This stimulation appears to reinforce its dominance of other individuals. Perhaps antennal contact during the first days has a role in increasing that kind of stimulation which is essential to the establishment of male status.

VI. 3.6 - Homosexual and pseudofemale behaviour of Nauphoeta cinerea in pairs of males of different ages

Five groups composed of pairs of males (one mature and the other immature) were established. The mature individuals were more than seven-days-old and had been kept isolated after the final moult. The immature males were used on the day of adult emergence (zero-day-old).

Figures VI.5 and VI.6 show the results obtained for four groups where homosexual and pseudofemale behaviour was observed. Encounters were subdivided into three types: aggressive (agonistic), non-aggressive (least agonistic) and sexual (where homosexual displays were observed). Figure VI.5 shows the encounters initiated by mature males during nine days observation periods and Fig. VI.6 shows the two most frequent responses performed by immature males in the same period.

Homosexual behaviour as well as the agonistic behaviour was observed immediately after the establishment of the groups. In both cases it was the mature male who performed the behaviour (Fig. VI.5). Pseudofemale responses were observed for the first time when the immature male was one-day-old (Fig. VI.6).

Agonistic behaviour by mature males was observed mainly on the day of establishment of the group and on the day following. This behaviour was not observed again until the immature individual was seven-days-old, and then only in one group (Fig. VI.5). Immature males showed pseudofemale behaviour when they were one-, three-, four-, five- and six-days-old (Fig. VI.6).

Attempts by the mature male to copulate were observed in one group when the immature male was three- and five-days-old.

After the immature male reached the age of seven-days homosexual behaviour by the mature male was seldom observed (Fig. VI.5).

Clearly homosexual behaviour depends on maturity, as in groups of males of the same age such behaviour was only observed when males were at least four-days-old (section VI. 3.4).

Individuals showing homosexual behaviour was always dominant (mature males): immature males exhibited only pseudofemale behaviour.

According to Sreng (1982) in *N. cinerea*, the chemical signal secreted by the sternal and tergal glands are utilized by the dominant males for maintaining the other males in submission. Sternal and tergal glands also have a fundamental role in sexual behaviour in *Nauphoeta cinerea*. Among Blattaria, tergal glands occur in adult males and have an important role in pre-copulatory behaviour while external glands are described as having a sexual role only in three closely related species: *Nauphoeta cinerea*, *Henchoustedenia flexivitta* and *Jagrehnia madecassa* (Sreng, 1979).

The suggestion of Sreng (1982) for *N. cinerea* may be applicable to *Henchoustedenia flexivitta* as the two species possess both glands. Perhaps the utilization of glandular (tergal and external) secretions by the dominant male for maintaining the other males in submission may explain the homosexual behaviour observed in dominant males and the pseudofemale response in subordinate males.

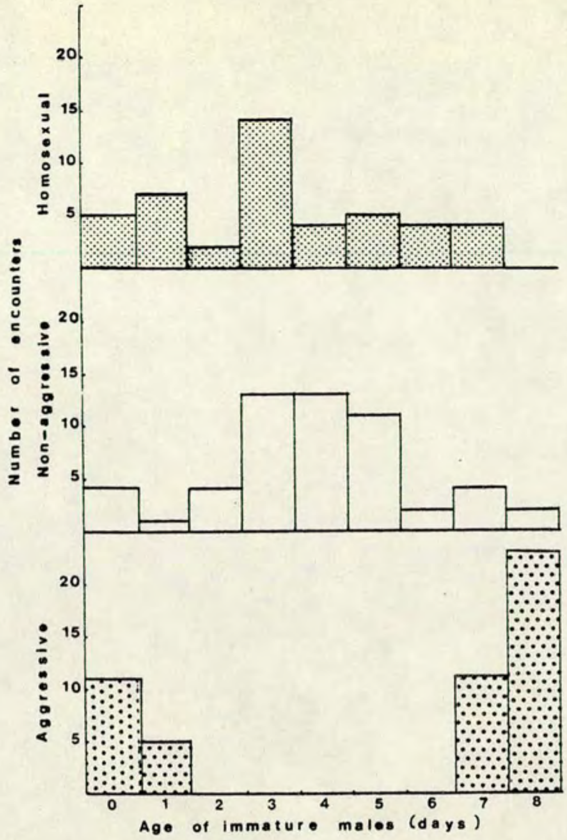

Fig. VI.5 - Types and numbers of encounters (aggressive, non-aggressive and sexual) performed by the mature male in relation to the age of immature males.

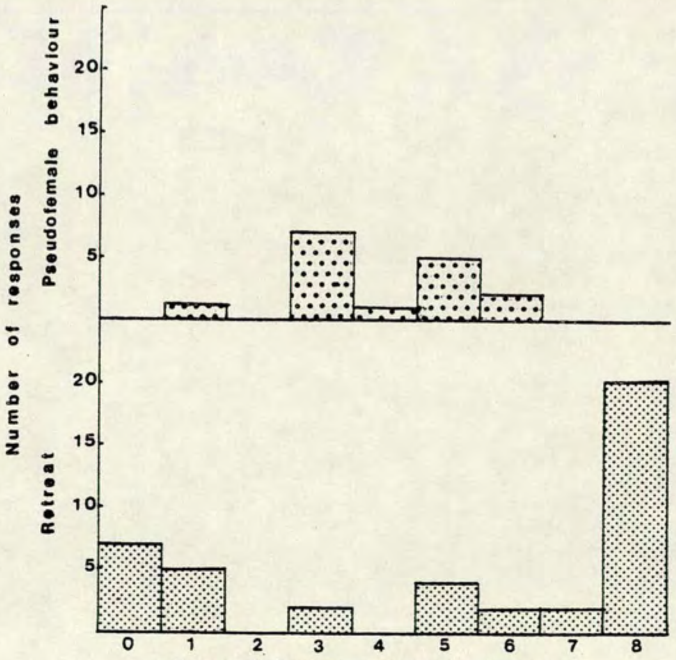

Fig. VI.6 - Types and numbers of response of immature males (retreat or sexual) to encounters initiated by mature males.

The basic difference between these groups and those made up of males of the same age (section VI. 3.4) is that in the former the males were active as soon as the groups were established, showing aggressive and sexual behaviour (Fig. VI.5).

Aggressiveness of the mature male was appreciable only when the immature individuals were zero to one-day-old, reappearing again in one case only when the subordinate individual was seven-days-old (Fig. VI.5). This behaviour may be explained in at least two possible ways:

(1) The mature male was not able to distinguish the immature male from a mature one and/or a female.

(2) The mature male tried to reinforce his status by showing aggressive behaviour immediately the group was set up, and in one case again when the younger individual reached maturity.

As the dominant male is always the mature male and the mature male generally shows homosexual behaviour, it appears that such sexual behaviour is involved in the setting-up of the male's status.

VI. 3.7 - Sexual behaviour among males in newly established groups

VI. 3.7.1 - Sexual behaviour in *Nauphoeta cinerea*

Four groups of five males kept in isolation for the whole nymphal period and for various lengths of time after the final moult were established and any homosexual and pseudofemale behaviour observed.

In two of these groups (3, 4) homosexual and pseudofemale behaviour were seen. In all four groups agonistic behaviour started immediately after the groups were set up.

In group 3 the ages of individuals 1 to 5 were 21-, 20-, 20-, 14- and 3-days-old respectively. Homosexual and pseudofemale behaviour were observed on the first and second day after establishment of the groups. In an observation period of one hour homosexual behaviour was shown by males 1, 2, 3 and 4 towards male 5 which was three/four-days-old. Individual 1, which later became the dominant male, showed homosexual courtship more frequently than the others. Male 5 showed pseudofemale behaviour only twice towards male 3. It retreated from all approaches by the other males.

In group 4 the ages of individuals 1 to 5 were 36-, 26-, 20-, 18- and 1-day-old respectively. Homosexual behaviour was observed for three consecutive days. Males 1, 2, 3 and 4 showed homosexual behaviour towards male 5 which was one, two and three-days-old acording to the day. Pseudofemale behaviour was observed only once and was shown by male 1 towards male 4. Male 5 retreated from all approaches.

Usually the acts which precede homosexual courtship behaviour are the least intensely agonistic. They consist primarily in approach →antennation and/or step-on.

