Behavioural and Physiological Aspects of Fighting in the Cockroach, *Nauphoeta cinerea* (Olivier).

by

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CHAPTER ONE

General Introduction

The widespread occurrence of fighting throughout the animal kingdom and the complexity of behaviour associated with it, suggest its survival value. Observations on vertebrates have shown that intra-specific fighting plays an important role in social organisation and in regulating population density. This aspect of fighting, which has been largely ignored in invertebrate studies, forms the central theme in this thesis on aggression in the cockroach, Nauphoeta cinerea.

The usefulness of insects and other arthropods as simple systems for investigating complex vertebrate problems, is often put forward. In many cases the simplicity is more apparent than real. The main advantage of using insects is in the ease with which they can be bred and in the low cost of maintenance. The use of an invertebrate in this study is to determine how far generalisations can be made about the role of aggression and where the limits lie. Since invertebrate studies lack a unified approach it seems relevant first to consider concepts which have been derived from more detailed vertebrate investigations, particularly as there appear to be, superficially, many parallels.

Broadly speaking, among vertebrates three types of social organisation exist, hierarchical, territorial/hierarchical and territorial. The relationship of fighting to these different animal societies and the role of rank and territory will be discussed. Invertebrate studies will then be examined in the light of these considerations.

Among social animals one outcome of fighting is the establishment of a hierarchy of dominance. Once individuals recognise their position in the hierarchy the amount of fighting is reduced. This is usually achieved by behavioural mechanisms which specifically inhibit fighting and killing con-specifics. Animals losing an encounter adopt a characteristic submissive posture which inhibits the winner from further attack. It is essential for the maintenance of the hierarchy that subordinate animals always respond appropriately to the threat postures of the superior animal and vice versa. Failure to do so leads to actual fighting or to the subordinate leaving the group, which may be disadvantageous.

The structure of baboon society reflects a strongly developed dominance hierarchy which is lead by one or several males. In a group studied by Devore and Hall, (1961) the dominant male mated with all the full-grown females at the height of their oestrus-cycle and fought off rival males to do so. The dominant male is not just the most aggressive male, he is also the most experienced and his position at the top of the hierarchy confers the responsibility of protecting the troop and in particular females with young. Because subordinates give way to dominant males, fighting is rare and, in addition, the leader of the group may actively interfere to prevent fights in the lower ranks. The structure of baboon society is strongly affected by the existence of a hierarchy but this is not the case for all primates and a wide range of social organisation exists. Chimpanzees form groups of a temporary nature and there is frequent inter-change of members between groups when they meet up (Reynolds and Reynolds 1965). A dominance order does exist but it is not an obvious feature of chimpanzee society. Dominant males do not have exclusive mating rights and although they lead the group, their influence is not always obvious. (Lawick-Goodall 1968).

Probably the most familiar hierarchy is the peck-order which Schjelderup-Ebbe described in the domestic fowl. At the top of the hierarchy one hen dominates the group and can peck at all other hens without being pecked back, while the bottom hen is pecked by all the others and itself pecks none. As in other hierarchical societies high-ranking individuals have certain privileges when it comes to food, rest-places and mating rights. Dominant females will not copulate with lower ranking males and dominant males win over inferior animals in competition for females. Stability of the group depends on stability in the peck-order. If members of a group are changed frequently there is more fighting and more wounding than in groups not so treated (Guhl 1956).

Some animals show two opposed tendencies, to form a group on the one hand and to hold a territory on the other. Social hierarchy may develop in such a group but it does not necessarily take the form of a sequential peck-order such as is found in chickens.

In some animals there is a limit to the number of males eligible for mating and these select few collect together on some traditional site to which the females are attracted. In the Uganda kob, *Adenota kob thomasi*, the males assemble on a stamping ground, an open area, some two hundred yards across, which is divided into fifteen to eighteen grassy plots. Each plot is defended by a territorial male, selected on the basis of rank from a herd of thousands. Females appear to be attracted most to the central territories which are owned by the older and highest ranking males. Males have priority over females only in their own plot (Buechner 1961).

Lek birds show very comparable behaviour. At the beginning of the mating season males of the ruff, *Philomachus pugnax* and of the black grouse, *Lyrurus tetrix*, assemble and display on a large open mating area, the lek. Central territories are owned by older birds of high rank. These central males appear to have greater mating success (Hogan-Warburg 1966, and Kruijt 1967).

Many rodents, like the lek birds, are at once social and territorial though territorial behaviour is not confined to a limited reproductive period. House mice show a wide range of social order from no fighting to complete dominance of the group by one male (Crowcroft 1955). The condition found seems to depend on population density. Davis (1958), holds the view that social hierarchy and territoriality are opposite poles of a continuum. At all densities animals rank but at low densities each group consists of only one individual and it is dominant. Under crowded conditions there is less chance of successful territory holding, there is room for fewer dominants and in a sense territories move with these few. Rats are also primarily gregarious but have a territorial society based on dominance. In colonies of Rattus norvegicus observed by Barnett (1958), males were found to be of three different types, animals of any one category being equal in rank. The top-ranking alphas are dominant over the rest of the group and will attack strange rats. Betas although strong and healthy show no aggression towards intruders. Omegas, sharing the fate of strange rats, are subject to frequent attacks and may die from shock if given no chance to escape.

A further example of the relationship between territoriality and social order is found in the South European green lizard, _Lacerta viridis_. A straight-line hierarchy develops between the males. Females of this species also have a rank order but all females are submisssive even to the weakest male. A strong female-biting inhibition, dependant on the characteristics of female smell, exists in the male. Since dominant animals of both sexes obtain the best territories, the top-ranking male and female form a pair in the same territory, without fighting because the female is subordinate to the male and he is inhibited from biting his mate (Kitzler 1942).

Lastly there are territorial animals. Many of the best examples are to be found in birds and suitably illustrate the main features of territorial behaviour. Characeristically a territory holder is dominant in its own territory but outside the boundaries of its territory responds submissively to the threat displays of neighbouring males. Various methods of delimiting the territory are found. Patrolling males display conspicuous structures which deter would-be intruders. The red breast of the robin and red belly of the stickleback, _Gasterosteus aculeatus_ are examples. Auditory signals are also utilised. Singing in birds, howling in wolves and monkeys serve to indicate territory occupation. In mammals scent-marking, either by urination and defaecation, which is found in dogs and bears or by deposition of secretions from specialised glands, as in rabbits (Lockley 1961), also serve to indicate territory boundaries.

The behaviour of an animal confronted by its neighbour at the boundary is typically ambiguous and consists of a series of attacks or retreats depending on whether the animal is nearer to its own or its neighbour's territory. Displacement activities are common on such occasions and Tinbergen has suggested that the grasspulling which he observed in the herring gull (1953) and sand digging behaviour which appeared out of context in the stickleback, <u>Gasterosteus aculeatus</u> appeared when the two tendencies, to attack and to flee, were in equilibrium.

Functions of ranking

One of the consequences of ranking is that the amount of damage from fighting is reduced. Fighting is wasteful of energy and it is advantageous that fighting should be reduced to brief encounters in which low-ranking animals submit or flee from dominant individuals. Hens in a stable group are healthier and gain more weight than their counterparts in a less stable group (Guhl 1956). A further advantage of reducing the amount of fighting is that it reduces risk from predators. Fighting animals are frequently noisy and otherwise conspicuous.

Lack (1966), holds the view that in a fight over food, a dominant-subordinate relationship will benefit both animals; the dominant on the one hand because it gets what it wants with the minimum of effort and the subordinate on the other because, as a result of its past experiences, it wastes no more effort in fighting and can spend time more profitably in seeking food. Most of the evidence suggests that the advantage is in favour of the dominant which usually has precedence over lower ranking individuals for rest-sites, food and often for mates. Rabbits, *Oryctolagus cuniculus*, showing greatest resistance to myxomatosis were the progeny of dominant animals (Mykytowycz 1961). This could have been due to an adverse effect on low-ranking animals rather than a positive effect in favour of dominant animals.

Under ideal conditions when food is plentiful subordinate animals probably do not suffer, though subordinate rats lose weight even when food is freely available (Barnett 1964). When food is limited low-ranking animals are the first to starve. They may be forced to take food after top-ranking individuals have had their fill. This is the case in the domestic fowl (Guhl 1956), and also in the house mouse, *Mus musculus*, where subordinate animals have to take food at daybreak and are thus more exposed to predators (Crowcroft 1954). The fate of subordinate animals is well illustrated by the red grouse, *Lagopus lagopus*. Low ranking males are non-territorial, occupy poor areas, and do not breed. Records on the effect of predation and disease in this bird show that it is the subordinate, non-territorial individuals that are most likely to succumb (Jenkins 1963). Errington's study (1946) on muskrat colonies describes how those without territories, "congregate on the fringes of areas dominated by muskrats already in residence. Transients, they form a biological surplus largely doomed by one medium or another".

Failure to obtain a territory and thus to breed, susceptibility to disease and predators appear to be related to low social rank. Under crowded conditons a correlation is found between intra-uterine mortality and social status in female rabbits, Oryctolagus cuniculus (Mykytowytcz 1960). Myer and Poole (1962), claim that both dominant and subordinate females are affected by crowding and that the main effect is on young animals. There are other examples where younger animals are also socially subordinate. These include the black grouse, the ruff and the Uganda kob to which reference has been made already. In all these animals peripheral males are younger and have lower rank than the central males. It is rather difficult, in the absence of relevant experiments, to determine which is the important factor but one assumes that rank decides which males will occupy the central territories. Young mice also have low rank and under crowded conditions both sexes show a delay in maturity (Christian 1961).

Perhaps the most dramatic effect on subordinate animals is death, not from the effects of starvation or disease, but from stress. This phenomenon is not confined to mammals and has also been reported in the lizard, Cnemidophorus sexlineatus (Carpenter 1960). There is no evidence for such deaths in fish or birds. Stress is the physiological response of an animal to deleterious external agents, stressors, whose action disturbs the internal homeostasis of the animal. The primary response of an animal to a stressor is adaptive but if the action of the stressing agent is too severe or is prolonged then irreversible changes occur and these lead to death (Munday 1961). The actual cause of death is not well understood. Social stress arising either from aggression or from crowding without overt fighting, is thought to act like other stressors such as heat, cold, disease and intoxication by alcohol. Many of the effects on subordinate animals, reduced resistance to disease, loss of weight when food is available and delay in sexual maturity can be attributed partially to the primary physiological effects of stress.

The immediate response of an animal to a stressor is governed by the autonomic nervous system and involves a rapid production of adrenalin by the adrenal medulla. If the action of the stressing agent is prolonged then there is an increase in the output of adrenocorticotrophic hormone, (ACTH), by the adenohypophysis. The consequent production of adrenocortical hormones assists the animal to meet the increased demands made upon it. Stimulation of the adrenals leads to a depletion of the hormone reserves which are then replaced by synthesis from cholesterol. In both fighting dominant rats and subordinate rats there is enlargement of the adrenal cortex, but only subordinates suffer from depletion of hormone precursor (Barnett 1955, 1964).

ACTH secretion particularly affects the production of glucocorticoids which affect carbohydrate metabolism and give rise to an increase in blood sugar and a loss of liver glycogen. This might explain the weight loss which occurs in subordinate animals even when food is available. Glucocorticoids also affect the normal defence reactions and lower resistance to pathogens (Chitty 1960). This might account for the lowered resistance to disease found in subordinate animals.

There have been many studies which correlate changes in adrenal weight with changes in population density. Chitty (1961), found that a seasonal change in numbers occurred in Microtus agrestis and that adrenal weights were highest when the number of voles was greatest. The implication from her finding is that stressful social interactions increase with the rise in number of animals. Similar results have been obtained for other species and these are covered by Christian and Davis (1964) in a comprehensive review on the subject. As Christian points out, adrenal weight is not an adequate index of adrenal function and other indices should be taken into account. Direct measurement of circulating hormone would provide the only complete evidence but so far this has not been practicable.

Many changes associated with reproductive capacity have been found to occur with increasing population density. These changes are indicative of reduced gonadotrophin secretion which is thought to occur when excess ACTH is produced. To date, however, no diredt measurement of gonadotrophin level has been made.

The structure of animal societies may vary with the density of the population. In the sunfish Lepomis gibosus, which is territorial, a hierarchy begins to develop as the number of animals increases and the higher the density of the population the more likely it is for one animal to dominate the group (Erickson 1968). Davis (1958), found an essentially similar situation in house mice. If two or more individuals are forced to share a limited space then ranking is a likely consequence. Competition for rank could act as a density regulating device by causing the subordinate animals to disperse, though direct evidence on this point is lacking. Part of the reason for this may be that many of the hierarchies studied have involved artificial colonies from which subordinate animals cannot escape because of the physical limitations imposed by the experimenter. One can question whether subordinates would move out anyhow, at least in the case of truly social animals in which behavioural mechanisms exist to attract animals to the group and to keep them there. One can also question whether hierarchy is not in many cases an artefact of confinement. It would be interesting to compare the space relations and behaviour of a group of animals in a large but limited space and in unlimited space.

In a confined space the number of subordinate animals increases and the number of dominants declines as the population expands. Stress arising from this situation is thought to be the major density dependent factor regulating mammal numbers though the exact way in which it operates over generations is debated (Chitty 1958, Christian and Davis 1961). Christian and Davis visualise an endocrine feed-back mechanism, operating through the pituitary-adrenocortical system, which regulates population growth in an overall response to social pressure resulting from an increase in numbers. The decline in numbers which this mechanism brings about may be accelerated by secondary factors such as disease. Food shortage undoubtedly contributes but in those populations which show cyclic fluctuations in numbers, the crashes have been found to occur before the food supply is exhausted, suggesting that food shortage is secondary in its effect (Chitty 1958). Predation may also add to the decline in numbers but probably by removing animals already weakened by the effects of stress or disease or hunger.

Summarising, we may say that under optimal conditions the peck-order unifies a group of animals and makes more or less peaceful co-existence possible. The hierarchy determines an elite for breeding. It may do so directly or indirectly, by ensuring that certain animals obtain territories. Ranking also confers certain benefits on the dominant individuals, such as priority at feeding and rest-sites. Ranking creates a subordinate class of animals which may be excluded from mating, from territory, and from food and these animals may have decreased resistance to disease and lowered reproductive capacity. These last mentioned effects can be related to stress from which subordinate animals may die directly. Stress, arising from crowding, is not marked only in subordinate animals but also in young animals which tend, in any case, to have low rank.

Territory, its function and relation to hierarchy.

The function of territory has been a favourite point of argument, particularly among ornithologists. It has become increasingly evident that there can be no one function of territory and that the function varies with the ecology and behaviour of the species concerned. Terns and other colonial birds, tits and other passerines which feed in flocks for at least part of the year, defend only the area immediately round the nest. Many carnivores including hawks and wolves have hunting territories. In non-social territorial birds the territory is usually large enough for the bird to carry out all its activities including foraging.

One advantage of territory is that it spaces animals, thereby reducing conspicuousness and giving possible protection from predators during courtship and mating when animals are particularly vulnerable, and while rearing young.

Ardrey (1966) stresses the value of territory in strengthening the pair bond. He maintains that an animal's attachment to territory, which he calls "the territorial imperative", is greater and more permanent than any attachment that the pair may have for each other. By mutual interest in a joint territory the bond (sexual) between them is reinforced and their behaviour is restrained and directed along lines which benefit survival of the young.

Territorial behaviour affects the density of animals in a given area and since the possession of a territory is a prerequisite for breeding, territory could act as a density regulating mechanism for the population as a whole. There are two currently held views as to how this could be brought about. If the lower limit of territory size is more or less constant, then so also will be the upper limit of numbers and for a given area the number of breeding pairs will be constant. Territories could also space animals in relation to the food supply. In this case, the number of animals will fluctuate with fluctuations in the food source. Evidence on these points is conflicting.

A study on the great tit, Parus major, by Kluijver and Tinbergen is quoted by Hinde (1957), as showing that territory sets an upper limit to the numbers in a favourable habitat. A parallel study begun by Lack and later continued by Perrins (1965) showed that in one year the number of tits in Marley wood was sixty per cent higher than in other years and yet no corresponding change in the environment was found. Van Den Assem (1967), suggests that this fluctuation may reflect the way in which settling took place. A given area can accommodate more individuals if they are introduced simultaneously and do not have to compete with individuals which are already established. This he found to be the case in the stickleback, Gasterosteus aculeatus.

A population of tawny owl studied by Southern (1959) was found to have a fairly constant number of breeding pairs and this number did not decrease even when the normal food supply was scarce. When food was limited, however, some pairs did not breed and among those which did there was an increase in infant mortality. Territory does limit the number of pairs in a given area but ultimately food is the limiting factor and adjustments to food supply are made through deaths in the infant population. It is not known whether the birds which do not succeed in obtaining territories in one area, then move to another area where they find a territory on which they can at least maintain themselves or whether these birds are 'surplus' and die. In other words, from the evidence evailable one cannot say whether territories disperse animals or limit their numbers.

There is no doubt that territory spaces animals and the effects of reducing the space round an individual beyond a certain point have already been discussed. Social animals can tolerate other individuals at a much closer distance than can non-social, territorial animals. In animals that are at once social and territorial the territory is said to move with the dominant animal. The usefulness of this concept is limited. It seems more relevant to consider the phenomenon of ranking which occurs even in animals which do not group in nature. Ranking, whether sequential or more complex, occurs at all densities but at low densities each group consists of only one animal or a pair which is "dominant". The territory boundary marks the point beyond which other individuals will not be tolerated. Just as individual distance can be reduced when crowding occurs, so also can territories be compressed when the population expands but not beyond a certain point. Van Dem Assem (1967) found a minimum size for a breeding territory in the three-spined stickleback. Below this minimum, reproductive success was reduced.

When several males were introduced simultaneously to a tank, the size of territories which could be maintained successfully closely approximated to the minimum size determined for isolated males.

The space round an animal is maintained by aggressive behaviour. Territory could have evolved through the selection of aggressive individuals with a reduced tolerance to other members of the same species. Such animals would develop a larger inter-individual distance. The boundaries of the resultant increase in space could then be fixed by the physical features of the environment. It is remarkable how often man-made boundaries such as fences and edges of fields are utilised as territory boundaries. In such cases the boundary presumably approximates to the limit of tolerance of con-specifics.

In certain cases, there is circumstantial evidence that territory holders are under considerable pressure (Lack (1966)), cites an instance where the garden territory of a blackbird was occupied by eight successive males, the owners dying from poison and the replacement appearing, more or less overnight, from less favourable adjacent territories. The brown rat shows non-cyclic fluctuations in numbers. An increase following a decline was shown to be due to recruitment from neighbouring areas. Barnett (1964), observes that rat populations reach a maximum at a declining rate and that before the maximum is reached, areas previously unoccupied by the rats were colonised. If crowding results in pressure for territorial space then an increase in aggression might be expected. This does appear to be the case in expanding populations of Microtus agrestis and the physiological consequences of increased agression in this animal have already been discussed.

Interest in the complex relationship between aggression and the structure of animal societies, between stress, a consequence of fighting, and the control of animal numbers, continues. The physiology of stress remains a matter of controversy and as yet there is no comprehensive explanation for stress death or for the other effects of stress on reproductive capacities. The results from many studies on territorial behaviour have suggested functions for territory but the evidence is often indirect and suffers from a lack of quantitative data.

Social hierarchy and the function of ranking in invertebrates.

Fighting has been described mainly in the Arthropoda among invertebrates. It is widespread among decapod crustaceans, occurs in several orders of insects and has been reported in spiders and scorpions. Many studies have revealed features shared by the vertebrates but on the whole the implications from these studies have not been so far reaching as those from vertebrates. Although functions for fighting have been suggested, this aspect has not been the major purpose of the investigation and there is a general lack of supporting evidence. It does appear that fighting is used to obtain the same ends, so far as establishing rank and maintaining territory are concerned.

Dominance hierarchies have been described in several crustaceans but the importance of this type of organisation in the wild is difficult to assess. Boubjerg (1953) observed aggressive interactions in natural populations of the crayfish, Orconectes virilis. Territorial behaviour appeared to obscure any dominance order that might exist and in order to eliminate the effects of territory, small groups of crayfish were placed in basins furnished only with gravel with the result that stable dominance hierarchies developed. In Procambarus alleni, an other crayfish studied by Boubjerg (1956), dominance did not appear to determine a class of male which could mate and subordinate males were found to mate with dominant females. Perhaps in the wild hierarchies would not develop and aggressive behaviour is confined to the establishment of territory.

Crane (1958), also observed a dominance order in laboratory populations of the fiddler crab, Uca species. In these crabs there is a semi-lunar rhythmn of social behaviour. Animals go through a sequence of five or six phases of behaviour which culminates in a display phase of courtship and mating. Only during the phases preceeding and including the display phase are the crabs aggressive. Rank is dependant on the phase of behaviour, animals in the display phase having the highest rank. Because the display phase lasts for but a few days, the hierarchy is stable for a few days only. The function of ranking if any, is obscure, it appears to be independant of sex, and it is not known whether top-ranking males and females mate with each other.

An artificial colony of crickets Gryllus campestris was found also to be capable of forming a hierarchy. Rank did not determine which males should have territories and even low-ranking males defended their territory with success against superior animals (Alexander 1961). It is not known whether dominant males had greater mating success. In this case, as in the other instances mentioned already, it seems likely that the tendency to form a hierarchy was enhanced by artificial conditions and that in the wild it may have no particular significance.

Territorial, hierarchical societies.

Endemic species of Hawaiian Drosophila show a kind of territorial behaviour which has been likened to lek behaviour (Spieth 1966). Unlike the mainland forms these insects do not court and mate on the food source. Males take up stations on nearby foliage where courtship and mating eventually occur. A leaf, or the pinna of a fern frond, is defended against intruding males but the resident does not necessarily win. Here the resemblance to the lek ends. There is no question that the fern or shrub is being used as a display-ground. *Drosophila laleakala*-like males take up stations some ten feet away from the food source where they would be invisible to the females and *Drosophila imparasetae* occupy the undersides of leaves where they would also be invisible. Territorial behaviour spaces males and makes them less conspicuous but not to the extent that male-female contacts become unlikely. Speith suggests that this behaviour has evolved in response to predation by the insectivorous Hawaiian honeycreepers and by the flycatcher, *Chasiempsis sandwichensis*. The fruit flies would certainly be conspicuous on the food source and there is the added disadvantage that *Drosophila* cannot fly *in copulo*. In addition to spacing the males, territories might provide for uninterrupted courtship but only if territorial males keep to their own sites. In some cases females also fight and this suggests that the primary function of the behaviour is related to spacing.

The cicada-killer wasp, *Specius speciosus* shows territorial behaviour which has been likened by Ardrey (1966) to lek behaviour but as with the previous example there is, in reality, very little resemblance. Male cicada-killer wasps do collect in a group and each male defends a small territory but the choice of territory is determined by the female. Territories are established close to the burrows from which females eventually emerge on maturing (Lin 1962). Males do not collect on a common area for purposes of display. Furthermore, hierarchy plays no role in structuring male society and each male is dominant in his own territory.

Territorial behaviour and the function of territory.

Male dragonflies have a beat (Aeshnidae) or a perch (Libellulidae) which is apparently defended. Moore (1952) claims, however, that what appeared to be defensive behaviour was in fact attempted copulation, males being unable to distinguish the sexes at a distance. The beats, though held for several hours by the same individual, were not defended and therefore not territories in the accepted sense of the word.

A New World dragonfly, Heterina americana, also takes up a particular perch during the day and one male may occupy the same perch for several days in succession, (Johnstone 1962). In this case there appears to be no doubt that the perch is defended and approaching males are pursued in circles of ever increasing diameter until one of the combatants leaves the territorial area. Two thirds of victories fall to the resident male. Johnstone found that the tendency to remain in a restricted area varied over the course of his observations and, rather surprisingly, that there was least movement when population numbers were highest and aggressive encounters most frequent. Territoriality did not appear to be operating as a mechanism of dispersal. As in the cicada-killer wasp the behaviour of the male in his choice of territory appears to be related to the habits of the female. She chooses a suitable oviposition site and the male takes up a perch nearby. When many females are concentrated in one area, so are there many males and more territorial disputes. Dispersal occurs with the decline in female numbers. Territoriality appears to be related to access to females but there is no evidence to prove that males without territories do not mate.

In both Heterina americana and Sphecius speciosus territorial behaviour is related to breeding. In neither case is it actually shown that only territorial males are successful in getting a mate but since males are dominant in their own territories, they might have a better chance of mating in their own territory than elsewhere. In many crustaceans, the fiddler crab, the crayfish, O. virilis and P. alleni mentioned previously, and the mantis shrimp, Gonodactylus bredini (Dingle and Caldwell 1969) both sexes are territorial and the function of the territory is not clear. Perhaps territory disperses animals or even limits their numbers.

Few studies have investigated intra-specific aggression from the stand point of population density regulation. In the pasture scarab, Aphodius howitti, the major factor governing density regulation is density-induced larval combat, (Carne 1958). Fighting does not occur during the initial larval stages in the oviposition shell and it is seen only when burrows have been constructed and inhabited. Mandibles are used in fighting and considerable damage may be inflicted to the soft parts of the body. Death appears to result from infection of wounds and from dessication. The excess of larvae produced is balanced by deaths from combat.

In the case of the pasture scarab, fighting leads to wounding which eventually kills the animal. It is also possible that aggression in invertebrates could lead to the development of a stress syndrome analogous to that found in vertebrates and that stress could affect reproductive capacity or could cause death and so play a role in regulating the number of animals.

The evidence that invertebrates could develop a stress-like syndrome, analogous to that found in mammals, came from Beament's experiments (1958) on Periplaneta americana nymphs which became paralysed after extreme mechanical or electrical stimulation. Recently a factor implicated in this phenomenon has been isolated (Cook et al 1969). To date there is no direct evidence for stress arising under natural conditions. Nevertheless there is some indirect evidence to which further attention could be given. Johnstone (1962) mentions that when the number of aggressive encounters was greatest in Haeterina americana so also was the number of deaths. Boubjerg (1953) records deaths in low-ranking crayfish. In neither case was the cause of death noted. The machilid Dilta hibernica, when captured may exhibit an escape reaction in which it jumps about wildly. Some individuals fall over and die, apparently from shock (Wygodzinsky, pers. comm). No studies in the invertebrate field investigate the effect of low rank or of crowding on health and reproductive capacity. Wilson (1968) advocates investigating the role of aggression in insect dispersal, to see how it is related to solitariness and gregariousness.

It appears that there is a need for a systematic study of the relationship of fighting to social organisation in invertebrates and also for an investigation of the physiological basis underlying this aspect of behaviour. The cockroach, Nauphoeta cinerea, in which fighting has been observed but not examined in any detail, seems ideally suited for such an investigation. The first part of this thesis will be concerned with the relationship between fighting, territory and hierarchy in N. cinerea. The second part involves an investigation of the dominant - subordinate relationship which develops in this insect. Emphasis will be placed on physiological aspects of this relationship and in particular on the possible involvement of the endocrine system in the appearance of a stress-like phenomenon.

CHAPTER TWO

Fighting Behaviour

Introduction

Like many other cockroach species, Nauphoeta cinerea shows intra-specific aggression. Roth and Willis (1960) describe how 'males would wrestle with each other, rolling over and over.' Kramer (1964) describes two other types of aggressive behaviour between adult males, during courtship. Males are seen to accost each other with abdominal segments fully distended, pointed slightly upward and raised from the floor. One male tries to flick the other onto its back by using its head and prothorax as a lever under the abdomen of its opponent. Males are also seen to charge and chase each other. The normal sequence of these events is described by Ewing (1967).

A description of fighting in Periplaneta americana suggests the importance of erect body stance and leg extension as a threat posture which occurs when two males meet (Ehrlich 1943). Without being explicit Ehrlich implies that the aggressive posture in Periplaneta is indicative of rank. He says, 'It may also be called an attempt of the animal to make an impression, since it can be seen that this position makes on fellow cockroaches an intimidating impression.

Only adult males of Nauphoeta cinerea fight (Kramer 1964). In Periplaneta americana fighting occurs in both sexes (Griffiths and Tauber 1942), and in Blattella germanica only the nymphs fight (Pettit 1940). These diverse observations raise questions relating both to the function and ontogeny of the behaviour pattern.

The first aim of my investigation was to build up a picture of the fighting pattern in N. cinerea through direct observation and then to determine by experiment some of the characteristics of fighting; when it first appears and whether its appearance is affected by the presence of females.

Materials and methods

1. Culture conditions. The cockroach, Nauphoeta cinerea, used in this study was originally obtained from Dr. Louis Roth, Natick, Massachusetts. The insects were maintained in large culture tanks at 25 ± 0.5°C, under an artificial light cycle of twelve hours light and twelve hours dark (LD 12:12). Water, rat cake and flake maize were provided ad lib.

2. Conditions for observation. Although Nauphoeta is a nocturnal animal its behaviour appears to be undisturbed by light and unless otherwise stated observations were made

in the light. Adult males were removed from the culture tank and placed in a small perspex container through which photographs could be taken. To begin with only qualitative observations were made and from these, aided by photographs, a description of the fighting sequence was built up.

3. Experimental Conditions. Male insects whether nymph or adult, paired or single, were kept in crystallising dishes with glass covers. The dishes were 9 cm. in diameter and 5 cm. deep. Ad lib food and water was provided.

To test for the appearance of fighting it was not possible to rely on observation alone and the appropriate stimulus had to be provided. From observations on fighting behaviour, antennal contact appeared to be important in initiating fighting. A test-animal whose antennal movements could be controlled was presented to an animal to see if it would respond aggressively. The test-animal had its legs removed to reduce body movements. A light balsa wood stick was attached to a thin metal wire threaded through the pronotum and this enabled almost complete control of the animal. Antennal contact between the test-animal and the experimental animal was allowed for two minutes. The experimental animal could respond in one of three ways; by attack, by submission (see below) or by ignoring the test-animal.

Observations and discussion

Fighting males adopt a characteristic aggressive posture which preceeds attack (Fig. 1a). Two animals face each other with abdomens fully extended and upturned and their legs stretched so that their bodies are carried well off the ground (Fig. 1b). A variable period of antennal fencing (usually of the order of a few seconds) follows and the two males then charge towards each other and butt on contact. Occasionally the charge may occur in the absence of antennal contact. A cockroach successfully engaging its pronotum under the thorax and abdomen of the other, springs in the air so tossing the opponent onto its back (Fig. 2a). This is essentially what Kramer (1964) described.

The least commonly observed event is grappling in which both animals fight with their legs locked together as they roll over. While wrestling in this fashion the two males take up a head to tail position and bite at each other (Fig. 2b). No damage appears to result from this type of encounter.

The fight may remain undecided for several minutes but soon one male emerges superior and from then on attempts to bite at its opponent's antennae, wings and abdomen. Torn wings and broken appendages are frequently seen after such chases. When the fighting pair is confined to a small container, chasing may persist for fifteen to twenty minutes but suddenly the inferior animal gives in. It lies still,

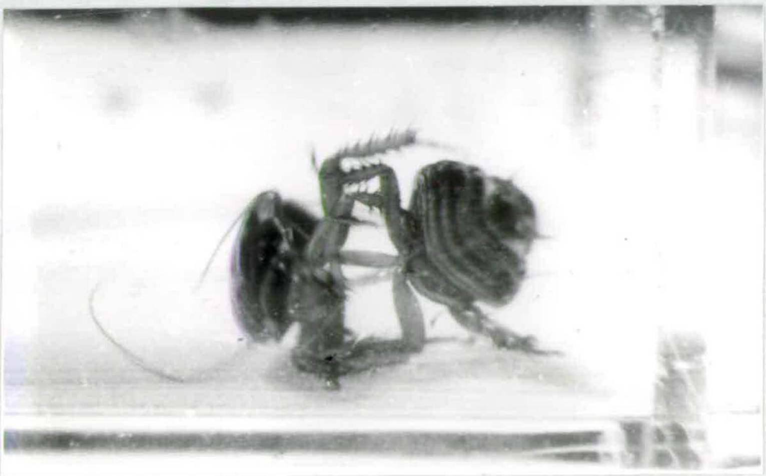
FIGURE I

Elements from the fighting sequence.

(a) Threat

(b) The aggressive posture.

a



b

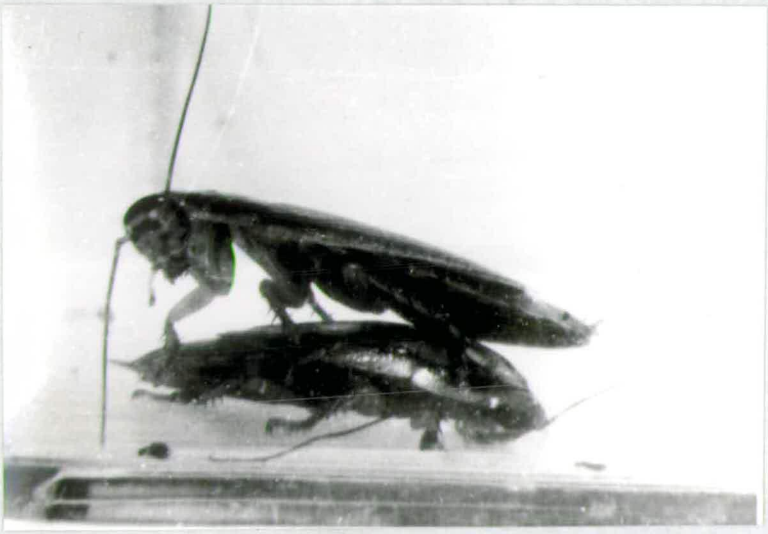
FIGURE II

Elements from the fighting sequence

(a) Tossing

(b) Grappling

a



b

FIGURE III

Elements from the fighting secuence

(a) Submission

(b) Assertion of dominance.

withdraws its limbs and retracts its head under the shield of the pronotum. The antennae lie most characteristically, flat on the ground, straight in front of the animal or less frequently pointing backwards, parallel to the animal's body which is always pressed close to the ground (Fig. 3a).

Once submission occurs, the dominant animal examines the loser with its antennae and maxillary palps. Eventually the dominant may climb onto the submissive's back where it often remains for long periods (Fig. 3b). Alternatively, particularly if other males are present, the dominant may court the submissive.

The foregoing sequence of events occurs only in pairs which appear (subjectively speaking) to be well-matched. The fight may be terminated at any stage, even after the initial antennal contact. This point can be recognised when one animal adopts the submissive posture. It is not clear what factors determine the outcome of a fight. Larger and heavier animals do not necessarily win. Sometimes the dominant persists in attacking even when the inferior animal adopts the submissive posture. A few subordinate animals can withstand prolonged attack but others die without obvious external damage. This observation will be considered in more detail in the second part of this thesis.

There are several points which merit further discussion. The first of these relates to the use of terms normally used in describing vertebrate behaviomr. 'Submissive' has a specific application in vertebrates but its use here seems justified since the posture has the same effect, it usually allays further attack. Once dominance is established, bouts of chasing become less frequent and the subordinate animal adopts the submissive posture when the aggressive posture is adopted by the dominant. It is not clear to which particular feature of the aggressive posture the subordinate animal is responding and therefore I hesitate to use the term threat in connection with the aggressive posture.

To the human observer the aggressive posture is a visible sign that a cockroach is ready for a fight but to a nocturnal insect such as *N. cinerea*, its value as a visual stimulus releasing aggression or flight is limited. The aggressive posture which involves extension of the abdominal segments, may expose the releasing sites of the male pheromone 'seducin' which attracts females to feed off the back of the male during courtship. *N. cinerea* does not have the well-developed tergal glands found in some cockroaches and the production site of the pheromone has not been exactly located. Highest quantities have been found in the abdomen (Roth and Dateo 1965). The possibility that 'seducin' arouses aggression in other males as well as courtship behaviour in females must not be overlooked.

Antennal contact between males appears to be an important though not essential factor in releasing agression in N. cinerea. This phase is prolonged in Blabera cranifer and may continue for up to thirty minutes (Gautier pers. comm.). The courtship wing-display in Nauphoeta cinerea is also released after antennal contact with the female (Roth and Willis, 1954) and the basis of sex discrimination may be contact pheromones.

The relationship between sex and aggression is complex and finds parallels in the vertebrates, noteably fish. Why dominant cockroaches should court their opponents once they have become submissive is puzzling. In Blabera cranifer homosexual behaviour may turn into aggressive behaviour but never the reverse (Gautier pers. comm.). It is interesting that the males first response to a female, receptive or otherwise, may be to adopt the aggressive posture during the examination phase. Abdomen raising is swiftly followed by abdomen depression typical of courtship. Any interruptions during courtship tend to produce abdomen raising before courtship is resumed.

During my observations on fighting behaviour no females were present though the influence of female pheromone was not eliminated. Kramer (1964) has suggested that fighting is associated with courtship. Probably his reason for assuming this is that fighting in Nauphoeta cinerea occurs only in adult males. Males do not begin to produce spermatophores until days 2 - 3 after the adult moult and they are not sexually mature until this time. In connection with this it would be interesting to see if the fighting pattern is present on emergence or whether it develops later.

Some simple experiments were set up to investigate the time at which fighting first appears and whether it appears in the absence of females and female pheromone.

Three experimental groups were used; paired males and single males collected from the culture tank as teneral adults immediately before the experiment was set up and paired, 'pheromoneless' adult males which had been removed from the culture tank as nymphs in their pre-penultimate instar. The purpose of isolating the animals as nymphs was to eliminate any trace of female pheromone which could have been picked up in the crowded culture tank. The nymphs were kept in a group and teneral adults paired as they emerged. Each adult male was presented with the test-animal once daily. The results for the paired males are shown in Table 1.1.

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

<u>Table 1.1</u>. <u>The day on which fighting is first detected by using the test-animal in paired males.</u>

Animals first respond aggressively to the test-animal on days 2 - 3. The criterion used was the aggressive posture coupled with either charging, butting or biting. Only one male out of each pair was found to attack the test-animal, the other responded submissively. Subsequent observations showed that the animal which attacked the test-animal was dominant over the other and that the relationship was stable and already established. 'Pheromoneless' males show similar results. These are shown in Table 1.2.

pair	1	2	3	4	5
day	3	3	2	3	2

<u>Table 1.2</u>. <u>The day on which fighting is first detected by using the test-animal in 'pheromoneless' males.</u>

Only five pairs were used because of the difficulty of obtaining individuals which had moulted to the adult stage at the same time.

These two experiments show that fighting as detected by the use of the test-animal, first appears on days 2 - 3 and that it can appear in the absence of females and female pheromone. A dominant-subordinate relationship is established between paired animals, the male which attacked the test-animal being dominant over the animal which responded submissively to it. The relationship becomes apparent immediately after one of the animals has attacked the test-animal. It can be postulated that fighting leading to the establishment of a dominant-subordinate relationship occurred at some time between presentations of the test-animal, most probably during the night when animals would be active. The alternative is that the attack on the test-animal represents the very first aggressive incident. Animals in which fighting has not developed respond submissively to all aggressive stimulation and provided that they remain with the same dominant, may never fight. This point could be resolved by continuous observation of pairs during the night.

Whether the dominant-subordinate relationship is established before or after presentation with the test-animal does not alter the fact that fighting occurs in the absence of females and female pheromone. Fighting therefore, is not directly related to courtship as Kramer (1964) has suggested.

The results from the third group of males, single males, open up an entirely new problem which has not been pursued because it leads away from the main theme which is concerned with the role of fighting rather than with the fighting pattern itself. The results are shown in Table 1.3.

male	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
day	-	7	-	-	-	5	3	8	7	9	3	-	-	10	4	-	-	3	-

TABLE 1.3 The day on which fighting is first detected by using the test-animal in single males.

Blanks indicate that no aggressive response was made to the test-animal on the tenth and last day of testing. The results show that the normal appearance of fighting can be affected by lack of contact with another individual. If animals are given a preliminary three-hour period of socialisation with another male while both are still teneral, the effects of isolation on the appearance of fighting are considerably reduced. The results are shown in Table 1.4.

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

TABLE 1.4 The day on which fighting is first detected in single animals which have had a three-hour period of socialisation before isolation.

The results suggest that an ontogenetic study of the fighting pattern would be well worth while. The observation that fighting does not begin until the third day may provide the key to the problem. Spermatophore production, the production of 'seducin' and the renewal of production of juvenile hormone by the corpus allatum all reach a peak at the same time as fighting is first detected. These events may not be unrelated.

Immediately after emergence young adult males are courted by older males that have already begun to fight. An experiment was set up to determine the time at which fighting males first attack young males in which fighting has not yet developed.

Teneral males were collected from the culture tank and kept in a group. Mature fighting males were also collected and these were kept singly, in vials. Each young male was placed daily, for seven days from the day of collection, with a mature fighting male in an arena. The animals were observed until one of the pair responded to the other by courtship or attack. Observations were terminated after five minutes. Mature fighting males were also collected and kept in a group. Each of these males was presented daily, for four days, to mature male which had been isolated. The purpose of this was to obtain some measure of how often fighting males attack each other when they meet for the first time. The results for the response of mature males to young males is shown in Table 1.5 and the response of isolated males to mature males which had been kept in groups is shown in Table 1.6. Five young males and five mature males were presented, each day, to the isolated males.

	Courtship		Attack	
Day	Fighting Males	Young Males	Fighting Males	Young Males
0 - 3	20	0	0	0
4 - 7	13	1	4	5

Table 1.5. The response of isolated, fighting males to individual young males which had been kept in a group. The response of the young males to the older males is also shown. The records cover a period of eight days including the day of emergence of the young males.

	Isolated males	Grouped Males
Courtship	2	10
Attack	7	2

Table 1.6. The response to each other of isolated fighting males and fighting males which had been kept in a group.
The records cover a period of four days including the day of collection.

In Table 1.5, the results are divided into two classes according to whether the observations were made before or after the day on which fighting normally appears in young adult males. No attacks are made on young males before day three and all young males are courted. After the third day young males either may be attacked or may be courted and, at the same time they, themselves, may court or attack. Observations on pairs of older males, known to have fought previously, show that when two such males meet for the first time in a new environment, they may also attack or court (Table 1.6).

Fighting males thus appear to treat young males as females until they are three days old. It is at this time that male pheromone production reaches a peak (Roth and Dateo 1965). It may be that before this time males cannot be identified as such and are therefore not attacked. The presence of male pheromone does not, however, inhibit courtship between males.

As a last point it should be mentioned that isolated males appear to show a greater tendency to attack than to court males that have been kept in a group and vice versa (Table 1.6). Further evidence suggesting that isolation increases aggression is given in the second part of this thesis.

It is convenient at this point to draw together, in the form of a summary, the diverse topics considered in this chapter.

Fighting occurs only in adult males and it does not make its appearance until days 2 - 3. The development of fighting over this period is affected by social isolation. Fighting leads to the establishment of a stable dominant-subordinate relationship and animals of different rank can be distinguished by different postures. Justification is given for the use of terms normally applied to vertebrate animals.

It is suggested that the aggressive posture will have limited value as a visual stimulus releasing fighting in other males. The posture could be involved in exposing the pheromone releasing sites thought to be localised in the abdomen. It is possible that male pheromone arouses aggression in other males. Antennal contact usually precedes attack though sometimes, if the animals are very close, attack appears to occur in the absence of contact. This suggests that chemoreception may be involved in identifying members of the same sex. In support of this suggestion it is shown that fighting males will touch, then court, young males in which fighting has not developed. After the third day, which corresponds to the time at which male pheromone is produced at peak level, young males are attacked as well as courted.

Attention is drawn to the readiness with which males will switch from courtship to aggression and vice versa. Once a male becomes submissive he may be courted. Males transferred to a new container may first court each other, then fight and even courtship of females initially contains elements associated with aggression.

Fighting occurs in the absence of females and of female pheromone and is therefore not directly related to courtship. Males will fight to establish rank. The next chapter is concerned with the role of fighting in territorial behaviour.

CHAPTER III

Territorial Behaviour

Introduction

Although many cockroach species show fighting behaviour only one example of territorial defence has been recorded, that found in Cryptocercus punctulatus (Ritter 1964). As marked males of Nauphoeta cinerea were seen to occupy the same position in a culture tank for periods of up to several months, the possibility that this species also shows territorial behaviour was examined in more detail.

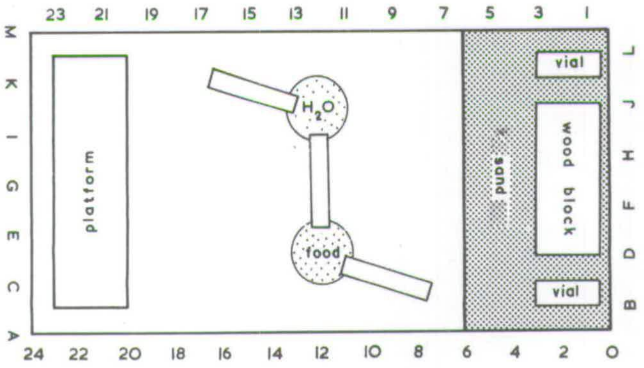
Materials and methods

Initially a group of ten males collectively referred to as T1, was observed over a period of three months and later two further groups of ten males T2 and T3, were watched for a shorter period to confirm the results of the first study.

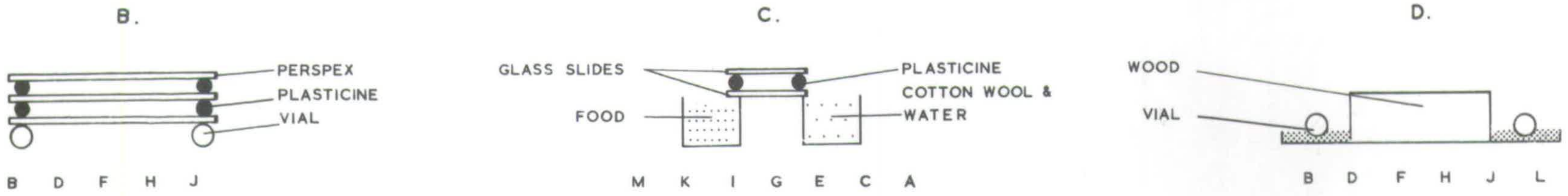
Teneral males were collected and code marked with quick-drying paint for individual recognition. After seven days in isolation the males were put into a large glass observation tank. The tank, measuring 24" x 12" x 12", had a perspex lid marked off in inch squares to facilitate plotting territories and movements of the animals. Several glass and perspex structures were provided inside as potential territory sites. They were, a platform of three

FIGURE 4 OBSERVATION TANK FOR STUDIES ON TERRITORIALITY

A . TOP VIEW



B.C.D. SIDE ELEVATION OF TANK COMPONENTS



perspex tiers supported at each end by a 1" x 3" glass vial, a chamber, bridging the food and water dishes, fashioned from two 1" x 3" glass slides, and two more glass vials. A block of wood was also provided and one third of the floor was covered by sand. There was only one source of food and water. The relationship between these structures is illustrated in Fig. 4.

Using the marked-off squares on the lid of the tank, the position of each male was noted, both during the day when the animals are at rest and at night when they are active. Records were made every few days and these can be found in Appendix 3.1.

T1 males were watched on twenty six separate occasions, for a total of seventeen hours over a period of eighty six days. Observation periods lasted from between thirty and sixty minutes. T2 and T3 males were watched over a period of thirty and forty days respectively. Observation periods lasted for sixty minutes and were made at a different hour each time until each hour of the night had been covered. This was then repeated thus totalling twenty four hours for both groups. Many items of behaviour were recorded but special attention was paid to aggressive encounters and to other behaviour associated with territoriality. Unless specifically stated all observations were made in red light.

My first aim was to establish that territoriality existed and then to describe its characteristics. The results are presented first as a description and then in a summary form in which the salient features are illustrated with tables and specific examples from the records.

