

Determinants of dominant-subordinate interactions in males of the cockroach *Nauphoeta cinerea*

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RESUME

Facteurs déterminant les interactions de dominance-subordination chez les mâles de la blatte *Nauphoeta cinerea*

Les événements successifs se qui produisent au cours de l'établissement de relations de dominance dans des paires de *Nauphoeta* mâles sont examinés.

L'âge est important dans la détermination du rang éventuel de mâles isolés, socialement inexpérimentés. Après la mue imaginale, les mâles déclenchent des manifestations sexuelles de la part de mâles plus âgés. Six à sept jours après la mue, les mâles déclenchent des actes agressifs (*e.g.* sauts en avant) de la part de mâles plus âgés. La reconnaissance de la classe d'âge est indépendante du fait que le sujet soit présenté comme étant un individu « étranger » ou comme un mâle « conditionné » exposé antérieurement à l'odeur de la cage expérimentale.

La vision a peu d'influence sur l'ontogenèse ou le résultat des interactions mâle-mâle. L'ablation des antennes d'un mâle dominant provoque une inversion de rang; aucune agressivité ne se manifeste quand les antennes des deux mâles sont supprimées.

La grosseur et/ou le poids ne peuvent prédire le résultat des confrontations agressives. Des transfusions sanguines entre mâles dominants et jeunes mâles inexpérimentés ne transforment pas ces derniers en mâles dominants au cour de combats avec des mâles inexpérimentés plus âgés. Inversement, les transfusions entre mâles subordonnés et plus âgés n'influencent pas le résultat des interactions avec des mâles les plus jeunes. L'ablation des testicules ou du *corpora allata* n'a eu aucun effet sur l'ontogenèse des hiérarchies de dominance.

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Chez des paires de mâles, le mâle dominant a un plus grand succès d'accouplement que le mâle subordonné, principalement à cause de son activité locomotrice élevée et de son intervention dans la cour du mâle subordonné.

Le soulèvement des ailes, normalement manifesté durant la cour, peut être un acte conditionnel contenant des informations, dans les affrontements mâle-mâle. Le mâle participant dans le plus de soulèvements d'ailes devient dominant. Le comportement sexuel de mâles en présence de jeunes mâles adultes (moins de 6-7 jours) suggère, que ces derniers sont perçus comme étant des femelles sexuellement réceptives. Puisque les femelles se retrouvent en groupes, probablement à cause de l'attraction mutuelle, il peut être avantageux pour des mâles plus âgés de permettre à des jeunes mâles inactifs l'accès à leur territoire où ils pourraient attirer des femelles.

Mots clés: Blatte. Comportement agonistique. Expérience sociale. Pariade.

SUMMARY

The sequential events occurring in the establishment of dominance orders in pairs of *Nauphoeta* males were investigated.

Age is important in determining the eventual rank of socially naive isolated males. Following the adult moult, males elicit sexual displays from older males. Six to seven days after ecdysis, males elicit aggressive acts (e.g. lunging) from older males. Age-class recognition is independent of whether the subject is introduced as a "foreign" individual or as a "conditioned" male previously exposed to the odour of the test cage.

Vision has little influence on the ontogeny or outcome of male-male interactions. Ablating the antennae of a dominant male causes a reversal in the rank order; agonism fails to occur when the antennae of both males are removed.

Size and/or weight do not predict the outcome of agonistic contests. Blood transfusions from dominant males to young naive males do not render them dominant in contests with older inexperienced males. Conversely, transfusions between subordinates and older males do not influence the outcome of interactions with younger males. Removal of testes or corpora allata did not affect the ontogeny of dominance hierarchies.

In pairs of males, the dominant has a higher mating success than the subordinate male, mainly because of his elevated locomotory activity and interference with the subordinate's courtship.

Wing-raising, normally a courtship display, may be a conditional act with information content in male-male encounters. The male engaging in the most wing-raising becomes dominant. Sexual behavior of males in the presence of young adult males (less than 6-7 days) suggests that the latter may mimic sexually receptive females olfactorily. Since females occur in groups, presumably because of mutual attraction, it may be advantageous for older males to allow sexually inactive young males on their territories to which they may attract females.