The other groups (1 and 2) where homosexual behaviour was not observed the youngest males were nine- and five-days-old respectively.

In the two groups of N. cinerea kept in isolation after the final moult no homosexual/pseudofemale behaviour was observed. In both groups the youngest male was six- and five-days-old respectively.

VI. 3.7.2 - Sexual behaviour in Henchoustedenia flexivitta

In the two groups of H. flexivitta kept in isolation after the final moult no homosexual or pseudofemale behaviour was not observed before day 11. In group 1 the age-structure was six-, five-, four-, and two-days-old. During the first two days after being put together males showed mutual antennation and only on the third day of observation was agonistic behaviour observed.

In group 2 the age-structure was eleven-, ten-, seven-, four- and zero-days-old. Agonistic behaviour was performed by individuals 1 and 2 immediately after being put together in the group.

These results for both species showed that young immature males less than three-days-old did not show homosexual behaviour. They are courted and very often showed pseudofemale behaviour. Homosexual behaviour was observed only in groups where there was a male three or less days old. It appears in that case that other males in the group were not able to distinguish this immature male from a female. This suggestion is supported by the fact that after two or three days homosexual behaviour was not observed anymore unless a female was introduced and then removed from the group after a certain period.

The homosexual behaviour observed in N. cinerea was not due to the fact that these males were strange to each other. In groups of males established immediately after the final moult, this behaviour developed in some groups by the fourth day after the final moult. These results disagree with those of Bell & Gorton (1978) when they suggested that in N. cinerea the homosexual behaviour is correlated with the association of strange males. It is not due also to the novel environment for the same reason.

VI. 3.8 - Sexual behaviour in mixed groups established during the nymphal instars

VI. 3.8.1 - Sexual behaviour in adult N. cinerea in groups established on the day of the nymphs hatching

Three groups of five individuals were observed. Group 1A was composed by two males and three females. A summary of sexual behaviour in this group is given in Appendix VI.1.

It is interesting to note that three females were courted on the day of their adult emergence by the only male present in the group by that time, and that copulation had probably occurred by the time the females were four-days-old as courtship then ceased (Appendix VI.1).

Group 1B of N. cinerea was composed of three males and two females. The sequential summary of sexual behaviour observed in this group is given in Appendix VI.2.

The data (Appendix VI.2) show that very consistent patterns of behaviour occurred in group 1B:

- Adult males and females can be courted on the day of adult emergence.
- Female nymphs in the last instar can be courted and can respond by mounting and showing feeding behaviour.
- Adult females can respond to a courtship as early as on the day of emergence.
- Males which show pseudofemale responses do so from day three to day ten.
- Stridulation was used by males courting males and females.
- Dominant males show homosexual behaviour towards the subordinates while the latter show pseudofemale behaviour.
- Dominant males which show homosexual behaviour are the first to court the new females in the group.
- Intensive female courtship is always shown by the dominant male.
- After the appearance of females in the group homosexual courtship ceases completely.

The events observed in this group (1B) may support the following hypothesis:

- Mature males are unable to distinguish immature males from females during the first three days after adult emergence.
- Males in a very stressed condition may court nymphs and

immature adults indiscriminately. - Homosexual behaviour is linked to dominant males and

pseudofemales behaviour to subordinate males. - Dominant males have a tendency to engage in more sexual

behaviour than the subordinate. - Possibly the male dominant pheromone "seducin" attracts

immature males and females although their response in mounting and dorsal feeding in the latter is not always related to their sexual receptivity.

Several authors had linked the N. cinerea male pheromone to two functions, i.e. attraction of the female and arousal of fighting behaviour in males. Such attraction might include immature males and might be important for the reinforcement of dominant status. When the males of the group were all mature and females were present homosexual behaviour ceased and fighting among males increased.

Group 1C of N. cinerea was composed of one male and four females. Although sexual behaviour was seldom observed the male started to show a posture with the abdomen extended and flexed upwards from the age of four-days-old and the oldest female was observed showing an ootheca when she was 13-days-old; another female was courted by the male when she was four-days-old.

VI. 3.8.2 - Sexual behaviour in adults N. cinerea in groups established in the penultimate nymphal instar

Three groups of five individuals were observed after the final moult of the component members. Group 1D was composed of three males and two females. Sexual behaviour observed in this group is summarized in Appendix VI.3.

In this group (1D) the sequence of acts during courtship behaviour was very variable especially when the female was not receptive or during homosexual courtship. Acts such as stridulation, abdominal extension, phallomere extrusion, step-on and climbing were frequently observed. It is clear that in normal courtship when the female is receptive the pre-copulatory phase is rapid and consists of a very simple sequence of acts such as approach→antennation→wing raising and jerking. In cases of homosexual courtship and when the female is not receptive this behaviour may take a long time and comprises more and variable acts including especially stridulation and several jerks. Probably this variable sequence strongly attracts females and immature males, as even unreceptive females can respond to this attraction by mounting and carrying out dorsal feeding acts.

The results obtained in group 1D (Appendix VI.3) are comparable to those obtained in group 1B (Appendix VI.2). In group 1D (Appendix VI.3) homosexual behaviour by males 4 and 2 was observed for the first time when male 5 had its final moult and by that time the two females in the group were supposed to be pregnant.

In group 1E of N. cinerea, composed of two males and three females, sexual behaviour was observed only once. In this group (1E) two females 20- and 22-days-old were established in the group when the first male had its final moult. Male 2 (nine-days-old) frequently showed phallomere extrusion and was observed courting female 3 when she was five-days-old.

In group 1F of N. cinerea, composed of three males and two females, courtship of the females was performed by all three males (since they were three-days-old).

No homosexual behaviour was observed in groups 1E and 1F. This could be explained by the fact that in group 1E the sequence of final moulting was: female 4 (day 0) - female 5 (day 2) - male 2 (day 21) - female 3 (day 25) - male 1 (day 28). Perhaps male 2 did not show homosexual behaviour towards male 1 because at that time there was a three-day-old female in the group. It was not possible to suggest any explanation for the absence of homosexual behaviour between male 5 and male 2 in group 1F: possibly it occurred outside the observation periods.

VI. 3.8.3 - Sexual behaviour in adults of *Henchoustedenia flexivitta* in groups established on the day of nymphs hatching

Two groups of five individuals were set up and observed after adult emergence. Group 1A was composed of four males and one female. A summary of the sexual behaviour in this group is given in Appendix VI.4.

V In group 1A of *H. flexivitta* (Appendix VI.4) the results were very similar to those obtained for *Nauphoeta cinerea* (Appendices VI.2 and VI.3). The homosexual behaviour of dominant males towards subordinates observed followed the same sequence as adult moulting, and seemed to reinforce the males status in the group. When the female underwent final moulting, the male hierarchy was stable in this sequence 1 → 3 → 2 → 4 and courting was not observed before she was five-days-old. However, at five-days-old she was courted by males 1, 2 and 3. Intensive courtship of the female was performed by male 2. For the first time males 1 and 3 were also courted by male 2, and male 2 attempted to copulate with male 3 which showed pseudofemale behaviour. It seemed that the presence of one receptive female in the group disrupted the male hierarchy, as on this day male 2 won more fights than any other male in the group.

Interestingly, male 2 showed homosexual courtship towards all other males in the group suggesting that this behaviour possibly has a role in the reinforcement of the male status.

Group 1B was composed of only two males and one female since two individuals died during nymphal instars. When the female underwent its final moult the males were 45- and 33-days-old and male 2 (45-days-old) was dominant. The summary of sexual behaviour observed in this group is given in Appendix VI.5.

In this group (1B), unlike 1A, the appearance of a female did not change male status. However, after the appearance of a female in the group no more homosexual display was observed.

In all groups of <u>Nauphoeta</u> <u>cinerea</u> and <u>Henchoustedenia</u> <u>flexivitta</u> most of the events followed a consistent pattern, e.g. homosexual behaviour and intensive courtship of new females was performed by the dominant males in the group.

VI. 3.8.4 - Sexual behaviour in adults of <u>Henchoustedenia</u> <u>flexivitta</u> in a group established in the penultimate nymphal instar

Only one group was established. Observations started after the component members had their final moult. The group (1D) was composed of two males with a gap of only one day between adult emergence and three females. The summary of sexual behaviour observed in group 1D is given in Appendix VI.6.