A General Description of Territoriality

Observations made during the day show that some males are found in the same place on successive days and that these animals are well spaced out. The other males occur in small groups and individuals also appear to have preferences for particular rest-sites, although this is not so marked. In the dark all animals are well spaced out. Once again certain individuals are to be found always in the same place and these animals defend their site against intruders.

Territorial males not only defend their chosen area but also patrol its limits at intervals throughout the night. The posture of males engaged in this activity is quite characteristic. The legs are maximally extended so that the body is well clear of the ground, the abdomen is also extended as in the aggressive posture. During periods of inactivity, when the territorial cockroach is nevertheless alert, the stance is also distinctive. The abdomen is fully extended and may be pumped up and down in a rhythmic fashion. The head is held rather low and quite often the animal faces into the rest-site on its territory (e.g. a glass vial). A male not actively engaged in defending or patrolling its territory may groom itself or forage. Food is sometimes brought back to the territory and returning males have been seen to fight off other males without dropping the food from their mandibles.

The area round the rest-site is variable in size but if the rest-site is a vial, usually covers a radius of 5-8 cm. round the entrance. Individuals from each of the three groups studied, occupied territory G12 which is strategically placed between food and water (Fig. 4). In this case animals rarely descended to ground level and only patrolled the food and water dishes. Animals occupying territory G20 often occupied J20 as well and patrolled the entire area beneath the platform. It was not clear what initiated patrolling but animals did appear to follow a particular routine. For example, one male occupying G12 had made several attempts over a period of days, to oust another animal from its rest-site under the water dish. The occasion came when the defending animals was not in occupation but the patrolling male nevertheless went through his usual routine and rushed under the dish to attack.

For some cockroaches at least, the territory is a place for maintenance activities such as resting, eating and grooming. Territory holders defend and patrol their chosen areas. This picture does not hold true for all cockroaches and the complicating factor of social hierarchy must be taken into account.

Cockroaches can be classified according to their grouping within the dominance hierarchy. The hierarchy is not in evidence when the groups are first set up. To begin with there is a great deal of fighting involving all individuals but eventually three categories can be distinguished. These have been designated alpha, beta and gamma. It should be made clear that while the extremes, alpha and gamma, are very obvious they represent opposite poles of a continuum of behaviour. Beta males form an intermediate class and are not so easy to characterise.

Alpha males

These are top-ranking animals which have territories in the sense already described. Their territories do not usually overlap and they are separated by rest-sites and more transient territories of lower ranking animals. Once established, alpha males usually do not leave their territories unless to forage and therefore only rarely come in contact with other males of the same rank. When a confrontation does occur, opponents grapple briefly but before the fight is resolved, both males break off to resume previous activities.

If all alpha males were placed together in a small container, one animal would become dominant over all the others but in the more spacious environment provided by the tank, for all practical purposes, they are equally ranked at the top of the hierarchy. An alpha male is usually successful in fights which occur inside his territory boundary, though occasionally one individual dominates the whole group. Fights between alpha males at the territory boundary are usually unresolved. Outside his territory, a top-ranking male will attack any lower ranking animal that he meets. The attack often has the appearance of threat; the aggressor rushes forward and the opponent runs off before contact is made.

Beta males

These are middle-ranking animals whose territory boundaries are more or less confined to the actual rest-site. The area which beta males patrol is either very small or non-existent. A beta animal is easily ousted from its territory by an alpha male but usually returns to it. Defence of the rest-site is successful only against other beta males or lower ranking animals. When two beta males meet outside their respective territories attack is not inevitable and often they will pass with a brief touch of the antennae followed by a marked avoiding movement. Top beta males may grapple but this is rare. Beta males not only avoid other individuals when they meet in the open they also avoid alpha territories where they have been beaten previously.

Once the hierarchy has been established a middle-ranking animal may retain its territory for up to several weeks.

Gamma males

These are submissive animals which are attacked by both alpha and beta males. They are usually unsuccessful in retaining even a rest-site for any length of time. For much of the active period gamma males make repeated non-aggressive attempts to get into an occupied territory. Gamma males occasionally attack other low ranking animals but often they do not fight at all.

Possession of a territory in Nauphoeta appears to depend on position in the dominance hierarchy. Once established the hierarchy is relatively stable but each position is not permanently fixed and an alpha male may be replaced by a lower ranking animal. An animal moving up the dominance hierarchy begins to win fights against animals to which it was previously submissive. Only when the position of such a male is stabilised does it settle down to permanent occupation of a territory. Territories may be held for periods ranging from one to five weeks at least.

Analysis of Data

Many of the events so far described depend on the correlation between territory possession and status in the dominance hierarchy. Before proceeding with examples from the records it is necessary to mention how the hierarchy was worked out.

The traditional criteria for ranking individuals in a hierarchy derive from the aggressive interaction itself, from the number of animals attacked by a particular male and from the number of males which that animal itself attacked. It could be argued that the total number of attacks scored by or against any one individual would provide a good indication of status but it is also possible that this would reflect unresolved status. Thus an animal having a high score against it, representing repeated attacks on separate occasions, cannot be very submissive. Similarly, a male with a high score of attacks against other males has not yet established its dominance over them. Therefore the traditional method, which takes account of the number of animals dominated by a particular individual, was adopted to construct the hierarchy. Tables 3.1a, 3.2a and 3.3a, show the record of attacks for the three groups observed, (T1, T2 and T3). Tables 3.1b, 3.2b and 3.3b show the hierarchies constructed from these results. In most cases attacks were one-sided but where they were mutual, attacks were recorded in favour of the winner.

T1 males were observed over a period of eighty six days. The observations shown in Table 3.1a have been

T1 MALES

Males attacking	1	2	3	4	5	6	7	8	9	10	Total males attacked
1		010	000	110	021	010	000	000	000	000	4
2	010		010	000	000	010	001	000	001	100	6
3	110	030		000	001	012	001	000	110	000	6
4	000	000	000		200	002	002	000	000	000	3
5	001	000	010	000		000	100	000	000	000	3
6	001	000	300	000	000		102	000	112	000	4
7	200	000	000	000	000	000		000	100	000	2
8	041	010	010	030	010	010	000		060	010	8
9	020	000	000	100	000	000	000	000		000	2
10	000	010	100	020	000	010	000	000	000		4
Total males attacking	6	4	5	4	4	6	5	0	5	2	

(Males attacked: columns 1–10)

TABLE 3.1a Record of Attacks up to Day 35

Dominant	8	10	3 =	2	4	6	9	5 =	1	7
Subordinate	1	2	1	1	5	1	1	1	5	
	2	3	2	3	6	7		7		
	3	4	5	6	7	9				
	4	6	6	7						
	5		7	9						
	6		9							
	9									
Status	Alpha		Beta					Gamma		

TABLE 3.1b Hierarchy up to Day 35

Males attacking	1	2	3	4	5	6	7	8	9	10	Total males attacked
1		000	000	001	000	000	000	002	000	000	2
2	001		010	011	000	304	314	005	000	000	6
3	010	000		020	000	022	034	001	040	000	6
4	010	000	000		000	000	000	001	000	000	2
5	000	002	000	040		200	000	000	010	020	5
6	000	000	000	000	000		000	000	000	000	0
7	000	000	000	000	000	000		000	000	000	0
8	100	000	000	310	000	120	101		100	000	5
9	001	000	000	000	000	000	000	000		000	1
10	100	000	000	000	000	000	100	000	000		2
Total males attacking	6	1	1	5	0	4	4	4	3	1	

(Males attacked: columns 1–10)

TABLE 3.1a Record of Attacks for days 36 - 69.

Dominant	5	10	2	3	9	1	4	8	7	6
Subordinate	2	1	1	1	1	4	8	6		
	4	7	3	4		8		7		
	6		4	6						
	8		6	7						
	10		7	8						
			8	9						
Status	Alpha		Beta			Gamma				

TABLE 3.1b Hierarchy for days 36 - 69.

Males attacking	1	2	3	4	5	6	7	8	9	10	Total males attacked
1		11	00	01	00	02	01	21	00	00	5
2	20		00	10	00	40	00	10	00	00	4
3	93	07		12	00	14	00	30	02	06	7
4	06	07	01		00	04v	02	01	01	01	8
5	00	00	00	31		00	00	05	01	02	4
6	10	00	00	10	00		00	00	02	00	3
7	00	00	00	10	00	00		02	03	00	3
8	00	00	00	00	00	01	00		00	00	1
9	01	00	00	70	00	00	01	11		00	4
10	06	04	00	00	00	04	00	00	02		4
Total males attacking	6	4	1	7	0	6	3	7	6	3	

(Males attacked: columns 1–10)

TABLE 3.1a Record of attacks for days 70 - 86.

Dominant	5	4 =	3	10	1	2	7	6 =	8
Subordinate	4	1	1	1	2	6	8	9	6
	8	2	2	2	6	8	9		
	9	3	4	6	7				
	10	6	6	9	8				
		7	8						
		8	9						
		9	10						
		10							
Status		Alpha		Beta				Gamma	

TABLE 3.1b Hierarchy for days 70 - 86.

Full explanations of Tables 3.1 - 3.3 can be found in the text.

T2 MALES

Males attacking	Males attacked 1	2	3	4	5	6	7	8	9	10	Total males attacked
1	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0
3	0	1	0	0	0	0	2	0	2	0	3
4	4	1	0	0	0	0	2	2	0	0	4
5	1	0	0	0	0	0	2	0	3	0	3
6	1	0	0	0	0	0	2	0	5	0	3
7	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	3	0	0	0	1
10	0	0	0	0	0	0	3	1	2	0	3
Total males attacking	3	3	0	0	0	0	6	2	4	0	

TABLE 3.2a Record of attacks for days 0 - 9.

Dominant	4	10	5	6	3	8	2	1	9	7
Subordinate	1	(3)	1	1	2				7	
	2	7	7	7	7					
	7	8	9	9	9					
	8	9								
Status	Alpha		Alpha				Gamma			

Table 3.2b Hierarchy for days 0 - 9.

Males attacking	Males attacked 1	2	3	4	5	6	7	8	9	10	Total males attacked
1	0	0	0	0	0	0	0	1	0	0	1
2	4	0	0	0	2	0	0	2	0	0	3
3	3	0	0	0	1	0	0	2	0	0	3
4	5	3	0	0	4	0	0	1	0	0	4
5	1	0	0	0	0	0	0	1	1	0	3
6	0	0	0	0	0	0	0	0	2	0	1
7	4	1	0	0	2	1	0	2	1	0	6
8	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	5	0	0	0	0	0	1
10	2	2	0	0	2	0	2	1	1	0	6
Total males attacking	6	3	0	0	6	1	1	7	4	0	

TABLE 3.2a Record of Attacks for Days 10 - 17

Dominant	10	7	4	3	2	6	9	5	1	8
Subordinate	1	1	1	1	1	9	5	1	8	
	2	2	2	5	5			8		
	5	5	5	8	8					
	7	6	8							
	8	8								
	9	9								
Status	Alpha		Alpha		Beta		Gamma			

TABLE 3.2b Hierarchy for days 10 - 17.

T^2 MALES (Continued)

Males attacking	Males attacked 1	2	3	4	5	6	7	8	9	10	Total males attacked
1	0	0	0	0	1	0	0	3	0	2	3
2	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	6	4	0	6	2	0	4
4	0	7	0	0	2	0	0	4	1	0	4
5	0	0	0	0	0	0	0	1	0	0	1
6	0	0	0	0	0	0	0	0	0	0	0
7	0	3	0	0	4	0	0	6	0	0	3
8	1	0	0	0	0	1	1	0	1	2	5
9	0	0	0	0	11	5	0	1	0	0	3
10	0	0	0	0	1	1	0	1	0	0	3
Total males attacking	1	2	0	0	6	4	1	7	2	2	

TABLE 3.2a Record of attacks for days 18 - 23

Dominant	3	4	8	1 =	7	9	10	2	5	6
Subordinate	5	2	1	(2)	2	5	5			
	6	5	6	5	5	6	6			
	8	8	7	10						
	9		9							
			10							
Status	Alpha		Beta				Gamma			

TABLE 3.2b Hierarchy for days 18 - 23.

Males attacking	Males attacked 1	2	3	4	5	6	7	8	9	10	Total males attacked
1	0	0	0	0	4	4	3	0	1	1	5
2	0	0	0	0	2	0	4	0	4	0	3
3	0	0	0	0	3	0	1	0	0	0	2
4	5	0	0	0	3	9	0	0	0	3	4
5	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	1	0	0	0	0	1	2
8	0	0	0	0	0	5	3	0	1	1	4
9	0	1	0	0	0	1	1	0	0	0	3
10	0	0	0	0	0	0	1	0	0	0	1
Total males attacking	1	1	0	0	5	4	6	0	3	4	

TABLE 3.2a Record of attacks for days 24 - 30. B

Dominant	8	4	3	1	2	9	10 =	7	6 =	5
Subordinate	6	1	5	5	5	6	7	10		
	7	5	(6)	6	7	7				
	9	6	7	7	9					
	10	10		9						
				10						
Status	Alpha			Beta			Gamma			

TABLE 3.2b Hierarchy for days 24 - 30.

T3 MALES

Males attacking	Males attacked 1	2	3	4	5	6	7	8	9	10	Total males attacked
1	0	0	0	0	0	0	0	0	0	0	0
2	3	0	6	0	0	3	5	9	8	3	7
3	4	0	0	0	0	3	5	3	0	1	5
4	3	1	9	0	0	0	2	3	3	2	7
5	3	14	3	0	0	4	12	10	7	1	8
6	0	0	0	0	0	0	0	0	0	0	0
7	1	4	2	0	0	1	0	1	2	0	6
8	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	1	0	1	0	0	2
Total males attacking	5	3	4	0	0	4	4	6	4	4	

TABLE 3.3a Record of attacks for days 0 - 10.

Dominant	5	4	2	7	3	9	10	6	1	8
Subordinate	1	1	1	1	1	(1)	1	1	6	1
	2	2	3	2	6	(6)	6	7	8	6
	3	3	6	3	8	(10)	8	8	10	10
	6	7	7	6	10			10		
	7	8	8	8						
	8	9	9	9						
	9	10	10							
	10									
Status	Alpha			Beta		Gamma				

Table 3.3b. Hierarchy for days 0 - 10.

Males attacking	Males attacked 1	2	3	4	5	6	7	8	9	10	Total males attacked
1	0	0	0	0	0	0	0	1	0	0	1
2	0	0	0	0	0	0	0	0	2	1	2
3	0	0	0	0	0	0	0	0	0	0	0
4	1	0	0	0	0	0	2	2	1	1	5
5	5	0	2	0	0	2	0	0	2	2	5
6	0	0	0	0	0	0	0	0	0	0	0
7	1	1	0	0	0	0	0	0	0	0	2
8=	1	0	0	0	0	1	0	0	0	0	2
9	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0
Total males attacking	4	1	1	0	0	2	1	1	3	3	

TABLE 3.3a Record of attacks for days 11 - 20.

Dominant	5	4	7	2	3	9	10 =	8 =	1	6
Subordinate	1	1	1	9			1=	1	6	1
	3	7	2	10			8=	8	10=	
	6	8						6		
	9	9								
	10	10								
Status	Alpha		Beta		Gamma					

TABLE 3.3b. Hierarchy for days 11 - 20.

	Males attacked										
Males attacking	1	2	3	4	5	6	7	8	9	10	Total males attacked
1	0	0	0	0	1	0	0	0	0	0	1
2	1	0	1	0	0	0	0	1	2	0	4
3	0	0	0	0	0	0	0	1	1	0	2
4	0	0	0	0	0	0	0	0	1	1	2
5	0	0	0	0	0	0	0	0	0	0	0
6	5	7	0	0	0	0	1	0	5	0	4
7	1	0	0	0	1	0	0	0	0	0	2
8	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	0	0	1	0	0	0	0	0	0	0	1
Total males attacking	3	1	2	0	2	0	1	2	4	1	

TABLE 3.3a Record of attacks for days 21 - 30.

Dominant	6	2	4=7		1	10	3	9	8	5
Subordinate	1	1	7	1	(3)	3	8			
	2	3	9	4	5		9			
	7	(7)	10	5						
	9	8								
		9								
Status	Alpha				Beta			Gamma		

TABLE 3.3b Hierarchy for days 21 - 30.

	Males attacked										
Males attacking	1	2	3	4	5	6	7	8	9	10	Total males attacked
1	0	0	10	0	3	2	5	19	8	1	7
2	14	0	3	0	5	22	9	12	13	1	8
3	2	0	0	0	2	1	5	2	1	0	6
4	0	0	0	0	1	0	6	4	3	0	4
5	0	0	0	0	0	0	0	0	0	0	0
6	0	0	4	0	1	0	0	16	5	0	4
7	0	0	0	0	0	0	0	0	1	0	1
8	0	0	0	0	1	0	0	0	0	0	1
9	0	0	0	0	0	0	0	0	0	0	0
10	0	0	5	0	6	1	4	7	9	0	6
Total males attacking	2	0	4	0	7	4	5	6	7	2	

TABLE 3.3a Record of attacks for days 31 - 40

Dominant	2=4		1	10	3	6	7	5=8		9
Subordinate	1	2	3	3	5	5	(5)	8	5	
	3	5	5	5	6	(7)	9	9		
	4	7	6	6	7	8				
	5	8	7	7	8	9				
	6	9	8	8	9					
	7		9	9						
	8		10							
	9									
	10									
Status	Alpha			Beta				Gamma		

TABLE 3.3b Hierarchy for days 31 - 40.

divided into three sub-tables corresponding to thirty five, thirty four and seventeen days. The hierarchies were constructed for each of these periods. The time scale of each sub-table is divided into periods which correspond approximately to ten days. T2 and T3 males were observed over a period of thirty and forty days respectively. The observations for both groups have been divided into four sub-tables each covering one week in the case of the T2 males and ten days in the case of T3 males. The hierarchies were constructed for each of these periods.

For each period over which the hierarchies have been calculated the ultimate criterion in allocating rank was the score made towards the end of that period. For example, if the beginning of the month male 5 is dominant over male 9 but at the end of the month the situation is reversed, then male 5 is ranked lower than male 9. (The daily scores are given in Appendix 3.2).

Constructing the hierachy was not always straightforward. In some cases no encounters between two individuals was observed because their patrolling areas did not overlap. Rank had to be determined from the rank of animals whose dominance relationships were known. E.g., if male 5 and male 6 have never met each other and male 5 is dominant over male 7, and male 7 is dominant over male 6, then male 5 is taken to be dominant over male 6 also. This situation was fairly common for top-ranking animals, and possibly my method of dealing with the problem creates a slightly artificial straight-line rank order. Nevertheless, a linear order was often apparent even within one class of male.

Encounters between two animals did not always end in attack and sometimes both individuals would flee in opposite directions after antennal contact. If this was the only type of encounter observed between two animals then they were taken to have equal status. This is indicated in the tables by an equals sign between the two males (thus, 5=6). This situation was common for low-ranking animals.

Sometimes one animal would flee from another without being attacked or even without antennal contact. If this was the only encounter observed between the two, the subordinate male is indicated in the table by brackets (thus, $\frac{5}{(6)}$).

Results

1. Rest-site versus territory

When it becomes light, animals seek out a rest-site, usually some structure which provides maximum contact round the body. Top-ranking males are found consistently in the same rest-site which becomes the centre of their territorial area which they patrol at night. Lower ranking males may occupy the same rest-site on several different occasions but not usually in succession. Out of eighteen or so popular rest-sites one animal will occupy only four or five.

Territory occupation in both light and dark was noted only in T1 males (the first group to be studied). The other two groups were watched only in the dark. Table 3.4a shows territory occupation in the light and dark for the first thirty five days and Table 3.4b covers the next thirty five days. Observations on this group cover a further ten days but none were made in the light over this period. Besides showing the total number of different territories (or rest-sites) occupied by a particular individual, the tables also show how frequently that animal was to be found in its preferred sites. The method of interpreting the tables can be demonstrated by taking male 1, Table 3.4a, as an example. In the light this male was observed on ten occasions over a period of thirty five days. During this time he occupied four different territories. One of these territories was occupied four times and this was taken to be his preferred site. The other territories were equally preferred and each was occupied twice.

From the tables it can be seen that some males were observed more often than others. The reason for this is that sometimes several males were crowded together in such a way that they could not be identified. Male seven is not recorded because it escaped twice for several days before being recovered.

Males		Territories (No.)	Times in 1st Preference	Times in 2nd Preference	Observations (No.)	Status
1	L	4	4	2	10	Gamma
	D	7	2	2	9	
2	L	6	5	1	10	Beta
	D	5	3	2	8	
3	L	5	3	3	11	Beta
	D	5	5	1	9	
4	L	5	4	2	11	Beta
	D	3	5	3	9	
5	L	3	10	1	12	Gamma
	D	4	4	2	8	
6	L	4	5	3	11	Gamma
	D	5	3	3	9	
8	L	2	11	1	12	Alpha
	D	3	6	2	9	
9	L	4	7	2	12	Gamma
	D	5	3	1	8	
	L	4	7	3	12	Alpha
	D	4	5	2	9	

Table 3.4a Territory occupation by males of different rank in the light (L) and dark (D) for T1 males. As well as showing the total number of territories occupied the table also shows how often the two most preferred sites were occupied. The observations cover the first thirty five days.

Males		Territories (No.)	Times in 1st Preference	Times in 2nd Preference	Observations (No.)	Status
1	L	5	3	2	8	Gamma
	D	3	2	2	5	
2	L	3	4	4	9	Beta
	D	2	7	1	8	
3	L	4	4	3	9	Beta
	D	2	4	1	5	
4	L	3	7	1	9	Gamma
	D	3	2	1	4	
5	L	1	8	0	8	Alpha
	D	1	7	0	7	
6	L	4	5	1	8	Gamma
	D	4	4	1	7	
8	L	6	2	2	9	Gamma
	D	3	2	2	5	
9	L	3	4	3	8	Gamma
	D	4	3	2	7	
10	L	1	9	0	9	Alpha
	D	1	7	0	7	

TABLE 3.4b. Territory occupation by males of different rank in the light (L) and dark (D) for T1 males. As well as showing the total number of territories occupied, the table also shows how often the two most preferred sites were occupied. Observations cover days thirty six to seventy.

The main features of interest are that:-

a) On the whole, a particular site is occupied more consistently in the light than in the dark. This is most true of low-ranking animals (Table 3.4a, males 1, 5 and 9).

b) Of all males, alphas occupy their preferred site more often than any other class of male (Table 3.4a, male 8 and male 10, Table 3.4b, male 5 and male 10).

Territory occupation in the dark was noted throughout observations on all three groups. The results have been divided into blocks which correspond to the periods for which hierarchies have been worked out. Tables3.5, 3.6 and 3.7 show the results for T1, T2 and T3 males respectively. T1 males were watched from the first day that the tank was set up but T2 and T3 males were left for fourteen days before observations were begun. In the tables day one refers to the first day of observation. The tables show whether on any one day of observation, a particular male is occupying the same territory as it was on the previous occasion. Social rank is given at intervals to demonstrate the change in territory holding which accompanies change in status.

(2) Territory holding and status

(a) Alpha males. As mentioned previously alpha males occupy only one territory so long as there is no change in rank. Very few individuals retained a top position in the hierarchy throughout the entire observation period, but those which did, occupied the same territory consistently. (Table 3.6, males 3 and 4, Table 3.7 male 4). An alpha male losing status to become a beta without further loss of rank during the observation period, does not necessarily lose its territory (Table 3.5, male 10),but in most cases loss of rank is accompanied by loss of territory (Table 3.5, male 8, Table 3.6, male 5, Table 3.7 male 5).

(b) Beta males. Middle-ranking animals as a class seem to be more variable than alpha males; some occupy the same territory consistently (Table 3.5, male 3, Table 3.6, males 1 and 9, Table 3.7, male 5.), but others are much more variable (Table 3.5, male 4, Table 3.6, male 8, Table 3.7, male 10). As with alpha males, loss of status is accompanied by loss of territory. Animals moving up the hierarchy become more established in their territories.

(c) Gamma males. Bottom-ranking males rarely occupy the same territory for any length of time. They are prevented from doing so by the activities of higher ranking individuals. If gamma males succeed in moving up the hierarchy then they also become established in a territory (Table 3.5, male 5, Table 3.7, male 1 and male 10).

These results confirm the general observation that the higher the rank of an animal the more likely it is for that animal to have a permanent territory.

	DAY							STATUS	DAY							STATUS	DAY						STATUS
Male	2	8	9	21	28	33	35		39	45	49	50	58	60	69		72	73	76	80	85	86	
1	+	-	-	-	-	-	-	Gamma	-	-	-	-	-	-	-	Gamma	+	+	-	+	+	-	Beta
2	-	-	+	+	-	-	-	Beta	+	-	+	+	+	+	+	Beta	+	+	-	-	-	+	Gamma
3	-	-	+	-	-	+	+	Beta	+	-	-	+	+	+	-	Beta	-	+	-	-	-	+	Beta
4	-	+	+	-	-	+	+	Beta	-	-	-	-	+	-	-	Beta	-	-	-	+	-	+	Alpha
5	-	+	+	-	-	-	-	Gamma	+	+	+	+	+	+	+	Alpha	+	+	+	+	+	+	Alpha
6	+	-	+	-	-	-	-	Gamma	-	-	-	-	-	-	-	Gamma	-	-	-	-	-	+	Gamma
7	-	-	+	-	-	-	-	Gamma	-	-	-	-	-	-	-	Gamma	+	+	+	-	-	+	Gamma
8	+	-	+	+	+	+	+	Alpha	-	-	-	-	+	+	-	Gamma	-	-	+	-	+	-	Gamma
9	-	+	-	-	-	-	+	Gamma	-	-	-	-	-	-	+	Gamma	+	+	+	-	-	+	Gamma
10	+	-	-	-	+	+	+	Alpha	+	+	+	+	+	+	+	Alpha	+	+	+	+	+	+	Alpha

TABLE 3.5 Territory occupation in T1 males. A positive (+) sign indicates that the animal is occupying the same territory as it was on the previous occasion of observation. Observations cover a period of eighty six days and status is given at the end of periods for which the hierarchy was worked out. The first observations were made on day one.

	DAY				DAY				DAY						DAY						
Male	2	3	9	Status	11	16	17	Status	18	19	20	22	23	Status	24	25	26	28	29	30	Status
1	-	+	+	Gamma	+	-	+	Gamma	+	+	+	+	+	Beta	+	+	+	+	-	+	Beta
2	-	-	+	Gamma	-	+	-	Beta	+	+	-	-	+	Gamma	-	+	+	+	+	+	Beta
3	+	+	-	Alpha	+	+	+	Alpha	+	+	+	+	+	Alpha	+	+	+	+	+	+	Alpha
4	+	+	+	Alpha	+	+	+	Alpha	+	+	+	-	+	Alpha	+	+	+	+	+	+	Alpha
5	-	+	+	Alpha	-	-	-	Gamma	-	-	-	-	-	Gamma	-	-	-	-	-	-	Gamma
6	+	+	+	Alpha	+	+	+	Beta	+	+	+	-	-	Gamma	-	-	-	-	-	-	Gamma
7	-	-	-	Gamma	-	-	-	Alpha	+	+	+	+	+	Beta	+	+	-	-	-	-	Gamma
8	-	-	-	Gamma	-	-	-	Gamma	-	-	-	-	-	Beta	-	+	+	-	+	+	Alpha
9	+	+	-	Gamma	-	-	-	Gamma	+	+	+	+	+	Beta	+	+	+	+	+	+	Beta
10	-	+	+	Alpha	+	+	+	Alpha	+	+	+	+	+	Beta	+	-	-	-	-	-	Gamma

TABLE 3.6 Territory occupation and status in T2 males. A positive (+) sign indicates that the animal is occupying the same territory as it was on the previous occasion of ovservation. Observations cover a period of thirty days and status is given at the end of periods for which the hierarchy was worked out.

	DAY							DAY				DAY				DAY						
Male	3	4	5	6	9	10	Status	14	15	20	Status	30	31	32	Status	34	35	36	38	41	43	Status
1	-	-	-	-	-	-	Gamma	+	-	-	Gamma	-	-	-	Beta	-	+	+	+	+	+	Alpha
2	-	-	-	-	+	+	Beta	-	-	-	Beta	-	-	+	Alpha	+	+	+	+	-	+	Alpha
3	+	-	-	-	-	-	Beta	-	-	-	Gamma	-	-	-	Beta	-	-	-	-	+	+	Beta
4	-	+	-	-	+	+	Alpha	+	+	+	Alpha	+	+	+	Alpha	+	+	+	+	+	+	Alpha
5	-	+	+	+	+	-	Alpha	-	+	+	Alpha	-	-	-	Gamma	-	-	-	-	-	-	Gamma
6	-	-	-	-	-	-	Gamma	-	-	-	Gamma	-	-	-	Alpha	+	+	+	+	-	-	Beta
7	-	-	-	+	+	-	Beta	-	+	-	Beta	-	+	+	Alpha	+	+	+	+	-	-	Beta
8	-	-	-	-	-	-	Gamma	-	-	-	Gamma	-	-	-	Gamma	-	-	-	-	-	-	Gamma
9	-	-	-	-	-	-	Gamma	-	-	-	Gamma	-	-	-	Gamma	-	-	-	-	-	+	Gamma
10	-	-	-	-	-	-	Gamma	-	-	-	Gamma	+	-	+	Beta	+	+	+	+	+	+	Beta

TABLE 3.7 Territory occupation and status in T3 males. A positive (+) sign indicates that the animal is occupying the same territory as it was on the previous occasion of observation. The observations were made over a period of forty three days and status is given at the end of periods for which the hierarchy was worked out.

(3) Fighting and status

The hierarchy is determined in such a way that high rank is given to a male which has beaten many other animals. High ranking males also initiate more attacks. There are two ways in which an animal can achieve a high score of attacks, either by chasing other males out of its territory and this usually applies to alpha males, or by wandering about the tank and attacking any animal which crosses its path and this usually applies to high ranking beta males before they achieve alpha status and become established in a territory. The relationship between fighting and status is shown in Tables 3.8a and 3.8b for T2 and T3 males respectively. The tables show the total number of successful attacks made by each male over the entire observation period (Twenty four hours of observation over a period of thirty days for T2 males and over a period of forty days for T3 males). Most males changed rank over the observation period and the score of attacks have been allocated to the appropriate rank. A blank in the table indicates that the individual never occupied that position in the hierarchy. Thus male 3, Table 3.8a, had periods as both a beta and a gamma but was never an alpha. This table does not show whether the animal is moving up or down in the hierarchy and for this information the original tables should be consulted (Tables 3.3b and 3.2b).

T2 MALES

	Alpha		Beta		Gamma	
	Attacks	Grappling	Attacks	Grappling	Attacks	Grappling
1	48	3	1	0	1	0
2	75	3	40	0		
3			31	0	0	0
4	46	2				
5	67	0			0	0
6	18	1	26	3	0	0
7	2	1	14	0		
8					3	0
9					0	0
10			33	0	2	0

TABLE 3.8a

T3 MALES

	Alpha		Beta		Gamma	
	Attacks	Grappling	Attacks	Grappling	Attacks	Grappling
1			11	1	1	0
2			18	0	0	0
3	33	0				
4	56	0				
5	6	0			4	0
6	8	0	2	0	0	0
7	11	1	13	0	2	0
8	10	0	6	0	0	0
9	0	0	20	1	8	0
10	18	0	4	0		

TABLE 3.8b

TABLES 3.8a and 3.8b. The relationship between fighting and status in T2 and T3 males.

Tables 3.8a and 3.8b show the number of attacks initiated by a particular male while it occupied different positions in the hierarchy and also the incidence of high intensity fighting, grappling.

Fighting is seen to be rare in gamma males and grappling, which is not very common in any group of animals, is seen only in alpha and beta males. When an alpha and beta grapple together it is usually obvious which of the two has the higher rank because the subordinate male soon runs off but when two alphas grapple the situation is not clear and grappling may be broken off without the fight being resolved. Alpha males rarely meet and it may be that they actively avoid each other. This point is difficult to prove but there is a noteable lack of encounters between alpha males. (See Tables 3.1 to 3.3). It was the difficulty in determining the dominance relations of top-ranking males that led me to suppose that the hierarchy was not linear. The fact that there are few encounters betwen top-ranking males indirectly supports the observation that these animals tend to remain on their territories. In the next chapter I shall present evidence that active avoidance may also be involved. On one occasion an encounter was recorded between two alphas from T3. Male 2, which occupied F12 and male 4 which occupied W (see Fig. 4) met while patrolling their respective territories. After grappling briefly, they broke off without resolving the fight and returned to their previous activities. No other encounter was observed between the two while they occupied top positions in the hierarchy.

Discussion

Social organisation in male Nauphoeta appears to differ from that described for other territorial insects, dragonflies, crickets and cicada-killer wasps. In these insects territory confers dominance on the territory holder while it is in residence but in Nauphoeta, rank determines the outcome of a fight, wherever it occurs, and rank determines which males can possess a territory. Many examples of this type of organisation are found in vertebrates as previously discussed.

In Nauphoeta the hierarchy itself has rather unusual characteristics. A top-ranking male is unable, in most cases to retain its rank and therefore its territory for more than four weeks. Alphas spend most of their time in territorial defence and possibly retire from exhaustion. Both beta and gamma males are able to move up the hierarchy and to achieve alpha status. Lorenz relates how subordinate males of the dwarf cichlid (Apistogramma species), may recover to dominate the worn-out territory holder.

There is one problem which is basic to any study of artificial colonies of animals in which a hierarchical organisation exists and that is, to what extent is the hierarchy a result of the restraints imposed by the experimenter ? To repeat Davis's observation (1958), a range of social organisation exists in *Mus musculus* from complete dominance of a group by one male, to a territorial situation where each male is dominant in its own territory, and the particular situation is dependant on population density. In the absence of any knowledge of what constitutes a natural group in *Nauphoeta* one can question the development of a hierarchy in this insect. This problem will be examined further in subsequent chapters but it must be said now, that the question cannot be answered fully until more is known of the habits of free-living *Nauphoeta* and of its non-domicilliary relatives.

Other problems which I shall be concerned with later in this thesis relate to the function of territorial behaviour; what are the benefits of possessing a territory, what are the disadvantages of low rank ?

CHAPTER FOUR

The Effect of Rank on General Activity

Introduction

In Nauphoeta cinerea, position in the hierarchy determines whether or not an individual can hold a territory. Low-ranking animals are unable to retain a territory and this is the most obvious difference between high and low-ranking animals. As discussed in the first chapter, low-ranking vertebrate animals also are unable to hold territories and in addition they are the first to be deprived when food is short, they have lowered resistance to disease and reduced reproductive capacity. It is possible that some of these effects could be found in subordinate N. cinerea. The effect of rank on feeding and drinking seemed most accessible to investigation and this is one of the main problems to be considered in this chapter. The other problem to be considered is the effect of rank on general activity. The amount of circadian activity, shown by Periplaneta americana isolates, in running wheels, varies according to the extent of the stressful treatment which they received beforehand (Brady 1967). If subordinate cockroaches, like subordinate vertebrates, are more stressed than dominant animals then they may show differences in activity.

To determine whether there is any correlation between rank and general activity in N. cinerea it was necessary first to obtain a picture of activity and feeding patterns. Two methods were adopted. The first was to run individual males in running wheels. The purpose of this was to check that the activity pattern for N. cinerea was similar to that found in other cockroaches. In alternating light and darkness, individual Periplaneta americana, in running wheels, become active just before the onset of darkness. Activity reaches a peak after two to three hours and declines over the next few hours after which it may cease altogether. Just before the onset of light there may be a second smaller peak of activity (Harker 1956).

The second method adopted involved watching groups of cockroaches directly and scoring activity for each hour of the night. The main object of this procedure was to see whether groups of males exhibited the same pattern of activity as single males in the wheels, whether a pattern of feeding and drinking exists and whether this pattern is affected by the rank of an animal.

(a) Single males

Materials and Methods

Day-old males were placed in running wheel actographs, basically similar to the design by Roberts (1960). Each balsa wood wheel was hexagonal, had sides 14 cm. long and a depth of 5 cm. The axle of the wheel revolved in a single ball race. A six-armed cardboard vane attached to the wheel interrupted a beam/photocell device in such a way that movement of the wheel could be monitored on a twenty channel, Esterline Angus pen recorder. Six pen marks were made per revolution of the wheel.

Seven males were run for four days, three for six days and seven for up to three weeks. The animals were run under an artificial light cycle of LD 12:12 at approximately 28°C.

Results

As expected the animals were more or less nocturnal but the pattern of activity during the night was rather different from that described for other cockroaches. Although most became active a few minutes after the onset of darkness the main bout of activity occurred after the middle of the twelve-hour dark period, before the onset of light. Table 4.1 shows whether the major bout of activity occurred at the onset of darkness and before mid-cycle or whether it occurred after mid-cycle and before the onset of light.

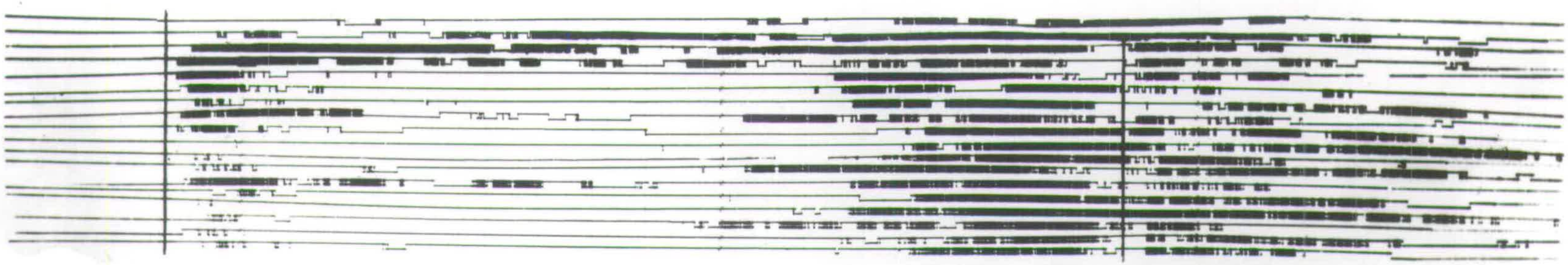
Most animals were more active on the first night than on any other night and several individuals which were more active after the onset of darkness on the first

Total Time in Minutes Spent Active

Males	After lights off	Before lights on	Males	After lights off	Before lights on
1	29.6	7.6	10	11.6	21.6
2		60.3	11	18.0	138.0
3	25.0	137.0	12	8.3	187.0
4	30.3	106.0	13	61.0	129.0
5	26.6	9.3	14	35.3	24.0
6	18.0	46.0	15	52.0	16.6
7	44.0	163.0	16	1.3	48.0
8	4.0	14.6	17	2.0	14.0
9	82.0	374.0			

TABLE 4.1. Mean time active in minutes for the main bouts of activity occurring before mid-cycle and after lights off and occurring after mid-cycle and before lights on.

night, were subsequently more active after mid-cycle. For both of these reasons, the mean time spent active during each of the major bouts was calculated from the records for days two, three and four. Daily records can be found in Appendix 4.1. The major bouts were picked out visually from the charts and any activity occurring thirty minutes before or after the main bout was considered as background and ignored. Activity was not always terminated by the onset of light and some animals were active for several hours during the day (Fig. 5). Bouts of activity beginning in the dark often continued into the light and the times given in Table 4.1 for bouts occurring in the latter half of the night may include some daytime activity.



LIGHTS OFF

LIGHTS ON

FIGURE V

Patterns of activity of males in running wheels.

(a) An active animal with the main bout of activity before dawn. This animal shows considerable daytime activity.

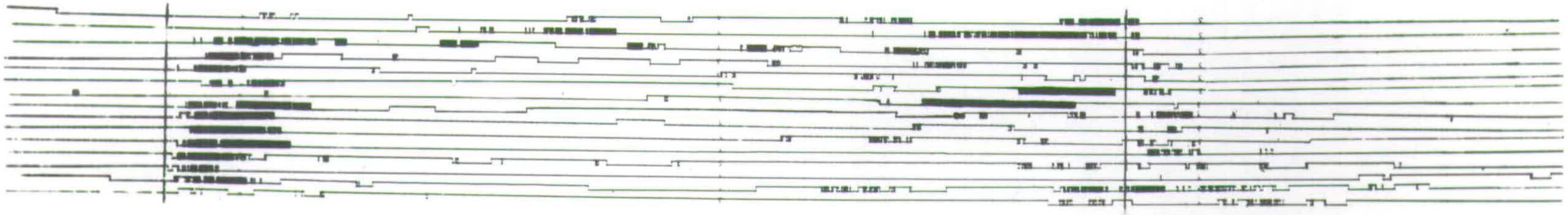
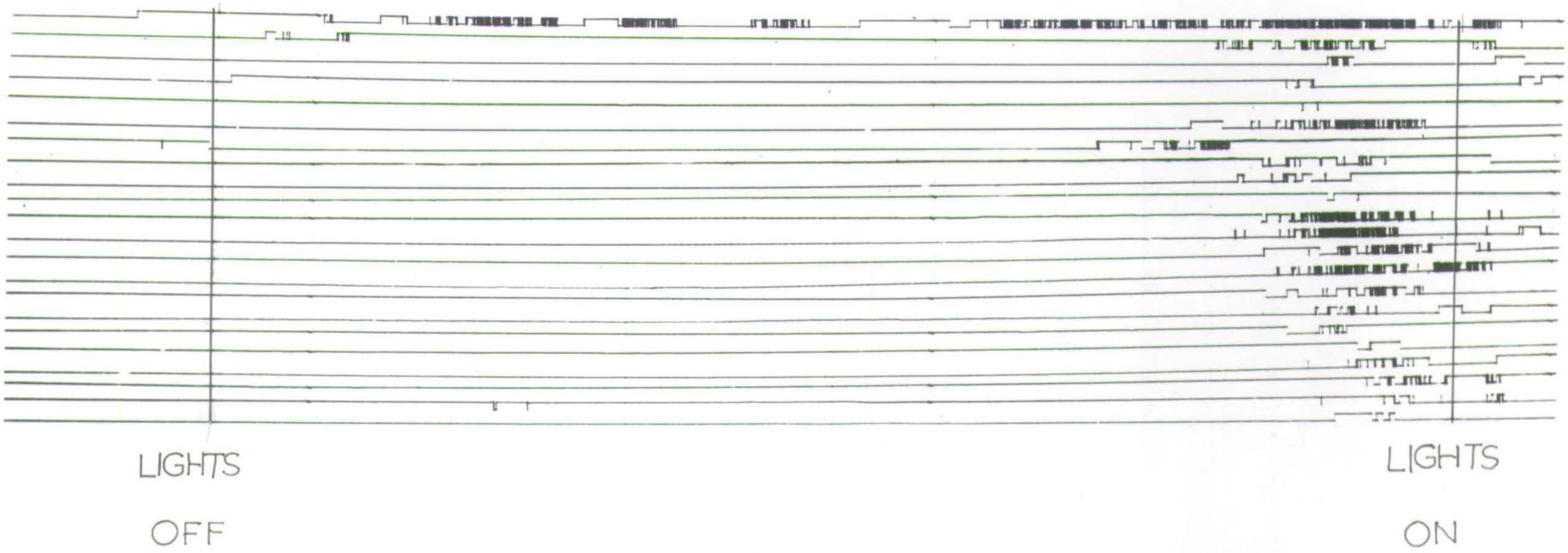

LIGHTS
OFF
LIGHTS
ON

FIGURE V continued

Patterns of activity of males in running wheels

(b) An animal with the main bout of activity early in the dark period.


LIGHTS
OFF
LIGHTS
ON

<u>FIGURE V</u> continued

Patterns of activity of males in running wheels.

(c) An inactive animal with the main bout of activity before dawn.

Three out of seventeen animals had the main bout of activity after the onset of darkness, thirteen had the main bout in the second part of the night, usually beginning a few hours before the onset of light and one was almost equally active during each of the major bouts.

As well as differences in the pattern of activity there were also differences in the total time spent active. This can be seen from Table 4.1. The results are best illustrated by examples from the records. Fig. 5 shows patterns of night activity in three different animals and also gives some idea of how much individuals can vary in the time they spend active. Fig. 5a shows the pattern of activity characteristic of most animals, in a particularly active individual whose main bout of activity continues into the day. Fig. 5b shows activity in an animal whose main bout of activity occurs early in the night and Fig. 5c shows activity in a relatively inactive animal.

The pattern of night activity in N. cinerea seems to be different from that found in other cockroaches although Periplaneta americana is more variable than one is led to believe. Most authors tend to emphasise the rhythms and their control and do not mention the percentage of animals possessing them (Sutherland 1969, pers. comm.). Since the activity of my insects was measured in alternating light and darkness and not in constant environmental conditions I have no evidence that the pattern which I find is part of an endogenously controlled circadian rhythm. If activity is measured in constant darkness the circadian element of the locomotor rhythm is most marked when the running wheel type of actograph is used. When a photocell box is used, the actographs show a decline in the peaks of activity which become difficult to distinguish from background after a few days (Brady 1967). Possibly, therefore, no particular pattern of activity would emerge in groups of males in the observation tank. Nevertheless, from the results on single males two predictions could be made. Firstly, one might expect animals in the tank to be more active in the latter part of the night, corresponding to the main bout of activity of animals in the wheel. Secondly one might predict that animals in the tank would feed in the middle of the night, corresponding to the time when animals in the wheel are inactive. Food and water arrangements in the wheel, are such that when an animal is eating or drinking the wheel is immobile.

(b) Groups of males

Materials and Methods

A method of recording and timing bouts of activity was developed during observations on T1 males and was eventually applied to T2 and T3 males. Only activity which would be likely to produce movement in a running wheel was included in the final activity score although most behaviour was recorded. Bouts of feeding and drinking were timed but not included in the activity score. The procedure adopted was as follows. The tank was scanned visually once every five seconds and at the same time a check was kept on the second hand of a clock. Whenever an animal moved, the time was noted and the behaviour recorded in a short-hand form. An animal had to be active for a minimum of fifteen seconds before any score was counted. If an animal began to move on one scan of the tank but had stopped by the next, then no score was made until the activity had been initiated three times and a score of fifteen seconds could be noted. Usually this procedure was called for only when an individual was walking slowly about the tank. Otherwise, once a particular activity was initiated, it was completed. If an animal was active for more than fifteen seconds the time was noted every thirty seconds. If, during a thirty second period, the activity was not performed continuously then it was recorded as lasting fifteen seconds.

HALF-HOURS OF THE NIGHT

GROUP	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
T2	2	5	3	3	4	9	6	7	7	6	8	5	9	5	6	9	8	6	3	5	8	8	5
T3	0	2	6	7	1	4	7	4	3	4	3	2	5	1	5	2	1	2	7	7	8	6	4

TABLE 4.2. The number of inactive animals (out of ten) in each half-hour of the night in T2 and T3 males.

A sample of recording might be as follows:

Time				
Min.	Sec.	Male	Activity	Interpretation
0	0	5	P	Male 5 is patrolling.
0	5	7	7/2	Male 7 attacks and beats male 2.
0	20	6	T	Male 6 goes to its territory.
0	30	5	P	Male 5 is still patrolling.
0	35	7	7/2 open	Male 7 beats male 2, 2 goes to open.
1	5	2	- pl	Male 2, still active goes tp platform.
1	15	6	- pl	Male 6 goes to platform.

The activity scores clocked up by the various males would be as follows:

Male	Score (sec.)
5	30
7	30
2	30 + 30
6	15 + 15

Both T2 and T3 males were watched on two occasions, for one hour at a time, for the twelve hours of darkness.