INTRODUCTION

Intraspecific agonism has many functions in the natural history of a species. Aggression in both immature and adult stages may lead to dispersal (Crane, 1956; Raisbeck, 1976; Tschinkel, 1978). The spatial

relations between individuals in a population may be maintained through aggressive encounters in territorial species (Alexander, 1961 ; Barlow, 1974). To balance the time and energy expenditures of aggression, the territorial individual derives benefits such as access to a predictable food source (*e.g.* Stiles, 1973); the site may attract receptive mates (*e.g.* Campanella and Wolf, 1974) and provide food for them and their young (*e.g.* Alcock, Jones and Buchmann, 1977). Territory holders may reduce energy expenditure by recognizing their neighbors and mutually de-escalating aggression (Emlen, 1971).

Agonistic encounters operate to maintain stability and to confer certain rights (food, water, shelter, mates) to the dominant individual in hierarchical dominance orders. Here, the usual proximity of individuals in the population allows for fighting to operate as a means of interference competition for mates.

The lower social Hymenoptera represent a specialized case of aggressive behaviour functioning in the maintenance of castes and queen control. In the more advanced Hymenoptera, aggression may function to institute changes in the colony. For instance, in honey-bees, workers aggressively exclude older drones from the hive (Frisch, 1954).

Several other functions of aggression have been reported. Breed, Hinkle and Bell (1975) hypothesized that increased aggression in egg case carrying females (*Blattella germanica*) is a mechanism to reduce cannibalism on the young. Zenone, Sims and Erickson (1979) presented evidence that male birds could induce a delay in ovulation by initiating social interactions aggressively with females. Thus, more time is secured for the male's sperm to compete with sperm from previous copulations. Post-copulatory behaviour of male crickets is aggressive in nature (Alexander, 1961). The male antennates the female and thus induces immobility. Here, aggression functions to protect the male's investment and to allow for repeated matings. In all of these cases, aggression confers enhanced fitness to the victor of the encounter.

Studies of agonistic behaviour in cockroaches have taken several approaches (review : Bell, 1981). Kramer (1964) described aggressiveness in *Nauphoeta cinerea*. Ewing (1967), Gautier and Morvan (1971), Bell and Sams (1973, Breed *et al.* (1975) and Simon and Barth (1977) followed with characterizations of aggressive repertoires in other species. Manning and Johnstone (1970), Olomon, Breed and Bell (1976), Gautier (1976), and Deleporte (1976, 1978) described ontogenetic patterns in agonistic behaviour. Territoriality and the spatial distribution of cockroaches were investigated in the field or in the laboratory by Ritter (1964), Ziegler (1972), Ewing (1972, 1973), Zanforlin, Cervato and Cescon (1973), Gautier (1974 a, b), Breed and Byers (1979), Gorton, Fulmer and Bell (1979), Gorton (1980) and Schal (1982). Informational analyses of agonism were performed by Bell and Gorton (1978), Bell, Robinson, Tourtellot and Breed (1978) and Bell, Gorton, Tourtellot and Breed

(1979), and agonistic strategies were studied by Breed and Rasmussen (1980). Bell (1978) investigated directional responses of cockroaches during agonistic encounters, and Breed, Smith and Gall (1980) reported on discriminatory abilities of ranked males. Although much is known about the reproductive endocrinology of female cockroaches, only Ewing and Ewing (1973) have investigated physiological correlates of agonistic behaviour in males.

In this study we report on physiological and behavioural correlates of dominance hierarchy formation in pairs of male *Nauphoeta cinerea*. Types of encounters are delineated relative to the sensory modalities used in these encounters. Roles of such partly heritable factors as size, and non-heritable factors (age, experience) are investigated. Sexual behaviour and homo-sexual displays in males, the ontogeny of agonistic behaviour and its role in the maintenance of a dominance hierarchy are discussed.

METHODS AND MATERIALS

Behavioural acts were recorded sequentially on tape. Observations were made on pairs of males in either 30 × 15 cm cages or in 15 × 15 cm cages. The cockroaches were restricted to the floor of the cage by coating the walls with vaseline. The floor was covered with white absorbant paper. Unless otherwise noted, observations were made during the first three hours of the scotophase; GE Ruby bulbs (590-640 nm) simulated darkness (Bell, Parsons and Martinko, 1972). Last instar male nymphs were isolated and the date of adult ecdysis recorded. They were then individually distinguished by numbered tags placed on the pronotum. The age and experience of animals used for experimentation were known. All cockroaches were maintained under a 12:12 hr light : dark cycle at approximately 26°C and 50 to 70 % RH.