Homosexual behaviour in group 1D was observed only once, but followed the same behaviour pattern of other groups, i.e. was shown by the older and dominant male.

In both species there was a very consistent sexual behaviour pattern in relation to male hierarchy in the groups. These results support the hypothesis that sexual behaviour might have a role in hierarchy formation and in the reinforcement of male status. Spontaneous homosexual courtship sequences were very common in Nauphoeta cinerea and Henchoustedenia flexivitta. This behaviour was observed also for other cockroach species such as Leucophaea maderae (Roth & Barth, 1967), Periplaneta spp and Blatta orientalis (Simon & Barth, 1977c).

Genital connection in homosexual courtship is rarely achieved. In N. cinerea it was observed occurring twice for a few seconds, while it was never observed in H. flexivitta.

The results obtained here for N. cinerea do not support the hypothesis proposed by Fukui & Takahashi (1980) that the wing-raising display by males was elicited by recognition of mature females through antennal contact with the female body surface. Males of N. cinerea were commonly observed displaying wing-raising to females and males of zero-, one- and two-days-old, and even to last instar female nymphs.

In summary in both N. cinerea and H. flexivitta the onset of courtship occurred slightly before the onset of fighting. The first male to initiate a courtship always became dominant in the group. The dominant males very commonly showed homosexual behaviour and the subordinate showed pseudofemale behaviour.

General Discussion

Sociality confers considerable advantages upon animals: the social insects and in particular the ants are of great significance because of their geographical range, biomass and consequent economic and ecological impact. In many tropical areas the termites also assume considerable importance. For these reasons and because of the inherent fascination of the phenomenon, social behaviour in insects has been intensively studied. The evolution of social behaviour is of particular interest and there is no consensus about the selective pressures that brought it about: undoubtedly many factors have been involved. It is therefore potentially useful to examine the subsocial insects as an aid to understanding this problem. The cockroaches are ideal candidates for such a project as they are closely related to the termites and, indeed, some authorities place both the cockroaches and the termites within a single order, the Dictyoptera.

The termites together with many of the Hymenoptera such as ants and wasps are termed 'truly social' or eusocial and show the following characteristics: co-operative brood care, overlap between generations and reproductive casts. The criptocercid cockroaches also show generation overlap and they, along with the termites are the only wood-eating insects which rely on symbiotic intestinal flagellates. This factor may help to explain how social life may have evolved in this case as a degree of social interaction would facilitate the transference of the flagellates across generations.

Dominance behaviour and aggression have been documented for many social and subsocial insects. In many of these cases there is a relationship between social status and physiological state and it has been shown that the behaviour of one individual can influence the development of others. In the hierarchical social system of the wasp Polistes the queen establishes her dominant position and controls the other wasps by direct aggressive behaviour. This behaviour has the effect of inhibiting development of the worker wasps' ovaries. Polistes workers also form a hierarchy among themselves and those that emerge early tend to become dominant over those emerging later. I have shown that this latter phenomenon also occurs in Nauphoeta cinerea and in Henchoustedenia flexivitta.

The development of social relationships between individuals of N. cinerea and H. flexivitta is influenced by three main facts which are -

(a) Isolation following last moult. The suppression of mutual interactions between males after the final moult can delay the onset of fighting. Thus normal social interactions appear to facilitate maturation of the behaviour and the establishment of dominant/subordinate relationships.

(b) Effects of males of different ages. Males that emerge first become dominant over those that eclose later. The presence of older males who behave aggressively affects the development of agonistic behaviour in young males. In these fighting is delayed and may even be totally suppressed. By contrast, the presence of younger males can lead to the acceleration of aggression in older males. A consequence of this effect is that within a group there is a tendency, at least initially, for there to be higher levels of aggression when the males are of a similar age than when there are large discrepancies in their ages.

(c) Presence of females. Even after the establishment of a stable dominance hierarchy within a group of males the introduction of females can lead to increased levels of aggression and to a change in the hierarchy.

These factors suggest that the social organisation found within groups of these two cockroach species is to a great extent a consequence of the order and timing in which males moult to the adult stage. Of particular interest in this respect was the large range of development times that was found. The social advantages of rapid development appear to be considerable and it would be interesting to identify the underlying control mechanisms, genetic, social and environmental, which influence development time. Two lines of enquiry would be worthwhile. Ethological observations of groups of cockroaches at different stages in their life cycle in large arenas would give an indication as to whether the factors outlined above in fact operate in a more natural situation. By contrast, a more experimental approach of using animals of different ages isolated for various periods could be used to characterise the factors more precisely and to see, for example, if critical periods were involved or whether any of the effects of isolation were permanent.

During the development of the social relationships in both species of cockroach males were often observed to exhibit pseudo-female and homosexual behaviour. Within a group of males homosexual behaviour was always performed by dominant males towards subordinates while the latter displayed pseudo-female behaviour. There are several possible functional explanations of this behaviour.

(a) The secretions of the tergal glands are eaten by females during courtship and by subordinate males during pseudo-female behaviour. It is possible that components of the secretions could have a direct effect upon males in maintaining them in a state of submission.

(b) Courtship feeding is a widely observed phenomenon in animals including insects. It was originally thought that this behaviour had a ritual significance only but it is now known that in many cases there is a considerable nutritional component. Thus subordinate males may be dominants by feeding on the latter's tergal gland secretions.

(c) The pseudo-female behaviour of subordinates may have the effect of reducing dominant male aggression with the consequent possibility of attack and physical injury.

Whether one or more of the above explanations is correct, one possible effect of the subordinate male behaviour is to enable him to remain in the vicinity of the dominant and thus gain access to females and possible mates. It is known that females are attracted to dominants and this type of strategy by subordinates has been widely reported as for example in Red Deer and crickets. It would certainly be unwise to conclude that benefits of homosexual and pseudo-female behaviour accrued mainly to the dominant individuals. The different hypotheses outlined above are capable of being tested: radioactive assays have been used to measure nutrient transfer during different stages of courtship and copulation and could certainly be used here. Extracts of the tergal glands could perhaps be extracted and fed to socially naive males and the effects on development of aggressive behaviour assayed.

There appeared to be a tendency for levels of aggressive behaviour to increase during the successive larval stages and this trend was clearest in N. cinerea. The repertoire of aggressive acts did not change throughout this period but the more aggressive acts characteristic of adults were observed infrequently in nymphs. Unlike adults the aggressive behaviour of nymphs did not result in the creation of a dominance hierarchy and dominant - subordinate relationships were not observed in the larval stages. The development of aggressive behaviour in nymphs is correlated with the occurrence of spacing. Larvae normally clump together and show levels of aggression but during the last instar the nymphs start to space out and disperse and this is accompanied by longer durations of aggressive encounters.

The natural habitats of N. cinerea and H. flexivitta are not known with certainty. The former species is in any case domiciliary and has spread from its original habitat in East Africa and is now widely distributed in the tropical and sub-tropical regions of the world. By contrast H. flexivitta, although occasionally reported a pest in greenhouses, is normally restricted to its original habitat. It is clear from their morphology and behaviour that these species are closely related and probably do not merit separate generic status. It is interesting to speculate of the relative success of these two species. Certainly there appears to be nothing in their behaviour or life cycles, as observed in the laboratory at least, to account for the differences. The species have almost identical behavioural repertoires while generation time and fecundity are only slightly less advantageous in H. flexivitta. It is perhaps significant that this species initially proved much more difficult to culture than did N. cinerea. A comparative study on the abilities of the two species to withstand environmental stress and their food and space requirements might be instructive.

VII. SUMMARY

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The objective of the present study was to investigate the development of social interactions in two closely related species of cockroach: Nauphoeta cinerea (O.) and Henchoustedenia flexivitta (W.).

Several aspects of nymphal development were considered together with the behaviour of immature males and the results obtained were the following:

(1) Nymphal development

Experiments were designed to evaluate the relationship between time of moulting and hierarchy formation.

Moulting in N. cinerea and H. flexivitta is not synchronized. In groups of five individuals there was considerable variation in moulting time.

In N. cinerea nymphal development took 134 ± 7 days for males and 146 ± 55 for females whilst in H. flexivitta the development took 131 ± 32 days for males and 137 ± 53 days for females. The number of moults also varied among individuals. In N. cinerea there were eight to nine moults in males and eight to ten moults in females. In H. flexivitta both sexes had eight to nine moults.