Results

(1) Activity

When the lights went off the animals came out of their hiding places almost immediately. In most cases all animals became active during the first half-hour of darkness,

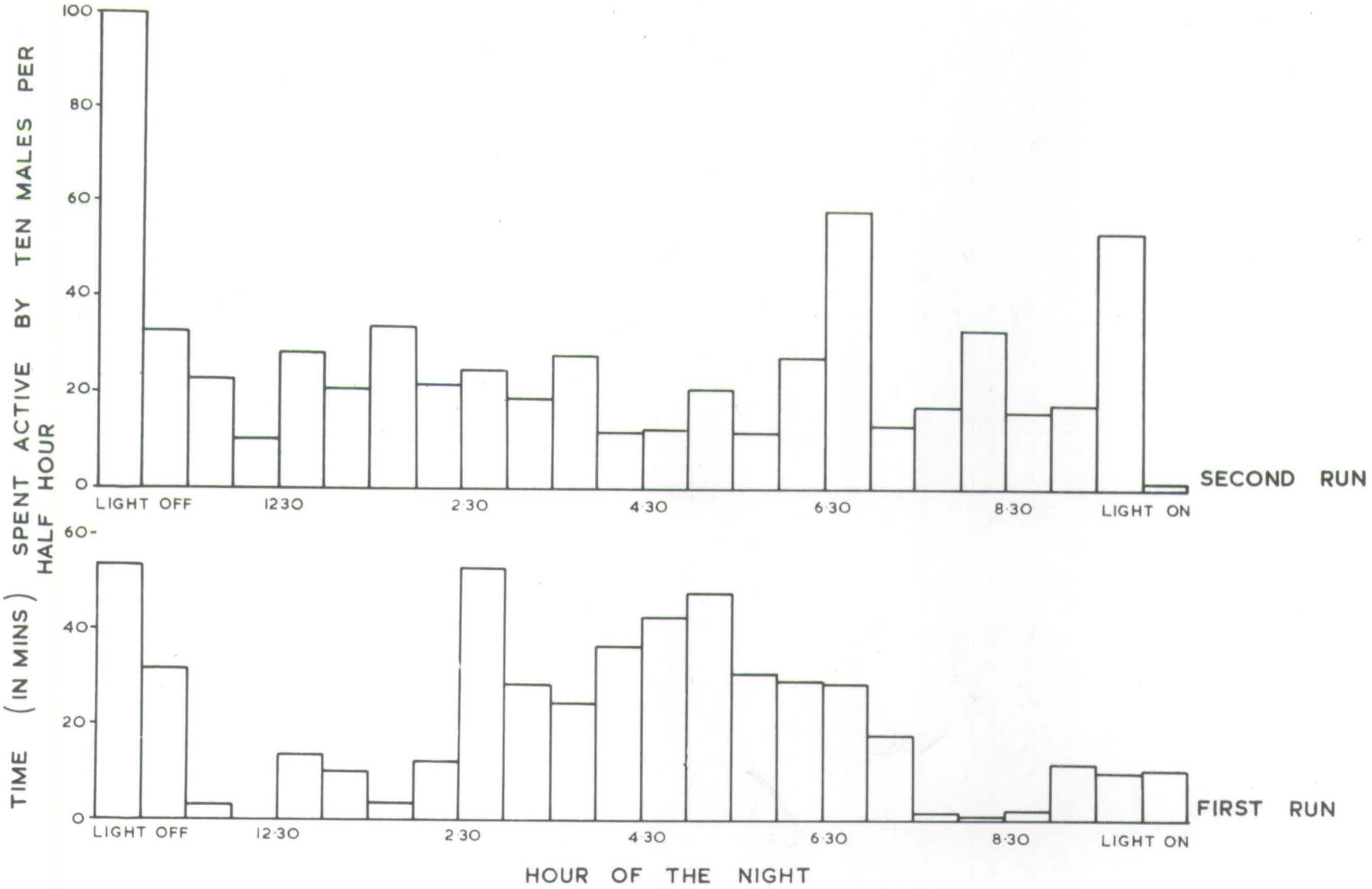

TIME (IN MINS) SPENT ACTIVE BY TEN MALES PER HALF HOUR
100
80
60
40
20
0
LIGHT OFF
12 30
2·30
4·30
6·30
8·30
LIGHT ON
SECOND RUN
60
40
20
0
LIGHT OFF
12·30
2·30
4·30
6·30
8·30
LIGHT ON
FIRST RUN
HOUR OF THE NIGHT

FIGURE VI

Activity in T2 males.

The histogram shows the total activity of all ten males for each half-hour of the night. The animals were watched twice for each hour of the night.

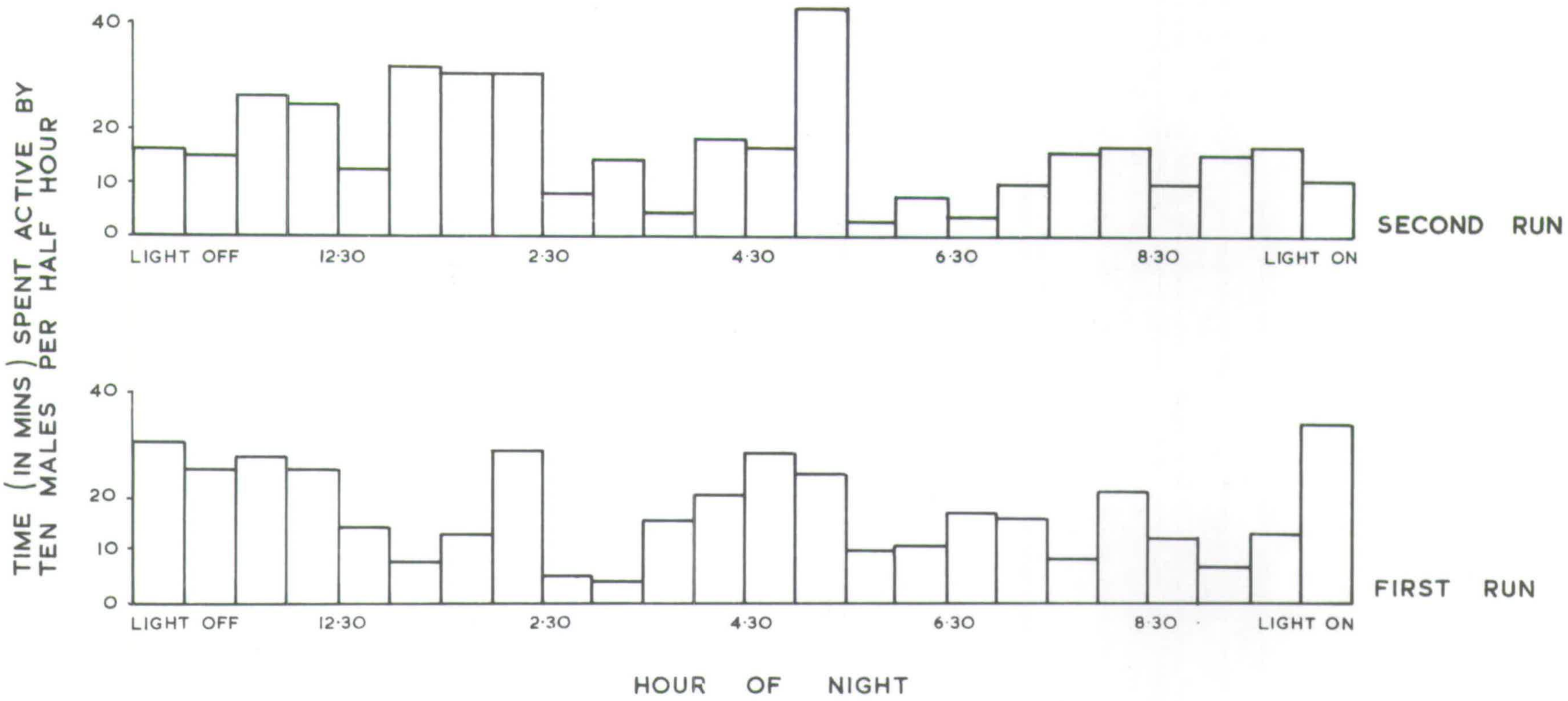

TIME (IN MINS) SPENT ACTIVE BY TEN MALES PER HALF HOUR
40
20
10
0
SECOND RUN
LIGHT OFF
12·30
2·30
4·30
6·30
8·30
LIGHT ON
40
20
10
0
FIRST RUN
LIGHT OFF
12·30
2·30
4·30
6·30
8·30
LIGHT ON
HOUR OF NIGHT

FIGURE VII

Activity in T3 males.

The histogram shows the total activity of all ten males for each half-hour of the night. The animals were watched twice for each hour of the night.

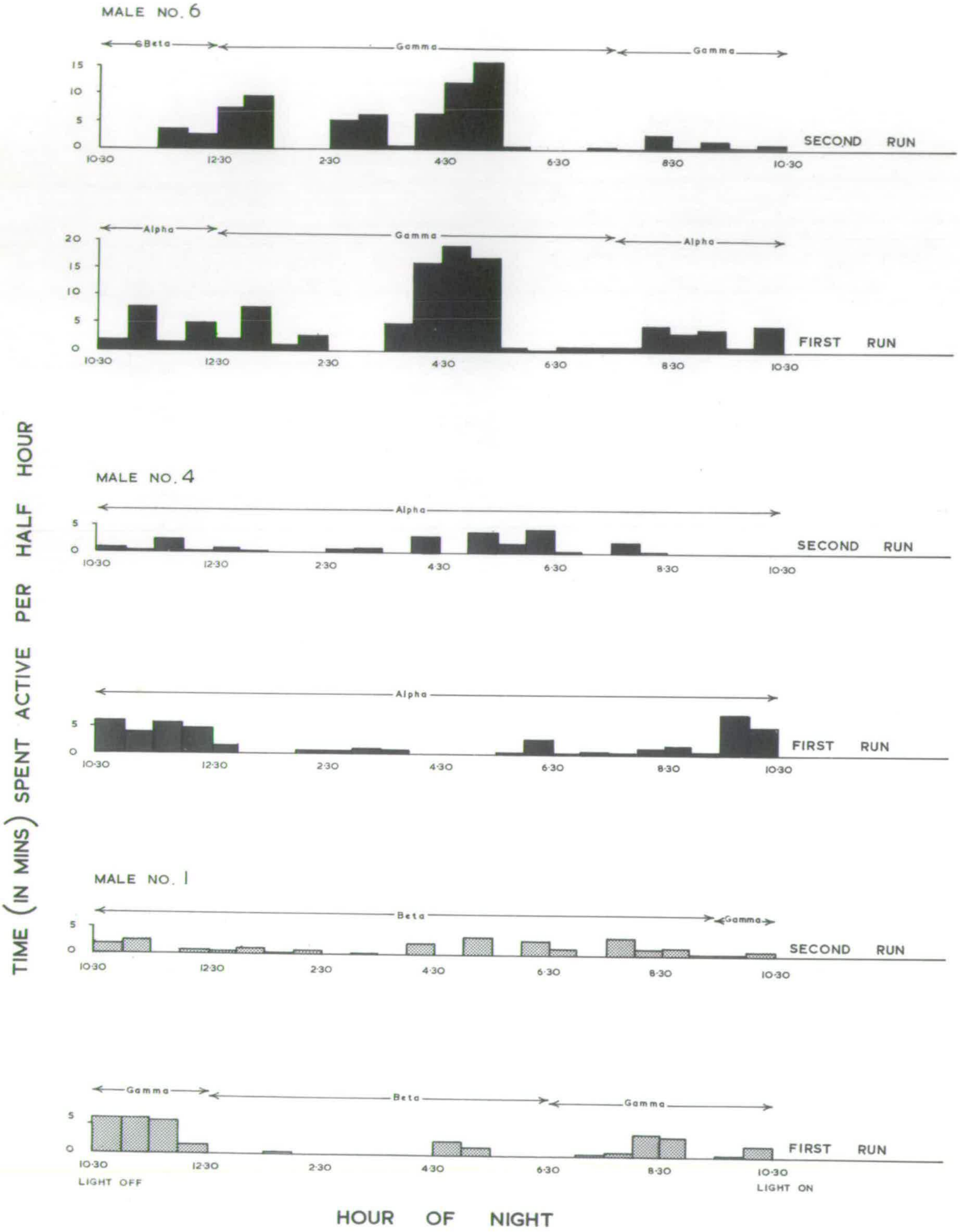

MALE NO. 6
Beta
Gamma
Gamma
15
10
5
0
10·30
12·30
2·30
4·30
6·30
8·30
10·30
SECOND RUN
Alpha
Gamma
Alpha
20
15
10
5
0
FIRST RUN
MALE NO. 4
Alpha
SECOND RUN
Alpha
FIRST RUN
MALE NO. 1
Beta
Gamma
SECOND RUN
Gamma
Beta
Gamma
FIRST RUN
LIGHT OFF
LIGHT ON
TIME (IN MINS) SPENT ACTIVE PER HALF HOUR
HOUR OF NIGHT

FIGURE VIII

Individual activity records.

Activity in some T2 males.

Male 6 An active animal which is both inactive and active during its gamma phase.

Male 4 An inactive alpha sometimes active at dawn and dusk, sometimes active at mid-cycle.

Male 1 An animal which is just as inactive during beta and gamma phases.

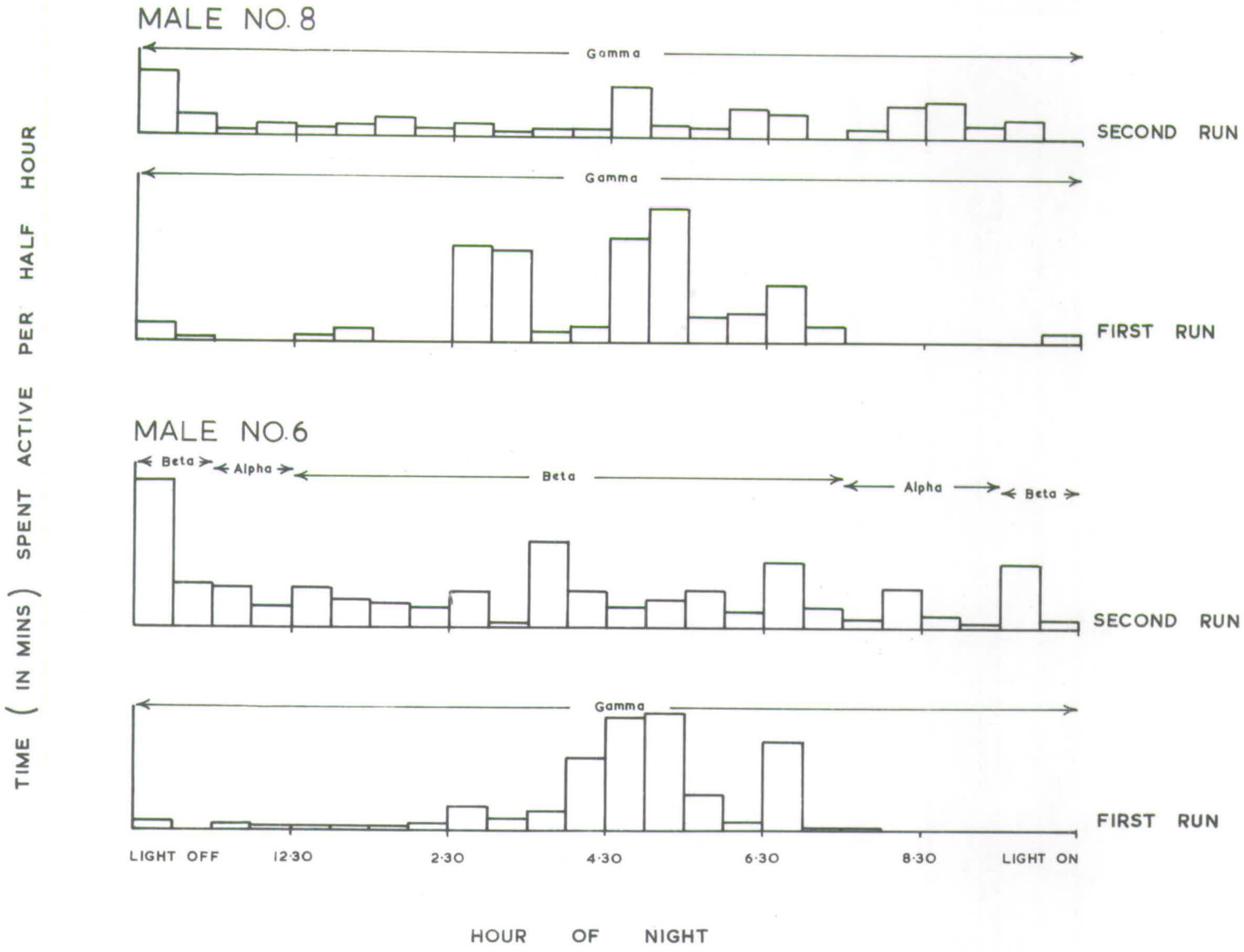

MALE NO. 8
Gamma
SECOND RUN
Gamma
FIRST RUN
MALE NO. 6
Beta
Alpha
Beta
Alpha
Beta
SECOND RUN
Gamma
FIRST RUN
LIGHT OFF
12·30
2·30
4·30
6·30
8·30
LIGHT ON
HOUR OF NIGHT
TIME (IN MINS) SPENT ACTIVE PER HALF HOUR

FIGURE VIII continued

Individual activity records.

Activity in some T3 males.

Male 8	A gamma male which shows no relationship between rank and activity.
Male 6	Like male 8, activity is high during mid-cycle on the first run, and more or less constant on the second run.

although there was no time when they were predictably active. Table 4.2 shows the number of animals which were completely inactive during each half-hour of the night.

The results for each half-hour represent the combined results from the two periods of observation.

Fig. 6 shows histograms of the combined activity scores of the ten males in T2 and Fig. 7 shows the same for T3 males. It was assumed that if most of the animals in the group had a similar pattern of activity, this would be reflected in the combined scores. However, the total activity of the group was found to be fairly constant. Periods in which most animals were inactive did occur but these were not consistent and some animals were particularly active when others were resting. A total lack of obvious activity pattern distinguishes group males from single males in the running wheels. Another distinguishing feature is the low level of activity in the group males. In the running wheels some animals are active for six hours at a stretch while the combined activity of the group males may not exceed ten and a half hours. (T3 males, second run).

Considered as a group, neither T2 nor T3 showed a particular pattern of activity. Fig. 8 shows a selection of individual records.

(a) T2 MALES

	ALPHA	BETA	GAMMA
1	-	12.75	0.00
2	-	0.25	0.00
3	0.50	-	-
4	0.00	-	-
5	0.00	-	9.50
6	3.75	0.00	4.50
7	0.25	0.50	18.25
8	0.00	2.50	0.50
9	-	0.00	0.50
10	0.25	0.00	0.00
Total	4.75	16.00	33.25

(b) T3 MALES

	ALPHA	BETA	GAMMA
1	5.25	0.25	0.25
2	13.50	11.50	-
3	-	10.50	0.00
4	0.45	-	-
5	0.00	-	11.00
6	0.00	1.25	0.00
7	2.00	4.50	-
8	-	-	15.00
9	-	-	7.00
10	-	29.00	0.25
Total	21.50	56.00	33.50

TABLE 4.3a and b. The total length of time spent eating in minutes by each male in T2 and T3.

Rank is shown and blanks indicate either that the animal never occupied that position in the hierarchy or that it held that rank for a short period only. In the T2 males there were 7 alphas, 7 betas and 8 gammas. In the T3 males there were 6 alphas and betas and 7 gammas. The total scores for each rank are shown. The results are obtained from observations over two, twelve hour dark periods.

(a) T2 MALES

	ALPHA	BETA	GAMMA
1	-	0.00	0.00
2	-	0.00	0.00
3	3.25	-	-
4	0.00	-	-
5	0.00	-	0.00
6	0.00	0.00	1.25
7	0.00	0.00	1.00
8	0.00	2.75	10.25
9	-	0.00	0.00
10	0.00	0.00	0.00
Total	3.25	2.75	12.55

(b) T3 MALES

	ALPHA	BETA	GAMMA
1	0.25	0.00	0.00
2	0.75	1.00	-
3	-	0.08	0.00
4	0.00	-	-
5	1.00	-	1.50
6	0.00	0.00	0.00
7	0.00	0.08	-
8	-	-	0.00
9	-	-	0.25
10	-	1.00	0.00
Total	2.00	2.16	1.75

TABLE 4.4a and b. The total length of time spent drinking in minutes for each male in T2 and T3.

Because drinking occurred so farely all bouts were timed, even if they lasted less than fifteen seconds. The results are obtained from two, twelve hour dark periods.

There is considerable individual variation in the amount and pattern of activity but this bears no relation to rank. Rank has been indicated in the records only when no change of rank has occurred over the observation period or when changes have been straightforward. Complete records can be found in Appendix 4.2.

(2) Feeding and Drinking

The main difficulty in detecting a rhythm in feeding and drinking was that the animals, particularly T2 males, ate and drank very little. The observations made would have to be repeated before definite conclusions could be drawn. Sufficient information however, was obtained to correlate feeding and drinking habits with rank.

Fig. 9 shows the total time spent eating by all T2 males and all T3 males during each half-hour of the night. Each point on the graph represents the sum of two observation periods. The results suggest a biphasic pattern of feeding. Fig. 10 shows the total time spent drinking in T2 and T3 males. There appears to be no pattern of drinking. Daily records can be found in Appendix 4.3.

Low-ranking animals do not appear to eat for shorter periods than males of higher rank. The results, which are shown in Tables 4.3a and 4.3b for T2 and T3 males respectively, indicate that alpha animals eat rather less than lower ranking males. This result is more obvious if account is

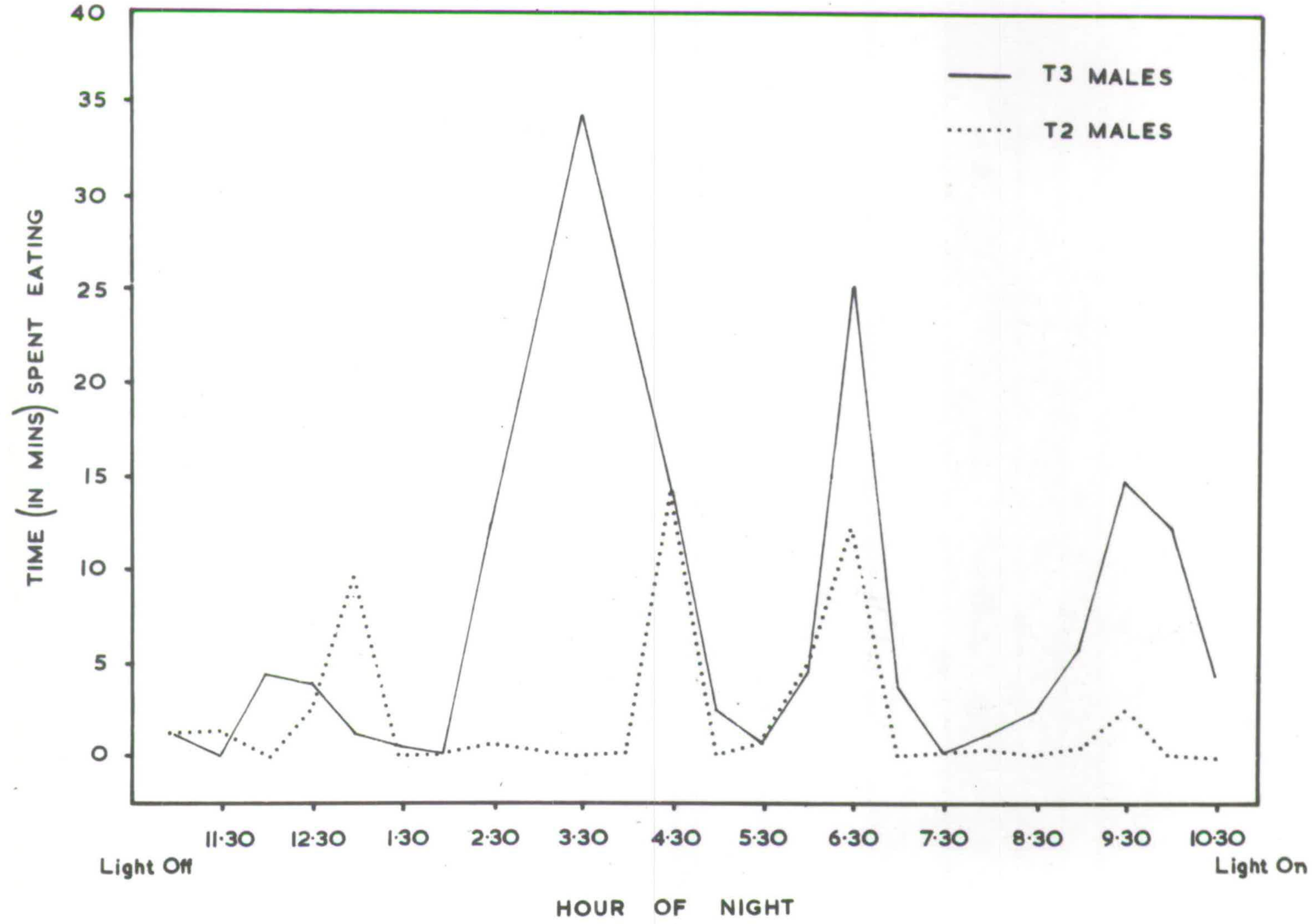

T3 MALES
T2 MALES
TIME (IN MINS) SPENT EATING
40
35
30
25
20
15
10
5
0
11·30
12·30
1·30
2·30
3·30
4·30
5·30
6·30
7·30
8·30
9·30
10·30
Light Off
Light On
HOUR OF NIGHT

FIGURE IX

The total time spent eating by all T2 males and all T3 males during each half-hour of the night.

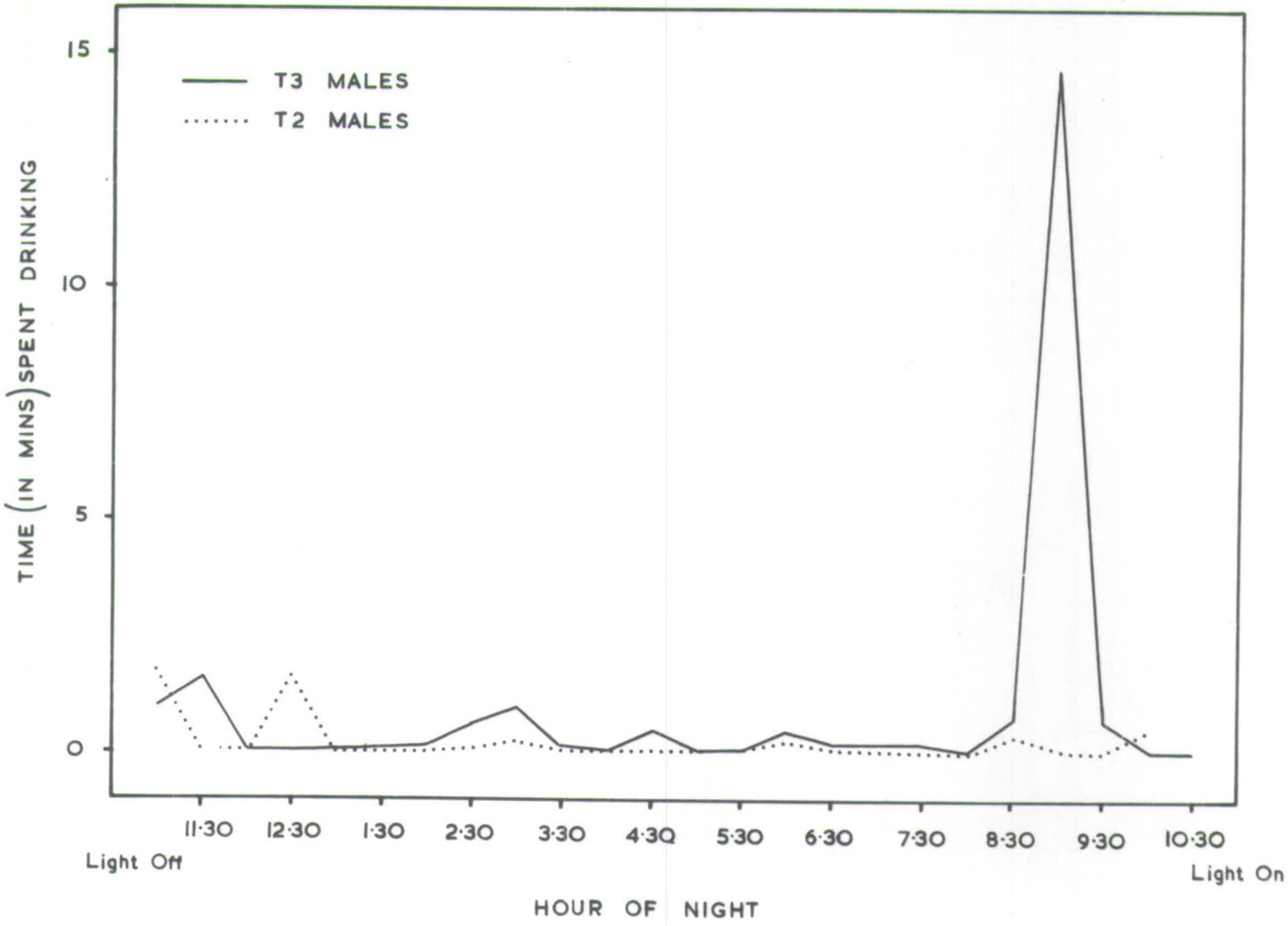

15
10
5
0
T3 MALES
T2 MALES
TIME (IN MINS) SPENT DRINKING
11·30
12·30
1·30
2·30
3·30
4·30
5·30
6·30
7·30
8·30
9·30
10·30
Light Off
Light On
HOUR OF NIGHT

FIGURE X

The total time spent drinking by all T2 males and all T3 males during each half-hour of the night.

taken of the fact that the only alpha male which eats for an appreciable length of time is male 2, (T3), which held the territory bridging the food and water supply.

Alpha males do not usually leave their territory and spend much of their active time patrolling. Low-ranking animals are free to forage and provided that they do not feed when the male in G12 (Fig. 4) is patrolling, can feed without interruption.

A very similar picture holds for drinking. The results are shown in Table 4.4a and b for T2 and T3 males respectively. The only alpha animal which drinks an appreciable amount is the owner of G12, male 3 (T2).

An alpha animal can hold a territory for up to six weeks but after this time usually loses rank. Perhaps prolonged territorial defence, combined with the effects of food and water deprivation, could account for the dominance shifts characteristic of the hierarchy in N. cinerea. Cockroaches are particularly resistant to food and water deprivation and Nauphoeta can survive up to eight weeks totally deprived (Cafferty 1969, unpublished work).

In the first chapter it was shown that males would fight to establish rank in the absence of females. It has now been shown that position in the hierarchy determines which males can hold territories. Although low-ranking males are excluded from territory holding there appears to be no other obvious effect of having low-rank. It remains to determine the role of territory and this will be considered in the next chapter.

CHAPTER FIVE

The Function of Territory

Introduction

In *N. cinerea* it seems unlikely that the defence of a territory is in anyway related to protecting the young or to providing food for them since there appears to be no specific association between adult males and nymphs. Mature males and females associate only to court and mate, a process which is completed in ten minutes. Territory, therefore, cannot be related to spacing out pairs in relation to the food supply. In other insects which are territorial, territory appears to ensure access to females, though there is no evidence that non-territorial males do not mate. Territory in *N. cinerea* could be related to mating behaviour, although how it operates in this gregarious insect is not immediately obvious.

Female *Nauphoeta* appear to be more gregarious than males. A small group of males and a small group of females were set up in identical containers, each provided with a platform of perspex tiers. The females remained clumped together while the males spaced out. This difference is illustrated in Figs. 11a and b and 12a and b. In a preliminary study on a small population of both sexes (twenty-two males and eight females) the low-ranking males were found to associate with the group of females while high ranking males took up territories outside this group.

a

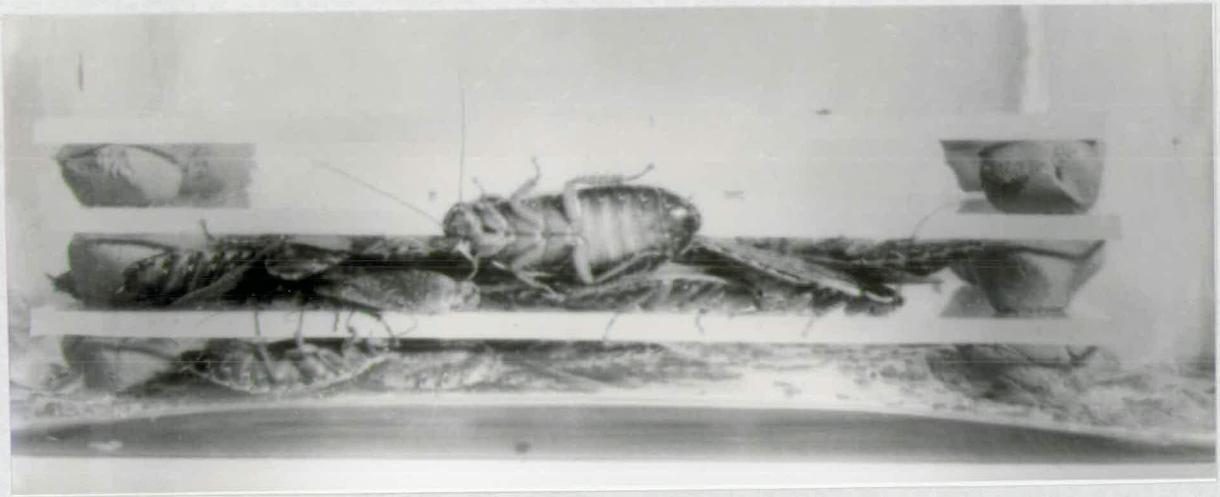
b

FIGURE XI

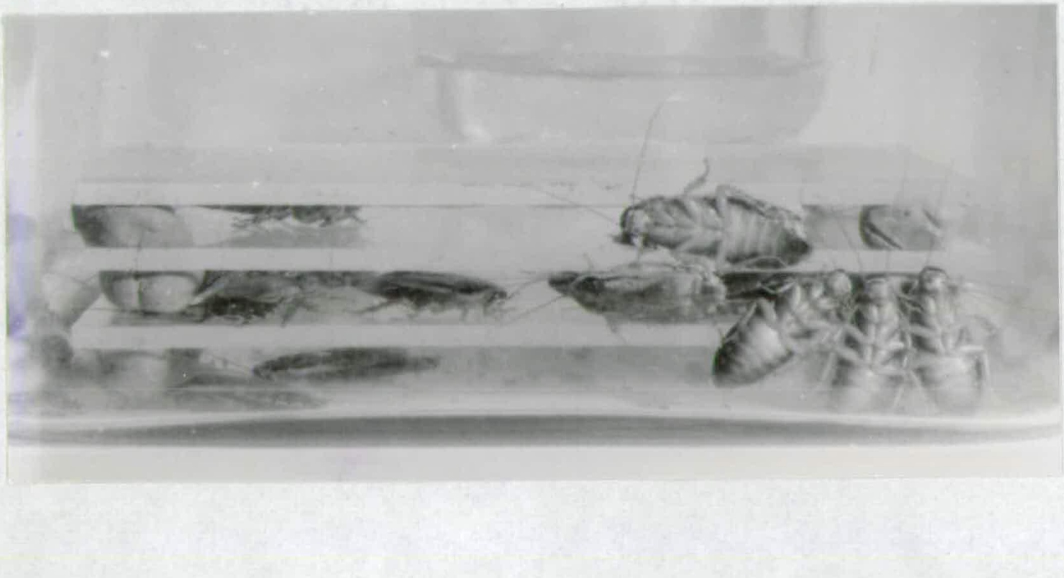
Spacing in males and females.

(a) Top view of a group of females. Notice the crowding.

(b) Top view of a group of males. Notice the spacing.



a



b

<u>FIGURE XII</u>

Spacing in males and females.

(a) Side view of females.

(b) Side view of males.

On the whole the females appeared to be rather inactive and little interaction was observed between the sexes. Only active females which left the group were courted.

One possibility which suggests itself from these observations is that when females become receptive, they leave the group and seek out the territorial males. This type of territorial behaviour would be rather similar to that of the vertebrate lek species in that only high-ranking animals have territories and females are attracted to the territorial area. I have already shown that only high ranking males have territories and I have some evidence that females become active during the period when they are receptive. Single females in running wheels exhibit cyclic locomotor activity which appears to be correlated to the reproductive cycle. Activity is high during the receptive period, gradually declines throughout pregnancy and for a time some animals become completely inactive. In a few cases there is a rise in activity just before parturition. Unmated females also show a decline in activity after the peak receptive period but this is less marked than in pregnant females and after a while activity returns to its previous high level. Full details of these results are given in Appendix 5.1. The observations on pregnant females are supported by a more thorough investigation on <u>Leucophaea maderae</u> (Leuthold 1966).

If a lek type system does operate in _N_. _cinerea_ then perhaps the territory provides an area where pairs can mate without interference from other males. If this is the main function, then mating success may be impaired by increasing the density of the population (or by reducing the area available for territory). There are two ways in which this could be brought about; either (1) indirectly, by reducing the number of high-ranking males (which was seen to be a feature of crowded mouse populations) and therefore the number of territorial individuals or (2) directly, by interference with mating. Bearing these points in mind I decided to investigate the effect of increasing the population density on the hierarchy and to see whether there was any correlation between rank and mating success.

(1) The effect of increasing population density on the hierarchy.

Materials and Methods

Two groups of ten males, T10a, and T10b, and two groups of twenty males, T20a and T20b, were used. Referring to the results from T1 - T3 males (ten males per group) it was possible to compare groups at increasing density. The increase in density was achieved in two different ways. T10 males were housed in half the area available to T1 - T3 males and T20 males, with twice the number of animals, were housed in the same area as T10 males.

Identical glass dishes, 25 cm. in diameter and 12 cm. deep, were provided for each group of males. Each dish was furnished with rectangular sheets of perspex arranged in three tiers, a water vial and a food dish. The animals were collected when teneral and marked with quick drying paint for individual recognition.

Observations were made in red light during the first hour of darkness and for three of the groups cover a period of one month. T10b males were watched over a period of three weeks only. Each group was observed at least twice a week (the exact occasions are recorded in Appendix 5.2). A record of attacks was made and hierarchies constructed for each week, as described in Chapter Three. Behaviour related to territoriality and to hierarchy was noted but no attempt was made to quantify the results because of the difficulty of recording the interactions between twenty males at once in the dense T20 groups. Positions of animals in the tanks were noted in the light, every few days, to see how territory holding was affected by density. These records can be found in Appendix 5.3.

Observations and Results

(a) T10 Males.

The main difference between these males and the T1-T3 males described in the preceeding chapters, is that it was easier to pick out an overall dominant in the more crowded

T10a MALES

	Dominant		
	8	4	5*
Subordinate	1	1	1
	2	3	2
	3	6	3
	6	7	7
	9	10	
	10		

Days 0 - 8

	Dominant			
	9	4	5*	2
Subordinate	1	1	1	1
	2	3	2	3
	3	6	3	7
	5	7	7	10
	6	8	10	
	7	10		
	8			
	10			

Days 9 - 16

	Dominant			
	5*	4	9	10
Subordinate	1	2	6	3
	2	3	7	6
	3	6	8	8
	4	7		
	6	8		
	7	10		
	8			
	10			

Days 17 - 23

	Dominant		
	7	5*	10
Subordinate	1	1	1
	2	4	3
	3	6	4
	4	9	6
	6		8
	8		
	9		
	10		

Days 24 - 31

TABLE 5.1. Dominance shifts in the hierarchy over a period of thirty one days in T10a Males. Only top-ranking males are shown and these are given in order of dominance. The full record of attacks is given in Appendix 5.3. * Indicates the owner of the food territory.

population. In both T10a and b, the top dominant was particularly active and patrolled the entire dish with the exception of the food container. The owner of the food container defended its territory with success against all except the top dominant. In both groups these males were not active and when patrolling rarely went farther than the edge of the container.

Hierarchies for each week of the observation period are shown in Tables 5.1 and 5.2, for T10a and b respectively. Daily scores are given in Appendix 5.2. The top dominants appear to lose rank sooner than males of equivalent status in the less crowded tank of the T1-T3 males, in which top alphas held their territory for a minimum of thirty days. In T10a there were two active top dominants, male 4, which lost rank after three weeks and male 9, which lasted for two weeks only. In T10b males there were no changes during the observation period of three weeks and there was only one active top dominant, male 4. In both groups the owners of the food territories retained rank throughout the observation period.

(b) <u>T20 males</u>

In the two most crowded tanks alpha males were easily distinguished and dominated the perspex platform, the water vial, the food container and sometimes the open space between the platform and the wall of the dish. During any

T 10b MALES

	Dominant	
	4	3*
Subordinate	1	2
	2	5
	3	6
	5	7
	6	
	7	
	8	

Days 0 - 6

	Dominant		
	4	5	3*
Subordinate	1	3	1
	2		7
	3		8
	5		9
	6		
	7		
	8		
	9		
	10		

Days 7 - 13

	Dominant			
	4	3*	9	2
Subordinate	1	1	2	1
	2	7		8
	5	8		10
	6			
	7			
	8			
	10			

Days 14 - 21

TABLE 5.2. Dominance shifts in the hierarchy over a period of twenty one days in T10b Males. Only top-ranking males are shown and these are given in order of dominance. The full record of attacks is given in Appendix 5.3.

* Indicates the owner of the food territory.

one thirty minute observation period, only two or three alphas were particularly active, although other alphas could be distinguished by their aggressive, guarding posture. Patrolling alphas marked centres of activity from which lower ranking animals were continually chased.

There was little sign of a linear hierarchy and apart from the alphas, most of the other males could only be described as 'non-dominant'. A few males, two or three in each group, were clear gammas. These animals became rather battered and were almost always to be seen in the submissive posture. Such extreme cases were not observed in either T1-T3 or T10 males.

A characteristic feature of T20 males was the lack of overt aggression in the 'non-dominant' males. Two types of non-aggressive interaction were commonly observed; either (1) two individuals would flee in opposite directions on contact or would sidle past each other, or (2) one male would give way without aggressive signals from the other. During periods of inactivity small groups of 'non-dominants' would crowd together. From time to time dominant males, patrolling nearby, would approach the group and randomly tap each member on the pronotum until the submissive response was evoked. This behaviour was seen to a lesser extent in T10 males but was never observed in T1 - T3 males. In <u>Blabera</u> <u>cranifer</u>, it has been shown that the

T20a MALES

	Dominant		
	*7	8	1
Subordinate	1	2	2
	2	3	3
	3	4	4
	4	5	5
	5	9	9
	9	19	17

Days 0 - 8

	Dominant				
	*7	8	3	14	4
Subordinate	4	1	1	1	1
	5	3	5	4	2
	9	4	6	9	3
	11	5	9	17	9
	16	9	14		11
	17	15	15		15
			16		18

Days 9 - 15

	Dominant	
	*7	12
Subordinate	1	1
	2	9
	9	11
	10	17
	15	
	16	
	20	

Days 16 - 23

	Dominant				
	15	3	12	6	4
Subordinate	4	9	1	4	2
	5	11	9		9
	12	13	13		11
	16	14	16		13
	17	17	17		16
					17

Days 24 - 31

TABLE 5.3. Dominance shifts in the hierarchy over a period of thirty one days in T20a Males. Only top-ranking males are shown and these are given in order of dominance. The full record is given in Appendix 5.3.

* Indicates the owner of the food territory.

pronotum is very sensitive to tactile stimulation and that reflex immobilisation may result from antennal tapping of the pronotal shield (Gautier 1965).

Hierarchies for each week of the observation period are shown in Tables 5.3 and 5.4 for T20a and b respectively. At any one time the total number of alphas in this group was more or less twice that found in the groups containing half the number of animals. Alpha males appeared to lose rank sooner than males of equivalent status in both T1-T3 and T10 groups. No alpha retained its position for more than three weeks. This suggests that as the density of the population increases the hierarchy becomes less stable. The owners of the food territory were able to retain rank for longest. A few encounters were recorded between alpha males but on the whole it was difficult to determine any linear relationship among these top-ranking animals. This phenomenon was commented on when describing the hierarchy in T1-T3 males and it was suggested that alpha males actively avoided each other. In the crowded tank housing the T20 males, the probability of encounter between two animals is very high and it thus seems likely that alphas must actively avoid the patrolling areas of males of the same rank.

Several conclusions can be drawn on the effect of increasing population density. In the large tank where the

T20b MALES

	Dominant			
	14	16*	11	9
Subordinate	1	9	3	3
	2	15	7	4
	3	17	9	5
	6	20	12	8
	12		19	20
	15			
	17			
	19			
	20			

Days 0 - 7

	Dominant							
	3	14	10	20	11	16*	5	17
Subordinate	4	2	2	8	2	5	2	4
	6	4	3	10	3	8	4	7
	7	7	7	11	4	12	7	15
	8	11	8	17	6		13	19
	9	12	9	19	7		17	20
	10	13	19		9		19	
	11	15	20		15			
	12	20						
	17							
	19							
	20							

Days 8 - 14

	Dominant					
	3	5	16*	4	10	2
Subordinate	1	1	4	6	1	6
	2	4	12	7	2	7
	6	7	18	10	11	12
	8	8		14	14	14
	10	11		15	18	15
	12	13		20	20	17
	16	14				18
	17	15				20
	18	18				
	20	19				

Days 15 - 22

	Dominant		
	18	20	5
Subordinate	3	1	1
	4	2	10
	7	3	12
	9	5	13
	11	6	14
	13	13	
	15	19	
	16		
	20		

Days 23 - 30.

TABLE 5.4. Dominance shifts in the hierarchy over a period of thirty days in T20b Males. Only top-ranking males are shown and these are given in order of dominance. The full record of attacks is given in Appendix 5.3. * Indicates the owner of the food territory.

structures provided for territories were separated by wide spaces, the hierarchy was stable and supported several alpha males which appeared to have equal status. The hierarchy which developed in the same number of animals in approximately half the area of the large tank, appeared to be less stable. There were also fewer active alphas. When the number of animals in the small tank was doubled, the number of alpha males was also more or less doubled. That is to say if at any one time there were three alpha males in T10 males, there might be six alphas in T20 males. However, in the more crowded tank, top-ranking males lost status after a shorter period and the hierarchy was less stable.

Since only top-ranking animals hold territories, frequent changes in the hierarchy will involve frequent changes in the number and position of territories. Low ranking animals will be less likely to learn to avoid specific areas and the territory owner will have to spend more time in defence. As the density of the population increases the structure of the group becomes less territorial/hierarchical and more hierarchical. This conclusion is supported by observations on the resting positions of males in more and less crowded tanks. In the T1-T3 groups it was found that even low-ranking males favoured a particular rest-site which they occupied during the day. In the T10 groups most animals occupied the platform but only the top dominant occupied the same tier repeatedly. The owner of the food territory was always found on the dish. In the T20 groups only the top-dominants were spaced out and apart from the male on the food territory, even these animals did not occupy the same site repeatedly. The remaining cockroaches would cram together at one end of the platform on one tier, with a few animals resting on the ends of the tiers. This crowding into a very small space is very reminiscent of the clumping exhibited by females.

In both T10 and T20 groups, males occupying the food territories retained them for as long or longer than other top-ranking individuals, despite the fact that these territories, above all others, were constantly approached by other males. This observation supports the suggestion put forward in Chapter Four that food shortage may contribute to the shifts in dominance which characterise the hierarchy in *N. cinerea*.

(2) The relationship between rank and mating success.