Ewing (1967, 1972, 1973) provided a basis for the characterization of the repertoire of agonistic acts in *N. cinerea*. Bell and Gorton (1978) expanded on Ewing's definitions, dividing the list into 18 distinct acts. These may be grouped into the following categories: (1) preliminary acts such as *approach* and *antennate*, (2) threat actions such as *stilt-walking*, (3) overt aggression (e.g. *lunge*), (4) submission (e.g. *crouch*), and (5) homo-sexual behaviour.

In this study we utilized all of Bell and Gorton's acts. Social rank and the state of the hierarchy were determined by the amount of time spent in *mutual antennation*, and the frequency of *lunges*, *wing-raising* and *crouching*. *Wing-raising* is a sexual act in which the displaying male presents his tergal glands to a male or a female.

RESULTS

1. ONTOGENETIC SEQUENCES OF AGONISTIC BEHAVIOUR

Three distinct patterns were observed in the formation and maintenance of rank order among randomly paired adult males. The most variable pattern, abbreviated as AN-WR-L, consisted of mutual antennation (AN) and wing-raising (WR) for up to nine days, followed by

lunging (L), which continued until either a reversal occurred in the dominance order or the subordinate male died. In the second pattern WR was absent and the dominant male proceeded from mutual antennation to lunging (AN-L) and the establishment of a stable rank order. In the final pattern, lunging initiated the relationship and the hierarchy was established after a few encounters. The last pattern occasionally involved grappling. The following manipulations were performed to elucidate and correlate these patterns with physiological events.

In the first experiment we paired socially naive males of the same age. The behavioural patterns observed were closely correlated with the age of the individuals (*table 1*). Males younger than two days of age followed the AN-L pattern; pairs between two and six days of age followed the AN-WR-L pattern. Lunging and grappling initiated the relation in pairs older than 6 days; AN and WR were not observed. To further examine the first and third types of patterns we paired males of various ages with males 6-7 days old (*table 1*). Here, again, AN and WR were followed by L in males less than six days of age. In these pairs, the older male performed sexual displays, lunged, and subsequently became the dominant male. The third pattern was most common in pairs of 6-7 day old males and older males; all encounters were initiated with lunging by the older male who assumed the alpha position. These patterns suggested a mechanism for age-related class recognition.

Next, we attempted to show that in fact, the age of the insect determined the ontogenetic sequence of agonistic acts and the relative ages of the pair determined their hierarchical rank. Newly ecdysed adult males were paired and a stable dominance hierarchy allowed to develop for two weeks (by which time lunging was the most common act). The subordinate male was then replaced with a previously isolated male of known age. The sequential acts of the dominant (resident) and the

Table 1: *Effect of age on dominant/subordinate hierarchy establishment in pairs of male Nauphoeta cinerea.*

Tableau 1: *Effets de l'âge sur l'établissement de la hiérarchie de dominance/subordination dans des paires de mâles Nauphoeta cinerea.*

	Ages of paired males**		Days AN x ± SEM	WR*	L*	N
	Dominant	Subordinate				
(a)	< 2 days	< 2 days	5.0 ± 0.0	(—)	(+)	3
(b)	2 to 6 days	2 to 6 days	5.4 ± 1.12	(+)	(+)	5
(c)	> 6 days	> 6 days	(—)	(—)	(+)	8
(d)	6 days	< 6 days	4.0 ± 0.82	(+)	(+)	6
(e)	> 6 days	6 days	(—)	(—)	(+)	6

Males were isolated since the imaginal molt.

AN = mutual antennation, WR = wing-raising, L = lunging.

* (+) occurs in the ontogeny of the hierarchy; (—) does not occur in the ontogeny of the hierarchy.

** In (a), (b), and (c) males in a pair were of the same age.

introduced males were recorded for 15 minutes. As shown in *table II* the dominant male lunged at males older than 6-7 days of age and displayed sexually (WR) to younger males.

In order to separate the possible effect of a "foreign odour" associated with an introduced male from the effect of age, a portion of the observation cage was set off with a double screen so as to isolate the inexperienced male in the cage for two days. Such treatment had no effect on age recognition when the divider was removed on day 3 (*table II*).