The males of both species had shorter instar duration than females. The first male to moult in the first instar continues to be first in all the following instars and becomes top-ranking when he reaches adulthood.

(2) Spacing-patterns

N. cinerea and H. flexivitta show gregarious behaviour throughout their nymphal instars. In N. cinerea nymphs the gregarious behaviour peaked at the sixth instar and decreased afterwards, while in H. flexivitta the gregarious behaviour was most developed in the third instar.

During the first days of adult life the individuals are still sociable. The tendency for N. cinerea males to space themselves increases after the third day following the final moult while in H. flexivitta this behaviour increases after the fourth day. The loss of gregarious behaviour in males coincides with the onset of fighting. The females of both species were still gregarious until at least 10 days after emergence.

(3) Agonistic behaviour in nymphs

Hierarchy does not appear to exist during nymphal instars although almost the entire agonistic behaviour pattern of adult males is displayed by the nymphs of both species. However, aggressive acts are infrequently observed. Usually, the nymphs in their encounters use simple non-aggressive acts such as approach, antennation and step-on.

There is an increase of aggressiveness during the nymphal development in N. cinerea, but this was not observed in H. flexivitta.

(4) Agonistic behaviour in adult males

In N. cinerea the onset of fighting in males occurs on the fourth day after adult emergence and in H. flexivitta on the sixth day. The dominance-subordinate relationship is then established as a result of fighting.

In the first four days of adult life in both species the most common acts performed by dominant and subordinate males were: approach, antennation and step-on. After the onset of fighting, unless homosexual behaviour occurs, step-on is not observed. Thereafter encounters consist primarily of lunging by one individual and retreating by another in N. cinerea. In H. flexivitta the encounters also consist of lunging and retreating but intention movements such as stilt-posture, stilt-walk and jerk are frequent.

(5) Influence of maturity on the establishment of male hierarchy

Social contact with mature males delays the onset of fighting in young males whereas contact with other young males tend to accelerate it.

In N. cinerea when a mature and an immature male are paired, the mature individual is generally dominant. The subordinate (younger male) responds to agonistic encounters by retreating or showing submissive behaviour.

(6) Influence of isolation on the establishment of male hierarchy

Isolation after the final moult can affect the hierarchy formation, as after isolation the male dominance hierarchy does not follow the sequence of adult moulting. Isolation can also delay the onset of fighting.

(7) Sexual behaviour

Onset of courtship appears on the second to fourth day after the final moult in both species. The male who first initiates courtship always becomes dominant.

In both species, the introduction of sexually mature females into the group may cause disruption of the previously established male hierarchy.

Homosexual courtship was often observed in both species. The dominant male very frequently shows homosexual behaviour while the subordinate shows pseudofemale behaviour. It seems that, sexual, especially homosexual behaviour, is involved in the establishment of dominance-subordinate relationships.

The relationships between maturation and previous social experience is very complex. Clearly, more behavioural experiments are required to clarify some aspects of the situation, especially concerning relations between development of maturity and previous social experience, the role of homosexual courtship and pseudofemale behaviour in the establishment of dominance-subordinate relationships.

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IX. APPENDICES

Appendix V.1 - Behaviour patterns of different individuals within groups of <u>Nauphoeta</u> <u>cinerea</u> (group 1A) (I to VIII represents instars)

I

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	2	6	2			1				4	
2	3	6	1							4	1
3	5	5									
4	2	2									
5											
T	12	19	3	0	0	1	0	0	0	11	1

$\chi_n^2 = -1.02$; df = 3 (NS)

II

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	5	5								3	
2	1	1									1
3											
4	2	2	1					2		2	
5	2	5	2	1			1			1	1
T	10	13	3	1	0	0	1	2	0	6	2

$\chi_n^2 = 1.62$; df = 3 (NS)

III

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1											
2	1	1									
3											
4	3	3	1								
5	1	4					4				2
T	5	8	1	0	0	0	4	0	0	0	2

$\chi_n^2 = -2.76$; df = 3 (NS)

IV

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	3	3		1						1	
2	4	3	1								2
3	1					1					1
4	1	1									1
5	1	2	1								
T	10	9	2	1	0	1	0	0	0	1	4

$\chi_n^2 = 10.5$; df = 3 ($p \leq .05$)

V

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	2	3	1							2	
2	2		1	1				1			1
3	6	7		1						5	1
4	1		1								
5	2	14					1			1	1
T	13	24	3	2	0	0	1	1	0	8	3

$\chi_n^2 = 2.82$; df = 3 (NS)

VI

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	8	4	5	1						2	
2	5	3	1	2				1		1	1
3	3	1	3						1		2
4	1		1								1
5	3	2	1		10	3	1	1			
T	20	10	11	3	10	3	1	2	1	3	4

$\chi_n^2 = 6.24$; df = 4 ; (NS)

VII

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	1	1								1	
2	17	5	12	3	1	1	2		3	3	2
3	5	4	3	1						1	
4	2		1						1		1
5	3	2	1	1			2	1		1	1
T	28	12	18	5	1	1	4	1	4	6	4

$\chi_n^2 = 2.24$; df = 4 (NS)

A = Acts ; I = Individuals

VIII

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	11	2	10						2	3	2
2	2	4	3							1	2
3	3	1	3								1
4	1			1							1
5	5	1	5			2	2				
T	22	8	21	1	0	2	2	0	2	4	6

$\chi_n^2 = 4.92$; df = 4 (NS)

Appendix V.1 - Behaviour patterns of different individuals within groups of <u>Nauphoeta</u> <u>cinerea</u> (group 1B)
(cont'd) (I to VIII represents instars)

I

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	4	7								3	
2	2	2	2							1	
3	4	4								1	
4	3	3	2							1	
5	2	3	2	1					1	1	
T	15	19	6	1	0	0	0	0	1	7	0

$\chi^2_r = 9.42$; df = 3 ($p \leq .05$)

II

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	3	2									1
2	2	1	1					1		2	
3	1	1	1							1	
4											
5	3	2	1								
T	9	6	3	0	0	0	0	1	0	3	1

$\chi^2_r = 3.12$; df = 3 (NS)

III

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	2	2								2	
2	2	5	1							3	1
3	1	2	2								
4	1	1	1							1	
5	1	1								1	
T	7	11	4	0	0	0	0	0	0	7	1

$\chi^2_r = 2.94$; df = 3 (NS)

IV

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	5	1	4	2			1				3
2											
3	3	5	1								2
4	3	11	2	2							3
5	1	1	1								
T	12	18	8	4	0	0	1	0	0	0	8

$\chi^2_r = 2.46$; df = 3 (NS)

V

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1								2			
2											
3											
4	1		1								
5	1	1	1								
T	2	1	2	0	0	0	0	2	0	0	0

$\chi^2_r = 1.32$; df = 3 (NS)

VI

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	1	1									
2	3	4									
3	4	2	2							2	2
4	5	1	3	1				1			3
5	2	1	1			1					1
T	15	9	6	1	0	1	0	1	0	2	6

$\chi^2_r = 5.4$; df = 3 (NS)

VII

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	10	1	8	2		1				2	4
2	2	3	1							1	
3	1		1								1
4	2		1	1							1
5	8		7	3					1		5
T	23	4	18	6	0	1	0	0	1	3	11

$\chi^2_r = 6.36$; df = 3 (NS)

A = Acts ; I = Individuals

VIII

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	2	1	2								1
2	3	2	1	3						1	1
3	3	2	2			1				1	
4	1	1									
5	2		3								2
T	11	6	8	3	0	1	0	0	0	2	4

$\chi^2_r = 4.74$; df = 3 (NS)

Appendix V.1 - Behaviour patterns of different individuals
(cont'd) within groups of <u>Nauphoeta</u> <u>cinerea</u> (group 1C)
(I to VIII represents instars)

I

A I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	2	4	1						1	1	1
2	3	3									
3	2	5								1	
4		1					1				
5	3	2	1								1
T	10	15	2	0	0	0	1	0	1	2	2

$\chi^2_{\wedge} = 9.18$; d f = 3 ($p \leq .05$)

III

A I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1											
2	2	5	1	1		1					
3	3	1	3				1		1		
4			3							1	1
5	3	3						2		3	
T	12	11	7	1	0	1	1	2	1	4	1

$\chi^2_{\wedge} = 3.0$; d f = 3 (NS)