Materials and Methods

T10 males were used in this investigation because their social structure was dominated by the presence of the hierarchy. At the end of the observations on the two groups, females were introduced to determine the relationship between

T10a MALES

	Hierarchy before introducing females	Hierarchy after introducing females	
Male	Males Defeated	Males Depeated	Males Grappled with
7	1 2 3 4 5 6 8(G) 9 10	3 6 8	3 8
10	1 3 4 6 8	5	
5	1 4 6 9	1 3	3 8
4	3		6 9
3	1 4		1 2 5 6 8 9
1	3	8 9	2 3 6 8
2			3 6
6		1 2 3 8 9	1 2 3 4 7 8 9
8		9 10	6 9 10
*9			3 4 6

TABLE 5.5. The effect on a hierarchy of introducing receptive females, in T10a Males.

The left-hand side of the table shows the hierarchy as it stood before the females were introduced. Grappling is indicated (G) and also the males achieving copulation (*). The right hand side of the table indicates which males are involved in encounters after the females have been introduced and also the males which grapple.

rank and mating success. Adult females were collected when teneral and kept in vials until they were six or seven days old and receptive. Three females still in their containers, were introduced one at a time, at ten minute intervals into each of the T10 groups.

Results

The effect of introducing females was to raise the level of arousal and aggression in the males and to disrupt the hierarchy completely. Some males examined the females after they emerged from the vials, took up the aggressive posture and began to fight with each other. Others began to fight without prior contact with a female. Although most males did at some time court, more time was spent in fighting. In the T10a group only one male achieved copulation, male 9, the lowest ranking male. In the T10b group three males copulated and only one, male 2, was high ranking, the fourth in the hierarchy. In all cases copulating couples were attacked and on several occasions copulation was prevented because of this interference.

The effect of introducing females on the general level of activity was most striking and in both groups most animals were active for the major part of the thirty minute observation period. During normal observation periods each animal is active for a short time only, apart that is, from one or two alpha males. Because interactions were more

T10b MALES

	Hierarchy before introducing females	Hierarchy after introducing females	
Male	Males Defeated	Males Defeated	Males Grappling
4	1 2(G) 5 6 7 8 10	1	7 10
3	1 7 8	1 6 8	
9	2	1 4 5 8	7 8 10
*2	1 8 10	4 5	7
10	5	1 2 4 6 7 8 9	4 7 8 9
*5	10		
*6		1	
7		2 4 6 8 9	2 4 10
8		4 9	10
1		6	

TABLE 5.6. The effect on a hierarchy of introducing receptive females in T10b Males.

The left hand side of the table shows the hierarchy as it stood before the females were introduced. Grappling is indicated (G) and also the males achieving copulation (*). The right hand side of the table indicates which males are involved in encounters after the females have been introduced and also which males grapple.

numerous in the more crowded tanks, I was able only to score attacks between males and have no quantitative data to illustrate the difference in activity before and after introducing the females. It is possible, however, to show that the general level of aggression is increased after introducing females. Two measures were taken in conjunction to demonstrate this point. They were, the incidence of high intensity fighting, grappling, and the appearance of fighting in previously submissive animals.

Tables 5.5 and 5.6 show the hierarchy for the week ending on the day that the females were introduced, in T10a and b respectively. There were very few incidents of grappling over this period but these are indicated thus (G), where they occur. The tables also show the animals which attack and grapple during the thirty minute period following the introduction of the females. The disruption of the hierarchy is very obvious, previously submissive animals not only attack other males but also grapple. For example, in Table 5.5, prior to introducing the female male 6 had initiated no aggressive encounters. Afterwards he defeated several males above him in the hierarchy and also grappled with most animals in the group. Top dominants are among those attacked and beaten by low-ranking males. For example in Table 5.6 males 8, 2, 10, 7 and 8 beat male 4, the previous top dominant. The incidence of grappling in the group as a whole is high. The males which achieve copulation are indicated by an asterisk. There is no correlation between rank and mating success. The main function of the hierarchy appears to be related to the determination of territorial males.

(3) The relationship between territory holding and mating success.

Materials and Methods

T2 and T3 were used in this investigation because their social structure was predominantly territorial. The object was not only to determine whether only territory holders mated but also whether females would seek out the males. The main difficulty in testing the female's behaviour was that she had to be presented with a choice between remaining in her home ground or moving to explore a new environment. Normally when a female is placed in new surroundings she rushes around in an agitated fashion. Such behaviour disturbs the males and makes it impossible to determine which sex has initiated sexual behaviour. In this experiment females were collected as teneral adults and kept in vials until the sixth or seventh day. The vial containing the female was then placed inside a crystallising dish containing food and water. Two glass slides, one propped up inside the dish and one outside, served as ramps. The dish was placed inside the large observation tank either between the platform and the food and water dishes or between the latter and the block of wood (see Fig. 4). Once the males had recovered from the disturbance the stopper was removed from the vial inside the dish. The behaviour of the males and the female was then noted.

Results

The females left the vial after a variable period of time and then spent some time exploring the dish. Within thirty minutes all the females had left the dish by way of the ramp and had begun to investigate the tank. The first female introduced into the T2 group climbed onto the food dish and mated with male 3, the owner of the territory bridging the food and water supplies. The second female wandered about the tank for five minutes or so before making her way to the platform where she mated with male 10 patrolling that area. The female introduced into the T3 group made straight for the block of wood and mated with male 4 whose patrolling area included the wooden block.

The most important observation is that in the relatively uncrowded tank of the T1-T3 groups in which the social structure is dominated by territorial behaviour, mating can take place without interference from neighbouring males. Furthermore, under these conditions females will approach males and males do not necessarily leave their territories when a female is in the vicinity. This is not the case in the more crowded groups in which the social structure is dominated by the hierarchy. Female Nauphoeta do produce a pheromone which will induce males to court and males will court filter paper which has been in contact with receptive females. Nevertheless it seems unlikely that female pheromone is very important as a sex attractant since males will court other males which have been isolated from females. Males, on the other hand, do produce a pheromone, 'seducin' (see Chapter Two) which attracts receptive females and to which pregnant females have a very high threshold. Purified extracts of the pheromone are very potent and females may respond to it over a distance of several inches, (Roth and Dateo 1965) although this is not evidence that females will do so under normal conditions. Perhaps when a male is patrolling, it is advertising to females as well as warning off rival males.

I have no good evidence that females will mate only with territorial males. In this experiment with such limited numbers, it may have been chance. When receptive females are introduced into crowded tanks, as shown by the T10 experiments, low-ranking males are able to court and mate normally. Perhaps in natural populations low-ranking males move out of the area or take up territories further away from the female group than the high-ranking males.

A more detailed investigation of groups containing both sexes would be useful and in particular it would be interesting to observe the spacing relationships which develop when a small group of young adults is put into a very large container. If the container could be partitioned it would be possible to observe the group in a confined space and then, by removing the partition, to see which males moved out to occupy the new space. Finally, from the evolutionary point of view, it would be interesting to find out if *N. flexivitta* and *N. punctipennis*, which come from grassland habitats in East Africa, also exhibit territorial behaviour.

The function of fighting, hierarchy and territory in Nauphoeta, a summary.

Male N. cinerea will fight to establish rank and at low densities a territorial/hierarchical society, in which only high-ranking males have territories, develops. Three classes of males can be distinguished and these have been called alpha, beta and gamma.

The characteristics of these three classes are discussed. Position in the hierarchy is not permanently fixed but high ranking males may retain rank for at least six weeks. Alpha males spend most of their time patrolling and eat and drink less than low-ranking animals. It is suggested that food and water deprivation may contribute to the dominance shifts which are characteristic of the hierarchy in N. cinerea. This is supported by the observation that in crowded groups, the males which own the food territories retain rank for as long or longer, than other top dominants.

N. cinerea is, like other cockroaches, nocturnal but the pattern of night activity seems to differ. Although single animals in running wheels show considerable individual variation, most animals have the main peak of activity before dawn. Grouped animals as a whole showed no particular pattern of activity and there was no correlation between rank and individual differences in amount of activity. There did appear to be a biphasic pattern of night feeding but on the whole the animals ate very little and this particular point would have to be examined in more detail, using larger groups, before definite conclusions could be drawn.

By altering the population density it is possible to change the social structure in a group of males. If the space is reduced the number of active dominants is decreased and dominance shifts appear to occur sooner than in less crowded groups. If the number of animals is increased, then the number of dominants increases more or less proportionately but dominance shifts occur sooner than in less crowded groups. As density increases, the structure of the group becomes dominated by the hierarchy and fewer animals have permanent territories.

When receptive females are introduced into a group which is hierarchical, rather than territorial/hierarchical, there is no correlation between rank and mating success. Hierarchy appears to determine only which males can have territories and nothing else. The effect of suddenly introducing receptive females into a crowded tank of virgin males was to increase arousal and also the level of aggression to the extent that the hierarchy became disrupted. This relationship between courtship and aggression was commented on in Chapter Two.

It is suggested that territoriality in N. cinerea may operate in a similar way to the vertebrate lek in which only high-ranking males have territories and the females are attracted to the territorial area. Female Nauphoeta appear to live in a group. Perhaps when females are receptive they leave this group and seek out territorial males. Evidence is presented that females are more active when they are receptive than when they are pregnant. When females are introduced into a group which is predominantly territorial, they will approach males on their territories and the males do not leave the territory when a female is in the vicinity. In crowded conditions mating pairs are subjected to attack and active interference of copulation was observed. In less crowded conditions when males are territorial no such interference was observed. It seems likely that the main function of territorial behaviour is to space males in such a way that the arrival of a female on one territory cannot be detected by males on neighbouring territories.

There is no evidence that females will not mate with low-ranking males. Perhaps in natural populations where space is not so limited they are able to take up territories but take those farther away from the females than the high ranking animals. Perhaps they move out of the area. In mixed groups, where no escape is possible, they appear to remain with the female group.

CHAPTER SIX

Stress and pharmacologically active substances from the central nervous system, an introduction.

In the crowded T20 groups of *N. cinerea* (Chapter Five) some of the low-ranking males remained at the bottom of the hierarchy throughout the observation period. These animals were easily identified; they moved about in a sluggish fashion and were frequently to be seen in the submissive posture. The symptoms of these animals are very similar to those found in young subordinate males paired from emergence with another male of the same age. In this situation a number of the subordinate males died on the day following the appearance of fighting in the dominant. Deaths were also found to occur in pairs of mature males. Both males were dominant when put together and deaths occurred in some of those males which had become subordinate. In both young and older males deaths occurred without obvious external damage. There were fewer deaths in the older pairs. (Ewing 1967). In *P. americana* mortality is high after the adult moult and although cannibalism of teneral animals is common this does not account for all the deaths (Wharton et al. 1967). Perhaps cockroaches are particularly sensitive to stressors at this time.

Before death occurs in N. cinerea a characteristic syndrome develops. The animals become quiescent, maintain the submissive posture and a paralysis affecting the hind limbs and abdomen sets in. The righting reflex disappears and once this stage is reached the animals do not recover. Death may occur very rapidly and in one pair of older males I saw the subordinate animal die only thirty minutes after the first attack. This phenomenon is strikingly similar to the stress deaths occurring in subordinate rats, Rattus norvegicus (Barnett 1958) and also in subordinate lizards, Cnemidophorous sexlineatus (Carpenter 1960). In this chapter I shall consider the other evidence for a stress syndrome in cockroaches and also discuss the physiological processes which could be involved in its appearance.

Stress paralysis, and the release of an active factor from the ventral nerve cord.

A syndrome which appears to be very similar to that found in Nauphoeta, also occurs in Periplaneta which have undergone prolonged mechanical immobilisation, or mechanical or electrical stimulation. Blood from cockroaches in which the symptoms were pronounced produce the same effects when injected into normal cockroaches

(Beament 1958). Beament suggests that under stressful conditions a blood-borne factor is released which, on injection in to a host insect, promotes a self-manufacturing process leading to stress paralysis. He gives evidence that it operates through the nervous system. Similar results have been obtained from cockroaches treated with the insecticide DDT, and a toxin in chromatographs of the blood from paralysed insects was found to have the same Rf value as the active factor in the blood from stress paralysed animals (Sternburg 1963).

Recently a neuromuscular excitatory substance, Factor S, has been found in insects and crustaceans (Cook 1967). The pharmacological activity and chemical properties of this substance suggest a close similarity to the DDT toxin and to the active factor in the blood of stress paralysed cockroaches (Cook 1969). Factor S was found to affect synaptic conduction in the terminal ganglion. The successive stages leading to stress paralysis in mechanically tumbled cockroaches showed a progressive increase in threshold and finally blockade of the post-synaptic response. Very low doses of Factor S resulted in facilitation of the post-synaptic response, resembling the action of adrenalin and other catechol amines. Although highest quantities of Factor S have been located in the head and nerve cord neither the site of production nor release has been identified. Cook suggests that Factor S is a neurohormone and a modulator substance whose main site of action is the synaptic junction.

Neurosecretory substances released from the corpus cardiacum during stress.

In *Periplaneta* enforced activity, whether by mechanical or electrical means, is accompanied by loss of material from the corpus cardiacum. From its staining properties, this material appears to be of neurosecretory origin (Hodgson and Geldiay 1959). Injection of corpus cardiacum homogenates produces a range of effects depending on the dose administered. At low concentrations of one gland pair in 0.5 - 1.0 ml. Ringer, the animals walked around their containers in a stereotyped fashion and with increasing concentrations there was a decrease in muscle tonus and an increase in abnormal posture until eventually the animals entered a quiescent state. On *in vitro* preparations of isolated nerve cord low doses resulted in an increase in spontaneous neuronal activity whereas high doses (which appear to be totally unrelated to any physiological quantity) of three hundred gland pairs / ml. had an inhibitory effect (Ozbas and Hodgson

1958). Only corpus cardiacum extracts were found to have these effects on behaviour and on spontaneous activity of the ventral nerve cord but if the nerves between the corpus cardiacum and the neurosecretory cells in the pars intermedialis of the brain were severed some time before the glands were removed, then the potency of the extracts was reduced. This suggests that some component from the brain is required to activate the corpus cardiacum factor.

There is some doubt as to whether the substances in the corpus cardiacum which are depleted during enforced activity and which stain with chemicals supposedly specific for neurosecretory products, are in fact responsible for the neuroactive properties of the corpus cardiacum homogenate. Geldiay (1959) found positive staining cells in the central nerve cord but extracts of the central nervous system failed to inhibit spontaneous activity in isolated nerve cords. Sternburg (1963) considers this sufficient evidence that the blue-staining material in the corpus cardiacum is not responsible for its active properties. It seems just as likely that this reflects a lack of specificity of the stain or that substances with an antagonistic action are also present in the nerve cord. It does appear, however, that the neuroactive factor in the corpus cardiacum is different from the active factor found by Beament, the DDT toxin and Factor S since these substances were found to have a very different Rf value from the corpus cardiacum factor. Occasionally, chromatograms of blood samples from *Periplaneta* showed spots corresponding both to the corpus cardiacum factor and to the paralysing agent, suggesting that they may be circulating simultaneously. The corpus cardiacum factor appeared to be less stable and to lose activity after five hours or so, (Sternburg 1963). After experiments in which cockroaches were either injected with corpus cardiacum extracts or extracts were applied to exposed nerve cords Milburn *et al.* (1961) concluded that the extracts suppressed the action of an inhibitory system and had no effect on excitatory synapses.

Other tissues besides the nerve cord are affected by corpus cardiacum. Davey (1961) found that a brise of the gland increased the rate of heart beat in the isolated heart of *Periplaneta americana*. When *Periplaneta* was subjected to enforced activity by tumbling the heart-accelerating activity of the corpora cariaca from these animals declined as enforced activity was increased. The action of the heart accelerating factor appeared to be indirect and it was thought to stimulate the pericardial cells to produce an amine which directly affected the rate of heart beat (Davey 1963). More recently Kater (1967) has found that there is a direct effect on the heart by a cardioaccelerator from the corpus cardiacum. Although his method of obtaining the active factor is quite different, this does not appear to account for the difference in the results. Although it was not possible to test the storage and secretory portions of the corpus cardiacum of <u>Periplaneta</u> separately, only the secretory portions of corpora cardiaca from <u>Schistocerca gregaria</u> had a pharmacological effect on heart rate (Davey 1963). Corpus cardiacum extracts were also found to increase peristalsis of the hind gut (Davey 1962).

The chemical identity of the factor affecting the activity of the heart and hind gut is uncertain. By means of paper chromatography, chymotrypsin digestion and bioassay, eight or nine active factors were detected in extracts of corpus cardiacum (Brown 1965). Of these nine, three factors appeared to be related to the cardioaccelerator described by Davey. These three factors designated P1, P2 and P3, which are probably chemically related, behave like peptides and could be either neurohormones from the brain, stored in the corpora cardiaca, or could be intrinsic secretions of the corpus cardiacum itself. Using a rather neat preparation of an isolated head of <u>Periplaneta</u> Kater (1968) obtained a cardioaccelerator substance which was released from the corpus cardiacum when the brain was stimulated electrically. Analysis of this factor indicated a peptide with a molecular weight around 1300. The active factor had a half-life of about ten hours. Kater suggests that this substance may be identical to the P factors isolated by Brown. Substances having the characteristics of neurohumours and affecting heart rate have also been found in the corpus cardiacum. The purpose of Kater's experiment was to determine which substance was actually released as a cardioaccelerator.

Other hormones from the corpus cardiacum which could be released during stress.

Another peptide with a hormonal mode of action is a hyperglycaemic factor which plays a similar role to glucagon in vertebrates (Steele 1963). It is thought that during periods of high activity the hyperglycaemic factor maintains sufficient blood trehalose levels by activation of fat body glycogen.

Neurohormones C and D were originally identified by Unger (1957). At high concentrations D caused the heart to stop beating in diastole and C caused it to stop in systole. Gersch (1960) showed that both hormones were a mixture of two substances. He designated the water soluble fractions C_1 and D_1 and the ethyl acetate fractions C_2 and D_2. The corpora cardiaca exhibit greatest C_1 and D_1 activity (Strejckova et al. 1965). Chromatographically separated extracts of D_1 induce a rise in spontaneous activity in the supraoesophageal and prothoracic ganglia. C_1 on the other hand depresses spontaneous activity, both when it occurs naturally and when it has been induced by application of D_1. These substances or one of them could be related to the active factors described by Ozbas and Hodgson and also Milburn et al. They appear to be quite distinct from the cardioaccelerator substance of Kater.

Neurohormones and water balance

Neurohormone D_1 may have other effects besides that on spontaneous activity. There is some evidence that it could be identical to activation hormone (Gersch 1962) though there is some controversy on this point. Gersch (1968) has shown that D_1 can affect membrane permeability in an in vitro preparation of the toad bladder and resembles the action of mammalian oxytocin. Like D_1, this hormone also has an effect on smooth muscle and such in vitro experiments have little value in determining the normal mode of action of the hormone.

Considerable circumstantial evidence suggests that the central nervous system may be involved in the control of water balance but differences between species have led to some confusion. As far as possible I shall confine myself to work carried out on cockroaches or at least the Orthoptera.

Destruction of the cells in the pars intermedialis in Locusta results in water retention and dilution of the haemolymph. Injection of water is accompanied by a depletion of the neurosecretory material in the A-cells of the pars intermedialis, and a redistribution of the stainable material in the corpus cardiacum to the area round the aorta, suggesting that secretion is taking place (Highnam 1965). In Blaberus giganteus the A-cells become full when the animals are water deprived (Wall 1962).

Malphighian tubules from dehydrated and salt loaded Periplaneta take up dye more slowly than those from normal animals. Extracts of corpora allata from normal animals have the same effect and so also do brain and suboesophageal ganglion from dehydrated animals. The corpora allata from dehydrated animals do not have this effect which may indicate that the antidiuretic factor is released from this site. Extracts of corpora allata, corpora cardiaca, and heart also have an antidiuretic effect on rectal water absorption. It is not known whether there are several factors affecting the rectum or whether the corpus allatum factor, which decreases the rate of uptake by the Malpighian tubules, also increases the rate of rectal reabsorption. In Periplaneta which have been deprived of water and then have been allowed to drink, the terminal abdominal ganglion releases a diuretic factor (Mills 1967).

The question remains as to the identity of the water regulating factors. Gersch suggests that neurohormone D_1 may be involved and his observations are supported by Unger (1965) who has isolated neurohormones C and D from the brain and found them to act antagonistically on the rate of dye uptake in an in vitro preparation of Malpighian tubules.

Products of the central nervous system, whether synthesised in the pars intermedialis and stored in the corpus cardiacum, or whether synthesised in the corpus cardiacum itself, affect a variety of physiological processes. In addition to those mentioned above, moulting, diapause and reproduction may also be affected (Cazal and Girardie 1969). In many cases there is only indirect evidence that the corpus cardiacum is involved and in vitro experiments leave the normal mode of action of suspected neurohormones open to question.

The main substances which I have discussed which could function as neurohormones include Factor S, which appears to be a modulator of neurones and when produced in excess is involved in the appearance of stress paralysis, a cardioaccelerator substance, a hyperglycaemic factor and two neurohormones, C and D, whose action on the supraoesophageal and prothoracic ganglia and on the Malpighian tubules is antagonistic. The efficiency of homogenates or extracts of corpus cardiacum to affect some of these processes is reduced after enforced activity and this is taken to mean that the neurohormones have been secreted. At the same time a depletion of neurosecretory material is seen in the corpus cardiacum but it is not known whether this material is identical to one or any of the active factors which have been identified. When diuretic activity is induced in Locusta by injection of water, the A-cells of the pars-intercerebralis are depleted of their neuroscretory material but here again the identity of this material with a diuretic factor is not proven and the handling of the animals itself is accompanied by depletion of neurosecretory material (Highnam et al 1965).

Many factors have contributed to the confusion over the role of neurohormones and other biologically active factors and it is worth while listing these. The corpus cardiacum has been shown to affect a variety of processes and eight or nine apparently different substances are associated with this endocrine organ. Different factors from the corpus cardiacum are found to have the same pharmacological effect and conversely, one substance may affect a variety of activities. The activity of the corpus cardiacum has been tested using different extraction methods and different concentrations of glands. In many cases so-called extractions have been crude homogenates.

Lastly, depletion of neurosecretory material from both the pars intermedialis and the corpus cardiacum occurs when neurosecretion is thought to be in process but the relationship between this material and the various active factors is not known.

Davey (1963) has suggested that under stressful conditions a chain of events is triggered, including the release of a cardioaccelerator from the corpus cardiacum, of a neurotoxin (Factor S) from the ventral nerve cord and the depletion of neurosecretory material from the corpus cardiacum. In locusts, handling is accompanied by depletion of material from the A-cells of the pars intercerebralis which may be involved in water balance. Steele (1963) suggests that the hyperglycaemic factor which he has found in association with the corpus cardiacum, may be produced during periods of high activity.

It seems very probable that Factor S is involved in the appearance of the stress syndrome preceeding death which I have observed in Nauphoeta. It could be that this substance is responsible for the appearance and maintenance of subordinate behaviour in animals which do not become paralysed. Equally, subordinate behaviour could be a consequence of the combined effects of the various processes which appear to be activated during stress.

With this point in mind I decided to investigate in more detail the dominant/subordinate relationship which develops in paired males.

CHAPTER SEVEN

Weight change in dominant and subordinate animals.

Introduction

Subordinate rats lose weight even when food is plentiful and when they are not prevented from eating by dominant individuals (Barnett 1958). It is not known whether these animals lose interest in food or whether their metabolic rate is increased. It was suggested in Chapter One that the over-production of a hyperglycaemic factor as a result of prolonged adrenal stimulation, may lead to a depletion of glycogen reserves and so to loss of weight.

Mention has been made already of the parallels between the dominant/subordinate relationships in rats and in the cockroach, Nauphoeta cinerea. Dominant/ subordinate pairs seemed ideally suited for an investigation of the effect of rank on body weight. The initial experiments, which involved weighing dominant and subordinate males over a period of time, were followed by an investigation of weight change and water content in dominant/subordinate pairs under different conditions of food and water deprivation. For convenience each set of experiments will be considered separately and details of experimental method given where appropriate.

1. The investigation of weight changes in dominant/ subordinate pairs.

Materials and methods

Teneral males were collected and those of the same approximate size were paired. Each animal was weighed on the day after pairing and again, either after twenty one days, or at weekly intervals for twenty eight days. In the interim, pairs were presented with a test-animal (see Chapter Two) on the third day after pairing to determine which member of the pair was dominant. Thereafter the test-animal was presented every six days to ensure that the relationship was stable and that no reversals of dominance had occurred.

Pairs were also watched during the first hour of darkness, on six separate occasions of fifteen minutes each. If, during the observation period, the dominant male attacked the subordinate or if the latter behaved submissively when touched by its partner, a score of one point was given to that pair. On the other hand, if both animals were clearly active and did not display evidence of dominance/subordinance, then no score was given to that pair. A point was also given each time a pair responded appropriately to the test-animal and thus, in all, each pair could 'score' a maximum of nine points. A pair scoring between 0/9 - 3/9 was considered to have a poorly developed dominant/subordinate relationship and was discarded.

In order to reduce the possibility that dominant males could actively prevent subordinates from eating and drinking, excess dry food and wet food in the form of carrots and one water vial was provided. Normally only one water vial, two pieces of rat cake and a few flakes of maize were provided and occasionally dominants were seen to fight off the subordinates when they attempted to feed. The squares of carrots provided in this experiment kept the humidity high and it was necessary to change the food frequently because of the growth of mould.

Two experimental groups were set up as follows:-

(1) 21 pairs weighed for the second time after 21 days.

(2) 15 pairs weighed weekly for 28 days.

The purpose of group (1) was to determine whether weight changes occur and the purpose of the second group was to determine the point at which changes can first be detected. This group also served as a control for handling.

Two control groups were set up as follows:-

(1) 22 pairs of one male and one female, of which the male was weighed for the second time after 21 days.

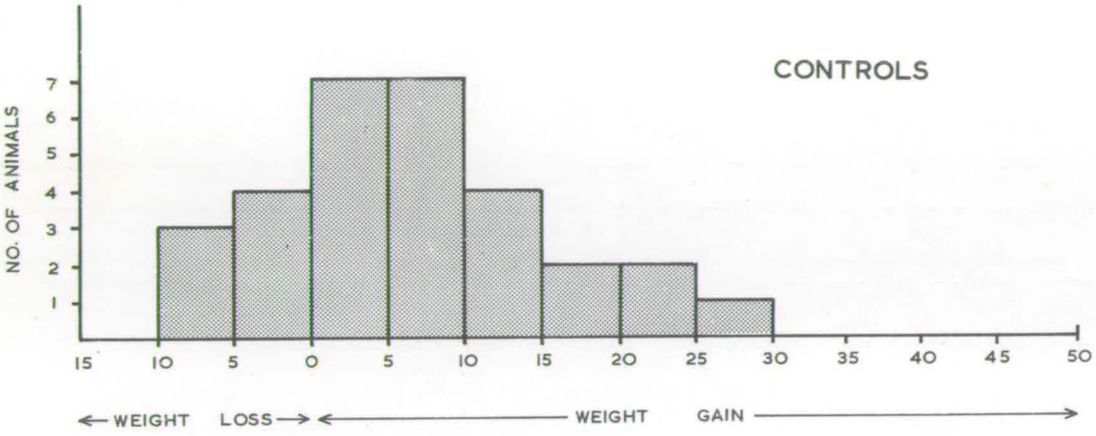
(2) 13 pairs of one male and one female of which the male was weighed once weekly for 28 days.

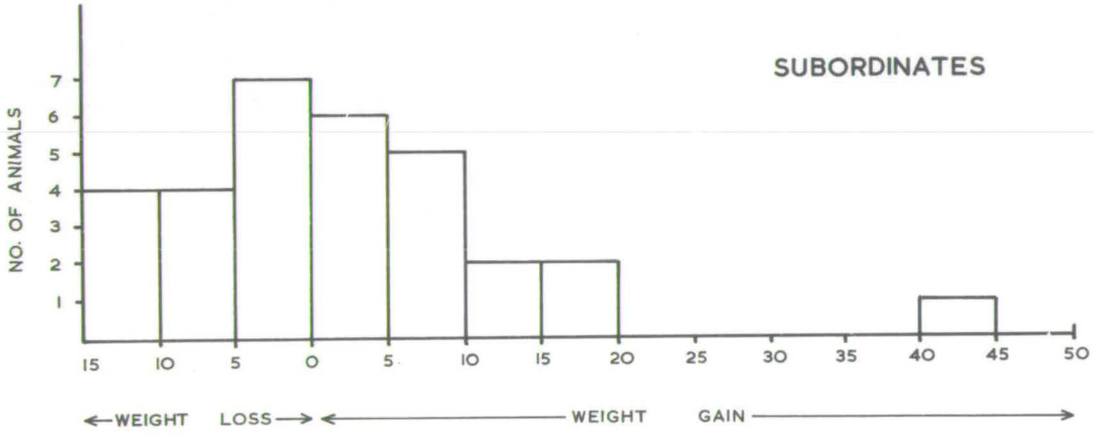
The purpose of these latter groups was to control for weight loss which might occur for reasons not related to rank. The choice was not ideal as the effects of courtship and mating on male feeding habits are not known. However, the use of single males seemed equally inappropriate because of the lack of social facilitation which appears to be involved in the feeding behaviour of groups of cockroaches. The use of a last instar male nymph instead of a female might have been a better choice.

Results

(a) Experimental groups (1) and (2).

Dominant males gained more weight or lost less than the subordinates with which they were paired in twenty eight out of thirty one cases, a highly significant trend ($p < .001$ on a Binomial test). The median value for weight increase is 11.9% for dominant animals and only 0.3% for subordinates. Furthermore, in fifteen out of thirty one cases subordinates actually lost weight while this is true of only one dominant. Fig. 13 summarises these results. In the two groups, five pairs of the thirty six showed reversal of dominance and their results have been excluded from the histogram.


CONTROLS
NO. OF ANIMALS
1
2
3
4
5
6
7
15
10
5
0
5
10
15
20
25
30
35
40
45
50
← WEIGHT LOSS →
← WEIGHT GAIN →


SUBORDINATES
NO. OF ANIMALS
1
2
3
4
5
6
7
15
10
5
0
5
10
15
20
25
30
35
40
45
50
← WEIGHT LOSS →
← WEIGHT GAIN →

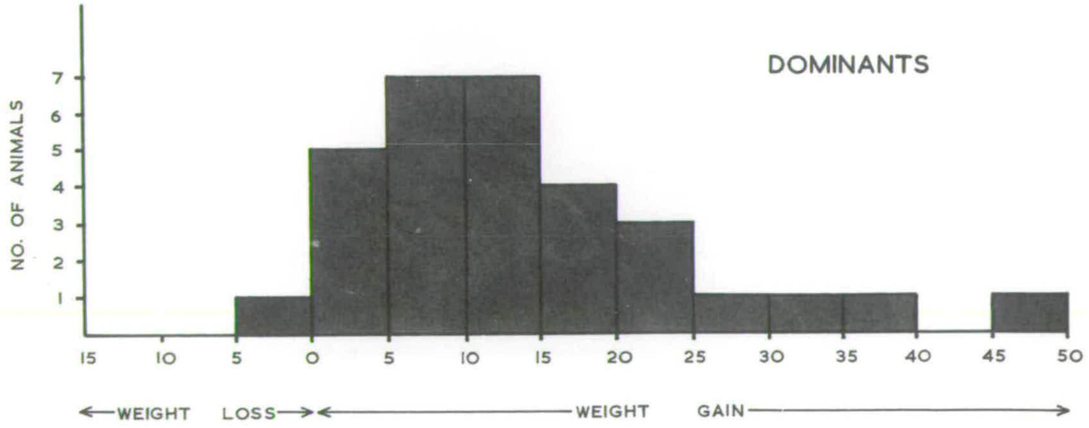

DOMINANTS
NO. OF ANIMALS
1
2
3
4
5
6
7
15
10
5
0
5
10
15
20
25
30
35
40
45
50
← WEIGHT LOSS →
← WEIGHT GAIN →

FIGURE XIII

Percentage weight change in dominant/subordinate pairs and in controls which were paired with a female.

PERCENTAGE WEIGHT CHANGE IN DOMINANT AND SUBORDINATE PAIRS OVER FOUR WEEKS

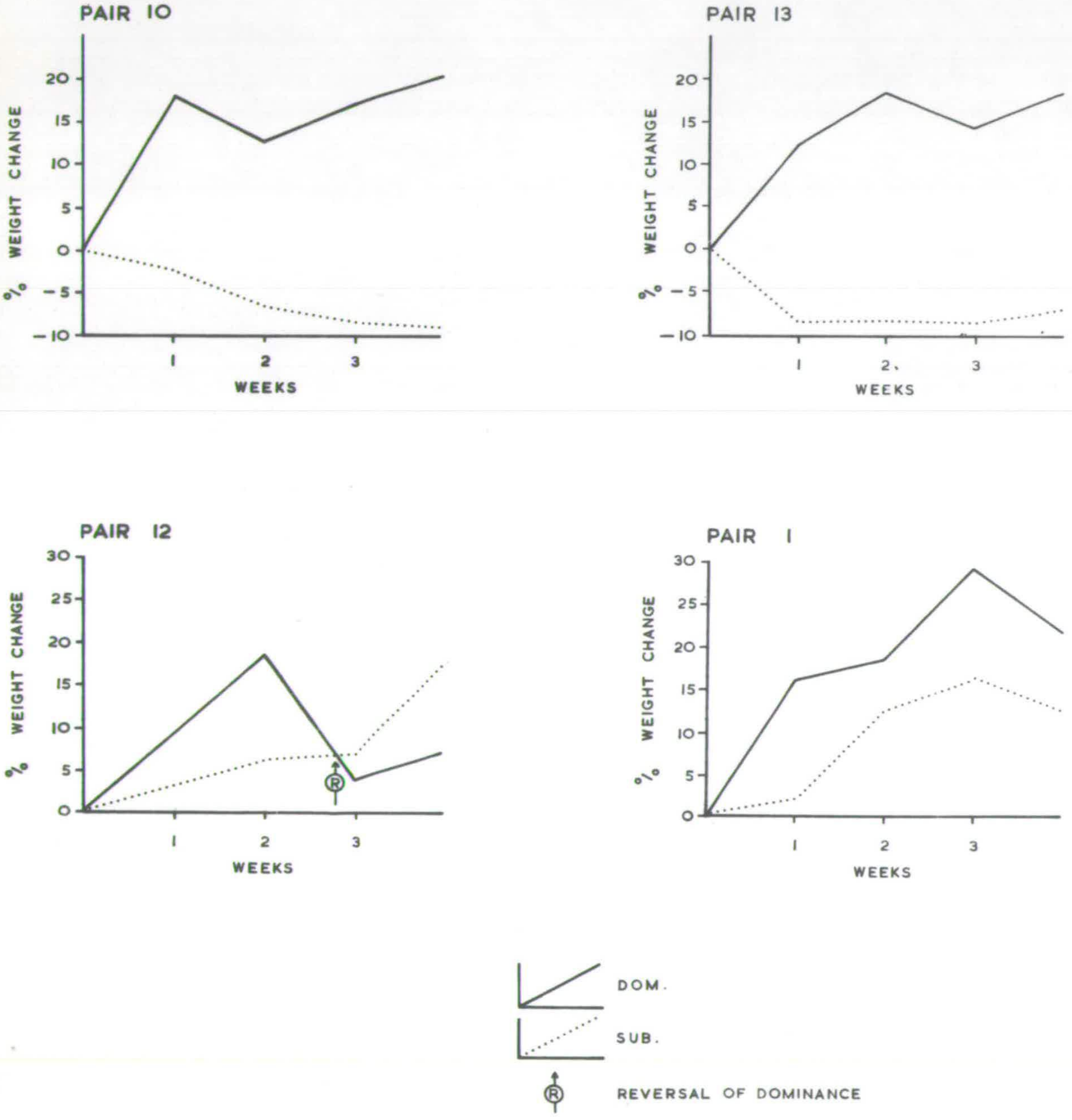
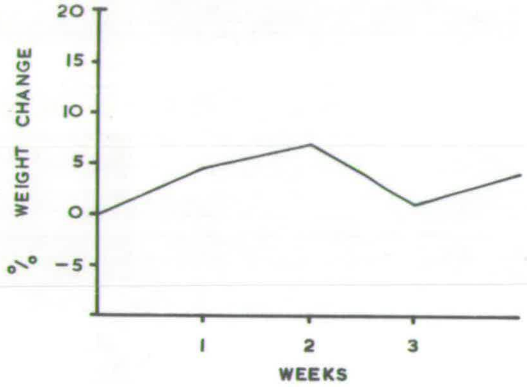


FIGURE XIV

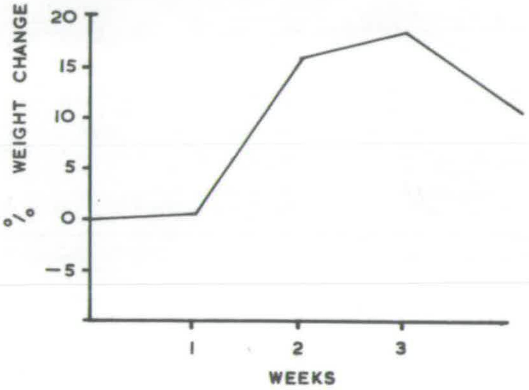
Percentage weight change in dominant/subordinate pairs after 28 days. Subordinate males either lose weight or gain less than the dominant. This trend is reversed when reversal of dominance occurs.

CONTROL ♂♂ PAIRED WITH ♀ PERCENT WEIGHT CHANGE OVER FOUR WEEKS

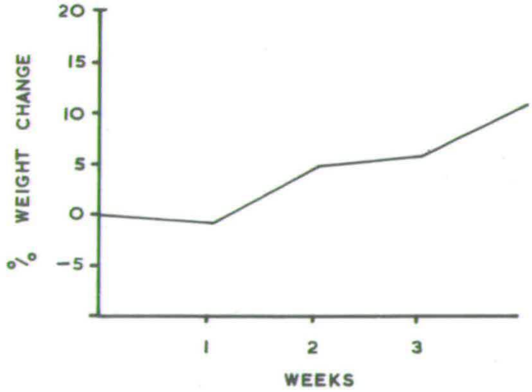
MALE 2C



MALE 12C



MALE 4C



MALE 15C

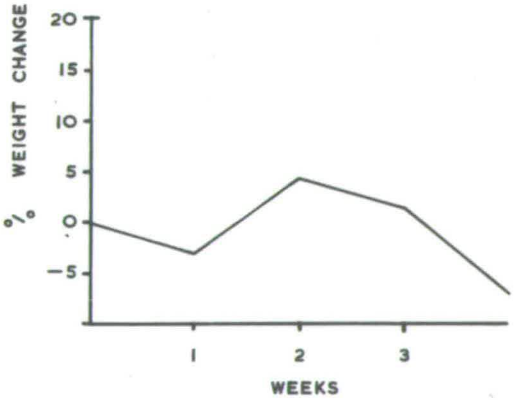


FIGURE XV

Percentage weight change in control males which were paired with a female. Most males gain weight but gain less than dominants.

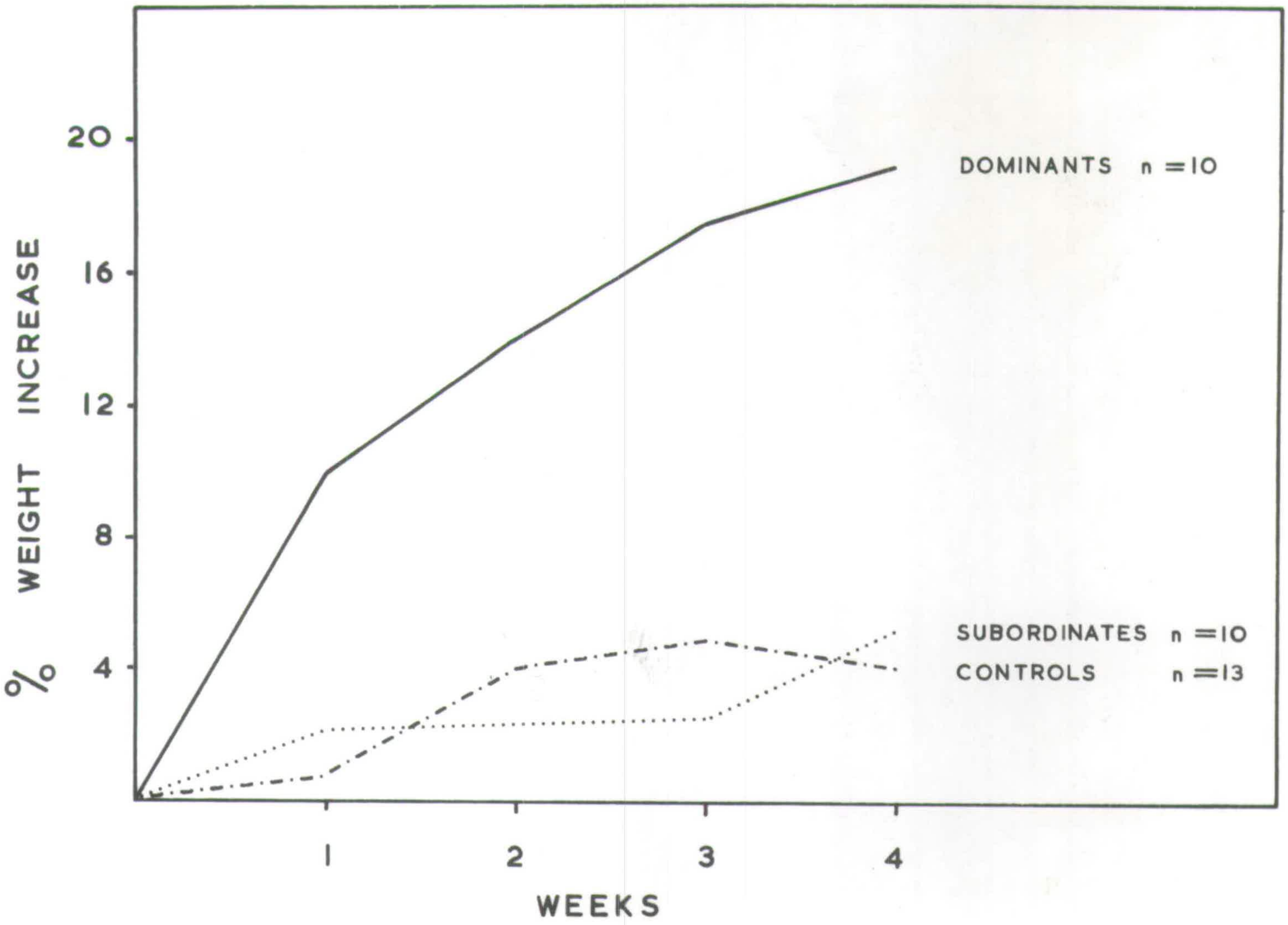

% WEIGHT INCREASE
20
16
12
8
4
1
2
3
4
WEEKS
DOMINANTS n =10
SUBORDINATES n =10
CONTROLS n =13

FIGURE XVI

Mean weight change in dominants, subordinates and controls over four weeks.

In the pairs weighed at weekly intervals (experimental group (2)) it can be seen that the effect on weight is obvious after one week. Dominant males on the whole show a steady increase in weight and subordinates show either a decline in weight which levels off or a gradual increase which falls off short of the dominant increase. When reversal of dominance occurs there is a reversal in the trend in weight change, the new dominant begins to gain weight whilst the old one loses weight. Examples of these results can be seen in Fig. 14.

(b) Control groups (1) and (2).

In the control groups most males gained weight but not so much as dominant animals in the experimental groups. Twenty six out of thirty males gained weight and the median value is 6.3%. These results are also shown in Fig. 13. From individual records of males weighed at weekly intervals, control group (2), it can be seen that the weights fluctuate more than in dominants (Fig. 15). If the weekly weight changes in all the groups are averaged out the controls do not differ significantly from the subordinates (Fig. 16). The data on which graphs and histograms are based can be found in Appendix 7.1.

Discussion

Subordinate males lose weight or gain less weight than the dominant with which they are partnered, an observation which is rather neatly confirmed by the reversal of this trend when dominance is reversed. There are several possible explanations for this. Either subordinate animals eat and drink less than dominant animals or their metabolism is altered in some way or both. The observations on control animals do not really clarify the situation. Although most of them increase in weight, less weight is gained than in dominants. Perhaps females have a depressant effect on the control animals. Single males weighed daily gain about 10% of their original weight after four weeks (Cafferty 1969, unpublished results) and this figure is very close to that obtained for dominants (11.9%).

When exposed to a variety of situations, including handling, exploration and attack by other animals, males may deposit a drop of water from the mouth (possibly from the salivary reservoir). Subordinate males may produce such a drop of water after the first bout of fighting by the dominant. Examination of the containers which have housed dominant/subordinate pairs reveals two types of faeces, one dry and the other watery.

Although defaecation was rarely observed in animals of either rank, when it was seen, dominant males did have normal, dry faeces, as do single males and subordinate males had watery faeces. In Periplaneta which has been subjected to enforced activity there is a marked loss of water from the haemolymph (Beament 1958). This could imply either an alteration in water balance or simply an increase in water loss via the spiracles which may be affected by stress paralysis. If metabolic processes are increased by the release of neurosecretory products during stress and this seems likely, then the rate of water evaporation will also increase. Nevertheless, the fact that subordinate animals produce watery faeces suggests that water balance could be affected and that there may be an increase in the production of a diuretic hormone or alternatively an exhaustion of the supplies of an antidiuretic factor which increases the rate of rectal reabsorption. Subordinate animals also lose water via the mouth and if this is indeed from the salivary reservoir the subordinates lose an important source of water reserve (Sutherland and Chillseyzn 1968). A comparison of the water content in dominant and subordinant animals could show whether a difference in water content accounts for the difference in weight.

(2) To determine the water content of dominant and subordinate animals.

Materials and methods

The animals from the previous experiment which had been weighed twice only, (experimental group (1)) were killed after the final weighing and desiccated in an oven at 60°C for five hours. The dried bodies were then weighed until an equilibrium point was reached. Faeces produced while the animals were killed under ether were also dried and weighed. Using the final fresh weight and the dry weight the percentage water content of each animal was calculated.

Results

No difference was found between dominant and subordinate animals with respect to water content. The mean water content was 62.0% for dominants and 61.9% for subordinates. These results are shown in Fig. 17. Full results are given in Appendix 7.2.*

Since subordinate males either lose weight or gain less weight than dominants, yet have the same water content, they must be regulating food and/or water intake to maintain a water content which is within the normal range.