Table II : Transition from wing-raising to lunging in paired males of different ages : effects of exposure to odours of future partners.

Tableau II : Transition du soulèvement des ailes aux sauts en avant chez des mâles appariés d'âges différents : effets de l'exposition aux odeurs des futurs partenaires.

Age of introduced male	Isolation procedure		Types of encounters	Numbers of pairs tested
	Same cage with divider for 48 hrs	Different cages		
2	+		WR	3
2.5	+		WR	3
3		+	WR	6
5	+		WR	2
		+	WR	3
6	+		L → WR	1
		+	L → WR	3
7		+	WR	1
		+	L → WR	1
		+	L	1
	+		L → WR	2
8	+		L	2
9	+		L	3
10		+	L	3
11		+	L	3
15	+		L	3
16		+	L	2
28	+		L	3

Another important factor that required controlled manipulation was the effect of isolation. Manning and Johnstone (1970) reported that non-aggressive contact led to a rapid development of aggressiveness, whereas aggressive contact and isolation retarded the development of aggression. Applied to these data, an alternative hypothesis to age recognition is that the behavioural sequence is coupled to the length of isolation prior to pairing. To test for the effect of contact on changes in age dependent behaviours, we introduced the same individual to a dominant male on successive days. Non-aggressive contact (AN and WR)

was expected to produce a more rapid switch to lunging. This was not borne out by the results. Here too, the dominant male initiated all encounters with lunges only after the introduced male was 6-7 days old. These results suggest that the dominant male recognizes the age of a foreign male or at least differentiates between two classes of males: less than 6-7 days old and older than 6-7 days.

Age was also shown to be important later in life. Only social experiences override the effects of age. *Table 1* shows that given equal social inexperience, the emergent dominant male is usually the older of the pair. Similar results were obtained by Gautier (1974 a) working with *Blaberus craniifer*.

2. DEVELOPMENT OF THE HIERARCHY

Bell and Gorton (1978) showed that hierarchical stability occurred after nine days in groups of five male *Nauphoeta*. Subsequently, reversals and shifts in rank order were common. In pairs of males the social hierarchy is stable for 25.4 ± 10.80 days ($x \pm SD$; $N = 10$). A reversal may follow, but the rank order is again stabilized in less than 24 hours. We were not able to correlate spontaneous reversals to discrete physiological or environmental events. The time to first reversal is a conservative estimate, since in five other pairs which we observed for up to 60 days, no reversal occurred.

Several instances of death were observed in subordinate males as previously noted by Ewing (1967). On the other hand a reduction in overt aggression occurred with a concomitant increase in ritualized threat and submissive displays. *Figure 1* illustrates two examples of the temporal pattern of aggression. The initial level of overt aggression is high, as the dominant male frequently chased the subordinate. Later, the frequency of lunging decreases and stilt-walking, body-jerking (threat displays), and crouching (submission) became more common. Lunging activity, however, remains at a relatively high level. In time, oscillations in the level of aggression become apparent. Peaks of aggressiveness may indicate periods in which the hierarchy is reinforced. Patrolling behaviour was more common and the dominant male engaged in fewer chases, lunging only when it occasionally encountered the other male.

The same pattern is repeated when a reversal in the rank order occurs. The frequency of overt aggressive acts was usually higher than in the few days preceding the reversal. Again, this pattern continued for a few days with a subsequent reduction in lunging by the new dominant male and a switch to reinforcing acts. A second reversal sometimes followed, but these were not common unless experimentally induced.