V

A I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	1	2								1	
2	4	2	4	1						1	2
3	3	2	1								
4	5	1	3	1							1
5	2		2								1
T	15	7	10	2	0	0	0	0	0	2	4

$\chi^2_{\wedge} = 4.98$; d f = 3 (NS)

VII

A I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	5	2	1	4							
2	1			1							
3	6	2	5					1		2	2
4	2	1	2			1	1				1
5	1		1							1	
T	15	5	9	5	0	1	1	1	0	3	3

$\chi^2_{\wedge} = 7.46$; d f = 4 (NS)

A = Acts ; I = Individuals

II

A I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1											
2		4		1							
3											
4	1	1								1	
5											
T	1	5	0	1	0	0	0	0	0	1	0

$\chi^2_{\wedge} = 0.96$; d f = 3 (NS)

IV

A I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	2	1	1	1	1						
2	2	2	2	1						1	
3	1	1	1								
4	1	2		1						1	
5	3	1	1	1							1
T	9	7	5	4	1	0	0	0	0	2	1

$\chi^2_{\wedge} = 5.52$; d f = 3 (NS)

VI

A I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	3		3								1
2											
3	1	1									
4	1		2				1				
5	4		3	1		1					1
T	9	1	8	1	0	1	1	0	0	0	2

$\chi^2_{\wedge} = 4.56$; d f = 3 (N.S)

VIII

A I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	1	1	1								
2	2	1	2								
3	3	2	2								
4											
5	1	1								1	
T	7	5	5	0	0	0	0	0	0	1	0

$\chi^2_{\wedge} = 10.62$; d f = 3 ($p \leq .05$)

Appendix V.2 - Frequencies and proportions of agonistic acts in male and female nymphs in each instar of Nauphoeta cinerea

Instars	I		II		III		IV		V		VI		VII		VIII	
Sex / Acts	M (n=6)	F (n=9)	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Ap	13 .342	24 .264	9 .257	11 .323	12 .273	12 .261	14 .229	17 .362	9 .250	21 .318	15 .268	29 .381	20 .328	46 .346	12 .343	28 .325
An	17 .447	36 .396	11 .314	13 .382	14 .348	16 .348	22 .361	12 .255	15 .417	17 .257	6 .107	14 .184	4 .065	17 .128	5 .143	14 .163
So	2 .053	9 .099	4 .114	2 .059	7 .159	5 .109	8 .131	7 .149	5 .139	10 .151	9 .161	16 .210	14 .229	31 .233	9 .257	25 .291
Bu		1 .011	1 .028	1 .029		1 .022	5 .082	4 .085	1 .028	3 .045	1 .018	4 .053	4 .065	12 .090	1 .028	3 .035
Bi								1 .021			10 .178			1 .007		
K		1 .011				1 .022		1 .021			3 .053	2 .026	2 .033	1 .007	3 .086	
Sp	1 .026		1 .028		4 .091	1 .022	1 .016		1 .028		2 .036		3 .049	2 .015	2 .057	
J			2 .057	1 .029		2 .043			2 .055	1 .015	2 .036	1 .013	1 .016	1 .007		
Cl		2 .022				1 .022						1 .013	1 .016	4 .030		2 .023
T	5 .131	5 .165	5 .143	5 .147	4 .091	7 .152	2 .033	1 .021	1 .028	9 .136	2 .036	3 .039	3 .049	9 .068	1 .028	6 .070
R / W		3 .033	2 .057	1 .029	3 .068	1 .022	9 .147	4 .085	2 .055	5 .076	6 .107	6 .079	9 .147	9 .068	2 .057	8 .093
Sum	38	91	35	34	44	46	61	47	36	66	56	76	61	133	35	86
Total	129		69		91		108		102		132		- 194		121	

Appendix V.3 - Frequencies and proportions of agonistic acts in each instar of Nauphoeta cinerea (groups 1A, 1B, 1C)

Instars	I			II			III			IV			V			VI			VII			VIII		
Groups / Acts	1A	1B	1C	1A	1B	1C	1A	1B	1C	1A	1B	1C	1A	1B	1C	1A	1B	1C	1A	1B	1C	1A	1B	1C
Ap	12 .255	15 .306	10 .303	10 .263	9 .391	1 .125	5 .250	7 .233	12 .292	10 .357	12 .235	9 .310	13 .236	2 .286	15 .375	20 .015	15 .366	9 .391	28 .333	23 .343	15 .349	22 .323	11 .250	7 .389
An	19 .404	19 .387	15 .454	13 .342	6 .261	5 .625	8 .400	11 .366	11 .268	9 .320	18 .352	7 .241	24 .436	1 .143	7 .175	10 .147	9 .219	1 .043	12 .143	4 .060	5 .116	8 .118	6 .136	5 .278
So	3 .063	6 .122	2 .061	3 .079	3 .130		1 .050	4 .133	7 .170	2 .071	8 .157	5 .172	3 .054	2 .286	10 .250	11 .162	6 .146	8 .348	18 .214	18 .269	9 .209	21 .309	8 .188	5 .278
Bu		1 .020		1 .026		1 .125			1 .024	1 .035	4 .078	4 .138	2 .036		2 .050	3 .044	1 .024	1 .043	5 .059	6 .089	5 .116	1 .015	3 .068	
Bi												1 .034				10 .147			1 .012					
K	1 .021								1 .024	1 .036						3 .044	1 .024	1 .043	1 .012	1 .015	1 .023	2 .030	1 .022	
Sp			1 .030	1 .016			4 .200		1 0 4		1 .019		1 .018			1 .015		1 .043	4 .047		1 .023	2 .030		
J				2 .053	1 .043				2 .048				1 .018	2 .286		2 .030	1 .024		1 .012		1 .023			
Cl		1 .020	1 .030						1 .024							1 .015			4 .047	1 .015		2 .030		
T	11 .234	7 .143	2 .061	6 .158	3 .130	1 .125		7 .233	4 .097	1 .036		2 .069	8 .145		2 .050	3 .044	2 .048		6 .071	3 .045	3 .070	4 .060	2 .045	1 .055
R	1 .021		2 .061	2 .053	1 .043		2 .100	1 .033	1 .024	4 .143	8 .157	1 .034	3 .054		4 .100	4 .059	6 .046	2 .086	4 .047	11 .164	3 .070	6 .090	4 .090	
Sum	47	49	33	38	23	8	20	30	41	28	51	29	55	7	40	68	41	23	84	67	43	68	35	18
Total	129			69			91			108			102			132			194			121		

Results of Friedman-test: $(\chi^2_r) \rightarrow n = 3$ groups ; $K =$ acts .

I (χ^2_r)= 10.74 ($P \leq .05$); II (χ^2_r) = 7.49 (NS) ; III (χ^2_r) = 5.93 (NS) ;

IV (χ^2_r) = 7.68 (NS) ; V (χ^2_r) = 2.55 (NS) ; VI (χ^2_r) = 4.04 (NS) ;

VII (χ^2_r) = 9.05 ($P \leq .05$) ; VIII (χ^2_r) = 8.72($P \leq .05$).

Appendix V.4 - Behaviour patterns of different individuals within groups of <u>Henchoustedenia flexivitta</u> (group 1A)
(I to VIII represents instars)

I

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	4	8	1		1	1	3				2
2	3	4	3						1		1
3	6	6			1					2	3
4	1	2	1				1				1
5											
T	4	20	5	0	2	1	4	0	1	2	7

$X^2_{\wedge} = 7.0$; df = 4 (NS)

II

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	1	3	1	1							
2	4	1	2	1				1			1
3	7	3	6		2				1		3
4	1	1						2			1
5	11	2	9		1		4		3		5
T	24	10	18	2	3	0	4	3	4	0	10

$X^2_{\wedge} = 6.9$; df = 4 ;(NS)

III

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	3	2	2				1	1			
2	4	2	2								
3	6	3	6					3	1		1
4	2	1	3	1	1						
5	6	3	5			1			3		3
T	21	11	18	1	1	1	1	4	4	0	4

$X^2_r = 14.4$; df = 4 ($P \leq \cdot 05$)

IV

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	18	7	17		6						16
2	3	2	2	1		1		5			1
3	9	5	9						2		6
4	3	4	2		1						1
5	1		1				2				
T	34	18	31	1	7	1	2	5	2	0	24