* See also Appendix 7.5

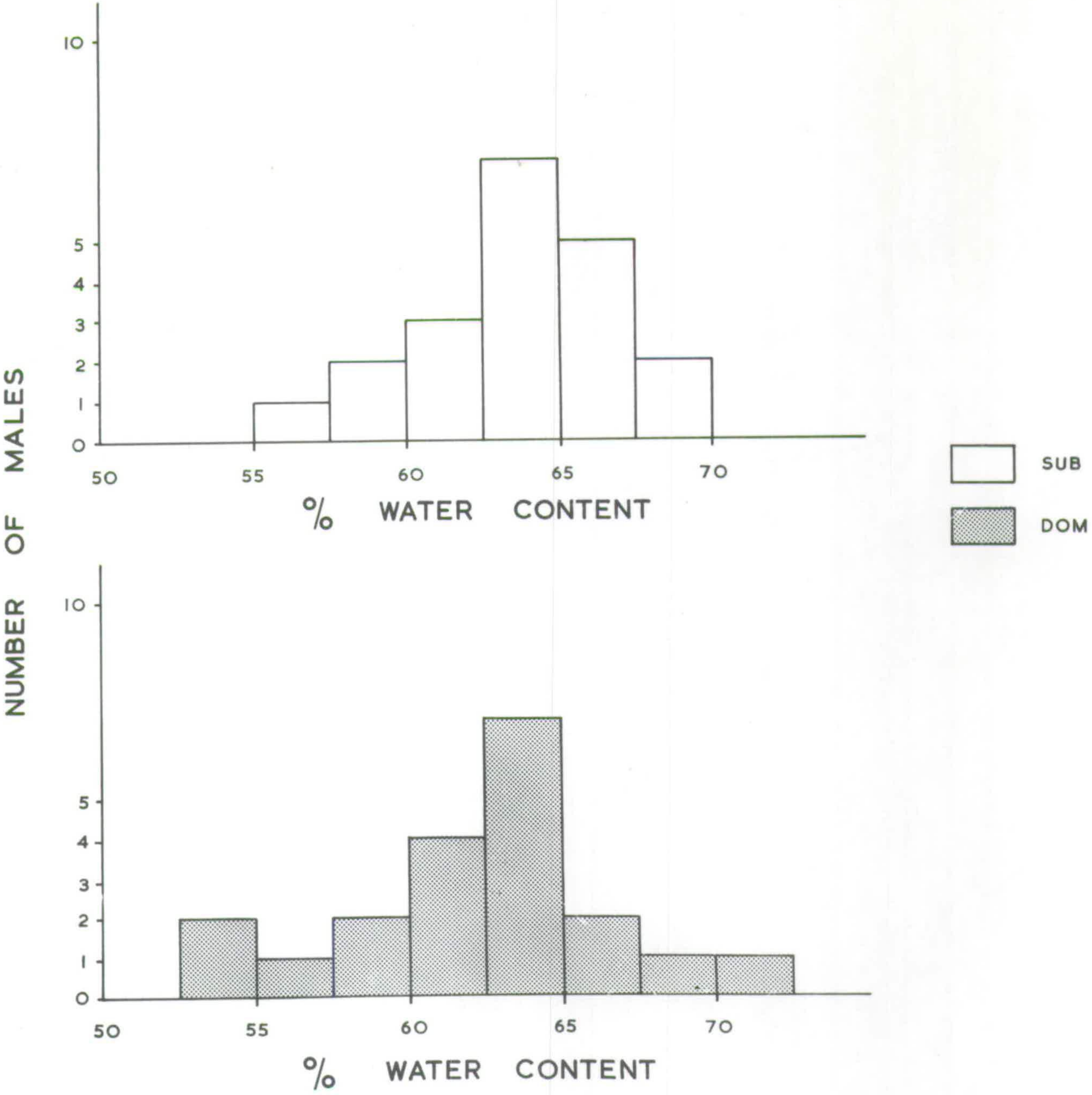

10
5
4
3
2
1
0
50
55
60
65
70
% WATER CONTENT
NUMBER OF MALES
SUB
DOM
10
5
4
3
2
1
0
50
55
60
65
70
% WATER CONTENT

FIGURE XVII

Percentage water content in dominant and subordinate animals.

There is no difference between the two groups.

This observation, however gives no insight into the cause of the difference between the two types of males.

If subordinate males drank less than dominants or if they actively lost water via the mouth and faeces (which they appear to do) then they would be effectively 'water deprived'. In this case one would predict that subordinates also eat less since it is observed that their water content is normal. If on the other hand subordinate animals initially ate less than dominants or if their metabolism was speeded up they would be effectively 'food deprived'. In this case one would predict that subordinates would subsequently drink less.

The initial cause of weight loss could be investigated by depriving pairs of food and water.

(3) Weight change and water content in dominant/submissive pairs deprived of food or water.

Materials and methods

Pairs were set up as before. The dominant/subordinate relationship was allowed to develop before depriving animals of food and water and the experimental treatment was begun after the animals had been together for ten days.

Two experimental groups were set up as follows:-

(a) Water deprived

(i) 19 pairs weighed after pairing and again after 28 days.

(ii) 15 pairs weighed at weekly intervals for 21 days.

(b) Food deprived

(i) 16 pairs weighed after pairing and again after 28 days.

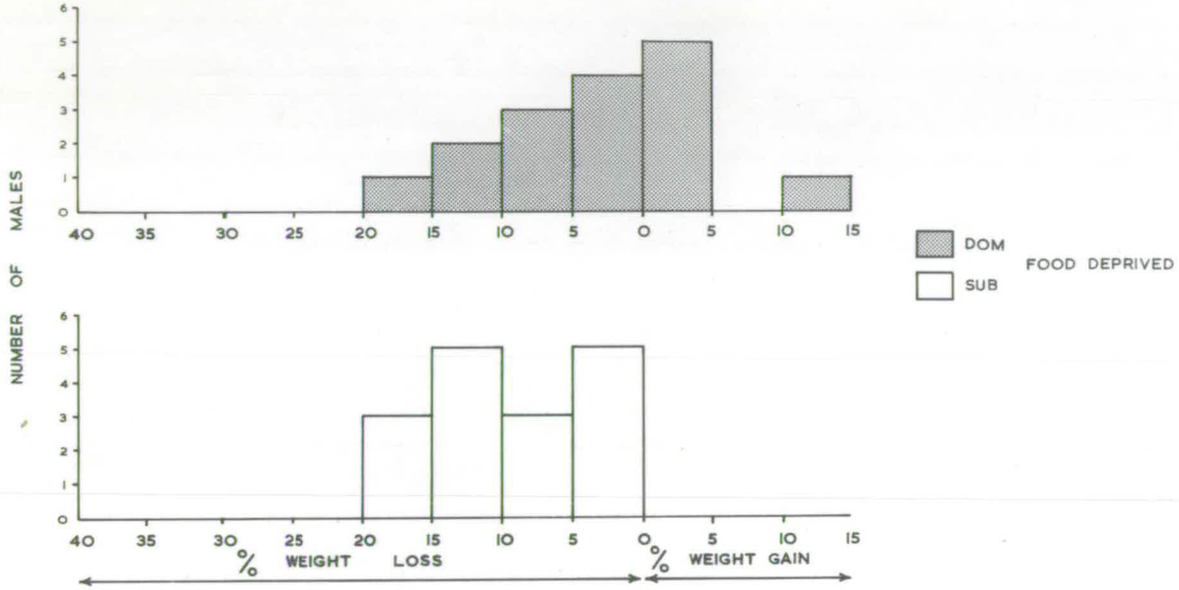
(ii) 9 pairs weighed at weekly intervals for 21 days.

The food deprived animals were provided with two vials of water and the water deprived animals with excess dry food. All animals were dessicated after the final weighing and the water content determined. The experiment was designed to determine (i) the effect of food and water deprivation on body weight and water content and (ii) the time course of any changes should they occur.

Results

(a) Water deprived

(i) Weight loss: Both dominant and subordinate males lose weight (Fig. 18). The tendency for dominants to lose less weight than subordinates is still apparent but less convincing; it occurred in thirteen out of nineteen cases ($p < 0.08$ on a Binomial Test). However, the weight differences between dominant and subordinate animals are not related to the deprivation


NUMBER OF MALES
0
1
2
3
4
5
6
40
35
30
25
20
15
10
5
0
5
10
15
% WEIGHT LOSS
% WEIGHT GAIN
DOM
SUB
FOOD DEPRIVED

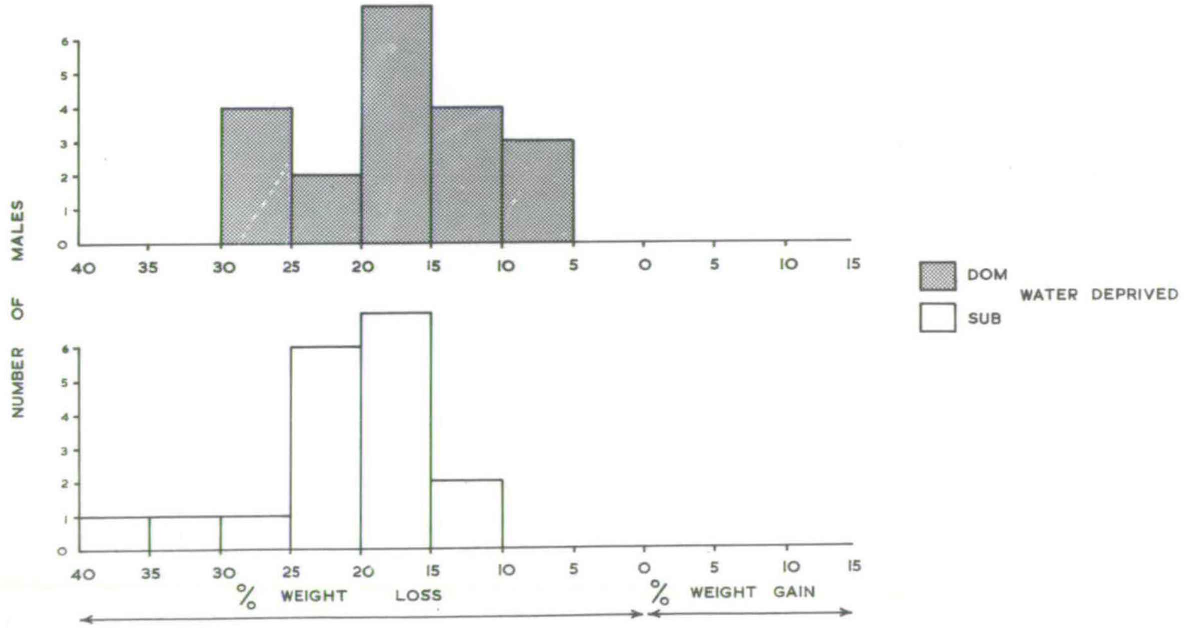

NUMBER OF MALES
0
1
2
3
4
5
6
40
35
30
25
20
15
10
5
0
5
10
15
% WEIGHT LOSS
% WEIGHT GAIN
DOM
SUB
WATER DEPRIVED

FIGURE XVIII

Percentage weight change in dominant and subordinate animals which have been deprived either of food or of water. Water deprived animals lose more weight than food deprived animals but the difference between dominants and subordinates is not significant.

WATER DEPRIVED PAIRS PERCENT WEIGHT CHANGE OVER THREE WEEKS

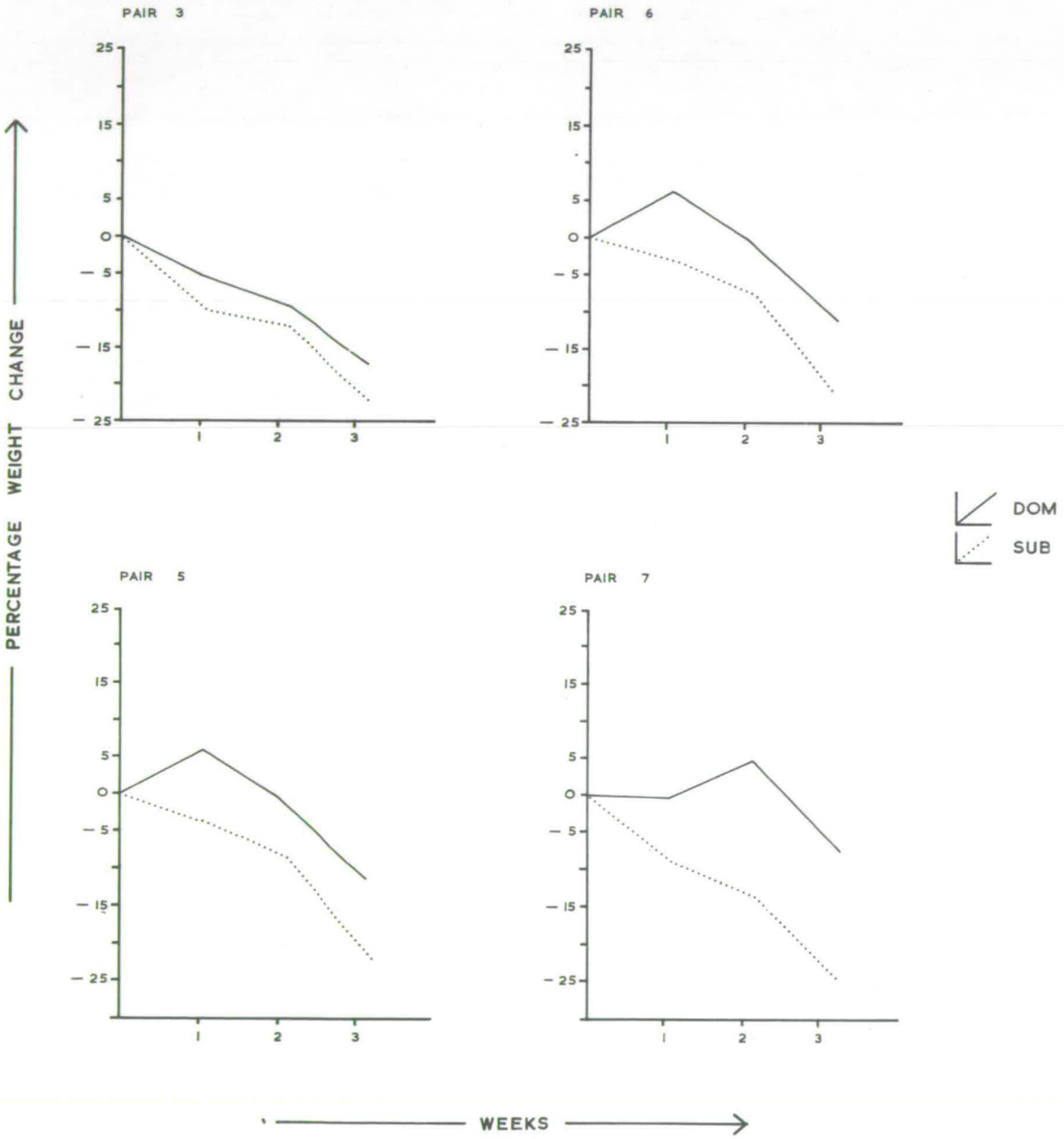
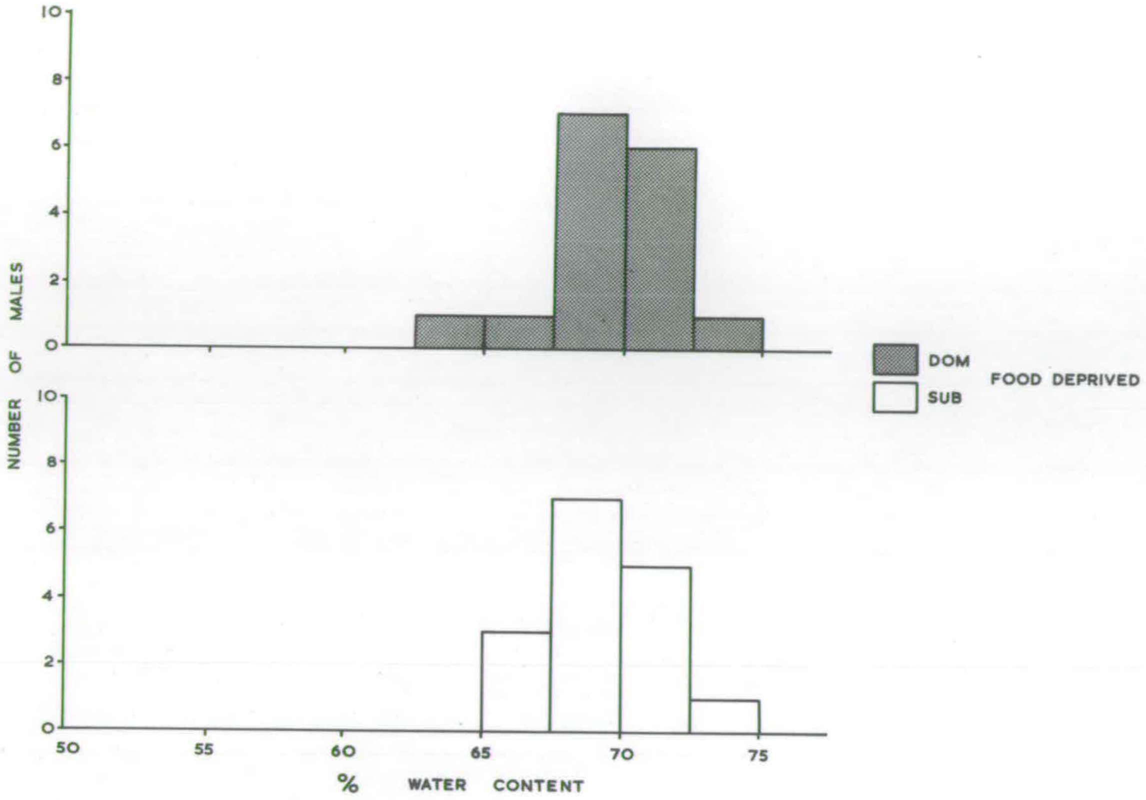


FIGURE XIX

Weight loss in water deprived pairs over three weeks. Water was removed on the tenth day and after this time both dominants and subordinates begin to lose weight at the same rate.


NUMBER OF MALES
10
8
6
4
2
0
DOM
SUB
FOOD DEPRIVED
50
55
60
65
70
75
% WATER CONTENT

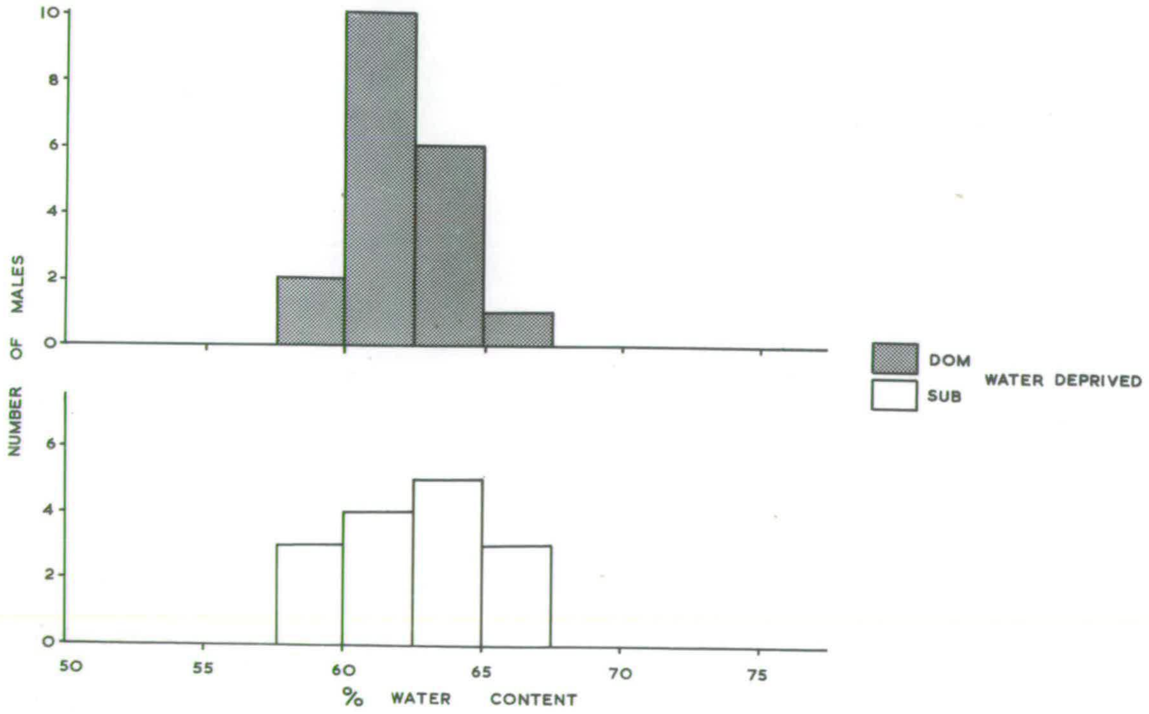

NUMBER OF MALES
10
8
6
4
2
0
DOM
SUB
WATER DEPRIVED
50
55
60
65
70
75
% WATER CONTENT

FIGURE XX

Percentage water content in dominant and subordinate animals which have been deprived either of food or of water. Food deprived males have a higher than normal percentage water content. Water deprived males are within the normal range. There is no difference between dominant and subordinate animals.

FOOD DEPRIVED PAIRS PERCENT WEIGHT CHANGE OVER THREE WEEKS

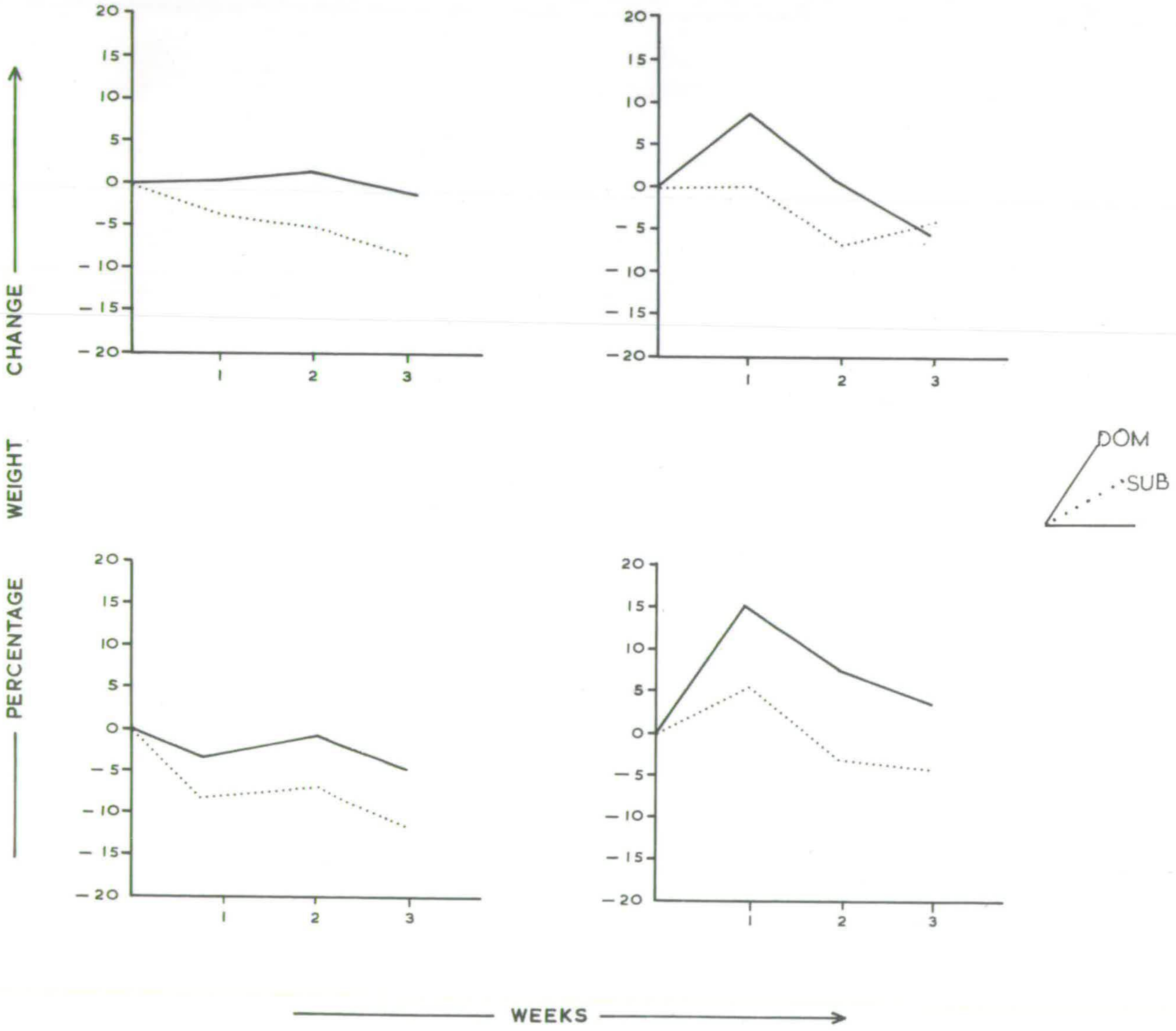


FIGURE XXI

Weight loss in food deprived pairs over three weeks. Food was removed on the tenth day and after this time both animals begin to lose weight at the same rate.

treatment. During the ten day period when food and water are present, dominant animals gain more weight or lose less then subordinates. This is essentially what was found in Experiment 1. Once the animals are deprived, both begin to lose weight at the same rate (Fig. 19).

(ii) Water content: Just as when food and water are present ad lib there is no difference in the percentage water in dominant and subordinate males (Fig. 20). After seventeen days of deprivation there is a slight but not significant decrease in the percentage water content of all water deprived animals.

(b) Food deprived

(i) Weight loss: Both dominant and subordinate males lose weight (Fig. 18) and as in the water deprived situation the difference in weight can be related to changes occurring before the experimental treatment was begun. Once the food was removed, both animals in a pair began to lose weight at the same rate (Fig. 21).

Animals lose more weight when deprived of food than when deprived of water. Another difference between the two treatments is that reversal of dominance is more frequent in food deprived pairs.

(ii) Water content: By three weeks, i.e., after ten days of food deprivation, the water content of both dominants and subordinates appears to be higher than in water deprived animals. With such a small sample and three out of nine reversals of dominance, this result by itself cannot be taken very seriously. However, after seventeen days of food deprivation it is quite clear that the water content of these animals is higher than in animals with no water (Fig. 20). Reversals of dominance have been included in Fig. 20 but this does not alter the situation. The data on which the graphs and histograms are based are given in Appendix 7.3.

Discussion

When animals are deprived of water a considerable amount of weight is lost. The percentage water content is the same as in animals provided with ad lib food and water. This suggests that in the absence of water, the food intake is regulated and a constant dry/wet weight ratio is maintained. Subordinate animals provided with ad lib food and water appear to respond in the same way as animals which are deprived of water; they lose weight but their water content is normal.

When animals are deprived of food they lose weight and show a significant increase in water per cent (the same results has been obtained in *Periplaneta americana* (Wharton et al. 1965)). Subordinate males with ad lib food and water do not respond in the same way as pairs deprived of food.

These experiments suggest that subordinate cockroaches with access to food and water are reacting as though they were water deprived. Subordinate animals have loose watery faeces and may also lose water via the mouth. Water loss does not appear to account for the difference in weight between dominant and subordinate animals and it is suggested that these animals must also eat less since the water per cent is normal. When water is freely available, the occurrence of dominance reversal is commoner. Thus when ad lib food and water was provided there were five out of thirty six cases of reversal, when water alone was provided, there were seven out of twenty six cases and when food alone was given there was only one out of thirty. This is fairly suggestive that the subordinate condition is affected by the availability of water and indirectly supports the observation that water loss is involved. Water loss could be due to changes in the amounts of diuretic or anti-diuretic factors. It could also be due to a secondary effect of the carcioaccelerator from the corpus cardiacum which also affects the rate of peristalsis.

The following chapter deals with some attempts to reverse dominance by various experimental procedures in order to gain some insight into the physiological processes underlying subordinate behaviour.

CHAPTER EIGHT

Reversal of Dominance

Introduction

When subordinate animals have access to water reversal of dominance appears to be more likely than when no water is available. If water loss is an important factor in the appearance of subordinate behaviour it might be possible to bring about reversal of dominance by injecting an antidiuretic factor. Extracts of corpus cardiacum from *Periplaneta americana* are found to have an antidiuretic effect (Wall 1967) although it is not known whether this is due to an antidiuretic hormone or to a secondary effect of the cardioaccelerator. Assuming that *Nauphoeta* resembles *Periplaneta* homogenates of corpus cardiacum could be used as a source of antidiuretic factor. The main difficulty in using this neuroendocrine organ is that it affects a variety of physiological processes and it can also affect behaviour when administered in high doses (Ozbas and Hodgson 1958). The first experiments in this chapter deal with an attempt to reverse dominance by injection of corpus cardiacum homogenates.

The second group of experiments are concerned with the reversal of dominance by other methods. Reversal of dominance has been observed in Gryllus campestris after the dominant was beaten by a yet superior animal (Alexander 1961). I repeated this experiment in N. cinerea and also tested the effect of separation on on the dominant/subordinate relationship.

(1) An attempt to reverse dominance by injection of corpus cardiacum homogenates.

Materials and Methods

Isolated adult males were maintained in the usual way for one week after which they were anaesthetised under ether and dissected alive in Hoyle's ringer (Hoyle 1953). The corpora cardiaca were dissected out, tranferred to a clean cavity slide where extraneous material was removed. The corpora allata were also removed. Some difficulty was encountered in this operation because the terminal portion of the corpus cardiacum forms a cup round the corpus allatum and there is no nerve stalk as in P. americana (see Chapter Nine for details of morphology). The gland pairs were transferred to a small tube and macerated in a drop of ringer with a small glass pestle until an even suspension was obtained.

Four pairs of glands were treated in this way and the volume of fluid made up to 150 µl.

Pairs of males were also set up in the usual way and left for one month. The animals were checked every six days to ensure that dominance reversal had not occurred. After the final check each animal was placed in a separate container in the refrigerator at $4^{o}C$ for ten minutes. The containers were then placed on ice until the animals entered chill coma. This method of anaesthesia was adopted because other methods produced severe convulsions and defaecation. Chilling also produced convulsions but they were less severe and there was no defaecation using this method. Immediately animals entered chill coma they were injected with 25 µl. of homogenate which was equivalent to approximately two thirds of one gland pair per animal. A Hamilton microliter syringe was used and the needle was inserted between the tergal plates of the abdomen. Ozbas and Hodgson (1958) injected from between one and six gland pairs in 0.5 - 1.0 ml. of saline into their animals (*Periplaneta* and *Blaberus*) but I found that injection of such large volumes caused considerable distention of the abdomen and also much fluid was lost. Using smaller quantities it was easier to ensure that the same amount was injected in each case. It was hoped that the behavioural effects which Ozbas and Hodgson obtained would be avoided with these concentrations.

After injection, the containers were removed from the ice and kept at room temperature. Each animal was presented with the test-animal at fifteen minute intervals over a period of one hour and again after two hours. The animals were left alone overnight without food or water and paired with their original partner the following day. Two points were noted: which animal initiated the first attack, and the outcome of the fight.

Three groups were set up as follows:

(1) 6 pairs chilled, injected with corpora cardiaca from isolated males and left overnight before re-pairing.

(2) 17 pairs chilled and separated overnight.

(3) 23 pairs separated overnight.

Results

In pairs which had been chilled (groups 1 and 2) the previously submissive animal attacked the test-animal in nineteen out of twenty three cases. Only five previously dominant males attacked the test-animal and those which did, appeared to attack later than the majority of subordinates. These results are shown in Table 8.1.

	Time after chilling (min.)					Observations (No.)
	15	30	45	60	120	
Subordinates	9	2	4	1	3	23
Dominants	0	0	1	1	3	23

TABLE 8.1. The number of subordinate and dominant animals which attacked the test-animal over the two hour period following chilling.

When chilled animals were paired again with their original partner almost always the previously subordinate animal either initiated the first attack and became dominant, or if the attack was mutual, subsequently became dominant. In only three out of twenty three cases was the situation unchanged. Control animals which had been separated overnight did not show this trend. These results are shmmarised in Table 8.2.

	Reversed	Unchanged	Total
Chilled	20	3	23
Untreated	2	21	23

TABLE 8.2. The incidence of dominance reversal in chilled and unchilled animals which have been separated for twenty four hours before re-pairing.

These results show that the chilling procedure itself can result in reversal of dominance. If there is any effect of the corpus cardiacum it is masked by chilling. All of the subordinate males which were injected attacked the test-animal and all became dominant on re-pairing. Thirteen out of seventeen chilled-only males reversed. With such small numbers it is not possible to say that the effect is more pronounced in the injected pairs.

(2) <u>The effect of previous wins and losses on dominance reversal</u>

Healthy adult males, not more than one month old, were collected from uncrowded tanks and allowed to develop a hierarchy. Altogether seven hierarchies were used. Each hierarchy comprised six animals and these were ranked 1 - 6. Pairs were set up as follows: 1+4, 2+5, 3+6. Each pair was left for three days and the middle pair, 2+5, was used to determine the effect on the relationship of (1) the dominant losing to a better male and (2) the subordinate winning over an inferior animal.

Three experimental situations were used:-

(a) The dominant male was beaten by pairing with the top-ranking male, male 1, and the subordinate was allowed to win by pairing with the bottom-ranking male, male 6. Both animals were left with the new partner for twenty four hours before re-pairing. Two repeats were made of this experiment.

(b) The subordinate male was allowed to win by pairing with the bottom ranking male, male 6, for twenty four hours before returning to its original partner. (The dominant, meanwhile, was isolated with food and water). One repeat was made of this experiment.

(c) The dominant was beaten by pairing with the top-ranking male, male 1, for twenty four hours before returning to its original partner. (The subordinate, meantime, was isolated with food and water). One repeat was made of this experiment.

The purpose of the experiments was to determine whether the submissive response was conditioned to a particular dominant which the subordinate recognised individually or whether it was more likely that the dominant induced a persistent physiological response in the subordinate.

Results

Dominance can be reversed if the dominant has recently been beaten by another male. If the submissive is allowed to win this does not appear to be sufficient to bring about reversal. The results are shown in Table 8.3.

Pair	Situation	Result
1a	Sub. Wins Dom. Loses	Reversal of Dominance
2a	Sub. Wins Dom. Loses	Reversal of Dominance
3a	Sub. Wins Dom. Loses	Reversal of Dominance
1a	Sub. Wins	No change
2b	Sub. Wins	No change
1c	Dom. Loses	Reversal
2c	Dom. Loses	Reversal

TABLE 8.3. The effect of wins and losses on the dominant/subordinate relationship when partners are re-paired.

These results indicate that even if the subordinate male is capable of recognising individual characteristics of the dominant this is not of overriding importance in the appearance and maintenance of subordinate behaviour.

Since a subordinate male only beats its dominant when the latter has just been beaten by a superior male, irrespective of whether the subordinate itself has just won, it is the change of state in the dominant which makes it possible for the subordinate to win.

(3) The effect of separation on the dominant/subordinate relationship.

Materials and methods

Healthy adult males, not more than one month old, were paired and the dominance relationship determined in the usual way. After three days each animal was kept in isolation for a specified period of time, before being paired again with its original partner. Seven time-intervals were chosen, 6, 12, 24, 48, 72, 96, and 120 hours. Twelve pairs were set up for each separation period thus totalling eighty four pairs. The purpose of the experiment was to determine whether subordinate animals show less submissive behaviour after they have been separated from the dominant and if so, how long it is before both members of a pair have equal status and the previously subordinate male has a chance to become dominant.

Each pair was observed for five minutes immediately after the two males had been put together again. Several measures were taken in conjunction to determine whether the subordinate was becoming less submissive. They were (1) the number of subordinate animals adopting the submissive posture within the five minute period, (2) the number of subordinates fighting back, (3) the incidence of grappling (this normally occurs between high-ranking males close in rank) and (4) reversal of dominance.

Results

With increasing separation time there is a decrease in the number of subordinate animals that become submissive during the first five minutes after pairing. There is also a gradual increase in the number of subordinate animals which fight back though this is not observed before 48 hours separation. Grappling is first observed after 72 hours but there were no reversals of dominance until the fifth day. These results are shown in Table 8.4.

Behaviour of the Subordinate	Hours of Separation						
	6	12	24	48	72	96	120
Submission	6	7	6	4	0	2	1
Retaliation	0	0	0	1	7	8	7
Grappling	0	0	0	0	2	3	4
Dominance	0	0	0	0	0	0	3

TABLE 8.4. The effect of separation from the dominant on the behaviour of the subordinate on re-pairing.

Twelve pairs were used for each separation period. The table shows the number of subordinates out of twelve which behave in a particular way.

Discussion

The effect of the corpus cardiacum on dominant/subordinate behaviour is inconclusive but chilling does result in a significant number of dominance reversals. Reversals are seen in 86% of pairs which suggests, not just that the previous effects of dominance have been cancelled out and animals have an equal chance of winning, but that there is a detrimental effect on the dominant which makes it less likely to win. The effect on the dominant can be detected immediately after recovery from chilling. Dominants adopt the submissive posture to the test-animal which they attacked beforehand.

In the previous chapter I discussed the possibility that subordinate animals are dehydrated. If these animals also have a higher haemolymph concentration then this could account for a better recovery after chilling. When chilling occurs the nerve membrane will become more permeable to Na^+ ions and water will enter the nerve. When the animals are warmed up the dominants will have more water to remove from the nerves (and other tissues). However, whilst this could explain the short-term changes, it seems unlikely that it could account for reversals which occur after twenty four hours. Dominants must be affected by some more permanent change.

Reversal of dominance can occur when the dominant has just been beaten by another male. This suggests that the subordinate does not recognise the individual characteristics of its dominant and supports the idea that the dominant induces a particular physiological state in the submissive. This state can be recognised by the outward display of submissive behaviour.

The effect of being beaten does wear off eventually. After two days of separation from its dominant the submissive male begins to fight back and gradually becomes more aggressive until on the fifth day reversal may occur.

When animals were paired for one month and then separated for twenty four hours before re-pairing (experiment 1, group 3) there were very few reversals but two pairs out of twenty three did reverse and yet when animals were paired for only three days, five days of separation were required before reversal occurred on re-pairing. This may reflect the difference between an adapted relationship of long-standing and a newly developed relationship. When pairs are first put together deaths appear to occur over the first three or four days or not at all. Perhaps during the early stages while the relationship is being established, the subordinates are more stressed than at any other time and the effects take longer to wear off. It is also possible that reversals occur when the relationship is poorly developed and the animals are close in rank.

These experiments show that the critical factor in the development of a dominant/subordinate relationship is the induction of a particular physiolgical state in the subordinate animal. Whatever changes do occur, they wear off when pairs that have been together for a few days, are separated. The ability of corpus cardiacum extracts to alter behaviour is not shown. It would still be possible to inject corpus cardiacum directly without anaesthesia, perhaps this would be no less stressing than the other procedures. Chilling both animals in a pair reverses dominance. This observation makes a good starting point for further investigation. There is little point in suggesting a mode of action of chilling until measurements of haemolymph concentrations in dominants and subordinates are made.

The next chapter is concerned with an examination of the neurosecretory system to see if there are any differences in the amounts of storage products or any other indications of differences in the rate of secretion in dominant and subordinate animals.

CHAPTER NINE

The pars intercerebralis and the retrocerebral complex in dominant/subordinate pairs.

Introduction

Two experiments in particular encouraged me to investigate the neuro-endocrine system in Nauphoeta cinerea. The first of these was the demonstration in Blaberus cranifer females that neurosecretory material was released from the corpus cardiacum during enforced activity or after repeated administration of electric shock (Hodgson and Geldiay 1959). The other was the observation in Blaberus giganteus that the A-cells of the pars intercerebralis accumulated neurosecretory material in water deprived animals (Wall 1962).

The treatment which subordinate cockroaches receive from dominant males would appear to constitute a more natural stressor than enforced activity and therefore it seemed worthwhile examining the corpora cardiaca of dominants and subordinates. My main interest was in establishing not only what factors are involved in the appearance of subordinate behaviour, but also what factors are involved in its maintenance. The most striking weight changes in subordinate males are seen around three weeks

(Chapter Seven) and I decided to look at pairs which had been together for that period. Hodgson and Geldiay's experiments involved only very short term exposure to the stressor and therefore his results cannot be used to predict the appearance of the corpora cardiaca in subordinate animals. As well as looking at the corpora cardiaca it was also necessary to examine the entire neurosecretory pathway from the pars intercerebralis to the corpora cardiaca. If the glands alone were examined the interpretation of any differences between dominants and subordinates would be open to question. The observation that water deprived cockroaches show an accumulation of neurosecretory material in the A-cells of the pars intercerebralis also indicated that the A-cells should be examined since I had found that subordinates were effectively water deprived (Chapter six).

There are two parts to the investigation. The first is concerned purely with a description of the morphology of the retrocerebral complex in Nauphoeta which I felt was necessary on the grounds that it might be different from that of Periplaneta which has been described in most detail (Willey 1961). More particularly, I wanted to familiarise myself with the anatomy to ensure proper removal of the glands for purposes of injection (Chapter eight) and also so that I could make valid comparisons between the glands from animals of different rank. The second part of the investigation involves a histological examination of the brain and retrocerebral complex in dominant and subordinate animals.

Materials and methods

1. General morphology

Mature healthy males were selected from the culture tank and used to investigate the gross morphology of the retrocerebral complex in *N. cinerea*. The animals were killed in ether and dissected in Hoyle's ringer. The head capsule was opened and once the tissue overlying the retrocerebral complex had been removed, one of two stains, Methylene Blue or Delafield's Haematoxylin, was applied to the dissected area. Drawings were made from the dissections and these were used to construct a general picture of the gross morphology. A few glands were removed and transferred to a cavity slide so that photographs could be taken.

2. Histology

Dominant/subordinate pairs were set up in the usual way and after three weeks were killed in ether. In some cases only the corpora cardiaca were dissected out and in others both the brain and the retrocerebral complex were removed. Two fixatives were tried, Bouin's 1898 fluid and Helly's fluid and eventually aqueous Bouin's with trichloracetic acid instead of acetic acid (Foot 1933) was used as this gave better fixation than Helly's fluid. Two stains, which are thought to stain neurosecretory hormones or more probably the protein carriers of the hormones, were employed. They were, Ewen's (1962) aldehyde fuchsin and also Bargmann's modification of Gomori's chrome alum haematoxylin phloxine (Pearse 1960). In addition some wholemount preparations were made using Dogra's (1964) bulk method with an aldehyde fuchsin stain.

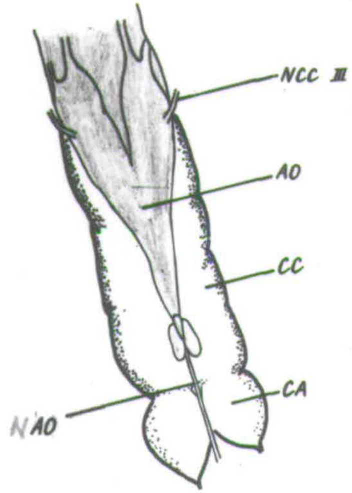
Tissues were either single-embedded in paraffin wax (melting point 58°C) or double-embedded in Peterfi's celluloidin paraffin which gave better sections of the brain. Serial sections were cut at 5µ.

No quantitative analysis was made of the amounts of neurosecretory material in either the type A-cells or the corpora cardiaca. The A-cells are those cells in the pars intercerebralis which stain positively with the two stains employed, blue-black with chrome alum haematoxylin phloxine (CAHP) and deep purple with aldehyde fuchsin (AF). In each case the pars intercerebralis was examined to see if the A-cells contained small, moderate or large amounts of neurosecretory material and this was carried out with reference to the animals having the smallest and the largest amounts of material. Diagrams were made of the main features of the brain so that as far as possible comparisons could be made between the same cells or at least the same group of cells. (There are at least four distinct groups of neurosecretory cells in the pars intercerebralis of the cockroach, Willey 1961). Each section of the corpus cardiacum was allotted to one of four categories according to the amount of neurosecretory material present. The categories were, none (-), small amounts (+), moderate amounts (++) and large amounts (+++). Wholemounts were analysed using similar criteria.

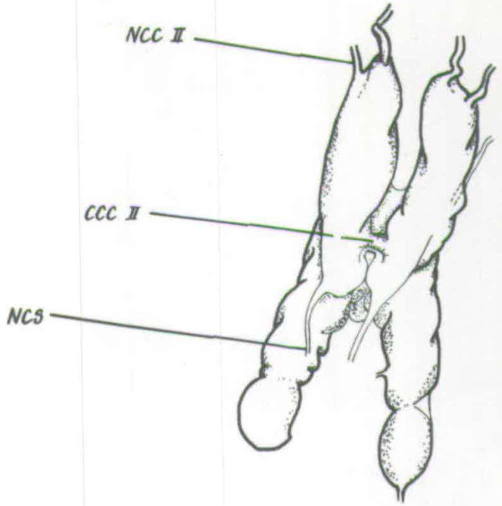
Results

1. Morphology

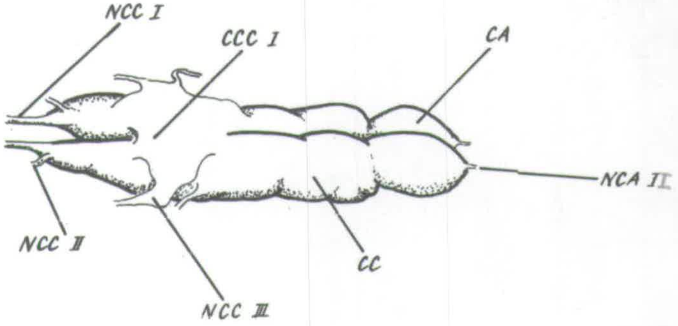
The retrocerebral complex in Nauphoeta is similar in its general features to those described for other species but there are some noteworthy differences. There also appears to be some variation in structure between individuals. Whether these differences have any functional significance, I do not know.


NCC III
AO
CC
CA
N'AO

a


NCC II
CCC II
NCS

b


NCC I
CCC I
CA
NCA II
NCC II
CC
NCC III

c

FIGURE XXIII

Gross morphology of the retrocerebral complex in *Nauphoeta cinerea*.

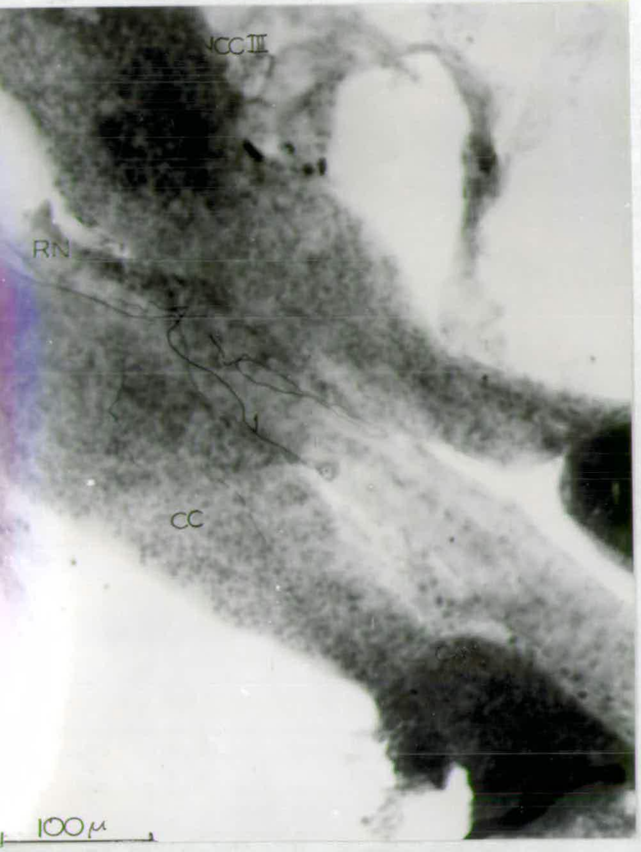
a) Dorsal view showing the aorta (shaded).
b) Ventral view showing the second commissure.
c) Lateral view showing the first commissure.

KEY: NCC I = Nervus corporis cardiaci I.
NCC II = Nervus corporis cardiaci II.
NCC III = Nervus corporis cardiaci III.
NCA II = Nervus corporis allati II.
NAO = Nervus aorticus.
AO = Aorta.
CC = Corpus cardiacum.
CA = Corpus allatum.
CCC I = Commissuris corporis cardiaci I.
CCC II = Commissuris corporis cardiaci II.

The corpora cardiaca are seen as two, elongate, blue-white bodies contrasting with the corpora allata, two, transparent, more or less pear-shaped glands, attached one to the distal portion of each corpus cardiacum. In Nauphoeta two commissures connect the two portions of the gland. The commissura corporis cardiaci I is anterior and dorsal and in most respects appears to be similar to the dorsal commissure in Periplaneta (Willey 1961). The commissura corporis cardiaci II is distal and ventrolateral and begins just behind the termination of the dorsal commissure. This ventral commissure, which is absent in Periplaneta, is probably similar to that found in Blaberus species though Willey (1961) gives little detail of its structure. In Nauphoeta the main crossing over of fibres in the distal commissure is lateral rather than ventral. Beyond the second commissure the main portion of the gland joins the corpus allatum without a conspicuous nerve stalk (the nervus corporis allati I of Periplaneta and Blaberus species). These general features are shown in Fig. 23, a, b and c.