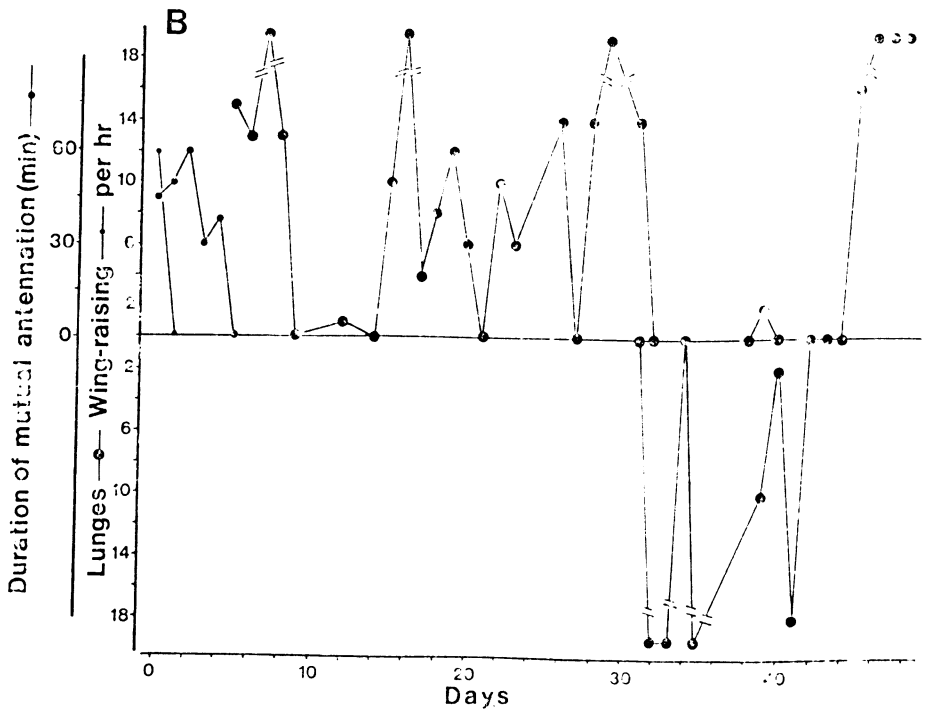
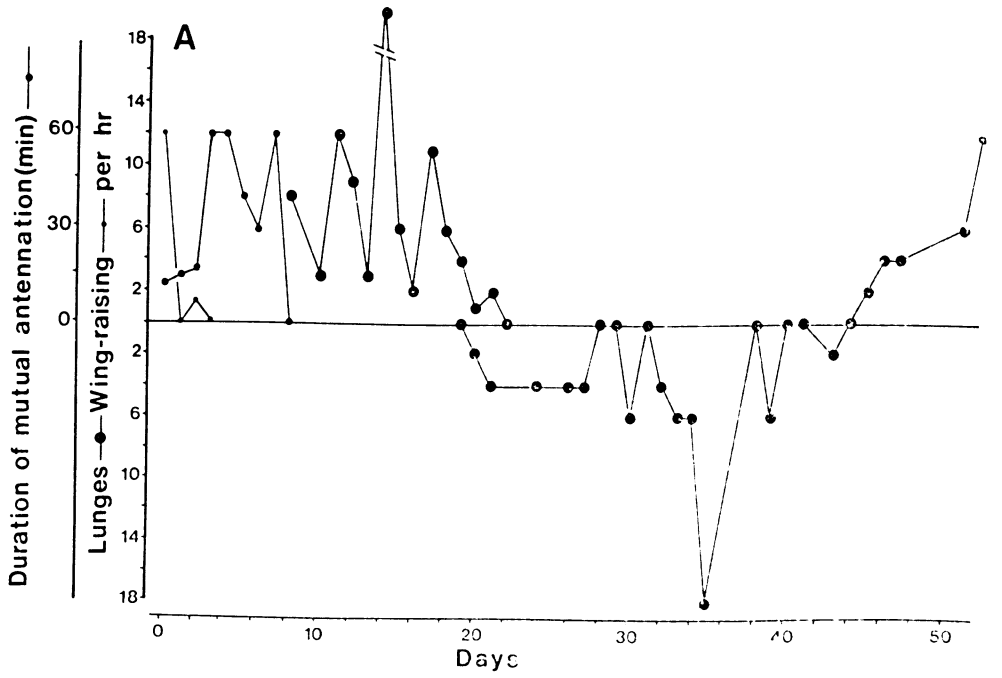


Fig. 1

3. SENSORY MODALITIES USED IN AGONISTIC BEHAVIOUR

In deciding whether to fight, submit, or retreat an animal needs to evaluate its antagonist. Vision may be important in the perception of body size and other physical characteristics of the rival individual. Four experiments show that vision or lack of it has no effect on the agonistic repertoire or on the outcome of agonistic encounters. Older males remain dominant in all cases whether their eyes are painted (India ink) before pairing with another male ($N = 5$) or after the establishment of a stable relationship ($N = 5$). Similarly, younger males remain subordinate when their eyes are painted before ($N = 3$) or after ($N = 3$) a dominance order is established.