$X^2_r = 5.88$; df = 4 ;(NS)

V

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	7	5	2	1	1					1	4
2	9		7	1							7
3	10	4	7		3		1			1	6
4	9	3	6		1	1	1	2			6
5	5	5	1	3		1		1			2
T	40	17	23	5	5	2	2	3	0	2	25

$X^2_r = 9.44$; df = 4 ; ($P \leq .05$)

VI

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	17	2	17			1	1				9
2	11	3	10		3	1			4		6
3	15	3	11	2					1		5
4	6	4	2				1				1
5	5	3	5						2		3
T	54	15	45	2	3	2	2	0	7	0	24

$X^2_r = 14.2$; df = 4 ; ($P \leq .05$)

VII

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	12	3	12	2		1	1		1	1	1
2	3		3	1							1
3	4	1	2			1					3
4	8	2	6	1					2	2	3
5											
T	27	6	23	4	0	2	1	0	3	3	8

$X^2_r = 9\ 48$; df = 4; ($P \leq \cdot 05$)
A = Acts ; I = Individuals

VIII

I \ A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	1		1								
2	2	1	3						1		1
3	3	2	2							1	1
4	2		2						2		2
5	3	2	1							1	1
T	11	5	9	0	0	0	0	0	3	2	5

$X^2_r = 13.$; df = 3 ; ($P \leq .05$)

Appendix V.4 - Behaviour patterns of different individuals
(cont'd) within groups of <u>Henchoustedenia</u> <u>flexivitta</u>
(group 1B)
(I to VIII represents instars)

I

A/I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	2	2	2					1	2		
2	1		2				2				1
3	8	5	7	1					1		7
4	4	2	4	1		4		3			2
5	5	6	1				2		1	1	3
T	20	15	16	2	0	4	4	4	4	1	13

$X_r^2 = 2.72$; d f = 4 ; (N S)

II

A/I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	4	4	1		1						2
2	4	4	1								2
3											
4	2	3						1			1
5	2	5	1								1
T	12	16	3	0	1	0	0	1	0	0	6

$X_r^2 = 8.46$; d f = 3 ; (N S)

III

A/I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	5	3	2								4
2	6	4	6								
3	4	3	2	1				2			1
4	5		5	1	2						4
5											
T	20	10	15	2	2	0	0	2	0	0	9

$X_r^2 = 5.7$; d f = 3 ; (N S)

IV

A/I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	6		6				1				2
2	13	4	11								10
3											
4	3	1	2	1							
5											
T	22	5	19	1	0	0	1	0	0	0	12

$X_r^2 = 7.7$; d f = 3 ; (N S)

V

A/I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	10	1	10						4		5
2						2	1				
3											
4	6	5	1					1	1	2	2
5											
T	16	6	11	0	0	2	1	1	5	2	7

$X_r^2 = 0.27$; d f = 4 ; (N S)

VI

A/I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	2	1	1						1	1	1
2	1		1								
3											
4	6	5	4						1	2	1
5											
T	9	6	6	0	0	0	0	0	2	3	2

$X_r^2 = 4.5$; d f = 3 ; (N S)

VII

A/I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	2		2						1		
2	1		1								1
3											
4	4	1	4								1
5											
T	7	1	7	0	0	0	0	0	1	0	2

$X_r^2 = 5.4$; d f = 3 ; (N S)
A = Acts ; I = Individuals

VIII

A/I	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1											
2	2	2								1	1
3											
4											
5											
T	2	2	0	0	0	0	0	0	0	1	1

$X_r^2 = 4.0$; d f = 3 ; (N S)

Appendix V.4 - Behaviour patterns of different individuals
(cont'd) within groups of <u>Henchoustedenia</u> <u>flexivitta</u>
(group 1C)
(I to VIII represents instars)

I

I\A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	2	2	1								1
2	4	2	3				1				
3	3	3	3						1		3
4	1		1								1
5	7	1	4	2					2		5
T	17	8	12	2	0	0	1	0	3	0	10

$X_r^2 = 3.48$; d f = 3 ; (NS)

II

I\A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	1			1		1					
2	4	8	4		1		1		1		1
3	3		3						1		1
4	1	2								1	1
5	7	6	5	1	1				1		2
T	16	16	12	2	2	1	1	0	3	1	5

$X_r^2 = 4.4$; d f = 4 ; (NS)

III

I\A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1							2	1			
2	1	1									1
3	11	6	11				1		2		8
4	5	4	1				4			1	2
5											
T	17	10	13	0	0	0	7	1	2	1	11

$X_r^2 = .35$; d f = 4 ; (NS)

IV

I\A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	12	3	7	2	1		1		1	1	5
2	7	1	5	1							
3	5	1	4								4
4	4	5	3				5		1		2
5											
T	28	10	19	3	1	0	6	0	2	1	11

$X_r^2 = 5.9$; d f = 4 ; (NS)

V

I\A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	3	1	2								3
2	5	5	4						1		5
3	10	6	8	1				1	2		10
4	5	3	3						2		2
5											
T	23	15	17	1	0	0	0	1	5	0	20

$X_r^2 = 9.9$; d f = 4 ; ($P \leq .05$)

VI

I\A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	4	3	4								2
2	2	2	2								1
3	1	1	1								1
4	7	3	7						3		5
5											
T	14	9	14	0	0	0	0	0	3	0	9

$X_r^2 = 4.05$; d f = 3 ; (NS)

VII

I\A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1	5	3	5								1
2	2		3				1		2		
3	3		3						1		
4	3	3	1	2							3
5											
T	13	6	12	2	0	0	1	0	3	0	4

$X_r^2 = 3.75$; d f = 4 ; (NS)

A = Acts ; I = Individuals

VIII

I\A	Ap	An	So	Bu	Bi	K	Sp	J	Cl	T	R
1											
2	1	1									1
3	4		3				4				
4	1								1		
5											
T	6	0	4	0	0	0	4	0	1	0	1

$X_r^2 = 3.37$; d f = 3 ; (NS)

Appendix V.5 - Frequencies and proportions of agonistic acts in male and female nymphs of <u>Henchoustedenia flexivitta</u>

Instars	**I**		**II**		**III**		**IV**		**V**		**VI**		**VII**		**VIII**	
Sex	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Acts	(n=6)	(n=6)														
Ap	17 .239	18 .295	21 .318	20 .282	26 .342	27 .281	52 .299	32 .348	45 .324	34 .288	52 .359	25 .291	30 .353	17 .333	10 .303	9 .375
An	22 .310	12 .197	16 .242	12 .169	15 .197	16 .167	22 .126	11 .119	13 .093	25 .212	13 .090	17 .198	6 .070	7 .137	5 .151	2 .083
So	9 .127	15 .246	11 .167	16 .225	21 .276	20 .208	47 .270	22 .239	32 .230	19 .161	42 .290	23 .267	26 .306	16 .314	8 .242	5 .208
Bu		1 .016	2 .030	1 .014	1 .013	1 .010	1 .005	4 .043	2 .014	4 .034	2 .014		4 .046	2 .039		
Bi	2 .028		3 .045	2 .028	1 .013		7 .040	1 .011	5 .036		3 .021					
K	1 .014			1 .014		1 .010	1 .005		3 .021	1 .008	2 .014		2 .023			
Sp	6 .084	1 .016		5 .070	1 .013	7 .073	1 .005	8 .087	3 .021		2 .014		1 .012	1 .020		4 .167
J	1 .014		3 .045		4 .053	3 .031	5 .029		2 .014	3 .025						
Cl	3 .042	2 .033	1 .015	5 .070	1 .013	5 .052	2 .011	2 .022	4 .029	6 .051	6 .041	6 .070	4 .046	3 .059	3 .091	1 .042
T	2 .028			1 .014		1 .010		1 .011	2 .014	2 .017	1 .007	2 .023	3 .035		2 .061	1 .042
R / W	8 .113	12 .197	9 .136	8 .121	5 .066	15 .156	36 .207	11 .113	28 .201	24 .203	22 .152	13 .151	9 .106	5 .098	5 .151	2 .083
Sum	71	61	66	71	75	96	174	92	139	118	145	86	85	51	33	24
Total	132		137		171		266		257		231		136		57	

Appendix V.6 - Frequencies and proportions of agonistic acts in each instar of <u>Henchoustedenia</u> <u>flexivitta</u> (groups 1A, 1B, 1C)