As in Periplaneta, there are at least three pairs of nerves from the brain to the corpora cardiaca. Two of these are easily found. They are the nervus corporis cardiaci I and the nervus corporis cardiaci II which can be traced from the protocerebrum of the brain to the anterior portions of the corpora cardiaca. The first nerve enters anteriorly and the second nerve somewhat laterally. The aorta covers the entire area from the brain to the anterior commissure, forming a funnel-like structure which terminates in the nervus aorticus. The aorta obscures the entrance of the nervus corporis cardiaci III at the anterior end of the first commissure. This can be remedied partially by the removal of the aorta (Fig. 23b) but several other nerve fibres also enter at this point (Fig. 24a) and in fact this nerve is best detected in sections. At the entrance of the nervus corporis cardiaci III the dorsal surface of the gland is folded into a wing-like structure and it is this portion which forms the ventral margin of the aorta (Fig. 24 b and c).

The junction between the corpora cardiaca and the corpora allata appears to differ both from *Periplaneta* and from *Blaberus* species. Some Methylene Blue preparations indicate that a half-cup of corpus cardiacum tissue surrounds the outermost edge of the anterior portion of the corpus allatum (Fig. 24a). Serial sections also show this tissue round the gland (Fig. 25a) but since it is not always observed there



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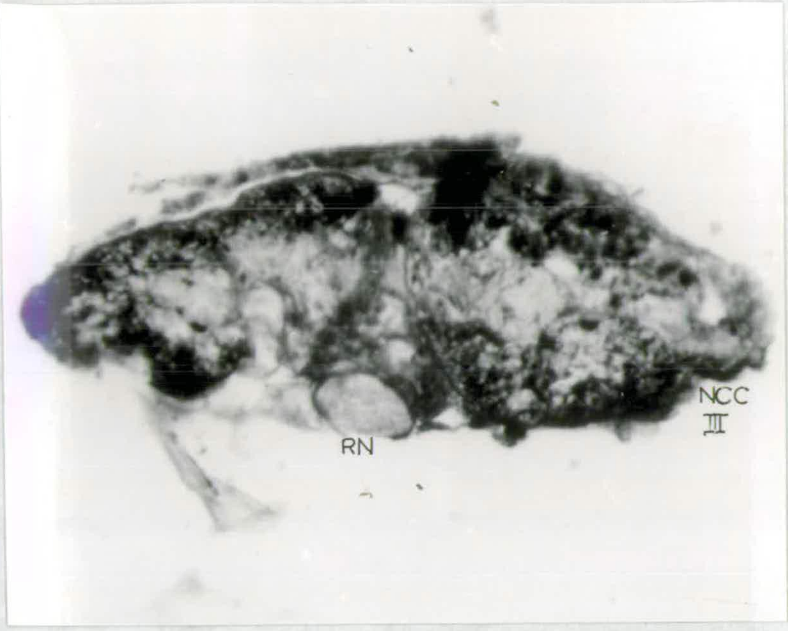

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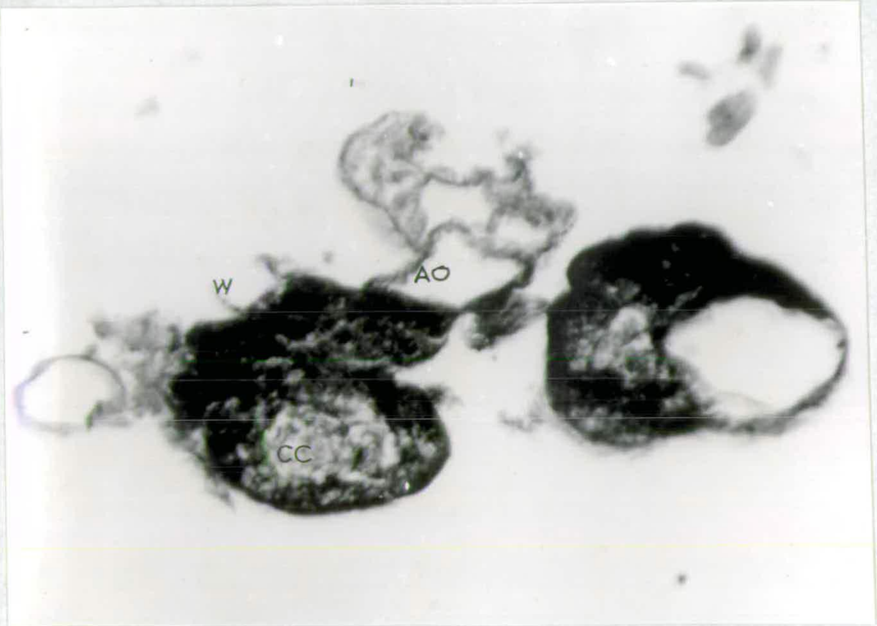


c

FIGURE XXIV

The anatomy of the corpus cardiacum.

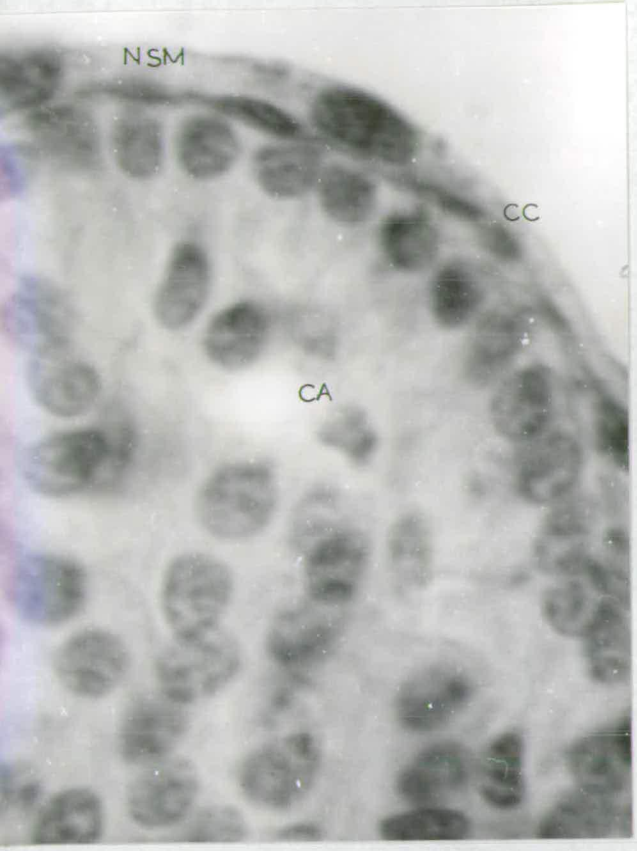
a) A methylene blue preparation of the corpus cardiacum. Several nerve fibres are seen to enter at the junction of the NCC III. Notice the corpus cardiacum tissue found the corpus allatum.

b) The entrance of the NCC III. The scale is shown in Figure 24a. AF was used as a stain.

c) The "wings" of the corpus cardiacum forming the ventral margin of the aorta. AF was used as a stain. The scale is shown in Figure 24a.

KEY: NCC III = Nervus corporis cardiaci III.
CC = Corpus cardiacum.
CA = Corpus allatum.
RN = Recurrent nerve.
AO = Aorta.
W = Wing.

XXV



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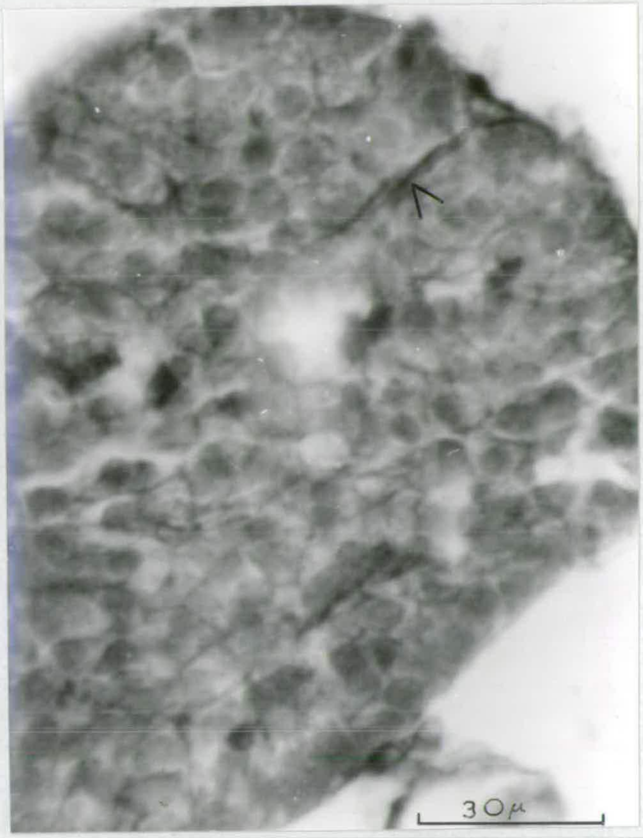

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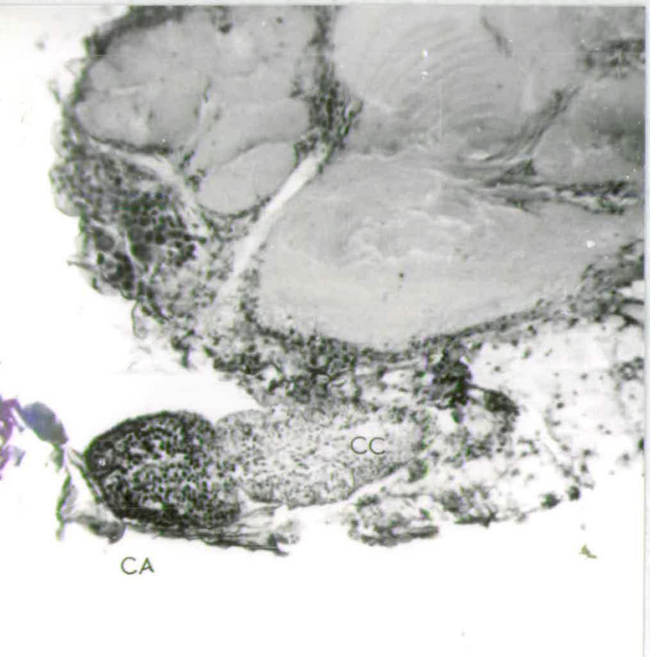

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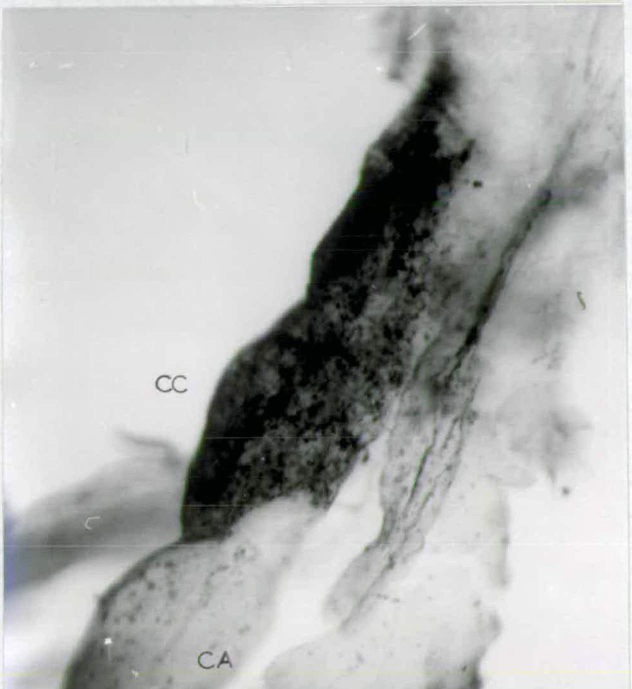

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FIGURE XXV

The junction of the corpus cardiacum and the corpus allatum.

a) Transverse section through the corpus allatum showing corpus cardiacum tissue with normal nucleii and neurosecretory material just visible as tiny granules. (X 100 oil immersion objective). CAHP was used as a stain.

b) Longitudinal section through the corpus cardiacum and corpus allatum. There is no nervus corporis allatum I. CAHP was used as a stain.

c) A transverse section showing the junction between the corpus cardiacum and corpus allatum. The arrow indicates material staining positively with AF.

d) A wholemount preparation using Dogra's bulk method with an AF stain. Only one half of the gland is complete. The corpus cardiacum is stained intensely. Neurosecretory material is also seen in the corpus allatum. The scale is shown in Figure XXVb.

KEY:
CA = Corpus allatum.
CC = Corpus cardiacum.
NSM = Neurosecretory material.

may be some individual variation. There is no nervus corporis allati I (Fig. 25b) although it is possible that the corpus cardiacum tissue linking the two glands represents the rudiment of this nerve. The connecting tissue appears to be non-nervous in origin and to contain both normal corpus cardiacum type nuclei and neurosecretory material. The membranes of the corpora cardiaca interdigitate with those of the corpora allata at the junction between the two glands. The membranes stain positive with AF and it may be that neurosecretory material is carried into the corpora allata at this point (Fig. 25c). Using Dogra's bulk method neurosecretory material can be detected as particles within the corpora allata (Fig. 25d).

Serial sections show that the corpus cardiacum is divisible into two portions, an anterior portion which contains the bulk of the fibres of the nerves from the brain and also, an apparently syncitial glandular region which partially surrounds the nerve fibres. The distal portion of the gland including the second commissure appears to be the main storage organ for neurosecretory material. Some such material does occur in the anterior portion but it is usually confined to a limited zone at the margin of the gland. These features are illustrated in Fig. 26a.

Pair No.	5		8		9	
Portion of the Corpus Cardiacum	Sec.	St.	Sec.	St.	Sec.	St.
Dominant	/	/	-	++	+	+
Subordinate	+	+++	/	/	/	/

Pair No.	15		16		17	
Portion of the Corpus Cardiacum	Sec.	St.	Sec.	St.	Sec.	St.
Dominant	+	++	+	++	-	+
Subordinate	+	+++	+	+	/	/

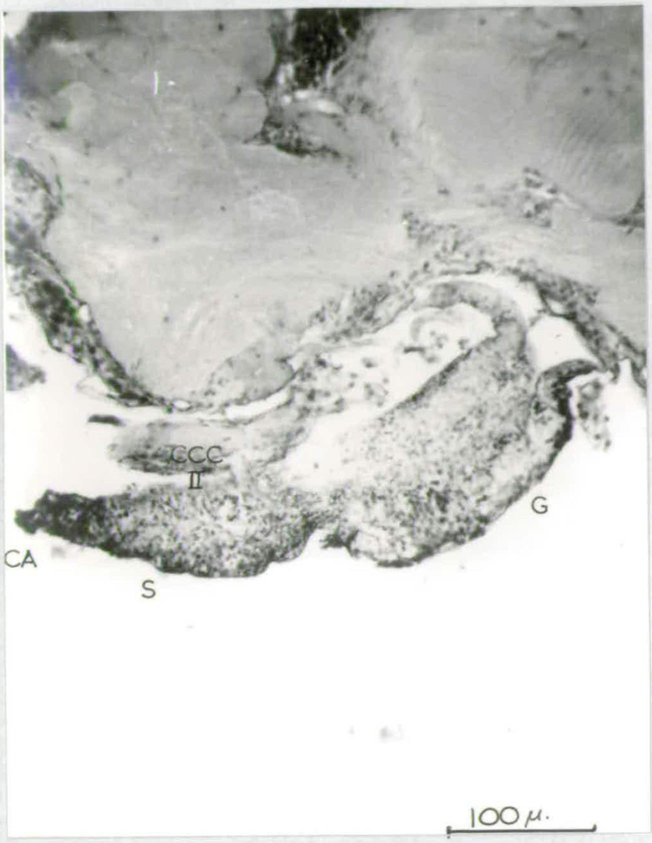
TABLE 9.1. The amounts of neurosecretory material in the copora cardiaca of dominant/subordinate pairs when CAHP was used as a stain. There are four possible categories from - (none) to +++ (large amounts of neurosecretory material). Specimens unsuitable for analysis are indicated / . Sec. = secretory. St. = storage, portions of the gland.

2. Histology of the brain and retrocerebral complex in dominant/subordinate pairs.

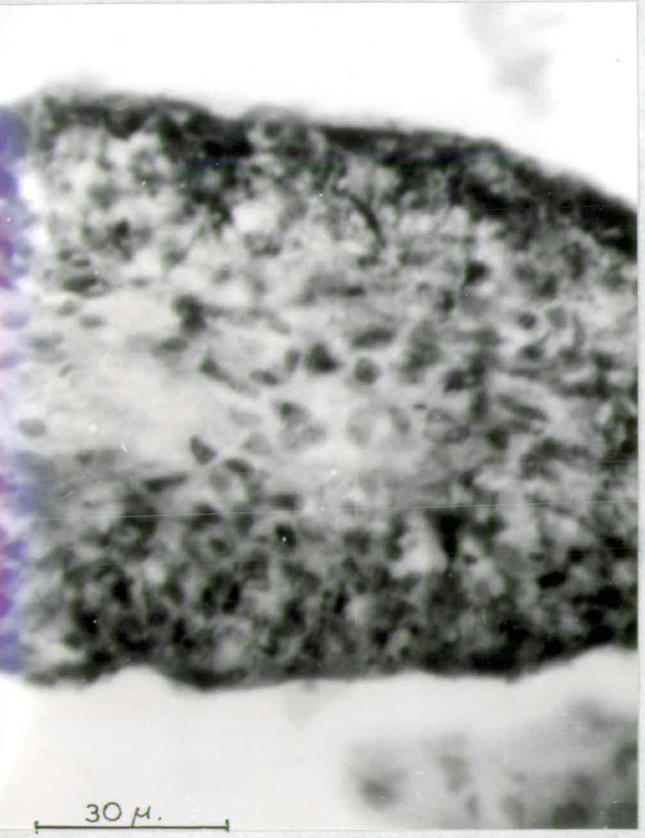
Examination of serial sections shows that although there are individual differences in the amounts of neurosecretory material in the corpora cardiaca there is no correlation between the amount of material and rank. Furthermore the neurosecretory cells of the pars intercerebralis contain only small amounts of material in all animals.

Comparisons can be made only between tissues which have been stained by the same method and the results for each method are given separately. Ideally comparisons should also be made only between pairs of males but there were relatively few pairs for which I obtained complete sections of the corpus cardiacum from the entrance of the nerves of the brain to the corpora allata and this is necessary for making accurate comparisons. Part of the trouble was that I lost sections as a result of over oxidation prior to staining. In other cases, particularly when the brain had been removed as well, the glands were lost. In such cases I have given the results for the other member of the pair alone.

Using CAHP the neurosecretory material is easily seen. It occurs as blue-black particles which are



a



b

c

FIGURE XXVI

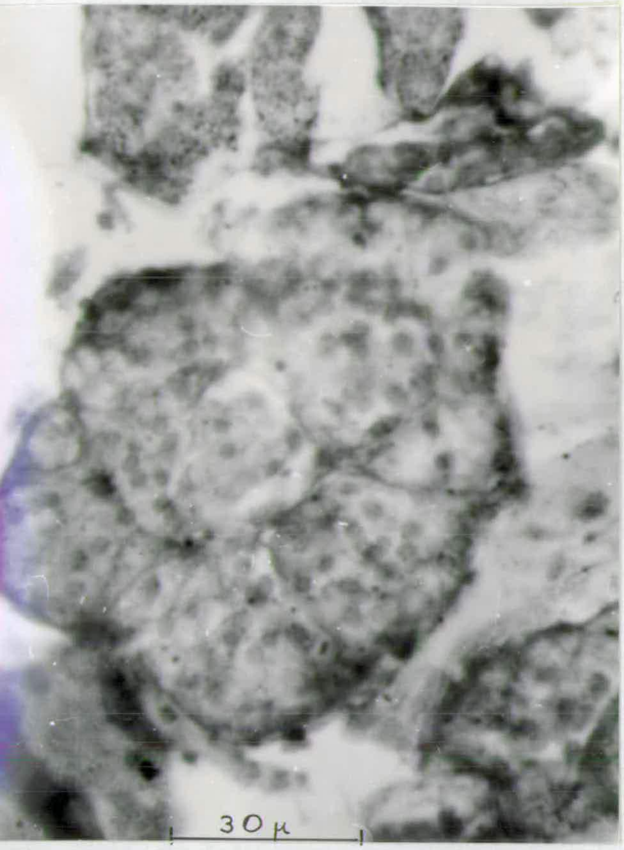
a) The glandular and storage regions of the corpus cardiacum . CAHP was used as a stain.

b) A longitudinal section of the storage region of the corpus cardiacum in a subordinate male (15S). Moderate amounts of neurosecretory material are seen. CAHP was used as a stain.

c) Transfer section of the storage region of the corpus cardiacum in a dominant male (15D). Moderate amounts of neurosecretory material are seen. CAHP was used as a stain. The scale is shown in Figure XXVIb.

KEY: CC = Corpus cardiacum.
CA = Corpus allatum.
CCC II = Commissuris corporis cardiaci.
G = Glandular.
S = Storage.
NF = Nerve fibres.

XXVII



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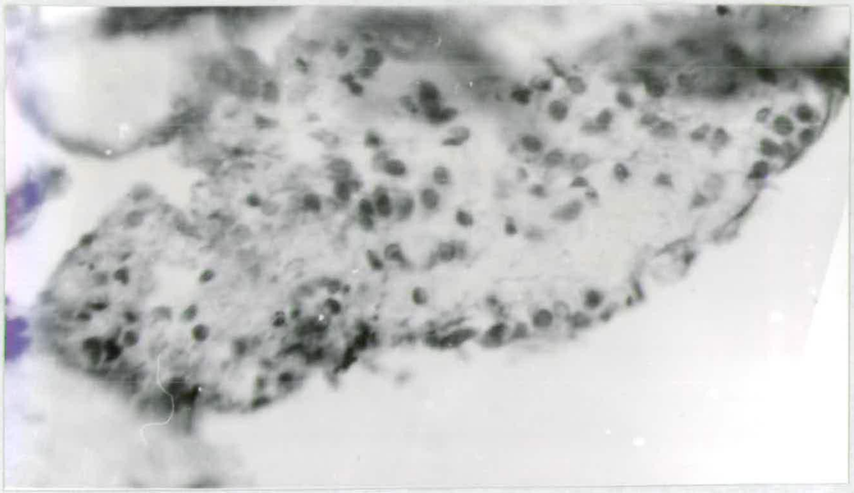

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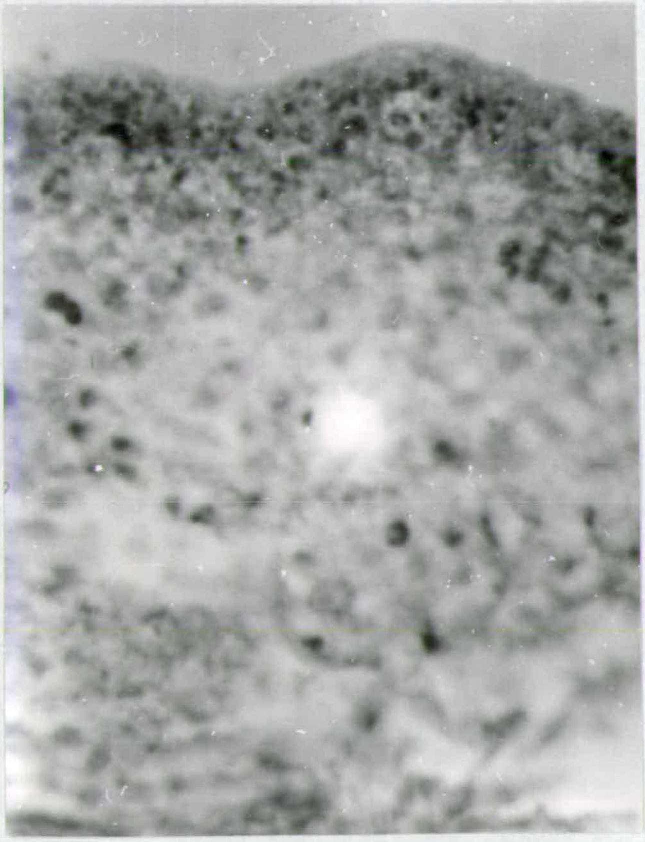


c

FIGURE XXVII

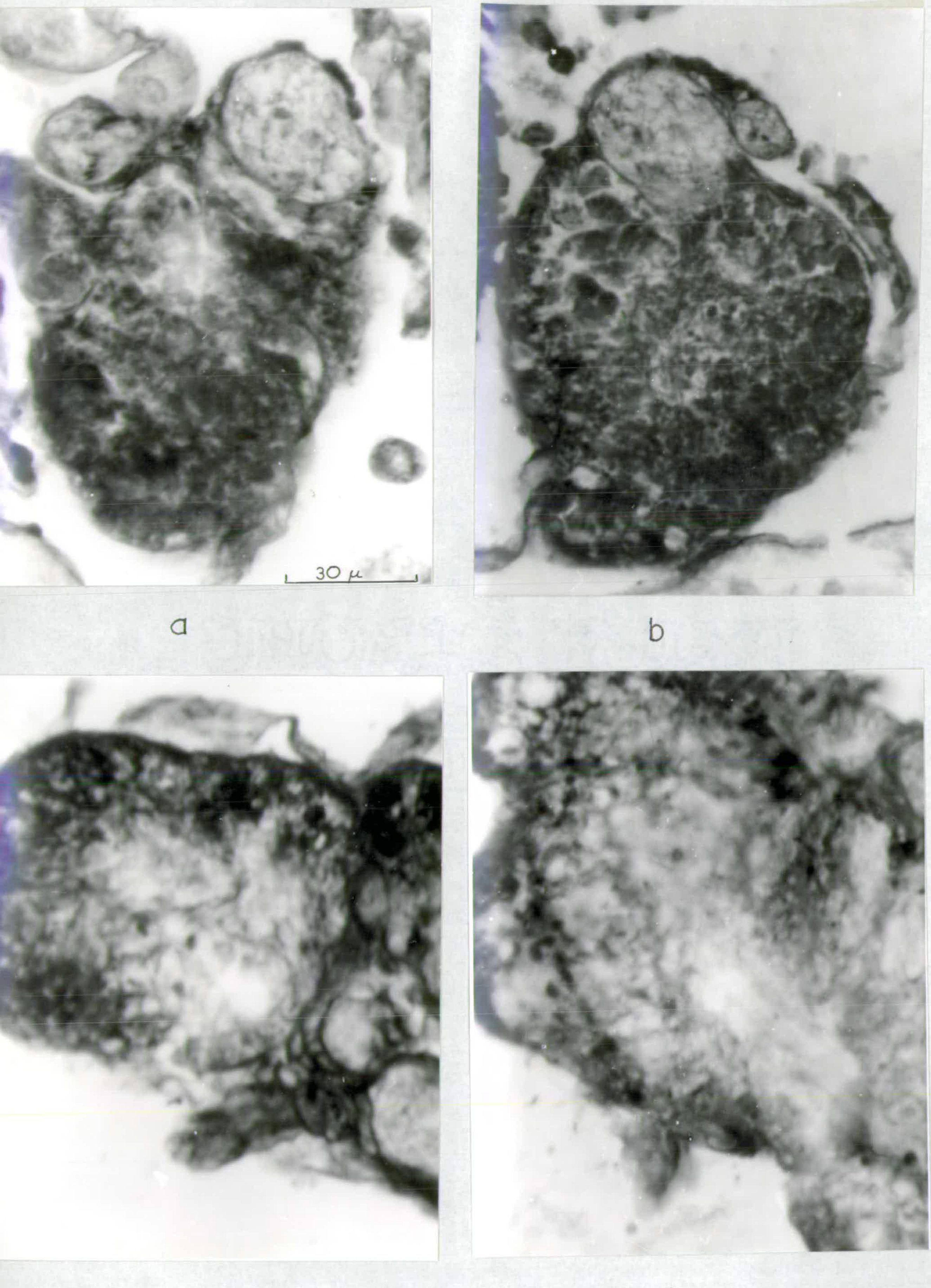
Secretory portions of the corpus cardiacum in a dominant/subordinate pair (8). CAHP was used as a stain.

a) A transverse section of the corpus cardiacum near the entrance of the NCC I in a subordinate male.

b) A longitudinal section of the corpus cardiacum in a dominant male. The scale is shown in Figure XXVIIa.

c) A longitudinal section of the corpus cardiacum in a dominant male. Only small amounts of neurosecretory material are visible.

XXVIII



a b

c d

FIGURE XXVIII

Neurosecretory material in the secretory and storage portions of the corpus cardiacum in dominant and subordinate animals. AF was used as a stain.

a) A transverse section through the secretory portion of the corpus cardiacum of a dominant male (43D). Large amounts of neurosecretory material are present.

b) A transverse section through the secretory portion of the corpus cardiacum of a subordinate male (43S). Large amounts of neurosecretory material are present. The scale is shown in Figure XXVIIIa.

c) A transverse section through the storage region of the corpus cardiacum in a dominant male (7D). Large amounts of neurosecretory material are present. The scale is shown in Figure XXVIIIa.

d) A transverse section through the storage region of the corpus cardiacum in a subordinate male (7S). Large amounts of neurosecretory material are present. The scale is shown in Figure XXVIIIa.

Pair No.	1		2		3		7	
Portion of the Corpus Cardiacum	Sec.	St.	Sec.	St.	Sec.	St.	Sec.	St.
Dominant	++	++	/	/	+++	+++	++	+++
Subordinate	+	++	+	++	/	/	+	+++

Pair No.	38		39		42		43	
Portion of the Corpus Cardiacum	Sec.	St.	Sec.	St.	Sec.	St.	Sec.	St.
Dominant	/	/	+++	+++	/	/	/	/
Subordinate	+	++	/	/	+	+++	+++	+++

TABLE 9.2. The amounts of neurosecretory material in the coppora cardiaca of dominant/subordinate pairs when AF was used as a stain. There are four possible categories from - (none) to +++ (large amounts of neurosecretory material). Specimens unsuited for analysis are indicated / . Sec. = secretory. St. = storage portions of the gland.

concentrated in the distal parts of the corpora cardiaca. The results obtained using this stain are shown in Table 9.1. Of the pairs from which complete serial sections were obtained (15 and 16) there was no obvious difference between the dominant and its subordinate. Fig. 16b shows a longitudinal section of the storage portion of the corpus cardiacum in the subordinate male of pair 15, 15S and Fig. 16c shows a transverse section through the same portion in the dominant male, 15D. By contrast, Fig. 17a and b show corresponding sections through the secretory portion of the corpora cardiaca in 8S and 8D. (8S is not included in the table as only sections of the anterior portion are present). Other animals showed varying amounts of neurosecretory material and some such as 17D had only small amounts confined to the periphery of the gland (Fig. 17c).

AF stain gave a very similar picture except that the actual amounts of neurosecretory material seemed to be greater and that the positive staining material in the anterior portion of the gland did not appear to be so localised. The results obtained with this stain are given in Table 9.2 and these confirm the results obtained from tissues stained with CAHP. The corpora cardiaca of subordinate males may contain as little or as much neurosecretory material as those from dominant animals.

Pair No.	7		8		11		19	
Portion of the Corpus Cardiacum	Sec.	St.	Sec.	St.	Sec.	St.	Sec.	St.
Dominant	–	+	+	+	+	+	+	–
Subordinate			++	+	+	+++	–	+

Pair No.	30		31		32	
Portion of the Corpus Cardiacum	Sec.	St.	Sec.	St.	Sec.	St.
Dominant			++	+	+	+
Subordinate	+	+	+++	+++	+	++

TABLE 9.3. The amounts of neurosecretory material in the corpora cardiaca of dominant/subordinate pairs using Dogra's bulk method with an AF stain. There are four possible categories from – (none) to +++ (Large amounts of neurosecretory material). Blank space indicates specimen lost.

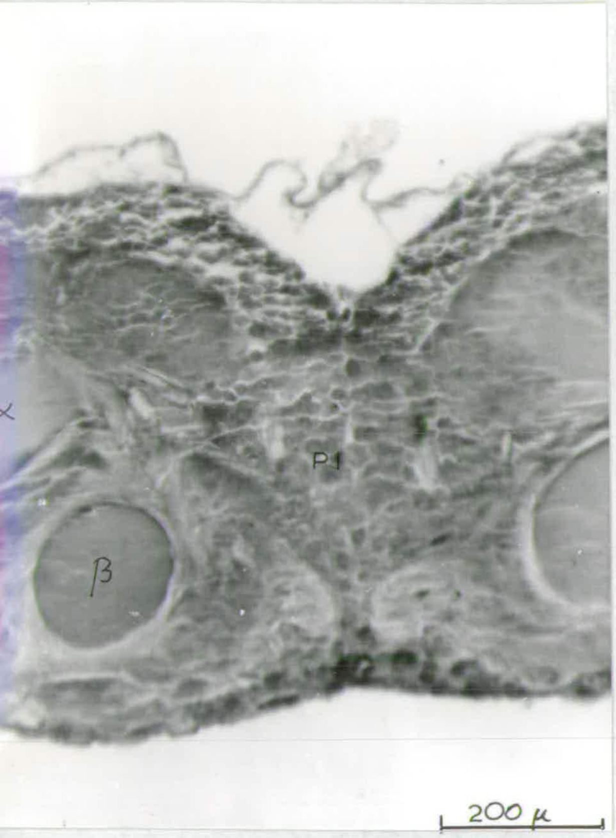
Figs. 28a and b show transverse sections through the anterior portions of the corpora cardiaca in 43 D and S respectively. Figs. 28c and d show transverse sections of the storage portions of the glands in 7D and 7S respectively.

I did not find Dogra's bulk method very satisfactory. In the first place I had difficulty in clearing the brains and in the second I had difficulty in distinguishing between internal particles and material which stained positively and adhered to the outside membranes. Also using this method there often appeared to be as much or more material in the secretory portion than in the storage portion which is not consistent with my previous findings. The results are given in Table 9.3 and perhaps indicate that there are greater amounts of material in the corpora cardiaca of subordinate animals.

2. Neurosecretory material in the pars intercerebralis of subordinate and dominant animals.

Different regions of the pars intercerebralis are shown in Fig. 29a, b and c. The neurosecretory cells appeared to be empty or to contain only small amounts of neurosecretory material. Figs. 30a and b show the pars intercerebralis in 15D and 15S respectively. CAHP was used as a stain and small amounts of positive material

XXIX



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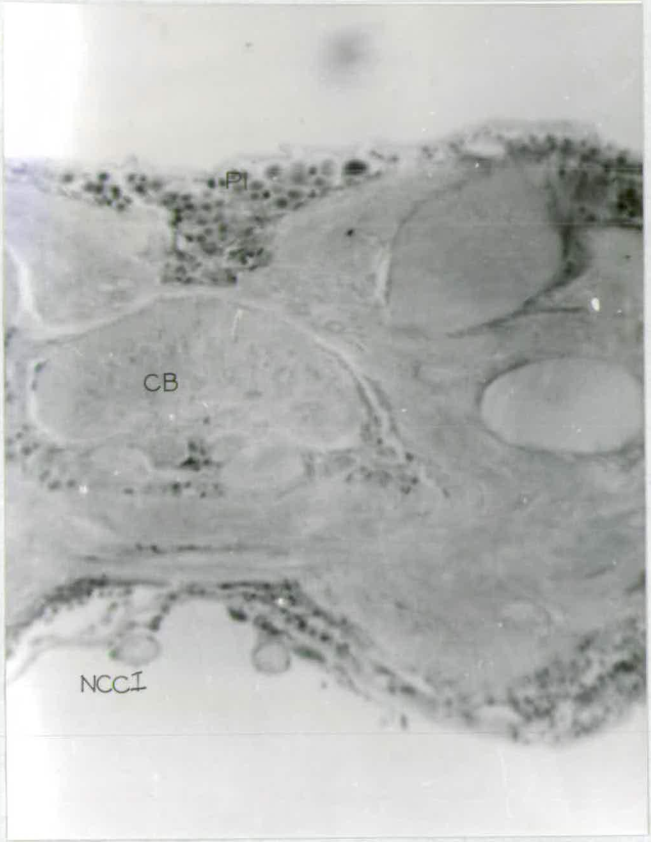

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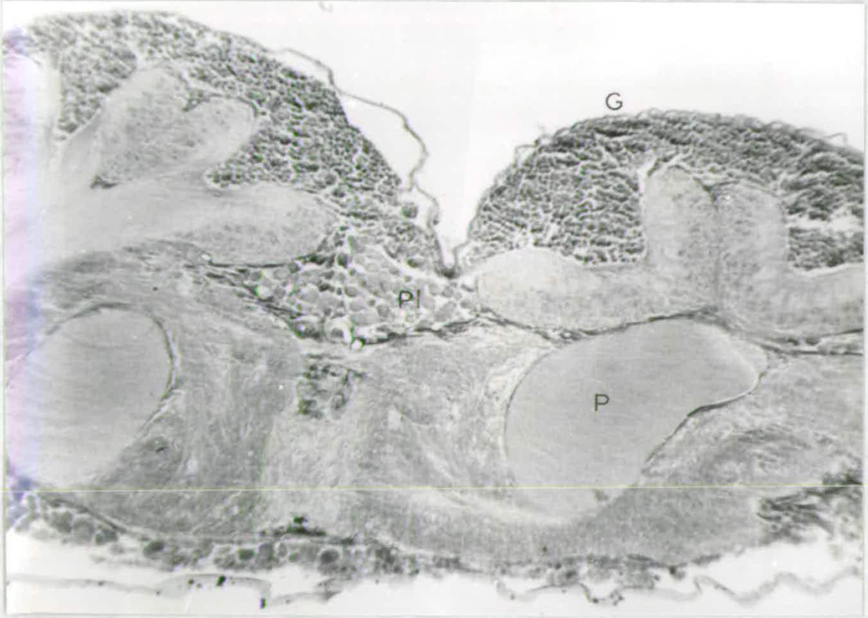


c

FIGURE XXIX

The pars intercerebralis.

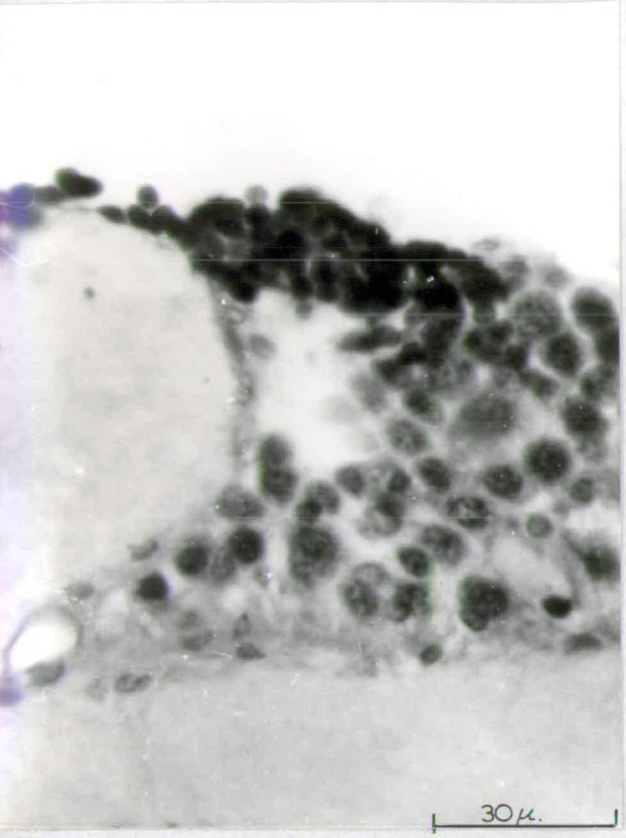
a) A frontal section through the pars intercerebralis. AF was used as a stain.

b) A horizontal section through the central body. CAHP was used as a stain. The scale is shown in Figure XXIXa.

c) A frontal section through the corpora pedunculata. AF was used as a stain. The scale is shown in Figure XXIXa.

Key:-
α = alpha lobe of corpus pedunculatum
β = beta " " " "
PI = pars intercerebralis
G = globuli cells
P = peduncle of corpus pedunculatum
NCCI = nervus corporis cardiaci I
CB = central body

XXX



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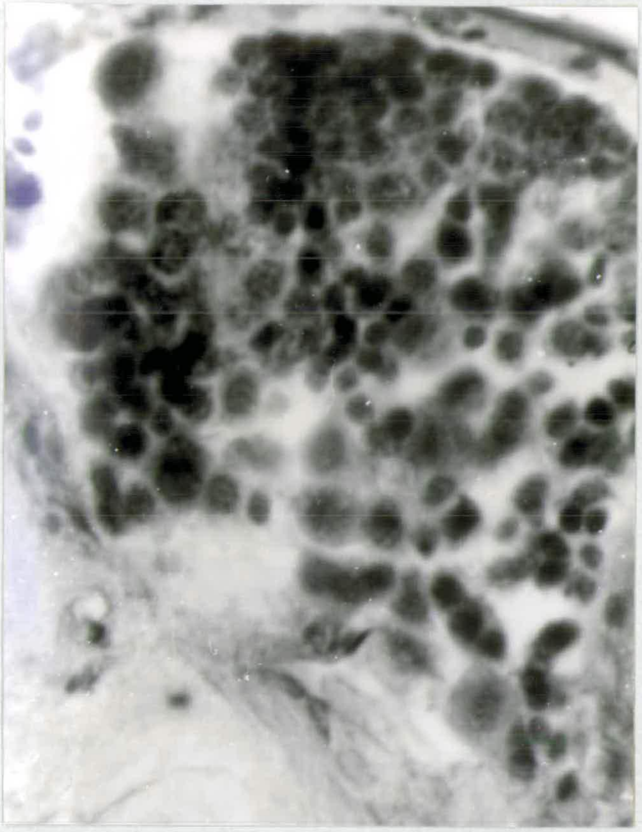

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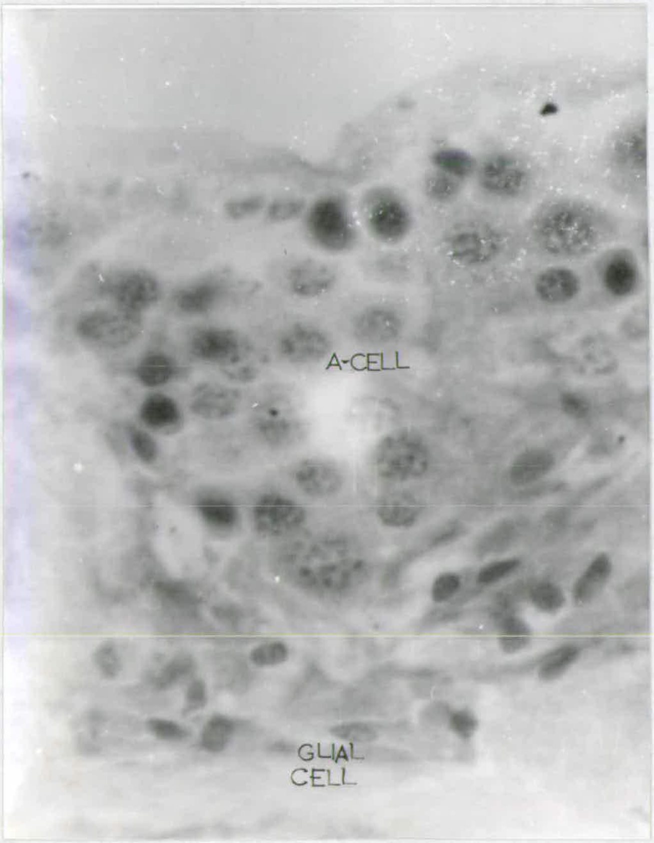


c

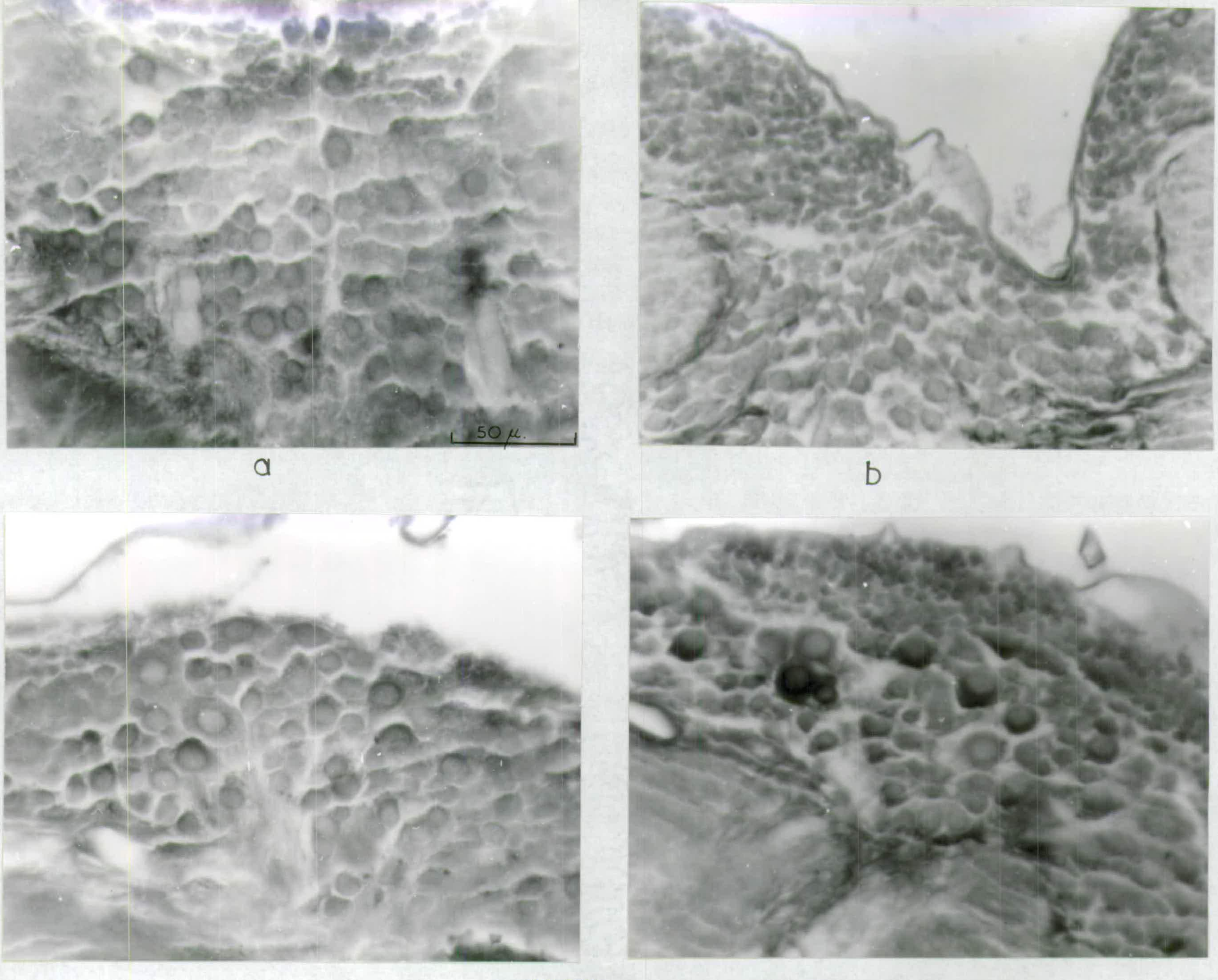
FIGURE XXX

The pars intercerebralis in dominant and subordinate males. CAHP was used as a stain.

a) The pars intermedialis in 15D. Small amounts of neurosecretory material can be seen in the A-cells.

b) The pars intermedialis in 15S. Small amounts of neurosecretory material can be seen. The scale is shown in Figure XXXa.

c) The pars intercerebralis in 17S. The A-cells are devoid of material. The scale is shown in Figure XXXa.