Instars	**I**			**II**			**III**			**IV**			**V**			**VI**			**VII**			**VIII**		
Groups **Acts**	**1A**	**1B**	**1C**	**1A**	**1B**	**1C**	**1A**	**1B**	**1C**	**1A**	**1B**	**1C**	**1A**	**1B**	**1C**	**1A**	**1B**	**1C**	**1A**	**1B**	**1C**	**1A**	**1B**	**1C**
Ap	14 .250	11 .250	10 .312	24 .308	8 .348	9 .250	21 .318	15 .349	17 .274	34 .272	22 .367	28 .346	40 .322	16 .281	23 .280	54 .351	9 .321	14 .286	27 .351	7 .389	13 .317	11 .200	2 .333	6 .105
An	20 .357	7 .159	7 .219	10 .128	8 .348	10 .278	11 .167	10 .232	10 .161	18 .144	5 .083	10 .123	17 .137	6 .105	15 .183	15 .097	6 .214	9 .184	6 .078	1 .055	6 .146	5 .143	2 .333	
So	5 .089	11 .250	8 .250	18 .231	2 .087	7 .194	18 .273	10 .232	13 .210	31 .248	19 .317	19 .234	23 .185	11 .193	17 .207	45 .292	6 .214	14 .286	23 .299	7 .389	12 .293	9 .257		4 .250
Bu		1 .023		2 .026		1 .028	1 .015	1 .023		1 .008	1 .017	3 .037	5 .040		1 .012	2 .013			4 .052		2 .049			
Bi	2 .036			3 .038	1 .043	1 .028	1 .015			7 .056		1 .012	5 .040			3 .019								
K	1 .018					1 .028	1 .015			1 .008			2 .016	2 .035		2 .013			2 .026					
Sp	4 .071	2 .045	1 .031	4 .051		1 .028	1 .015		7 .113	2 .016	1 .017	6 .074	2 .016	1 .017		2 .013			1 .013		1 .024			4 .250
J		1 .023		3 .038			4 .061	2 .046	1 .016	5 .040			3 .024	1 .017	1 .012									
Cl	1 .018	3 .068	1 .031	4 .051		2 .055	4 .061		2 .032	2 .016		2 .025		5 .088	5 .061	7 .045	2 .214	3 .061	3 .039	1 .055	3 .073	3 .039		1 .062
T	2 .036					1 .028			1 .016			1 .012	2 .016	2 .035			3 .107		3 .039			2 .057	1 .167	
R	7 .125	8 .182	5 .156	10 .128	4 .174	3 .083	4 .061	5 .116	11 .177	24 .192	12 .200	11 .136	25 .202	7 .123	20 .244	24 .156	2 .214	9 .184	8 .104	2 .111	4 .098	5 .143	1 .167	1 .062
Sum	56	44	32	78	23	36	66	43	62	125	60	81	124	51	82	154	28	49	77	18	41	35	6	16
Total	132			137			171			266			257			231			136			57		

Results of Friedman-test: $(X_r^2) \rightarrow$ II = 4.56 (NS); VI = 7.81 (NS);

VII = 7.94 (NS); VIII = 3.26 (NS).

Results $X^2 \rightarrow$ df = 6: I = 10.94 (NS); III = 8.86 (NS);

IV = 8.97 (NS); V = 5.19 (NS).

Appendix V.7 - Frequencies of agonistic acts in paired adult males of <u>Nauphoeta cinerea</u> (Ages Day 0 to Day 10)

Age-days	0		1		2		3		4		5		6		7		8		9		10	
Status / Acts	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S
Ap	2	6	5	3	3	2	6		3		1		9	1	3		3		3		2	
An	1	10	5	1	1	2			3	1	1	1	6	1	2	1	1		1		1	
So	1	6	2		1	2	3		1		1		3									
Bu											1						1		1			
Bi							1		1				1									
K					2								2									
Sp	1	2	2	3	2	1	2						2		1		1		1		1	
J					2																	
Cl		1																				
T		3	3	2	1	1	1				1	1	4		1				1		1	
W			2		2		1															
L							1		2				1									
G							1		2				1									
Ae								3														
Cr								2						2								
R				1		1		1		4				1								
Sum	5	28	19	10	14	9	16	6	12	5	5	2	29	5	7	1	6	0	7	0	5	0
Total	33		29		23		22		17		7		34		8		6		7		5	

D = Dominant ; S = Subordinate

Appendix V.8 - Frequencies of agnostic acts in adult males of
<u>Nauphoeta</u> <u>cinerea</u> in groups composed of two
males and one female
(Ages Day 0 to Day 10)

Age-days	0		1		2		3		4		5		6		7		8		9		10	
Acts \ Status	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S
Ap	2	2	1			6	4	2	20		12	2	1		1		6		1	1	1	
An	1	2				6	3	3	6	5		2	1		1				1		1	
So	2	2	1			3	2	1	2		1											
Bu									2								1					
Bi									1								2					
K				3																		
Sp						2	2		7		3						1			1		
J									11													
Cl		2					1				3											
T	2	2				6				5			1		1				1		1	
W																						
L									3		4						3					
G									2		3						2					
Ae						1			2													
Cr										1		2										
R								2		3		10						10				
Sum	7	10	2	3	0	24	12	8	56	14	26	16	3	0	3	0	15	10	3	2	3	0
Total	17		5		24		20		70		42		3		3		25		5		3	

D= Dominant ; S = Subordinate

Appendix V.9 - Frequencies of agonistic acts in paired adult males of <u>Henchoustedenia flexivitta</u> (Ages Day 0 to Day 10)

Age-days	0		1		2		3		4		5		6		7		8		9		10	
Acts \ Status	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S
Ap			6	8					3	1	1		18	5	37	4	13	5	32	2	13	2
An			6	8					3		1		14	1	15	4	14	4	9	2		
So																						
Bu																						
Bi													3		14	2	7		16		8	
K																						
Sp											1	1	11	2	9		8	2	3			3
J																						
Cl																						
T			6	8					3		1		2	2	1				6			
W															3	3	2	2	2	8		
L														3	2				16		8	
G															10		3		5		3	
Ae																						
Cr																						
R										1				11		24		11		18		11
Sum	0	0	18	24	0	0	0	0	9	2	4	1	48	24	91	37	47	24	89	30	32	16
Total	0		42		0		0		11		5		72		128		71		119		48	

D= Dominant ; S = Subordinate

Appendix V.10 - Frequencies of agonistic acts in adult males of <u>Henchoustedenia</u> <u>flexivitta</u> in groups composed of two males and one female (Ages Day 0 to Day 10)

Age-days	0		1		2		3		4		5		6		7		8		9		10	
Status / Acts	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S
Ap	2		2				1		1		3	2	10	8	10	6	1		9	3	8	1
An	2						1		1		2	2	6	2	6	2	1		6	2	3	1
So			2																			
Bu																						
Bi														3	2	1			3		4	
K																1				1	1	
Sp			1				1				1	1	2		3	2				2		1
J																						
Cl																						
T	1								1						5	1					3	
W											1		4		3		1		3			
L											1		4	6	3	3			3	1	4	
G														2	2	1			2		2	
Ae																						
Cr																						
R												1		21		3		1		5		2
Sum	5	0	5	0	0	0	3	0	3	0	8	6	26	42	34	20	3	1	26	14	25	5
Total	5		5		0		3		3		14		68		55		4		40		30	

D = Dominant ; S = Subordinate

Appendix VI.1 - Sexual behaviour in *Nauphoeta cinerea* (group 1A)
(The numbers in brackets indicate the age in
days after adult emergence)

Behaviour	Sequence	Participants
Courtship	Ap → J → Sp → Wr	M 5(37) x F nymph 2 – immediately after the 9th moult –
"	"	M5 (52) x F3 (0)
"	Ap → An → J → Wr	M5 (55) x F3 (3)
"	Ap → An → Wr	M5 (56) x F3 (4)
"	"	M5 (59) x F1 (0)
Female response	M → Feeding	F1 (0) x M5 (59)
Attempt copulation		M5 (59) x F1 (0)
Courtship	Ap → An → J → St → Wr	M5 (63) x F2 (0)
"	"	M5 (64) x F2 (1)
"	Ap → An → J → Wr	M5 (66) x F2 (3)
"	Ap → An → Wr	M4 (5) x F2 (14)