XXXI

FIGURE XXXI

Neurosecretory cells in dominant and subordinate animals using AF as a stain.

a) The pars intercerebralis in a dominant male, 42D. Small amounts of neurosecretory material are present in the A-cells.

b) The pars intercerebralis in a subordinate male, 43S. Small amounts of neurosecretory material are present. The scale is shown in Figures XXXIa.

c) The lateral bouquet in a dominant male, 42D. Moderate amounts of neurosecretory material are present. The scale is shown in Figure XXXIa.

d) The lateral bouquet in a subordinate male, 43S. Moderate amounts of neurosecretory material are present. The scale is shown in Figure XXXIa.

can be seen as fine granules in the cytoplasm. There is no correlation between the amount of material and rank. Fig. 30c shows the typical appearance of empty neurosecretory cells (17S). As with the corpora cardiaca, AF stain gave the appearance of larger amounts of neurosecretory material but here again there was no difference between dominants and subordinates. Figs. 31a and b show the pars intercerebralis in 42D and 43S respectively. Some positive A-cells are seen in both animals. The lateral group of neurosecretory cells which supplies fibres to the nervus corporis cardiaci II (Willey 1961) appeared to contain cells with larger amounts of neurosecretory material but dominants and subordinates did not differ in this respect. Figs. 31c and d show the lateral bouquet in 42D and 43S respectively. Using Dogra's bulk method the pars intercerebralis cells took up no stain.

Discussion

In Chapters seven and eight I presented evidence that subordinate Nauphoeta are stressed and that they undergo various physiological changes while paired with the dominant. A subordinate animal may die but if it survives the initial period of intensive fighting, it may survive as long as the dominant. Dominants and single males gain on average about 10% of their post adult mount weight over a period of one month. Subordinate males only gain 0.3% on average and many animals lose weight. Subordinate animals have watery faeces but since it is observed that the percent water content is normal they must either eat less than dominants or have a higher metabolic rate. Lastly, subordinates can be identified by characteristic behaviour patterns. If subordinate animals are separated from their dominant submissive behaviour gradually disappears and after five days subordinates may be indistinguishable from the dominant so far as behavioural criteria are concerned. These observations are consistent with the idea that subordinate animals may, as a result of exposure to a stressor, suffer from a surfeit or from a lack of a hormone. Hodgson and Geldiay (1959) suggested that the corpora cardiaca may be involved in the cockroach's response to a stressor and they have observed a loss of neurosecretory material from these glands after short-term exposure to enforced activity. On the basis that the most pronounced weight differences between dominant and subordinate Nauphoeta are seen around three weeks, I decided to look at the corpora cardiaca of pairs of males which had been together for this time. Although there was individual variation in the amount of neurosecretory material present there was no correlation with rank. Thus from my observations, neither subordinate behaviour nor the physiological changes which accompany long-term exposure to a dominant, can be accounted for in terms of a surfeit or a lack of neurosecretory material stored in the corpus cardiacum. I feel, and I speculate here, that if dominant and subordinate animals were to be examined immediately after the initial establishment of dominance, which would be the equivalent of Hodgson and Geldiay's experiment, the corpora cardiaca of both animals would be depleted, since both animals are equally active until the loser gives in. In this particular instance it is argueable whether the fight is causing stress; the subordinate, if removed, would very soon recover to fight again. When animals are paired for long periods more permanent changes affect the subordinate and the presence of the dominant, is a stressor in a real sense.

The corpora cardiaca of adult Periplaneta are normally only partially full (Prabhu and Hema 1970). Nauphoeta may differ from Periplaneta but even so, I cannot account for the variation which I find between individuals. With hindsight I would question the advisability of making comparisons of the amounts of neurosecretory material in the corpus cardiacum.

Using Dogra's bulk method Prabhu and Hema found the neurosecretory cells of the brain to be devoid of material. Using the same method I obtained similar results for Nauphoeta. Serial sections stained with CAHP or AF never showed more than small amounts of neurosecretory material in the cells of the pars intercerebralis.

My results do not imply that the corpus cardiacum is not involved in the appearance and maintenance of subordinate behaviour. I have already discussed products of the corpus cardiacum other than the positively staining material which could be involved. Although I have tried to alter behaviour by injection of corpus cardiacum any effects were masked by chilling (which did reverse dominance). It should still be possible to inject glands without prior chilling and possibly the storage and secretory portions of the gland could be injected separately though there is risk of contamination from neurosecretory material of extrinsic origin. It might be better to test fractions separated by chromatographic methods or by gel electrophoresis. The observation that chilling can reverse dominance is interesting, in itself, and provides a starting point for further research. Specifically the spontaneous activity in the nerve cords of dominant and subordinate males could be examined as the animals recover from chill coma. If subordinate animals are more aroused this could be related to their increased aggressiveness. It would also be interesting, though technically difficult, to chill only the head of dominants and subordinates as this might help to localise the system affected.

The dominant/subordinate relationship is a useful system for investigating certain aspects of insect social behaviour and insect physiology. Its main attraction is that it is natural and, in fact, it plays an important role in the structure of cockroach society.

Stress and its implications in the cockroach Nauphoeta cinerea, a summary.

Subordinate cockroaches, particularly young adult males, may die if they are paired with a dominant male from which they cannot escape. Before death occurs a characteristic syndrome develops. Death may occur without external damage and the phenomenon bears striking resemblance to the stress deaths which have been recorded in some vertebrates. The possibility that stress deaths in *Nauphoeta* may be related to a recently characterised substance released from the ventral nerve cord is discussed.

Death is only likely to occur if the dominant ignores the submissive posture of the subordinate and persists in its attacks. In most cases submissive behaviour is successful in preventing further attacks. Most subordinates survive but unlike the low-ranking males described in the first part of this thesis, these animals are less active than dominants and are frequently to be seen in the submissive posture.

Experiments were carried out to test the idea that submissive behaviour, adaptive in itself, is the outward expression of a particular physiological state induced by the dominant. Throughout the second part of the thesis I have tried to relate my experiments to current work on stress and to neuroendocrine products which

could be involved in the syndrome. Chapter Six is particularly concerned with this aspect.

On average subordinate cockroaches were found to gain less weight than dominants and half of subordinates lost weight. When reversal of dominance occurred there was a reversal of this trend. Subordinate animals have watery faeces and may lose water via the mouth (probably from the salivary reservoir). I examined the percentage water content in dominants and subordinates and found no differences between them. Animals treated in the same way except that they were deprived of either food or water all lost weight. Food deprived males had a higher than normal percentage water content and water deprived males were within the normal range. From these results I concluded that subordinates with free access to food and water were reacting as though they were deprived of water. Since the water content of subordinates if normal, these animals, in addition to losing water view the faeces (which could contribute to weight loss) must also eat less. This is supported by the observation that water deprived animals lose more weight than food deprived animals. That water balance is somehow related to subordinate behaviour is supported by the observation that reversal of dominance appears to be more likely when water is available than when it is not.

I attempted to reverse dominance by injection of corpus cardiacum homogenate and used chilling as a method of anaesthesia prior to injection. The chilling procedure itself was found to reverse dominance. The change in behaviour could be detected immediately after recovery from chilling. Whatever changes are involved in this change of behaviour they are long term and even after over-night separation reversal of dominance occurred in 86% of cases. This might indicate that the endocrine system is affected.

It is possible to reverse dominance by means other than chilling. I allowed groups of six males to develop a hierarchy and used the middle pair to test the effect of the dominant losing to a better male and the subordinate being allowed to win over an inferior animal. If the dominant is left overnight with a superior male and then returned to its original partner then reversal of dominance is observed. If, on the other hand, the subordinate is allowed to win, reversal does not occur. These observations support the idea that the dominant induces a apecific state in the subordinate. They also show that even if the subordinate is able to recognise the individual characteristics of its dominant, this is not important in the appearance of submissive behaviour.

When dominant and subordinate animals are separated for increasing periods of time the subordinate gradually becomes less submissive and after five days it may be able to beat the dominant. This also supports the hypothesis that physiological changes accompany the appearance of submissive behaviour. The time for recovery is consistent with the idea that subordinate males may suffer from a surfeit or from a lack of a hormone or hormones.

Work of other authors suggested that the corpus cardiacum might be involved in the cockroach's response to stress. Both this suggestion and the observation that the A-cells of the pars intermedialis accumulated neurosecretory material in water deprived cockroaches led me to investigate the brain and retrocerebral complex in dominant and subordinate males.

Before undertaking such an investigation I found it necessary to examine the gross morphology of the retrocerebral complex, mainly so that accurate comparisons could be made and also to see whether *Nauphoeta* differed from *Periplaneta*. Unlike *Periplaneta* and like *Blaberus* species, *Nauphoeta* has two commissures joining the two half-glands of the corpus cardiacum. Unlike both *Periplaneta* and *Blaberus* species, *Nauphoeta* has no conspicuous nerve stalk between the corpus cardiacum and the corpus allatum. Attention is drawn to other points of interest, such as the presence of neurosecretory material within the corpus allatum.

The results of the histological examination of the brain and retrocerebral complex were negative. Individual variation in the amounts of neurosecretory material in the corpus cardiacum were found but there was no correlation with rank. The A-cells of the pars intercerebralis were either devoid of material or contained only small amounts. These results do not imply that the corpus cardiacum is not involved in the appearance and maintenance of submissive behaviour, merely that differences in the amounts of neurosecretory material from the brain and stored in the corpus cardiacum, are not related to the rank of the animal.

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APPENDIX 3.1

T1 Males

Territory occupation in the light.

Male	1	2	3	4	5	6
1	C20	K20	K20	K20	K20	122(1)
2	K23	L3	L3	L3	L3	L3
3	C20	OUT	K20	H21(2)	H21(2)	E20(1)
4	122(1)	120(2)	122(1)	120(2)	J21(2)	K20
5	C20	C20	C20	C20	C20	C20
6	E21(1)	H20T1)	H20(2)	H20(1)	H20(1)	D12
7	C20	OUT	D12	C22	OUT	OUT
8	121(2)	G12	G12	G12	G12	G12
9	O20(2)	O20(2)	C20	D12	D12	D12
10	G22	K20	K20	D20(2)	K21	L3

Male	7	8	9	10	11	12
1	H21(2)	H21(2)	K20	K20	OUT	J22(2)
2	OUT	OUT	C22(3)	K20(2)	D12	H22(3)
3	K20	K21	H20	F21(1)	F21(1)	F21(1)
4	120	120	F20(2)	OUT	F20(2)	E21(1)
5	C20	C20	D12	K20	C20	C20
6C20	C20(2)	C20(2)	C20	OUT	C20(1)	C20
7	OUT	OUT	OUT	B22(1)	B22(1)	C20
8	G12	G12	G12	G12	G12	G12
9	D12	D12	K20	D12	K20	D12
10	L3	L3	L3	L3	L3	L3

Male	13	14	15	16	17	18
1	K20	D12	D12	D12	K20	B22(2)
2	C20	C20	C20	K20	C20	D12
3	H20(1)	H20(1)	H20(1)	G20(2)	H20(1)	K20
4	J20(2)	120(1)	J20(2)	J20(2)	J20(2)	J20(2)
5	OUT	G12	G12	G12	G12	G12
6	C20(2)	120(1)	OUT	120(1)	K20(2)	C20(2)
7	J20(1)	J20(1)	OUT	J20(1)	K20(2)	C21(1)
8	K20	C20	J20	J21(2)	J21(3)	J20(1)
9	OUT	K20	C20	K20	C20	C20
10	L3	L3	L3	L3	L3	L3

Territory sites are shown in Fig. 4
1 - 21 = observations
(1) - (3) = tier of platform.

Appendix 3.1 (continued) T1 Males. Territory occupation in the light.

Male	19	20	21
1	C20	C22(1)	OUT
2	D12	D12	D12
3	C20	C20	C20
4	J20(2)	J20(2)	C21(2)
5	G12	G12	G12
6	C20(2)	C20(2)	C20
7	C20	C20	C20
8	F20(1)	F21(1)	C21(1)
9	C20	K22	122(2)
10	L3	L3	L3

T1 Males - Positions in the dark

Male	1	2	3	4	5	6
1	D19	F18	110	K20	G201	A15
2	120	B22(2)	L3	L3	L3	H22(3)
3	H20(1)	H20	K20	K20	C13	K20
4	D22(2)	G20(3)	G20(3)	G20(3)	D9	F21(1)
5	F20(2)	C20	C20	C20	OUT	D12
6	E22(1)	E20(1)	H20(2)	H20(2)	C14	E20(1)
7	E22(3)	C21(1)	C20	C20	OUT	K20
8	F22(3)	122(3)	G12	G12	G12	G12
9	H22(3)	D22(2)	D20(2)	K20	OUT	C20
10	D22(1)	H22(1)	115	G22(3)	L3	L3

Male	7	8	9	10	11	12
1	D8	D12	K20	D12	OUT	G22(2)
2	B23	OUT	C22(2)	122(2)	D12	D12
3	K20	K20	K20	C20	OUT	C20
4	C20(2)	E22(2)	F20(2)	G21	OUT	OUT
5	G20(1)	C20	D12	G12	G12	G12
6	B20(2)	C20	K17	B20(2)	OUT	G20(3)
7	OUT	J20(2)	J22(1)	C20	OUT	K20
8	G12	D12	G12	OUT	K20	C20(1)
9	J20(3)	J20(3)	J20(3)	K20	C20	K20
10	L3	L3	L3	L3	L3	L3

Male	13	14	15	16	17	18
1	G20(3)	D22(2)	K20(3)	J20	J20	J20
2	D12	D12	D12	D12	D12	D12
3	C20	C20	OUT	K20	C22	C20
4	J20(3)	J20(3)	J22(1)	OUT	C20	E20(1)
5	G12	G12	G12	G12	G12	G12
6	OUT	H23	K20	G20(1)	F12	B12
7	OUT	OUT	K20	G20(1)	G20(1)	J20(1)
8	G20(1)	G20(1)	C20(1)	OUT	K21	E24
9	C20(2)	K20	122(2)	J22(2)	J22(2)	J22(2)
10	L3	L3	L3	L3	L3	L3

Appendix 3.1 continued T1 Males - positions in the dark.

Male	19	20	21	22
1	D12	D12	F14	J20
2	K9	OUT	OUT	C20
3	J20	OUT	C20	C20
4	J12	K10	D12	B12
5	G12	G12	G12	G12
6	C22	K22	C20	C20
7	G20(1)	OUT	J20(1)	J22(1)
8	C20	K20	K20	B22(1)
9	G21(2)	OUT	C20(2)	G21(2)
10	L3	L3	L3	L3

T2 Males - Positions in the dark.

Male	1	2	3	4	5	6	7
1	OUT	A3	W	D12	A3	A3	A3
2	OUT	L3	OUT	L3	D12	D12	W
3	G12	G12	G12	G12	G12	PLAT	OUT
4	L3	L3	L3	L3	L3	L3	L3
5	OUT	C20	OUT	PLAT.	C20	C20	PLAT.
6	PLAT.	PLAT.	G22(2)	PLAT.	G22(2)	G22(2)	PLAT.
7	OUT	OUT	OUT	C20	OUT	OUT	C20
8	OUT	OUT	OUT	OUT	K20	OUT	K20
9	PLAT.	PLAT.	OUT	PLAT.	F11	G12	PLAT.
10	OUT	K20	K20	K20	K20	K20	K20

Male	8	9	10	11	12	13	14
1	A3	A3	L0	A3	A3	A3	A3
2	OUT	G1	G1	OUT	G1	122(2)	122(2)
3	G12	G12	G12	G12	G12	G12	G12
4	L3	L3	L3	OUT	L3	L3	L3
5	OUT	OUT	K20	OUT	OUT	OUT	OUT
6	PLAT.	G22(2)	G22(3)	OUT	OUT	G1	J12
7	C20	PLAT.	C20	C20	K20	C20	C20
8	OUT	OUT	OUT	OUT	K20	C20	C20
9	PLAT.	OUT	PLAT.	PLAT.	PLAT.	PLAT.	PLAT.
10	K20	K20	K20	K20	K20	K20	E12

Male	15	16	17	18
1	A3	A3	C20	A3
2	122(2)	122(2)	122(2)	L22(2)
3	G12	G12	G12	G12
4	L3	L3	L3	L3
5	OUT	OUT	OUT	OUT
6	G1	ROOF	PLAT.	E12
7	J12	F20(1)	PLAT.	E12
8	K20	OUT	K20	K20
9	PLAT.	PLAT.	PLAT.	PLAT.
10	E12	ROOF	A3	J12

Appendix 3.1 continued **T3 MALES** - positions in the dark.

Male	1	2	3	4	5	6	7
1	A16	H22(2)	A3	K20	G1	A24	A3
2	D20(2)	122(3)	G12	C20	G12	G12	G12
3	G1	G1	K20(1)	G1	L3	A3	K20
4	J12	L3	L3	L3	L3	L3	L3
5	H22(3)	C20	C20	C20	C20	C20	E22(2)
6	G1	G12	F22(2)	G1	J20(3)	K20	K22(3)
7	C20	OUT	K23	G12	K20	K20	E12
8	G1	OUT	OUT	K20(1)	G1	K20(3)	G1
9	B21	G12	C20	G1	K20	C21(2)	G1
10	A24	G1	G1	G1	A24	E12	A24

Male	8	9	10	11	12	13	14
1	A3	J20(2)	E10	G1	K20	H23	OUT
2	L20	C20	120(2)	J12	H20(1)	E12	G12
3	A3	K20	C20(2)	122(1)	122(2)	D21(2)	122(1)
4	L3	L3	L3	L3	L3	L3	L3
5	C20	C20	K20	C20	B3	E10	D20
6	OUT	C20(3)	G1	K22(3)	D20	C20	D20
7	G12	G12	K20	E10	OUT	A3	A3
8	G1	OUT	G1	K20	C20(2)	C20	OUT
9	E12	C20(3)	C20(3)	G1	C21(2)	G1	K20
10	E22(1)	E10	F5	E1	E1	E1	121(2)

Male	15	16	17	18	19	20	21	22
1	C20	J12	J12	J12	J12	J12	J12	J12
2	G12	G12	G12	G12	G12	K20	C20	C20
3	OUT	K20	C20	L3	K20	A3	A3	A3
4	L3	L3	L3	L3	L3	L3	L3	L3
5	120(2)	OUT	122(1)	OUT	K20(3)	E12	OUT	OPEN
6	K20	C20	K20	C20	C20	K20	OUT	C24
7	A3	A3	A3	A3	A3	A3	G1	K20
8	OUT	A9	A9	C20	K20	A10	D22(2)	C20
9	J12	E20(1)	A18	G1	F12	J14	K20	K20
10	H22(1)	H21(111)	H20(2)	F21(2)	120(1)	C21(1)	F22(3)	F22(3)

APPENDIX 3.2

Record of attacks in T1, T2 and T3 males. The tables indicate which males attack and beat other members of the group. If more than one attack was made on a particular individual then the number of attacks is indicated in brackets. The attacking males are indicated along the vertical axis and the males beaten along the horizontal axis of each table.

Date 15/5

♂	♂ ♂ beaten
1	4
2	10
4	5
6	3 7 9
10	3

Date 21/5

♂	♂ ♂ beaten
3	1
9	4

Date 23/5

♂	♂ ♂ beaten
3	9
5	7
6	3
7	1(2) 9

Date 26/5

♂	♂ ♂ beaten
2	1
3	1 2 (3) 9
8	1(3) 4 9(2) 10
9	1(2)

Date 4/6

♂	♂ ♂ beaten
1	4 6
2	3 6
6	9
8	2 4 6 9

Date 5/6

♂	♂ ♂ beaten
1	2 5(2)
3	6
5	3
8	1 3 4 5 9(3)
10	2(2) 4(2) 6

Date 10/6

♂	♂ ♂ beaten
4	6

Date 13/6

♂	♂ ♂ beaten
1	5
2	7 9
3	5 6(2) 7
4	6 7(2)
5	7 9(2)

Date 17/6

♂	♂ ♂ beaten
6	1 7
8	1

APPENDIX 3.2 continued

Date 19/6

No attacks
observed

Date 20/6

No attacks
observed

Date 28/6

♂ ♂ ♂ beaten

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

Date 2/7

♂ ♂ ♂ beaten

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

Date 3/7

♂ ♂ ♂ beaten

2 7
3 6(2) 7(2)

Date 5/7

♂ ♂ ♂ beaten

3 1 9
8 4 6

Date 11/7

♂ ♂ ♂ beaten

2 7

Date 13/7

♂ ♂ ♂ beaten

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

Date 22/7

♂ ♂ ♂ beaten

1 4
2 4 8(4)
3 8

Date 25/7

♂ ♂ ♂ beaten

1 8
2 4 6(3) 8
3 1(5) 4 6 8(2)
5 4(3)
6 4
9 4

Date 26/7

♂ ♂ ♂ beaten

1 8
2 1(2) 6
3 1(5) 6 8
6 1
7 4
9 4 8

Date 29/7

♂ ♂ ♂ beaten

1 2

Date 2/8

♂	♂♂ beaten
1	4
3	1 2(3) 4 6 9(2)
4	1(3) 10
5	4 9 10(2)
7	9(3)
8	6
9	1 7
10	1(6) 2(4) 6(4) 9(2)

Date 7/8

♂	♂♂ beaten
3	6
4	1 8 9

Date 8/8

♂	♂♂ beaten
1	2 6(2) 7 8
3	1(2) 2(4) 4 6(2)
4	2(7) 6(4) 7(2)
7	8(2)
9	8

T2 MALES

Date 14/10

♂	♂♂ beaten
3	2
5	1
6	1 9(2)

Date 15/10

♂	♂♂ beaten
3	9
4	1(3) 2 7(2)
5	7 9(3)
6	7 9 (3)
10	8

Date 17/10

♂	♂♂ beaten
3	7(2)
4	1
5	7
9	7(2)
10	7(3)

Date 22/10

♂	♂♂ beaten
3	9
4	8(2)
6	7
9	7
10	9(2)

Date 24/10

♂	♂♂ beaten
1	8
2	1(2) 5(2) 8(2)
3	1
4	1(2) 2 5(3) 8
5	9
6	9
7	1 2
9	5(3)
10	8

Date 29/10

♂	♂♂ beaten
2	1(2)
3	8
5	1
9	5
10	1 5 9

Date 30/10

♂	♂♂ beaten
3	1(2) 5 8
4	1(3) 2(2) 5
5	8
7	1(3) 5(2) 6 8(2) 9
9	5
10	1 2(2) 5 7(2)

Date 31/10

♂	♂♂ beaten
4	2 (2) 8
9	5 (2) 6 (4)

Appendix 3.2 continued

Date 1/11

♂	♂ ♂ beaten
1	5 8(2)
3	5(2) 8(6) 9(2)
4	2(5) 5(2) 9(3)
5	8
7	5(2) 8(2)
9	5(5) 6 8
10	5 8

Date 2/11

♂	♂ ♂ beaten
1	8
3	5(4)
7	2 5(2) 8(2)
8	9
9	5(4)
10	6

Date 4/11

♂	♂ ♂ beaten
7	8

Date 5/11

♂	♂ ♂ beaten
1	10(2)
3	6(4)
8	1 6 7 10(2)

Date 6/11

♂	♂ ♂ beaten
2	7
4	1(2) 6(4)

Date 7/11

♂	♂ ♂ beaten
1	6(2)
4	1(3) 6 10(2)
8	6 10

Date 8/11

♂	♂ ♂ beaten
4	6(3)
8	6(2) 7(2)

Date 11/11

♂	♂ ♂ beaten
1	5 6(2) 7(3) 9 10
2	6(2) 7(2) 9(4)
3	7
4	5(2) 6
8	6
9	2 6 7
10	7

Date 12/11

♂	♂ ♂ beaten
1	5(3)
2	5(2)
3	5(3)
4	5
7	5
8	5(4) 6 7 9

T3 MALES

Date 6/5

♂	♂ ♂ beaten
2	1 6(2) 8(2) 9(2) 10
3	1(3) 6(2) 8(3)
5	1 2(4) 6(2) 7 8(2)
7	6
10	6 8

Date 9/5

♂	♂ ♂ beaten
2	8(2)
3	6 7(3)
4	7(2) 9
5	2(2) 3 6(2) 7 8(3) 10

Appendix 3.2 continued

Date 10/5

♂ ♂ ♂	beaten
3	7

Date 11/5

♂ ♂ ♂	beaten
2	1 3 6 7(2) 8(2) 9
3	1 7
4	3(3) 9(2)
5	1 2(5) 7(5) 8(4)
7	8 9

Date 12/5

♂ ♂ ♂	beaten
2	8(2) 9(3) 10
4	8(2)
5	1 9(2)
7	1 9

Date 15/5

♂ ♂ ♂	beaten
2	7(3) 10
3	10
4	10
5	2 9(2)

Date 16/5

♂ ♂ ♂	beaten
2	1 3(5) 8 9(2)
4	1(3) 2 3(6) 8 10
5	1 2(2) 3(2) 7(5) 8 9(3)
7	2(4) 3(2)

Date 20/5

♂ ♂ ♂	beaten
4	1
5	1(2) 3 10(2)
8	1 6

Date 21/5

♂ ♂ ♂	beaten
1	8
2	9(2)
4	8
5	1 3 6(2)
7	8 9

Date 26/5

♂ ♂ ♂	beaten
2	10
4	7(2) 8 10
5	1(2) 9(2)
7	1 2 9

Date 5/6

♂ ♂ ♂	beaten
2	1 8
3	8 9
4	9
6	1(3) 2(4) 7
7	1

Date 7/6

♂ ♂ ♂	beaten
1	5
2	3 5(4) 9(2)
6	1(2) 2(3) 3(7) 9(5)
7	5
10	3

Date 8/6

♂ ♂ ♂	beaten
1	3
4	8
6	3(2) 8
10	3 9(7)

Date 9/6

♂ ♂ ♂	beaten
1	3(2) 6 8(7) 9
2	8
6	3 8(4) 9
7	9

D

Date 10/6

♂ ♂ ♂	beaten
1	3 5 8(5) 9(2)
2	6(2) 7(7) 8
3	8(3)
4	8(4) 9(2) 10
6	7 8(6) 9(3)
10	5(2) 7(3)

Date 11/6

♂ ♂ ♂	beaten
2	1(3) 3(3) 5 6(5) 7 8(3) 9(3)
3	1(2) 5 6 8 9
6	8
10	5

Appendix 3.2 continued

Date 12/6

♂ ♂ ♂ beaten

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

Date 16/6

♂ ♂ ♂ beaten

1 5 9 10
2 1 5 6(5) 8(2) 9(3)
10 8(5)

Date 18/6

♂ ♂ ♂ beaten

1 5 6(2) 8 10
2 1(3) 5 6 8
8 5
10 6 7 8 9(2)

APPENDIX 4.1

The total time spent active in hours and minutes during the two main bouts of activity occurring (1) after lights off and before mid-cycle and (2) after mid-cycle and before lights on.

Male	First Peak	Second Peak	Male	First Peak	Second Peak	Male	First Peak	Second Peak
1	34	5	2	52	None	3	75	4
	30	6		214			168	30
	25	12		154			168	41
Total	89	23	Total	420		Total	311	75
Mean	29.6	7.6	Mean	140		Mean	103	15

Male	First Peak	Second Peak	Malec	First Peak	Second Peak	Male	First Peak	Second Peak
4	80	9	5	19	6	6	57	10
	138	20		20	12		40	26
	90	62		41	10		41	18
Total	308	91	Total	80	28	Total	138	54
Mean	102	30.3	Mean	26.6	9.3	Mean	46	18

Male	First Peak	Second Peak	Male	First Peak	Second Peak	Male	First Peak	Second Peak
7	174	32	8	12	5	9	451	77
	136	40		17	5		325	83
	180	60		15	2		348	86
Total	490	132	Total	44	12	Total	1124	246
Mean	163	44	Mean	14.6	4	Mean	374	82

Male	First Peak	Second Peak	Male	First Peak	Second Peak	Male	First Peak	Second Peak
10	57	19	11	236	20	12	165	0
	4	13		226	101		188	20
	4	2		138	18		210	5
Total	65	34	Total	600	139	Total	563	25
Mean	21.6	11.3	Mean	200	46.3	Mean	187	8.3

APPENDIX 4.1 continued

Male	First Peak	Second Peak	Male	First Peak	Second Peak	Male	First Peak	Second Peak
13	100	92	14	48	30	15	72	22
	220	-		52	30		48	24
	108	92		16	12		36	4
Total	428	184	Total	116	72	Total	156	50
Mean	142	61	Mean	38.6	24	Mean	52	166

Male	First Peak	Second Peak	Male	First Peak	Second Peak	Male	First Peak	Second Peak
16	36	4	17	30	6			
	660	0		8	0			
	48	0		4	0			
Total	144	4	Total	42	6			
Mean	48	1.3	Mean	14	2			

APPENDIX 4.2

The total time spent active in T2 and T3 males. Observation periods lasted for one hour and were made twice for each of the twelve hours of darkness. The tables show the total time spent active in each half hour of the hour period. The dark period began at 10.30 a.m. and continued until 10.30 p.m.

T2 Males

Date 30/10 Time 10.30-11.30.

Male	Time (min)	
	0-30	30-60
1	13	13
2	5½	2
3	4½	1½
4	12	8
5	4½	6
6	7	7
7	7½	7
8	½	3½
9	4	0
10	3½	2½

Date 11/11 Time 10.30-11.30.

Male	Time (min.)	
	0-30	30-60
1	3½	5
2	8	0
3	7	1
4	2	1
5	½	1½
6	0	7
7	5	4
8	4½	9½
9	2	½
10	1	½

Date 24/10 Time 11.30-12.30.

Male	Time (min.)	
	0-30	30-60
1	12	3½
2	8	5
3	2½	1
4	11½	8½
5	4½	7½
6	3	10
7	3½	2
8	10	9½
9	1½	5
10	½	0

Date 1/11 Time 11.30-12.30.

Male	Time (min.)	
	0-30	30-60
1	0	1½
2	0	0
3	3½	7
4	5	½
5	5½	13½
6	7½	5
7	½	2½
8	16½	13½
9	14	3½
10	½	2

Appendix 4.2 continued.

Date 10/11 Time 12.30-1.30

Male	Time (min.)	
	0-30	30-60
1	0	0
2	1	0
3	½	0
4	3	0
5	0	0
6	4	16
7	0	0
8	0	0
9	½	0
10	20½	0

Date 12/11 Time 12.30-1.30.

Male	Time (min.)	
	0-30	30-60
1	½	2
2	0	6½
3	3	1½
4	2	½
5	15	26
6	1½	6½
7	0	3½
8	3	6½
9	0	7½
10	0	3½

Date 2/11 Time 1.30-2.30

Male	Time (min.)	
	0-30	30-60
1	½	0
2	½	½
3	0	4
4	0	1½
5	3½	15½
6	2½	6
7	3½	5
8	11½	5½
9	5	15½
10	½	1

Date 4/11 Time 1.30-2.30.

Male	Time (min.)	
	0-30	30-60
1	0	1½
2	0	2
3	0	0
4	0	0
5	0	0
6	0	0
7	½	5½
8	60	49
9	½	4
10	0	0

Date 31/10 Time 2.30-3.30

Male	Time (min.)	
1	0-30	30-60
1	0	0
2	½	1
3	1½	0
4	1½	2½
5	1	½
6	0	½
7	0	0
8	0	½
9	6	4½
10	0	0

Date 6/11 Time 2.30-3.30.

Male	Time (min.)	
	0-30	30-60
1	0	½
2	1	6
3	1½	0
4	1½	2½
5	0	0
6	10½	13½
7	0	1
8	0	½
9	2	4½
10	0	1

Appendix 4.2 continued

Date 8/11 Time 3.30-4.30.

Male	Time (min.)	
	0-30	30-60
1	0	0
2	0	½
3	0	0
4	2	½
5	0	0
6	10	32
7	4½	4½
8	13½	1
9	1½	2½
10	0	0

Date 11/11 Time 3.30-4.30.

Male	Time (min.)	
	0-30	30-60
1	0	4
2	1½	2
3	½	½
4	0	6½
1½	1½	8½
6	1½	13½
7	0	7
8	0	0
9	3	4½
10	1½	10

Date 5/11 Time 4.30-5.30

Male	Time (min.)	
	0-30	30-60
1	5	3
2	2	0
3	6	½
4	0	0
5	0	0
6	38½	34
7	0	1
8	1	5½
9	½	3
10	1	2½

Date 7/11 Time 4.30-5.30.

Male	Time (min.)	
	0-30	30-60
1	0	6½
2	½	1
3	½	1
4	0	8
5	0	0
6	24½	32½
7	0	0
8	4	11½
9	2½	7
10	1½	19

Date 1/11 Time 5.30-6.30

Male	Time (min.)	
	0-30	30-60
1	0	0
2	½	2½
3	0	1½
4	1½	6
5	4½	1
6	2½	½
7	½	2
8	5½	2
9	5	4
10	0	1

Date 6/11 Time 5.30-6.30

Male	Time (min.)	
	0-30	30-60
1	0	5½
2	0	0
3	0	0
4	2	9
5	0	0
6	1½	0
7	0	0
8	1½	0
9	0	0
10	0	0

Appendix 4.2 continued

Date 31/10 Time 6.30-7.30

Male	Time (min.) 0-30	30-60
1	0	½
2	0	1½
3	0	0
4	½	1½
5	4	4
6	2½	2½
7	1	2
8	0	½
9	18	20
10	½	1

Date 11/11 Time 6.30-7.30

Male	Time (min.) 0-30	30-60
1	0	2½
2	2	9
3	½	1
4	1½	0
5	1½	2
6	0	1
7	0	0
8	0	½
9	1	2½
10	0	0

Date 17/10 Time 7.30-8.30

Male	Time (min.) 0-30	30-60
1	6½	2½
2	3½	½
3	4½	½
4	5½	1
5	0	0
6	½	6
7	1	9
8	5½	6
9	5	7
10	1	½

Date 22/10 Time 7.30-8.30

Male	Time (min.) 0-30	30-60
1	0	½
2	0	1½
3	0	0
4	½	1½
5	4	4
6	2½	2½
7	1	2
8	0	½
9	18	20
10	½	1

Date 14/10 Time 10.30-9.30

Male	Time (min.) 0-30	30-60
1	7	0
2	1	0
3	4	0
4	4	2
5	0	2
6	7	8
7	0	0
8	0	0
9	2	1
10	0	13

Date 29/10 Time 8.30-9.30

Male	Time (min.) 0-30	30-60
1	2½	1
2	0	½
3	1½	½
4	0	½
5	4	½
6	1½	2
7	0	0
8	4	4½
9	1½	2½
10	4½	19

Appendix 4.2 continued

Date 15/10 Time 9.30-10-30

Male	Time (min.) 0-30	30-60
1	1	4
2	½	3½
3	½	7
4	15½	10½
5	0	3
6	3	9½
7	5	20½
8	0	0
9	0	9
10	2	1½

Date 11/11 Time 9.30-10-30.

Male	Time (min.) 0-30	30-60
1	1	2
2	10½	2½
3	0	½
4	0	0
5	9½	0
6	1	3
7	8½	2
8	0	2½
9	2½	8
10	0	½

T3 MALES

Date 16/5 Time 10.30-11.30

Male	Time (min.) 0-30	30-60
1	14	11
2	23½	2
3	8	4
4	17½	9½
5	17½	14
6	1	0
7	10½	14
8	4	½
9	3½	6½
10	4½	2½

Date 10/6 Time 10.30-11.30

Male	Time (min.) 0-30	30-60
1	9½	5
2	31	½
3	14	0
4	3	½
5	9	0
6	16	2
7	1½	0
8	4½	0
9	11	0
10	10	0

Date 10/5 Time 11.30-12.30

Male	Time (min.) 0-30	30-60
1	0	0
2	0	0
3	1½	½
4	1	0
5	0	0
6	1½	1
7	1	0
8	0	0
9	1½	0
10	0	0

Date 5/6 Time 11.30-12.30

Male	Time (min.) 0-30	30-60
1	2	2½
2	6½	3½
3	18	2½
4	4	0
5	0	0
6	9	5
7	0	1
8	1½	2½
9	6	2
10	1	4½

Appendix 4.2 continued

Date 20/5 Time 12.30-1.30

Male	Time (min) 0-30	30-60
1	5½	6½
2	1	4
3	4	1
4	3	0
5	10	5
6	1	1
7	½	0
8	1	3
9	0	0
10	0	0

Date 15/5 Time 1.30-2.30

Male	Time (min.) 0-30	30-60
1	0	7
2	1	3
3	½	2½
4	3	0
5	½	6
6	1	1½
7	0	4
8	0	0
9	0	½
10	1½	1

Date 26/5 Time 2.30-3.30

Male	Time (min.) 0-30	30-60
1	28½	12
2	4	2
3	8	0
4	4	2½
5	9½	5
6	6	2½
7	16	5
8	24	21½
9	3½	3
10	3½	4½

Date 7/6 Time 12.30-1.30

Male	Time (min.) 0-30	30-60
1	3	8½
2	9½	3
3	12½	2
4	½	0
5	1	11
6	22½	7
7	0	1
8	1½	2½
9	6	2
10	1	4½

Date 13/6 Time 1.30-2.30

Male	Time (min.) 0-30	30-60
1	3	½
2	26	15
3	1	0
4	0	1
5	3½	2½
6	6	4½
7	6	0
8	4½	1½
9	5½	1½
10	12½	18

Date 9/6 Time 2.30-3.30

Male	Time (min.) 0-30	30-60
1	4½	2
2	0	0
3	4	0
4	½	0
5	1	0
6	9	1
7	0	0
8	3	½
9	3	0
10	25	3

Date 9/5 Time 3.30-4.30

Male	Time (min.) 0-30	30-60
1	1	1
2	3½	½
3	1½	5
4	0	6½
5	5	18½
6	13	19
7	7½	9½
8	2½	8½
9	0	5½
10	7	4½

Date 10/6 Time 3.30-4.30

Male	Time (min.) 0-30	30-60
1	7½	4
2	3	½
3	½	1½
4	0	1½
5	4½	0
6	21	9½
7	0	0
8	2½	2
9	0	1
10	17½	4

Date 6/5 Time 4.30-5.30

Male	Time (min.) 0-30	30-60
1	4½	6½
2	8	11
3	5	2
4	0	0
5	10½	7½
6	28	29½
7	0	3½
8	25½	33½
9	3	2
10	3½	2

Date 26/5 Time 4.30-5.30

Male	Time (min.) 0-30	30-60
1	0	4
2	½	4½
3	0	2½
4	0	3½
5	1½	2½
6	5	7
7	½	8
8	12	2½
9	6	3½
10	0	4½

Date 11/5 Time 5.30-6.30

Male	Time (min.) 0-30	30-60
1	4	4½
2	9	7½
3	10½	4½
4	6	3½
5	6	9½
6	4½	2
7	7½	6
8	6½	7½
9	7½	12½
10	½	2

Date 9/6 Time 5.30-6.30

Male	Time (min.) 0-30	30-60
1	3½	16½
2	0	3
3	0	3
4	0	0
5	½	1
6	9½	3½
7	0	3
8	2½	7
9	5	10
10	3½	8½

Appendix 4.2 continued

Date 21/5 Time 6.30-7.30

Malec	Time (min.) 0-30	Time (min.) 30-60
1	3	9½
2	2	1½
3	4½	6
4	½	0
5	5	½
6	22½	½
7	2½	½
8	14	3½
9	1	9½
10	4	5½

Date 10/6 Time 6.30-7.30

Male	Time (min.) 0-30	Time (min.) 30-60
1	12	0
2	11	3½
3	5½	½
4	4½	1½
5	1½	1
6	16½	5½
7	32½	10½
8	5½	0
9	15	1½
10	14	3

Date 5/6 Time 7.30-8.30

Male	Time (min.) 0-30	Time (min.) 30-60
1	0	0
2	0	0
3	½	1½
4	1	½
5	½	0
6	½	0
7	0	0
8	0	0
9	1	0
10	0	½

Date 16/6 Time 7.30-8.30

Male	Time (min.) 0-30	Time (min.) 30-60
1	4	6
2	7½	22
3	0	0
4	0	1½
5	½	3
6	1½	10
7	0	0
8	2	7½
9	1	5
10	18	10

Date 6/6 Time 8.30-9.30

Male	Time (min.) 0-30	Time (min.) 30-60
1	½	0
2	0	0
3	0	½
4	2½	6
5	½	3
6	½	0
7	0	8
8	0	0
9	0	1
10	0	5½

Date 18/6 Time 8.30-9.30

Male	Time (min.) 0-30	Time (min.) 30-60
1	5½	4½
2	4	9
3	0	0
4	0	0
5	2	2
6	3	1½
7	1	0
8	8½	3
9	3½	1
10	6	16½

Appendix 4.2 continued

Date 12/5 Time 9.30-10.30.

Male	Time (min.)	
	0-30	30-60
1	2½	½
2	6½	4½
3	0	0
4	0	5½
5	4	1
6	0	0
7	6½	2
8	0	2½
9	5	3
10	0	4

Date 10/6 Time 9.30-1030

Male	Time (min.)	
	0-30	30-60
1	9½	0
2	31	½
3	14	0
4	3	½
5	9	0
6	16	2
7	1½	0
8	4½	17
9	11	0
10	10	0

APPENDIX 4.3

The duration of eating in minutes for each half hour of the twelve-hour dark period in T2 and T3 males. Two observations were made for each half hour. In the tables the half hours are numbered 1 - 24.

		1	2	3	4	5	6	7	8	9	10	11	12
T2	1	¾	½	0	0	0	0	0	½	¼	0	0	0
	2	0	¼	0	2½	9½	0	0	0	0	0	0	14
T3	1	¾	0	0	0	¼	½	0	5	0	16	0	0
	2	1½	¾	4½	6¼	10¼	½	0	13	¼	34½	0	14

		13	14	15	16	17	18	19	20	21	22	23	24
T2	1	¼	0	0	0	0	0	0	7	0	0	0	0
	2	0	¼	4½	12½	0	0	¼	0	¼	2¾	0	0
T3	1	2¼	0	0	12	½	0	1½	0	0	0	4½	3½
	2	0	½	0	13½	3¼	0	0	2½	6½	15	8½	0

The duration of drinking in minutes for each half hour of the twelve hour dark period in T2 and T3 males. Two observations were made for each half hour. In the tables the half hours are numbered 1 - 24.

		1	2	3	4	5	6	7	8	9	10	11	12
T2	1	¾	0	0	0	0	0	0	0	¼	0	0	0
	2	1¼	0	0	1⅔	0	0	0	0	0	0	0	0
T3	1	1	0	0	0	0	0	0	½	1	0	0	0
	2	0	1½	0	0	0	0	0	0	0	¼	0	½

		13	14	15	16	17	18	19	20	21	22	23	24
T2	1	¾	0	0	¼	0	0	0	0	0	0	0	0
	2	½	0	0	0	0	0	0	0	15	¾	0	0
T3	1	0	0	¼	¼	0	0	0	0	0	0	½	0
	2	0	0	¼	0	0	0	0	¼	0	0	0	0

APPENDIX 5.1

Introduction

When males and females are housed in the same container the females tend to clump together in a group while the males spread out and take up territories. On the whole females appear to be rather inactive though sometimes one or two may be seen moving among the territorial males. It seemed possible that receptive females might be more active than pregnant females and to test this hypothesis I measured the activity of females throughout the reproductive cycle and also compared the activity of mated and unmated females.

Materials and methods

One day old adult females were placed in running wheels and were provided with food and water. (The wheels were those used to measure activity of males, Chapter Four). Activity was recorded on a tally counter and six digits were clocked up for each turn of the wheel. After seven days a male was introduced into the running wheel and the female was either courted for five minutes or mated. The male was removed immediately after the five minute period or after copulation. Mated females were left in the running wheel until just before the young were expected or for about forty two days in the case of unmated insects. One of the main difficulties encountered was that many animals escaped.

Also several females were removed rather too soon before the young were born. Only records which were complete up to thirty days were used. There were thirteen females in each group.

Results

(a) Mated females

In all cases activity was high over the receptive period (day three until mating) and in half of the animals there was an increase in activity over this period. Not all females exhibited the same pattern of activity after mating but it was characteristic of all animals except one that activity dropped to a low level at some point before the young were born. Two patterns of activity predominated; either activity fell off soon after mating and gradually declined to a low level, or activity remained more or less constant and dropped off rather abruptly three weeks after mating. In three cases a marked rise in activity was observed before the young were born. The data from which these results were obtained are shown in Tables 1 and 2. The tables show the mean tally counter scores for every three days that the animals were in the wheels.

(b) Unmated females.

In all cases activity was high over the receptive period and in ten out of the thirteen cases there was an increase in activity over this period. As with the mated females not all animals showed the same pattern of activity after courtship. Three patterns were seen. The most common of these was a cyclic rise and fall of activity with 18 - 21 days between the peaks of activity. In most cases the second activity peak was as high or higher than the first peak but in a few cases it was apparent that the overall activity was falling off. In two cases no cycle of activity was evident and activity was more or less constant. Overall activity in unmated females was higher than in the mated animals. The data from which these results were obtained are shown in Tables 3, 4, and 5. The tables show the mean tally counter scores for every three days that the animals were in the wheels.

Conclusions

Virgin females are active over the receptive period and in most cases activity increases slightly over this period. If females are mated on the seventh day activity either begins to decline immediately or drops off by the third week after mating. All mated females except one became inactive during pregnancy. In females which have been courted by a male but not mated, activity continues to rise after the encounter with the male, drops off slightly and rises again to a peak some eighteen days after the first peak.

If the behaviour of females in activity wheels can be applied to the behaviour of females in the observation tank then receptive females would be more active than pregnant females and might therefore leave the female group to seek out the territorial males. From the behaviour of females in the activity wheels one would also predict that unmated females would remain active.

TABLE 1 Mated females showing a decline in activity after mating on day seven. The tables show the mean tally counter score for every three days that the animals were in the activity wheel.

Wheel 3

Days	Mean
1 - 3	2391.0
4 - 6	3774.0
7 - 9	1224.0
10 - 12	703.6
13 - 15	145.3
16 - 18	301.0
19 - 21	400.0
22 - 24	1094.0
25 - 27	489.3
28 - 30	192.6
31 - 33	86.3

Wheel 4

Days	Mean
1 - 3	1322.0
4 - 6	2936.0
7 - 9	2140.0
10 - 12	47.3
13 - 15	12.6
16 - 18	8.0
19 - 21	8.3
22 - 24	7.3
25 - 27	5.0
28 - 30	9.0
31- 33	7.0

Wheel 11

Days	Mean
1 - 3	1917.6
4 - 6	1533.6
7 - 9	4129.6
10 - 12	3409.3
13 - 15	3506.0
16 - 18	1360.0
19 - 22	787.6
23 - 24	1988.3
25 - 27	1012.6
28 - 30	749.6
31 - 33	909.6
34 - 36	251.0
37 - 39	62.0
40 -	0.0

Wheel 12

Days	Mean
1 - 3	5943.0
4 - 6	4047.0
7 - 9	1110.6
10 - 12	1517.0
13 - 15	204.6
16 - 18	3.6
19 - 21	1.6
22 - 24	40.6
25 - 27	3.0
28 - 30	1.6
31 - 33	3.6

Table 1 continued

Wheel 10

Day	Mean
1 - 3	1841.0
4 - 6	1324.0
7 - 9	1256.3
10 - 12	513.0
13 - 15	109.0
16 - 18	24.6
19 - 21	47.0
22 - 24	123.6
25 - 27	64.0
28 - 30	50.6
31 - 33	16.6

Wheel 10

Day	Mean
1 - 3	2971.0
4 - 6	912.6
7 - 9	2880.6
10 - 12	1321.3
13 - 15	159.6
16 - 18	95.3
19 - 21	154.0
22 - 24	285.0
25 - 27	310.0
28 - 30	38.6
31 - 33	210.3
34 - 36	145.3
37 - 39	45.6
40 -	266.0

Wheel 18

Day	Mean
1 - 3	4121.6
4 - 6	2564.3
7 - 9	6974.0
10 - 12	3355,0
13 - 15	467.6
16 - 18	37.3
19 - 21	239.6
22 - 24	32.3
25 - 27	4.0
28 - 30	1.6

Wheel 20

Day	Mean
1 - 3	4617.3
4 - 6	3018.3
7 - 9	2975.6
10 - 12	4799.3
13 - 15	4276.6
16 - 18	31.3
19 - 21	59.0
22 - 24	42.5
25 - 27	63.3
28 - 30	186.3
31 - 33	12.6
34 - 36	8.6
37 - 39	0.0

Wheel 9

Day	Mean
1 - 3	4369.0
4 - 6	2382.3
7 - 9	1295.6
10 - 12	4943.6
13 - 15	183.0
16 - 18	1444.6
19 - 21	1927.6
22 - 24	270.6
25 - 27	501.6
28 - 30	501.6
31 - 33	653.3
34 - 36	4.3
37 - 39	0.0
40 - 42	4.0
43 - 45	0.3

Wheel 5

Day	Mean
1 - 3	3669.0
4 - 6	3236.3
7 - 9	4799.3
10 - 12	6803.3
13 - 15	4917.6
16 - 18	2254.6
19 - 21	3210.6
22 - 24	3294.6
25 - 27	3119.3
28 - 30	0.0
31 - 33	3.3
34 -	2.0

TABLE 2 Mated females showing a decline in activity soon after mating on day seven and also showing a rise in activity before parturition.

Wheel 4

Day	Mean
1 - 3	1917.0
4 - 6	897.6
7 - 9	3042.6
10 - 12	1549.6
13 - 15	3031.6
16 - 18	3047.6
19 - 21	1598.3
22 - 24	1360.0
25 - 27	2245.3
28 - 30	999.3
31 - 33	556.6
34 - 36	453.0
37 - 39	1505.0
40 - 42	4511.0

Wheel 13

Day	Mean
1 - 3	3559.3
4 - 6	7458.0
7 - 9	5526.0
10 - 12	3046.0
13 - 15	158.6
16 - 18	2.0
19 - 21	18.6
22 - 24	3.0
25 - 27	85.6
28 - 30	3045.0

Wheel 18

Day	Mean
1 - 3	1834.3
4 - 6	3221.6
7 - 9	2283.6
10 - 12	1058.3
13 - 15	352.3
16 - 18	783.0
19 - 21	277.3
22 - 24	40.0
25 - 27	29.6
28 - 30	43.6
31 - 33	31.0
34 - 36	47.0
37 - 39	255.6
40 - 42	3688.0

TABLE 3. Unmated females showing a cycle of activity with 18 - 21 days between peaks of activity. In these females the second peak was as high or higher than the first.

Wheel 4

Days	Mean
1 - 3	2010.3
4 - 6	1219.0
7 - 9	475.0
10 - 12	326.6
13 - 15	320.0
16 - 18	301.0
19 - 21	126.3
22 - 24	82.3
25 - 27	1.3
28 - 30	50.6
31 - 33	121.0
34 - 36	239.6
37 - 39	189.3
40 -	129.0

Wheel 3

Days	Mean
1 - 3	369.6
4 - 6	395.0
7 - 9	1348.6
10 - 12	2259.6
13 - 15	2055.3
16 - 18	2413.0
19 - 21	1173.6
22 - 24	68.0
25 - 27	3598.6
28 - 30	1529.0
31 - 33	1417.3
34 - 36	740.3
37 - 39	632.3
40 -	389.0

Wheel 3

Days	Mean
1 - 3	4517.0
4 - 6	3311.3
7 - 9	3755.0
10 - 12	3002.0
13 - 15	1971.3
16 - 18	3670.0
19 - 21	3313.3
22 - 24	365.0
25 - 27	2763.0
28 - 30	5988.6
31 - 33	5590.6
34 - 36	3942.3
37 - 39	2755.0
40 - 42	4941.0

Wheel 8

Days	Mean
1 - 3	3920.3
4 - 6	4444.6
7 - 9	7919.3
10 - 12	3547.3
13 - 15	14105.3
16 - 18	10749.0
19 - 21	3702.3
22 - 24	3298.3
25 - 27	1209.0
28 - 30	154.3
31 - 33	1321.6

Table 3 continued

Wheel 8

Days	Mean
1 - 3	3064.6
4 - 6	4286.3
7 - 9	3951.3
10 - 12	4860.3
13 - 15	7000.6
16 - 18	2876.6
19 - 21	61.0
22 - 24	71.3
25 - 27	53.0
28 - 30	1657.0
31 - 33	2156.0
34 - 36	2062.0
37 - 39	232.3
40 - 42	547.0

Wheel 8

Days	Mean
1 - 3	4236.0
4 - 6	5019.3
7 - 9	11633.6
10 - 12	21153.0
13 - 15	19014.6
16 - 18	15459.0
19 - 21	4909.0
22 - 24	2611.3
25 - 27	1816.3
28 - 30	5835.0
31 - 33	9515.3
34 - 36	4146.3
37 - 39	3658.6
40 -	1766.0

Wheel 11

Days	Mean
1 - 3	2042.3
4 - 6	3005.6
7 - 9	1960.3
10 - 12	3401.6
13 - 15	3134.0
16 - 18	2080.3
19 - 21	3018.0
22 - 24	3162.6
25 - 27	1414.0
28 - 30	254.3
31 - 33	540.3
34 - 36	10.3
37 - 39	308.0
40 - 42	496.6
43 -	2380.0

TABLE 4. Unmated females showing a cycle of activity of 18 - 21 days and an overall decline in activity.

Wheel 2

Days	Mean
1 - 3	93.6
4 - 6	67.6
7 - 9	559.3
10 - 12	1118.3
13 - 15	1874.3
16 - 18	2167.0
19 - 21	3115.3
22 - 24	575.3
25 - 27	13.0
28 - 30	11.3
31 - 33	0.6
34 - 36	1.6
37 - 39	1.6
40 - 42	27.6
42 - 45	16.0

Wheel 10

Days	Mean
1 - 3	861.6
4 - 6	4251.3
7 - 9	5009.0
10 - 12	11262.6
11 - 15	9860.0
16 - 18	2254.0
19 - 21	2071.6
22 - 24	484.0
25 - 27	33.0
28 - 30	98.0
31 - 33	876.3
34 - 36	45.3
37 - 39	896.3
40 - 42	645.0

Wheel 11

Days	Mean
1 - 3	1103.0
4 - 6	1539.5
7 - 9	3102.3
10 - 12	2404.6
13 - 15	3977.6
16 - 18	6501.0
19 - 21	3968.0
22 - 24	328.6
25 - 27	146.6
28 - 30	32.3
31 - 33	49.0
34 - 36	80.3
37 - 39	39.0

Wheel 18

Days	Mean
1 - 3	1636.3
4 - 6	1089.0
7 - 9	8135.6
10 - 12	9689.3
13 - 15	12568.6
16 - 18	5236.0
19 - 21	3467.6
22 - 24	1907.6
25 - 27	16.3
28 - 30	14.0
31 - 33	25.6
34 - 36	2.6
37 - 39	12.6
40 -	0.0

TABLE 5. Unmated females showing more or less constant activity.

Wheel 1

Day	Mean
1 - 3	1503.3
4 - 6	1707.6
7 - 9	1370.3
10 - 12	1140.3
13 - 15	3045.0
16 - 18	2531.3
19 - 21	3683.6
22 - 24	1885.6
25 - 27	2285.0
28 - 30	1036.3
31 - 33	368.3
34 - 36	1552.6
37 - 39	3093.3
40 - 42	3984·0

Wheel 19

Day	Mean
1 - 3	1452.3
4 - 6	971.3
7 - 9	3363.0
10 - 12	2197.6
13 - 15	848.3
16 - 18	1123.3
19 - 21	1879.0
22 - 24	1948.0
25 - 27	1643.0
28 - 30	2694.6
31 - 33	2662.6
34 - 36	1570.3
37 - 39	2308.0
40 -	c706.0

APPENDIX 5.2

Record of attacks in T10a males.

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

Day 8

♂	♂ ♂ beaten
1	3
3	7 8
4	3 10
5	1 3
9	1

Day 9

♂	♂ ♂ beaten
4	7 10
5	3 7
9	1 3 5 6 7 8
10	8

Day 13

♂	♂ ♂ beaten
2	7 10
4	1 6 10
5	3
9	2 6 7 10

Day 16

♂	♂ ♂ beaten
2	1 3 7 10
4	1 3 6 7 9 10
5	2 7 10
9	2 3 7

Day 18

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

Day 20

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

Day 26

o	o o beaten

R Record of attacks in T10b males

♂	♂ ♂ beaten
2	1
4	2 3 6 7 8

Day 1

♂	♂ ♂ beaten
1	6
3	2 5 7
4	3 5

Day 2

♂	♂ ♂ beaten
3	7 8
4	1 2 8

Day 5

♂	♂ ♂ beaten
4	1 2 6 7 8 10

Day 7

♂	♂ ♂ beaten
3	8
4	2 3 6 7 9 10

Day 8

♂	♂ ♂ beaten
4	3 5 7

Day 9

Appendix 5.2 continued

♂	♂ ♂ beaten
3	9
4	5 6 7 8 9
5	3

Day 12

♂	♂ ♂ beaten
3	1 7

Day 13

♂	♂ ♂ beaten
2	1
4	7
9	2
10	5

Day 17

♂	♂ ♂ beaten
3	1 8
4	1 2 6 7 10

Day 18

♂	♂ ♂ beaten
2	8 10
3	1 7 8
4	1 2 5 6 7 8
5	10

Day 19

Record of attacks in T20a males

♂	♂ ♂ beaten
1	2 4 17
2	9
7	1 2 3 5 9
8	2 4 5 9 19
20	9

Day 6

♂	♂ ♂ beaten
1	3 5 9
7	3 4 5
8	3 5 9

Day 7

♂	♂ ♂ beaten
7	9
8	1 3 4 5 9

Day 10

♂	♂ ♂ beaten
3	1 5 6 9 14 15 16
7	9 16
8	3 4 9
14	1 4 9

Day 11

♂	♂ ♂ beaten
1	13 18
2	11
3	9
4	1 2 3 9 11 15 17
6	1
7	4 9 11 17
8	5
12	2 11 15
14	17

Day 13

♂	♂ ♂ beaten
3	2
4	1
6	15
7	2 9 10 15 16 20
12	1 9

Day 17

♂	♂ ♂ beaten
1	14
3	9 11
4	17
7	1
12	9 11 17

Day 23

♂	♂ ♂ beaten
2	6
3	9 11 13 14
4	2 9 11 13 16 17
6	4
7	9 11 20

Appendix 5.2 continued

Record of attacks in T20b males

♂	♂ ♂ beaten
2	9 11
4	6 20
7	3 4 8 10 12 13
9	3 5 8 20
11	19
14	19
17	4 10 14
18	3 5 11
20	4 14

Day 3

♂	♂ ♂ beaten
11	9
12	3 19
14	12 20
16	9 15 17

Day 4

♂	♂ ♂ beaten
4	1
5	1
6	7
8	11
8	4
10	1 4 9 17
11	3 7 12
14	1 2 3 6 15 17 19 20
15	12
16	20
17	2
20	6

Day 5

♂	♂ ♂ beaten
5	2 4 7 13 17 19
6	2
8	7 11
9	2 4
11	15
12	2
14	2 4 8 11 12 13 15 20
16	5 8
17	4 15 19
20	10 17

Day 8

♂	♂ ♂ beaten
2	3
3	9
4	10 15
5	13
7	3
10	3 9
11	2 3 4 6 7 9 15
14	13
16	12
18	4 9 17

Day 9

♂	♂ ♂ beaten
3	6 7 20
5	13
7	8
10	2 7 8 19
17	3 4 15 20

Day 13

Appendix 5.2 continued

♂	♂♂ beaten
3	4 6 8 10 11 12 17 19 20
4	19
10	20
11	4
17	7
20	8 11 17 19

Day 14

♂	♂♂ beaten
2	6 7 12 14 15 17 18 20
3	1 2 6 8 12 16 17 18 20
4	14
5	1 4 7 8 11 13 14 15
7	14
10	1 2 4 11 14 18 20
16	12 18
20	18

Day 16

♂	♂♂ beaten
3	2 6 10
4	6 7 10 15 20
5	18 19
16	14

Day 22

♂	♂♂ beaten
2	4
3	1 14
5	1
16	14

Day 28

♂	♂♂ beaten
2	8 13
4	14
5	10 12 13 14
9	4 6 14
13	9
15	7 13
18	3 4 7 9 11 13 15 16

Day 30

APPENDIX 5.3

Positions of T10a males in the tank during the day.

P = platform   0 - 3 = tiers of platform   S = side

o	Day 3	Day 4	Day 7	Day 8	Day 10	Day 11
1	P 2	P 1	P S	P 0	P 2	P 1
2	P 0	P 2	P 2	P 0	P 3	P 2
3	P 2	OUT	P 3	Food S	Food S	P 1
4	P 1	P 2	P 2	P 2	P 1	P 2
5	P 1	P 1	Food	Food	Food	Food
6	P 1	P S	P S	P 0	P 0	P 1
7	P 2	P 3	P 3	P 1	P 2	P 2
8	P 3	P 0	P 1	P 1	OUT	P 1
9	P 0	Food S	P 0	P 3	Water	P S
10	P 3	P 3	P S	P 0	P 0	P S

o	Day 14	Day 15	Day **21**	Day **25**	Day 28	Day 29
1	P S	P 3	P 3	P 3	Food S .	P 2
2	P 2	P 1	P 1	P 1	P 1	P S
3	P 1	P 1	P 3	P 2	P 3	P 1
4	P 2	P 2	P 2	P 1	P 0	P S
5	Food	Food	Food	Food	Food	Food
6	P 1	P S	Water	P 2	P 2	P 0
7	P 2	P 1	Water	P 0	P 0	P 2
8	P 1	P 0	P 2	OUT	P 2	P 0
9	P 0	P 0	P S	Food S	OUT	P 0
10	P 1	P 3	P 1	P 3	Food S	P 1

Positions of T20a males in the tank during the day.   R = Remainder

o	Day 1	o	Day 3	o	Day 5
1	P 3 alone	1	P 2	3	Food
4	P 3 alone	R	P 1	4	P S
5	P 3 alone			5	P S
R	P 2 all touching			R	P 1

Appendix 5.3 continued

Positions of T20a males in the tank during the day   R = Remainder

o	Day 6
5	P 2 alone
7	Food
R	P 1 all touching
R	P 2 all touching

o	Day 7
5	P 3 alone
7	Food
R	P 1 all touching

o	Day 10
1	P 0 alone
2	P 2 alone
5	P 0 alone
7	Food
R	P 2 all touching

o	Day 12
2	Food S
3	P 1 alone
5	P 3 alone
7	Food
8	P 0 alone
4	Water
13	Water
17	Water
R	P 1 all touching

o	Day 17
7	Food
8	P 0 alone
12	Water
15	OUT
R	P 1 all touching

o	Day 21
7	Food
12	Water
15	P 3 alone
R	P 1 all touching

o	Day 24
6	P 1 alone
7	Food
12	Water
16	P 2 alone
17	P 2 alone
R	P 1 spread out

o	Day 26
7	Food
12	Water
14	P 2
R	P 1 all touching

o	Day 28
7	Food
12	Water
R	P 1 all touching

APPENDIX 7.1

Weight change in dominant/subordinate pairs after 21 days.

R = Reversal G = Gain L = Loss

Pair		Initial Weight (gm)	Final Weight (gm)	Percentage Change
1	S	0.4844	0.4363	L 9.9
	D	0.3874	0.5411	G 39.6
2	S	0.4994	0.4880	L 2.2
	D	0.4549	0.4870	G 7.0
3	S	0.4124	0.4369	G 5.9
	D	0.4623	0.5131	G 10.9
4	S	0.4193	0.4153	L 0.9
	D	0.4704	0.5260	G 11.8
5	S	0.5867	0.4864	L 0.0
	D	0.4360	0.4742	G 8.7
6	S	0.3741	0.3308	L 11.5
	D	0.4280	0.4402	G 2.8
7	S	0.4126	0.4639	G 12.5
	D	0.4451	0.5390	G 21.9
8	S	0.3653	0.3794	G 3.8
	D	0.4615	0.4896	G 6.0
9	S	0.4435	0.4418	L 0.3
	D	0.5548	0.6144	G 10.7
10	S	0.4311	0.4612	G 7.0
	D	0.5513	0.5997	G 8.7
11	S	0.4221	0.4247	G 0.6
	D	0.4692	0.5220	G 12.7
12	S	0.3427	0.3427	0.0
	D	0.4497	0.4732	G 5.2
13	S	0.4465	0.4247	L 4.8
	D	0.4459	0.4328	L 2.9
14	S	0.3970	0.3830	L 3.5
	D	0.4081	0.4290	G 5.1

Pair		Initial Weight (gm)	Final Weight (gm)	Percentage Change	
15	S	0.4051	0.4237	G	4.5
	D	0.3911	0.4385	G	12.1
R16	S	0.4656	0.4761	G	2.5
	D	0.4131	0.4290	G	3.8
17	S	0.4329	0.4201	L	2.9
	D	0.3535	0.4367	G	23.5
18	S	0.4012	0.4633	G	15.4
	D	0.3906	0.4715	G	20.2
19	S	0.4430	0.4713	G	6.3
	D	0.4639	0.5353	G	16.3
20	S	0.2972	0.2991	G	0.6
	D	0.3593	0.4718	G	31.3
	S	0.4359	0.4766	G	9.3
	D	0.4777	0.5032	G	5.3

Experiment 1, Control Group 1

Animal	Initial Weight (gm)	Final Weight (gm)	Percentage Change
1	0.4439	0.4869	9.6
2	0.5626	0.5403	3.9
3	0.3735	0.3698	0.9
4	0.3400	0.3633	6.8
5	0.3774	0.4059	7.5
6	0.4750	0.4429	6.3
7	0.4182	0.4761	13.8
8	0.3481	0.3826	9.9
9	0.4440	0.5125	15.4
10	0.4732	0.5708	20.6
11	0.3273	0.3967	21.1
12	0.3936	0.5048	28.2
13	0.4210	0.4094	2.7
14	0.4992	0.5362	7.4
15	0.5207	0.5354	2.8
16	0.3469	0.3611	4.0
17	0.3863	0.4612	19.3
18	0.4072	0.4507	10.6
19	0.4080	0.4082	0.0
20	0.4188	0.5207	26.7
21	0.4783	0.4906	2.5

Appendix 7.1 continued

Weight change in dominant/subordinate pairs weighed weekly for 28 days.

			Percentage Weight Change							
	Pair No.		Week 1		Week 2		Week 3		Week 4	
	1	S	G	2.2	G	12.4	G	16.7	G	12.5
		D	G	15.1	G	18.3	G	29.0	G	21.7
R	2	S	L	3.5	G	3.0	G	9.9	G	17.3
		D	L	2.8	L	4.9	L	4.2	L	10.6
R	3	S	L	4.6	G	7.0	G	8.8	G	23.7
		D	L	5.7	G	13.2	G	18.7	G	0.3
R	4	S	G	5.7	G	5.6	G	4.7	G	28.7
		D	L	1.9	G	4.4	G	4.3	G	3.9
	5	S	G	8.1	G	20.0	G	11.7	G	25.6
		D	G	6.9	G	15.1	G	25.0	G	16.7
	6	S	L	0.9	L	3.8	L	1.1	G	6.3
		D	G	13.4	G	12.2	G	13.4	G	12.1
	7	S	L	8.0	L	12.0	L	11.5	L	4.8
		D	G	6.5	G	12.1	G	16.3	G	21.1
	8	S	G	7.3	G	10.7	G	0.3	L	0.3
		D	G	1.4	G	7.0	G	3.7	G	9.9
	9	S	G	18.4	G	19.4	G	19.4	G	24.8
		D	G	23.4	G	41.0	G	45.3	G	55.0
	10	S	L	2.5	L	6.2	L	8.7	L	9.3
		D	G	15.7	G	9.5	G	20.5	G	20.2
	11	S	G	29.2	G	37.6	G	37.0	G	44.0
		D	G	2.4	G	9.3	G	8.2	G	9.7
R	12	S	G	6.3	G	6.7	G	15.7	G	16.8
		D	G	18.5	G	3.6	G	7.1	G	2.0
	13	S	L	8.2	L	8.2	L	8.7	L	7.0
		D	G	12.4	G	18.3	G	14.3	G	18.2
	14	S	L	0.0	L	10.4	L	7.8	G	4.2
		D	G	9.1	G	11.1	G	8.3	G	8.6
	15	S	G	4.7	G	4.5	G	6.4	G	11.3
		D	L	2.8	L	3.5	G	1.0	G	0.9

Appendix 7.1 continued

Experiment 1, Control Group 2.

Animal	Percentage Weight Change							
	Week 1		Week 2		Week 3		Week 4	
1	G	4.5	G	21.8	G	23.1	G	19.2
2	G	4.8	G	7.2	G	1.4	G	4.4
3	L	1.1	G	4.5	G	5.8	G	10.9
4	G	11.0	G	15.0	G	12.9	G	15.4
5	L	3.3	L	9.0	L	5.5	L	4.0
6	G	0.3	G	16.3	G	18.8	G	11.0
7	G	2.1	L	2.3	G	0.4	G	0.5
8	L	2.3	L	2.7	G	4.0	G	2.1
9	L	3.1	G	4.4	G	1.6	L	7.6
10	L	7.0	L	2.3	G	1.7	G	4.3
11	G	12.7	G	7.4	G	9.4	G	7.6
12	L	4.1	L	2.3	G	8.1	L	1.6
13	L	5.3	L	5.1	L	6.4	L	7.7

APPENDIX 7.2

Percentage water content in dominant/subordinate pairs.

Pair No.		Fresh Weight (gm)	Dry Weight (gm)	Percentage Water Content
1	S	0.4363	0. 091	
	D	0.5411	0. 334	
2	S	0.4880	0.1793	63.29
	D	0.4870	0.1695	71.75
3	S	0.4369	0.1634	62:61
	D	0.5131	0.2143	58.24
4	S	0.4153	0.1415	65.96
	D	0.5260	0.1905	63.81
5	S.	0.4864	0.1678	65.61
	D	0.4742	0.1556	67.00
6	S	0.3308	0.1134	65.74
	D	0.4402	0.1852	57.93
7	S	0.4639	0.1489	67.93
	D	0.5390	0.1999	62.93
8	S	0.3794	0.1207	67.93
	D	0.4896	0.1502	73.15
9	S	0.4418	0.1507	65.65
	D	0.6144	0.2431	60.45
10	S	0.4612	0.1646	64.35
	D	0.5997	0.2227	62.89
11	S	0.4247	0.1621	61.72
	D	0.4732	0.1973	62.22
12	S	0.3427	0.1256	63.37
	D	0.4732	0.1947	58.88
13	S	0.4247	0.1645	61.27
	D	0.4328	0.1516	64.97
14	S	0.3830	0.1358	64.55
	D	0.4290	0.1640	61.80

Appendix 7.2 continued

Pair No.		Fresh Weight (gm)	Dry Weight (gm)	Percentage Water Content
15	S	0.4237	0.1529	64.68
	D	0.4385	0.1549	63.93
16	S	0.4761	0.2098	55.92
	D	0.4290	0.1602	62.69
17	S	0.5329	0.1491	64.52
	D	0.3535	0.1403	72.46
18	S	0.4633	0.1899	59.03
	D	0.4715	0.1869	60.38
19	S	0.4713	0.2030	56.75
	D	0.5353	0.2432	54.58
20	S	0.2972	0.2166	54.11
	D	0.3593	0.1058	64.64
21	S	0.4359	0.1867	67.43
	D	5032	0.1966	60.82

APPENDIX 7.3

Weight change in dominant/subordinate pairs deprived of water or food.

Experiment 3a Group 1 Water deprived males weighed once after pairing and again after 28 days.

Pair No.		Initial Weight (gm)	Final Weight (gm)	Percentage change
1	S	0.4065	0.3534	-13.0
	D	0.4170	0.3626	-13.0
2	S	0.4602	0.3835	-16.6
	D	0.5902	0.5085	-13.8
3	S	0.3786	0.3171	-16.2
	D	0.3610	0.3133	-13.2
4	S	0.4599	0.3196	-30.5
	D	0.4362	0.3657	-16.6
5	S	0.5157	0.4057	-21.3
	D	5143	0.3857	-25.0
6	S	0.4160	0.3585	-13.8
	D	0.5003	0.4132	-17.4
7	S			
	D			
8	S	0.4246	0.3530	-18.7
	D	0.4386	0.3667	-16.3
9	S	0.4389	0.3568	-18.7
	D	0.3098	0.2825	-8.8
10	S	0.4138	0.3499	-15.4
	D	0.4355	0.3670	-15.7
11	S	0.3852	0.2914	-24.3
	D	0.4108	0.3345	-18.5
12	S	0.4685	0.3631	-22.5
	D	0.5008	0.4621	-7.7
13	S	0.4396	0.3441	-21.7
	D	0.3693	0.3212	-13.0
14	S	0.4442	0.3705	-16.5
	D	0.4861	0.3435	-29.3
15	S	0.4252	0.2779	-24.7
	D	0.5486	0.4129	-34.6

Appendix 7.3 continued

Experiment 3a Group II Males deprived of water and weighed every nine days for twenty eight days.

	Pair No.		Percentage Weight Change		
			Week 1	Week 2	Week 3
	1	S	− 0.6	− 1.3	− 9.6
		D	− 8.2	+ 7.5	− 1.5
	2	S	+ 1.4	− 9.1	−21.6
		D	− 1.4	− 7.7	−17.9
	3	S	− 9.6	−12.0	−22.3
		D	− 5.3	− 9.4	−17.5
	4	S	− 3.2	− 7.7	−21.4
		D	+ 6.2	− 0.3	−11.5
	5	S	+ 0.6	− 5.8	−20.6
		D	+11.4	+ 7.7	− 5.9
	6	S	− 8.5	−13.0	−23.5
		D	− 0.3	+ 4.6	− 7.4
	7	S	+14.6	+ 9.4	− 7.7
		D	− 0.7	+ 3.8	−16.2
R	8	S	+ 3.3	−10.1	−22.4
		D	− 1.9	− 2.7	−18.0
	9	S	− 2.4	+ 2.9	−10.4
		D	− 3.2	+ 1.9	−11.9
	10	S	−10.1	−20.5	−27.4
		D	− 7.0	−19.2	−26.2
	11	S	− 8.1	−16.5	−23.4
		D	−10.9	−14.1	−18.7
	12	S	−10.1	−16.3	−20.3
		D	−22.5	−26.4	−29.4
	13	S	− 3.7	−10.1	−15.9
		D	+ 6.7	− 1.6	− 6.9
	14	S	− 6.5	−15.1	−21.5
		D	+ 1.2	− 9.0	−17.2

Appendix 7.3 continued

Experiment 3b, Group 1. Food deprived males weighed once after pairing and again after 28 days.

	Pair No.		Initial Weight (gm)	Final Weight (gm)	Percentage Change
	1	D	0.4042	0.4136	+ 2.3
		S	0.4412	0.4007	- 9.1
	2	D	0.4623	0.4728	+ 4.5
		S	0.4197	0.3844	- 8.4
R	3	S	0.4127	0.3827	- 7.2
		D	0.4299	0.3868	-10.0
	4	D	0.4312	0.4218	- 2.1
		S	0.4263	0.3811	-10.6
	5	S	0.4983	0.4832	- 3.0
		D	0.5196	0.4670	-10.1
	6	D	0.4422	0.5128	+14.4
		S	0.5407	0.4388	-+ 8.8
R	7	D	0.5019	0.4988	- 0.6
		S	0.5227	0.4785	- 8.4
	8	S	0.3916	0.3859	- 1.5
		D	0.5000	0.5233	+ 4.6
	9	S	0.4784	0.4043	-15.4
		D	0.3921	0.3558	- 9.2
R	10	S	0.3966	0.3310	-16.5
		D	0.4576	0.4238	7.3
	11	S	0.4906	0.4397	-10.3
		D	0.4523	0.4640	+ 2.5
	12	S	0.3997	0.4103	+ 2.5
		D	0.4187	0.4083	- 1.3
R	13	D	0.4460	0.4397	- 1.4
		S	0.4567	0.4374	- 4.2
	14	D	0.4321	0.4549	+ 5.2
		S	0.4569	0.4437	- 2.6
	15	D	0.4514	0.4051	-10.2
		S	0.4593	0.4015	-12.5
R	16	D	0.4185	0.3723	-11.0
		S	0.4686	0.4531	- 3.3

Appendix 7.3 continued

Experiment 3b, Group II. Males deprived of food and weighed every nine days for 28 days.

	Pair No.		Percentage Weight Change		
			Week 1	Week 2	Week 3
R	1	S	+ 0.6	− 6.6	− 4.3
		D	+ 8.7	+10.0	− 5.3
	2	S	− 3.9	− 5.5	− 8.6
		D	+ 0.9	+ 1.7	− 0.7
	3	S	− 1.2	+ 6.5	+ 0.0
		D	− 2.4	+12.3	−16.8
R	4	S	− 5.5	−13.0	−10.6
		D	− 5.4	− 0.2	− 6.1
	5	S	+ 0.0	− 4.2	− 8.5
		D	+11.3	+ 3.4	+ 3.3
	6	S	− 7.8	− 6.7	−11.1
		D	− 3.3	− 5.3	− 4.7
	7	S	− 2.6	− 6.6	− 8.2
		D	− 2.2	− 6.1	− 8.1
	8	S	+ 5.5	− 3.0	− 4.1
		D	+15.8	+ 7.8	+ 7.3
R	9	S	− 4.1	+ 6.3	− 2.6
		D	+ 1.1	+ 1.3	−11.9

APPENDIX 7.4

Percentage water content in water deprived pairs after three weeks.

Pair No.		Fresh Weight (gm.)	Dry Weight (gm)	Percent Water
1	D	0.3730	0.1312	64.8
	S	0.3841	0.1471	61.7
2	D	0.3258	0.1280	60.7
	S	0.3920	0.1427	63.6
3	S	0.3493	0.1296	62.9
	D	0.3878	0.1496	61.4
5	D	0.4463	0.1672	62.5
	S	0.4492	0.1780	60.3
6	D	0.4317	0.1775	58.8
	S	0.3279	0.1303	60.2
7	D	0.4806	0.1728	64.0
	S	0.3816	0.1434	62.4
8	D	0.3856	0.1406	63.5
	S	0.4827	0.1836	61.9
9	D	0.2655	0.1014	61.8
	S	0.3309	0.1250	62.2
10	S	0.3304	0.1635	61.1
	D	0.4133	0.1487	64.0

Appendix 7.4 continued

Percentage water content in food deprived pairs after three weeks.

Pair No.		Fresh Weight (gm.)	Dry Weight (gm)	Percent Water
1	S	0.4417	0.1540	65.1
	D	0.3906	0.1372	64.8
3	S	0.3857	0.1422	63.1
	D	0.4100	0.1266	69.1
4	D	0.3627	0.1263	65.1
	S	0.3831	0.1467	61.7
5	D	0.3711	0.2482	66.8
	S	0.4267	0.1200	71.8
6	D	0.4059	0.1145	71.8
	S	0.3437	0.1400	59.2
7	D	0.3915	0.1327	66.1
	S	0.3664	0.1920	69.9
8	D	0.4836	0.1321	72.7
	S	0.4128	0.1111	73.1
9	S	0.3688	0.1657	55.0
	D	0.3843	0.1384	64.0
10	S	0.4672	0.1108	76.3
	D	0.4138	0.1185	71.0
	S	0.3824	0.1144	70.0
	D	0.4005	0.1368	65.8

Appendix 7.4 continued

Percentage water content in water deprived pairs after four weeks.

Pair No.		Fresh Weight (gm.)	Dry Weight (gm.)	Percent Water
1	S	0.3534	0.1376	61.0
	D	03626	0.1292	64.3
2	S	0.3835	0.1624	57.6
	D	0.5085	0.1917	61.4
3	S	0.3171	0.1157	63.5
	D	0.3133	0.1107	64.7
4	S	0.3196	0.1299	59.3
	D	0.3657	0.1397	61.8
5	D	0.3857	0.1398	63.7
	S	0.4957	0.1484	63.4
6	D	0.4132	0.1564	62.1
	S	0.3585	0.1244	65.0
7	D	0.3935	0.1806	60.6
	S	0.3743	0.1311	64.9
8	D	0.3667	0.1279	65.0
	S	0.3568	0.1288	63.0
9	D	0.2825	0.1069	62.1
	S	0.3568	0.1341	63.6
10	D	0.3670	0.1301	64.5
	S	0.3499	0.1304	62.7
11	D	0.3345	0.1376	58.8
	S	0.2914	0.1110	61.9
12	S	0.3631	0.1234	66.0
	D	0.4621	0.1778	61.5
13	S	0.3441	0.1092	68.3
	D	0.3212	0.1234	61.6
14	S	0.3705	0.1332	64.0
	D	0.3435	0.1419	58.7
15	D	0.4129	0.1602	61.2
	S	0.2279	0.1136	59.1

Appendix 7.4 continued

Percentage water content in food deprived pairs after four weeks.

Pair No.		Fresh Weight (gm.)	Dry Weight (gm)	Percent Water
2	D	0.4136	0.1255	69.6
	S	0.4007	0.1227	69.3
3	D	0.4728	0.1390	70.6
	S	0.3844	0.1102	71.3
4	D	0.3827	0.1095	71.4
	S	0.3868	0.1166	69.8
5	D	0.4218	0.1279	69.6
	S	0.3811	0.1182	69.0
6	S	0.4832	0.1522	68.5
	D	0.4670	0.1430	69.3
8	D	0.5128	0.1670	71.3
	S	0.4531	0.1152	74.9
9	D	0.5128	0.1670	71.3
	S	0.4388	0.1430	67.4
10	D	0½4988	0.1518	69.5
	S	0.4775	0.1652	65.4
11	S	0.3859	0.1058	72.6
	D	0.5233	0.1640	68.6
12	S	0.4043	0.1208	70.1
	D	0.3558	0.1068	70.0
13	S	0.3310	0.1183	64.2
	D	0.4238	0.1269	70.0
14	S	0.4397	0.1314	70.1
	D	0.4640	0.1400	69.8
16	S	0.3997	0.1185	70.3
	D	0.4083	0.1275	68.7
17	D	0.4397	0.1326	69.8
	S	0.4374	0.1258	71.2
18	D	0.4549	0.1304	71.3
	S	0.4437	0.1448	67.3
20	D	0.4051	0.1250	69.1
	S	0.4015	0.1246	69.0

APPENDIX 7.5

Merrill et al. (1946) obtained different results for the percentage water content of P. americana. The mean water content was found to be 69.8% and this was determined as the weight of water lost after drying to constant weight in dry air at 105°C. The difference in the results could be due to species differences, to differences in the technique employed or to insufficient desiccation of the insects in the case of Nauphoeta. In order to check that five hours desiccation at 60°C was sufficient to remove all the water from the corpses I weighed ten males after five hours of desiccation in the usual way and then weighed them at hourly intervals until the weights appeared to have reached an equilibrium. I found that more water was lost after five hours and that equilibrium was reached after seven hours. However, the percentage water content was not significantly different from that of my experimental animals. The mean was 64.1%, the range 60.6% - 68.2%. The results are given on the next page.

It is worth commenting that Merrill et al. find that after 18 hours water deprivation weight loss is as much as 12%. Such losses are not observed in Nauphoeta until seven days of deprivation or more.

Appendix 7.5 continued

Fresh Weight (gm.)		0.4904
Dry weight after	5 hrs.	0.1809
	6 hrs.	0.1785
	7 hrs.	0.1772
	8 hrs.	0.1772
Water Content		63.8%

Male No. 1

Fresh Weight (gm.)		0.4758
Dry weight after	5 hrs.	0.1742
	6 hrs.	0.1725
	7 hrs.	0.1720
	8 hrs.	0.1726
Water Content		63.8%

Male No. 2

Fresh Weight (gm.)		0.4284
Dry weight after	5 hrs.	0.1376
	6 hrs.	0.1363
	7 hrs.	0.1360
	8 hrs.	0.1369
Water Content		68.2%

Male No. 3

Fresh Weight (gm.)		0.4805
Dry weight after	5 hrs.	0.1569
	6 hrs.	0.1558
	7 hrs.	0.1556
	8 hrs.	0.1565
Water Content		67.6%

Male No. 4

Fresh Weight (gm.)		0.6243
Dry weight after	5 hrs.	0.2448
	6 hrs.	0.2415
	7 hrs.	0.2405
	8 hrs.	0.2422
Water Content		61.5%

Male No. 5

Fresh Weight (gm.)		0.6108
Dry weight after	5 hrs.	0.2353
	6 hrs.	0.2315
	7 hrs.	0.2304
	8 hrs.	0.2308
Water Content		62·3%

Male No. 6

Fresh Weight (gm.)		0.5502
Dry weight after	5 hrs.	0.2202
	6 hrs.	0.2170
	7 hrs.	0.2167
	8 hrs.	0.2174
Water Content		60.6%

Male No. 7

Fresh Weight (gm.)		0.5632
Dry weight after	5 hrs.	0.2102
	6 hrs.	0.2082
	7 hrs.	0.2078
	8 hrs.	0.2084
Water Content		63.1%

Male No. 8

Appendix 7.5 continued

Fresh Weight (gm.)		0.4775
Dry weight after	5 hrs.	0.1764
	6 hrs.	0.1746
	7 hrs.	0.1743
	8 hrs.	0.1749
Water Content		63.5%

Male No. 9

Fresh Weight (gm.)		0.5079
Dry weight after	5 hrs.	0.1692
	6 hrs.	0.1675
	7 hrs.	0.1676
	8 hrs.	0.1685
Water Content		67.0%

Male No. 10

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10

Fighting and Death from Stress in a Cockroach

Abstract. *Fighting behavior, leading to the establishment of stable dominant-subordinate relationships between pairs of males, is described for the cockroach* Nauphoeta cinerea. *Deaths, which do not appear to be due to external damage, occur in subordinate animals as a result of fighting. The situation is likened to death from stress as found in mammals.*

Intraspecific fighting between males has been described for a number of insects including field crickets (*1*), cicada-killer wasps (*2*), ants where fighting occurs between colonies of the same species (*3*), and for a wood roach where the male defends a mating chamber against rivals (*4*). Although no published records have been found, fighting can be observed commonly between adult males of the cockroach *Nauphoeta cinerea*, where it appears to be associated with a loose territorial system. Fighting, which first appears on the 2nd and 3rd days after the imaginal molt, involves a complex sequence of events that eventually establishes a stable dominant-subordinate relationship between members of a fighting pair.

In an encounter between two more-or-less evenly matched males, a fairly consistent sequence of events can be observed. Both animals, with heads lowered, extend upwards the last three or four abdominal segments, simultaneously lifting the body high off the ground (Fig. 1). This posture may be assumed on sight, when one aggressive male crosses the path of another, or after brief but rapid antennal flagellation (fencing) between the two animals. This posture could be described as aggressive. It always preceeds fighting but may cause a less aggressive male to flee. Following this display, two aggressive animals charge towards each other with their heads lowered and butt on contact. If one cockroach successfully engages its pronotum under that of its opponent, it may toss the rival in the air so that it falls on its back. Less frequently, males may grapple with their legs locked together and bite at each other as they roll over and over. A critical stage is usually reached within a few minutes, and one animal emerges superior.

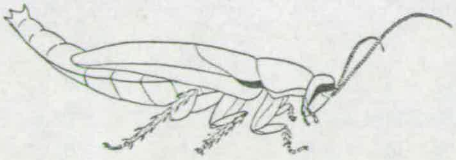

Fig. 1. The aggressive posture.

The behavior of the loser is quite characteristic. After prolonged chasing and tucks its limbs under its body and its head under the shield of the pronotum. The antennae either lie flat on the ground, straight in front of the animal, or, less frequently, pointing backwards, parallel to the body, which is always pressed close to the ground (Fig. 2). Once this posture has been adopted, the subordinate animal no longer attacks the dominant; it runs underneath its superior and adopts the subordinate posture if subjected to attack itself.

It is possible to determine the dominant-subordinate relationship within a pair of males from their response to a test animal, a live adult male attached to a thin balsa-wood stick by means of a wire threaded through the pronotum. Amputation of its tibiae and tarsi restricts the movements of the test animal, thus facilitating manipulation. Antennal contact is allowed between the test animal and the subject, this generally being sufficient to elicit a response. Dominant animals typically adopt the aggressive posture and may attack the test animal, whereas subordinate animals do not respond aggressively and adopt the subordinate posture. Test animals can also be used in the determination of the earliest age at which the fighting response can be elicited in young adult males. Indeed, until fighting has appeared, dominant-subordinate relationships cannot be established.

In the course of experiments to determine the time at which fighting first appears, it was noticed, incidentally, that, over the first few days after the adult molt, the death rate among paired males was rather high. I set up three groups of young adults to see if there was some connection between these deaths and fighting (Table 1).

Table 1. The relationship between fighting and death. Single males, still teneral, were left untouched as controls (group 1); pairs of males, still teneral, were left untouched (group 2); and pairs of males, still teneral, were confronted once daily with the test animal (group 3).

Group	Males (No.)	Deaths (No.)	Deaths in subordinates (No.)
1	30	3	
2	30	7	
3	30	15	12

The numbers of deaths occurring in the first two groups do not differ significantly ($\chi^2 = < .3$). The findings for the third group indicate that there is an increase in the number of deaths following repeated presentation with the test animal and that, where deaths do occur, they occur in subordinate animals in 80 precent of the cases. In all 12 subordinate animals, death occurred on days three and four, that is, after fighting had first appeared in the dominant. The increase in death rate is significantly different from that of the control group ($\chi^2 = .01$) and probably significantly different from group 2 ($\chi^2 = .05$).

It would seem that there is some connection between deaths in subordinate animals and fighting. It is puzzling, however, that more deaths do not occur in group 2. Casual observation suggests that, if these animals fight at all, they fight considerably less than animals of group 3. It may be that cage mates reared together from the time of emergence do not fight each other unless presented with a novel stimulus—in this case, the test animal. This phenomenon is not unknown and has been called passive inhibition. It occurs in young mice that normally fight at 35 days of age but do not fight cage mates with which they have been reared (*5*).

To test whether deaths from fighting occurred in older cockroaches, I set up two more groups. Pairs of males were left together for 24 hours, then presented once with the test animal. As controls, single animals were treated in the same way. Both groups were observed for a period of 10 days, and the deaths were recorded.

No deaths occurred in the control group of 30 animals. Four of the 30 experimental males died, and all of these were subordinate animals. This offers some support for the suggestion that there is some connection between being subordinate and dying after fighting. It also suggests that older adults are less susceptible to death under these conditions.

Some mention must be made of the events leading up to deaths. Once a dominance relationship has been established, the frequency and intensity of

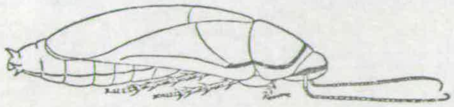

Fig. 2. The subordinate posture.

however, the adoption of a subordinate posture on the part of the inferior animal fails to allay attack, and the dominant animal may continue to fight for long periods of up to 30 minutes. Towards the end of this time the movements of the submissive become sluggish and stiff; the righting reflex disappears; and a state of semi-paralysis, affecting the abdomen and limbs, sets in. Animals in this state apparently do not recover, and death soon follows. They die after an extended bout of fighting but characteristically show no signs of external damage. Some animals do survive prolonged attack over a period of several weeks. Such animals may have entire wings or limbs removed by their superiors.

The situation bears striking resemblance to the social stress found in mammals. Male rats in particular show a well-marked dominant-subordinate behavior. Prolonged aggression produces stress in the subordinate, and ultimately a disease state, characterized by the stress syndrome, leads to death, which cannot be attributed to external damage (*6*). Subordinate cockroaches may die from some internal changes comparable to those accompanying the stress syndrome in mammals.

Several problems arise from these observations; the corpus cardiacum may play some role in the development and maintenance of dominant-subordinate behavior and in death from stress. Indeed, it repeatedly shows severe depletion of neurosecretory material during artificially induced stress, such as forced hyperactivity and electrical shocks (*7*).

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References and Notes

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9. I thank the Department of Zoology, Edinburgh for use of facilities, Dr. A. Manning for criticism of the manuscript, and Dr. L. Roth for the original culture of *Nauphoeta cinerea*.

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ABSTRACT OF THESIS

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Title of Thesis Behavioural and Physiological Aspects of Fighting in the Cockroach Nauphoeta cinerea (Oliver).

This thesis is concerned with the role of fighting in the cockroach, Nauphoeta cinerea. As a general introduction the role of fighting in vertebrates and invertebrates is described and discussed.

(1) The fighting sequence in Nauphoeta is described and some of the characteristics of fighting behaviour are determined by experiments. Males are found to fight not for females but for rank.

(2) The social structure of a group of male cockroaches is found to be territorial/hierarchical. Rank determines which males can possess territories. The hierarchy is not linear and alpha, beta and gamma categories of males can be distinguished. Rank is not permanently fixed and shifts in the hierarchy may occur after four weeks.

(3) The pattern of night activity of single males differs from that of other cockroaches. Groups of males show no particular pattern except that they are more active at night. There is no correlation between the rank of animal and its activity. There appears to be a biphasic pattern of night feeding but no rhythm of drinking. Top-ranking males eat and drink less than bottom-ranking males and this may contribute to the dominance shifts characteristic of the hierarchy in Nauphoeta.

(4) It is possible to alter the structure of the society of a group of males by altering the population density. At low densities the structure of the group is dominated by territory and at high densities by hierarchy. The hierarchy becomes less stable with increasing population density.

(5) At high density mating can take place but mating couples are attacked and copulation may break off. There is no correlation between rank and mating success. At low densities, mating can take place without interference from other males. Since only high-ranking males have territories only high-ranking males mate. It is suggested that a lek-type system may operate in Nauphoeta.

The second half of this thesis is concerned with the dominant/subordinate relationship which develops between two adult males.

(6) There is a correlation between low rank and death in male cockroaches. Death can occur without obvious external damage and is preceded by a characteristic syndrome which involves paralysis. The possible involvement of the neuro-endocrine system is discussed in detail.

(7) Subordinate males lose weight or gain less weight than dominants. Experiments show that subordinate males respond like water deprived males rather than food deprived males. The water content of subordinate males is normal and yet these animals lose water via the faeces. It is suggested that subordinate males either eat less than dominants or have an increased metabolic rate.

(8) In an attempt to alter behaviour by injection of corpus cardiacum homogenates the pre-injection chilling treatment was found to be very effective and dominance was

reversed/

Use other side if necessary.

reversed. The time scale of events is consistent with an effect on the endocrine system. Dominance can be reversed by other methods and several experiments are described which indicate that the dominant animal induces a particular physiological state in the subordinate and that even if the subordinate is capable of recognising the dominant this is not important in the appearance of submissive behaviour.

The corpus cardiacum is implicated in the cockroaches response to stress and this thesis concludes with a two-part investigation of the brain and retro-cerebral complex.

(9) The morphology of the retrocerebral complex is described and compared to other cockroach species. A comparison is made of the neurosecretory cells in the brain and of the amounts of neurosecretory material in the corpora cardiaca in dominant and subordinate animals. There is considerable individual variation but no correlation with rank.