Wr = Wing-raising ; M = Mounting ; M5 = Male 5 , and F = Female

Appendix VI.2 - Sexual behaviour in *Nauphoeta cinerea* (group 1B)
(The numbers in brackets indicate the age in
days after adult emergence)

Behaviour	Sequence	Participants		
H. courtship	Ap→J→Wr Ap→Ae→St→J→Wr	M3 (6)	x	M1 (1)
"	Ap→An→J→Wr→Sp	M3 (8)	x	M1 (3)
P. response	M→Feeding	M1 (3)	x	M3 (8)
Attempt copulation		M3 (8)	x	M1 (3)
H. courtship	Ap→An→Sp→Ae→J→Wr	M3 (9)	x	M1 (4)
P. response	Ap→M→Feeding→R	M1 (4)	x	M3 (9)
H. courtship	Ap→An→Sp→J→St→Ae→Wr	M3 (10)	x	M1 (5)
Attempt copulation				"
P. response	Ap→M→Feeding→R	M1 (5)	x	M3 (10)
H. courtship	Ap→An→Ae→Wr	M3 (13)	x	M1 (8)
"	Ap→An→J→Wr	M3 (16)	x	M4 (0)
"	Ap→An→Wr	M3 (17)	x	M4 (1)
"	Ap→An→J→Wr	M3 (20)	x	M4 (4)
Courtship	Ap→An→Ae→Wr	M3 (23)	x	F2 (0)
"	Ap→An→Ae→Wr	M3 (24)	x	F2 (1)
"	Ap→An→Wr	M4 (8)	x	"
F. response	Ap→M→Feeding	F2 (1)	x	M4 (8)
Courtship	Ap→St→J→Wr	M4 (9)	x	F2 (2)
"	"	M1 (21)	x	F2 (3)
H. courtship	Ap→J→Wr	"	x	M4 (10)
P. response	Ap→M→Feeding	M4 (21)	x	M1 (21)
Courtship	Ap→An→Wr	M3 (28)	x	F2 (5)
"	"	M4 (12)	x	"
"	"	M3 (29)	x	F2 (6)
"	"	"	x	F5 (nymph - n)
F. response	Ap→M→Feeding	F5 (n)	x	M3 (29)
Attempt copulation		M3 (29)	x	F5 (n)
Courtship	Ap→An→Wr	M3 (30)	x	F2 (7)
"	Ap→An→Wr→J	M1 (5)	x	"
F. response	Ap→M→Feeding	F2 (7)	x	M3 (30)

Appendix VI.2 - cont'd

Behaviour	Sequence	Participants
Courtship	Ap→An→Wr	M3 (31) × F2 (8)
"	"	M4 (15) × "
"	Ap→An→Wr→J→Wr	M1 (28) × F2 (10)
"	"	M4 (17) × "
"	Ap→An→Wr	M1 (29) × F2 (11)
"	"	M3 (38) × F2 (15)
"	"	× F5 (0)
F. response	Ap→M→Feeding	F2 (15) × M3 (38)
"	"	F5 (0) × "
Courtship	Ap→An→Wr	M3 (39) × F5 (1)
"	"	M1 (34) × "
"	"	M4 (23) × "
F. response	Ap→M→Feeding	F5 (1) × M4 (23)
Courtship	Ap→An→J→Wr	M3 (40) × F2 (16)
"	Ap→An→Wr	" × F5 (2)
"	"	M1 (35) × "
"	Ap→An→J→Wr	M4 (24) × "
F. response	Ap→M→Feeding	F5 (2) × M1 (35)
"	"	" × M4 (24)
Courtship	Ap→An→Wr	M3 (41) × F5 (3)
"	"	M1 (36) × "
"	"	M4 (25) × "
F. response	Ap→M→Feeding	F5 (3) × M3 (41)
"	"	" × M4 (25)
Courtship	Ap→An→J→Wr	M3 (44) × F5 (6)
Attempt copulation		"
F. response	Ap→M→Feeding	F5 (6) × M3 (44)
Courtship	Ap→An→Wr	M1 (43) × F5 (10)
"	"	M4 (32) × "

Appendix VI.3 - Sexual behaviour in <u>Nauphoeta cinerea</u> (group 1D)
(The numbers in brackets indicate the age in days after adult emergence)

Behaviour	Sequence	Participants
Courtship	Ap→An→Wr Ap→An→J→Ae	M4 (3) x F3 (0)
"	Ap→St→Ae→Pe¨	M4 (4) x F1 (0)
F. response	M→ Feeding	F1 (0) x M4 (4)
Courship	Ap→An→Wr	M4 (5) x F3 (2)
"	"	" F1 (1)
"	"	M4 (6) x F3 (3)
"	"	" F1 (2)
"	"	M2 (4) x F3 (3)
"	"	" F1 (2)
"	"	M2 (9) x F3 (8)
"	"	M4 (16) x F1 (12)
"	"	M4 (25) x F1 (21)
H. courtship	"	" M5 (1)
"	Ap→An→Sp→J→Wr	M2 (23) x "
P. response	Ap→M→ Feeding	M5 (1) x M4 (25)
Courtship	Ap→An→Wr	M2 (4) x F1 (22)
H. courtship	Ap→St→Cl→Wr	" M5 (2)
"	Ap→An→Wr	M4 (27) x M5 (3)
"	Ap→So→An→Wr	M2 (25) x "
F. response	Ap→M→ Feeding	F1 (3) x M4 (27)
H. courtship	Ap→An→Wr	M4 (30) x M5 (6)
Attempt copulation		"
Courtship	"	M2 (28) x F1 (26)
H. "	"	" x M5 (6)
P. response	Ap→M→ Feeding	M5 (6) x M4 (30)

¨Phallomere extrusion

Appendix VI.4 - Sexual behaviour in <u>Henchoustedenia</u> <u>flexivitta</u>
(group 1A)
(The numbers in brackets indicate the age in days after adult emergence)

Behaviour	Sequence	Participants
H. courtship	Ap → J → Wr	M1 (11) x M3 (3)
"	"	M1 (18) x M3 (10)
"	Ap → An → Wr → J	M1 (24) x M2 (4) " M4 (1)
"	Ap → Wr	M1 (39) x M4 (16)
"	"	M3 (31) x M2 (19)
"	"	" M4 (16)
P. response	M → Feeding	M2 (19) x M3 (31)
Courtship	Ap → An → Wr	M1 (40) x F5 (5)
H. courtship	Ap → Wr	" M3 (31)
intensive courtship	Ap → An → J → Wr	M2 (20) x F5 (5)
H. courtship	"	" x M4 (17)
Attempt copulation		" x "
Courtship	Ap → An → Wr	M4 (17) x M2 (20)
P. response	Ap → M → Feeding	M3 (32) x "
Courtship	Ap → J → Wr	M1 (43) x F5 (8)
"	Ap → An → Wr	M2 (25) x F5 (10)

P. response = Pseudofemale response

Appendix VI.5 - Sexual behaviour in <u>Henchoustedenia</u> <u>flexivitta</u>
(group 1B)
(The numbers in brackets indicate the age in days after adult emergence)

Behaviour	Sequence	Participants
H. courtship	Ap → An → J → Wr	M2 (15) x M1 (3)
"	Ap → An → Wr	M2 (25) x M1 (13)
"	"	M2 (32) x M1 (20)
Courtship	Ap → An → Wr → J → Wr	M2 (46) x F4 (1)
"	Ap → An → J → Wr	M2 (47) x F4 (2)
" "	" "	M2 (48) x F4 (3) M1 (36) x "

Appendix VI.6 - Sexual behaviour in Henchoustedenia flexivitta
(group 1D)
(The numbers in brackets indicate the age in
days after adult emergence)

Behaviour	Sequence	Participants
Courtship	Ap→An→Wr	M5(16) x F3(0)
H. courtship	"	M2 (23) x M5 (22)
Courtship	"	M2(23) x F3 (7)
"	"	M5 (22) x "
"	Ap→An→J→Wr fhallomere extruded	M2 (27) x F1 (0)
"	Ap→An→J→Wr	M5 (26) x F3 (11)
"	Ap→An→Wr	M2 (36) x F3 (20)
"	"	M5 (35) x F4 (7)
"	"	" x F1 (9)

H. courtship = Homosexual courtship