When the antennae of both males were ablated ($N = 7$ pairs), agonistic behaviour ceased or did not develop in all cases, regardless of the age of the males and the state of the rank order establishment. Removing the antennae of a subordinate male did not change the relationship ($N = 5$ pairs), but removing the antennae of the dominant male resulted in a reversal in the dominance order ($N = 5$ pairs).

Other non-heritable disabilities had variable effects on the dominance order. Cutting off the wings of dominant males did not affect the rank order. Ablations of single legs had little effect in a stable hierarchy but rendered the disabled male subordinate when paired with a healthy male of the same age.

Bell and Gorton (1978), in examining the ontogeny of social hierarchies in *Nauphoeta* males suggested that wing-raising was a response elicited by the presence or odours of strange males and by exposure to a novel environment. However, their discussions and those of Ewing (1972, 1973) did not elaborate on the functions of WR in hierarchy formation, a task more easily performed with pairs of males than with larger groups.

Our finding that older males did not WR when paired (*table 1c, e*) showed that WR is a response to a specific class of males rather than to all strange males. In addition, WR correlated significantly with dominance. The younger male (less than 6-7 days) always became subordinate after the older male WR. In pairs of young males of the same age, the eventual dominant male was always the individual that engaged most actively in WR.

Fig. 1: *Temporal patterns of agonistic acts in two pairs of male Nauphoeta cinerea. Age (days since adult emergence) of males at the time of pairing: (A) upper, 4.5d, lower, 1.5d, (B) upper, 38d, lower 1.5d.*

Fig. 1: *Modèles temporels d'actes agressifs chez deux paires de mâles Nauphoeta cinerea. Age (jours depuis l'émergence adulte) des mâles au moment de l'appariement: (A) supérieur, 4.5j, inférieur, 1.5j; (B) supérieur, 38j, inférieur, 1.5j.*

That WR is an important step in gaining dominance was borne out in the following experiment. The subordinate male in a stable hierarchy was isolated with a female for 24 hours (the male was allowed to court but not to copulate). When this male was placed back in its home cage it engaged the dominant, for the first time, in extensive grappling bouts: in 6 of the 12 cases this behaviour led to a reversal in the dominance order. That this dramatic change in behaviour was not caused merely by exposure to a female was shown by pairing the subordinate male with a teneral male; here also, the subordinate exhibited more aggressive behaviour when paired again with the dominant male. Of course, it is rather difficult to separate the act of WR and general motivational or reactional state experimentally. We do not know whether WR by the subordinate causes a behavioral change or results in an elevated state of excitation which in turn results in more aggressive encounters.

Another line of evidence supporting this conclusion is the occurrence of WR after spontaneous dominance reversals. In some cases, prior to the reversal or concurrent with it, the new alpha male wing-raised and stridulated to the new subordinate. In this case both males were familiar with each other and with the cage environment; only their relative ranks in the hierarchy changed. These results suggest that WR has a high predictive value in the eventual dominance order and therefore may be an important act in the agonistic context. Similar results are reported by Gautier (1974 a), but sexual displays in *Blaberus craniifer* elicit aggressive acts in the younger male in some cases; the latter may become temporarily dominant. We have no record of a < 7 days old male being dominant over a > 7 day old male.

The effects of "novel environment" (including novel cage mates), female odour, and possibly an imperfect sexual recognition mechanism are easily recognized in groups of males. Whereas WR rarely occurs upon pairing previously isolated older (> 7 days) males, when several males are caged together the incidence of WR increases. We maintained all male colonies of various sizes (but equal densities) wherein males were tagged with colony-specific colours. Then, we randomly paired males from the same colony in a clean cage for 5 minutes. The occurrence of WR was a function of the number of males in the parent colony (fig. 2). Apparently, sexual recognition may be disrupted in a large group of males, perhaps due to the greater heterogeneity of individual odours.

To test the possibility that *Nauphoeta* has a deficient sexual recognition mechanism, we replaced the subordinate male in a stable hierarchy with an unreceptive female and recorded the frequency of WR by the dominant male for 5 minutes. On successive days a male from a mixed colony and a male from an all male colony were introduced in random order, utilizing the same procedure. Table III combines the data for 7 cages in each category. The dominant male is fooled by the

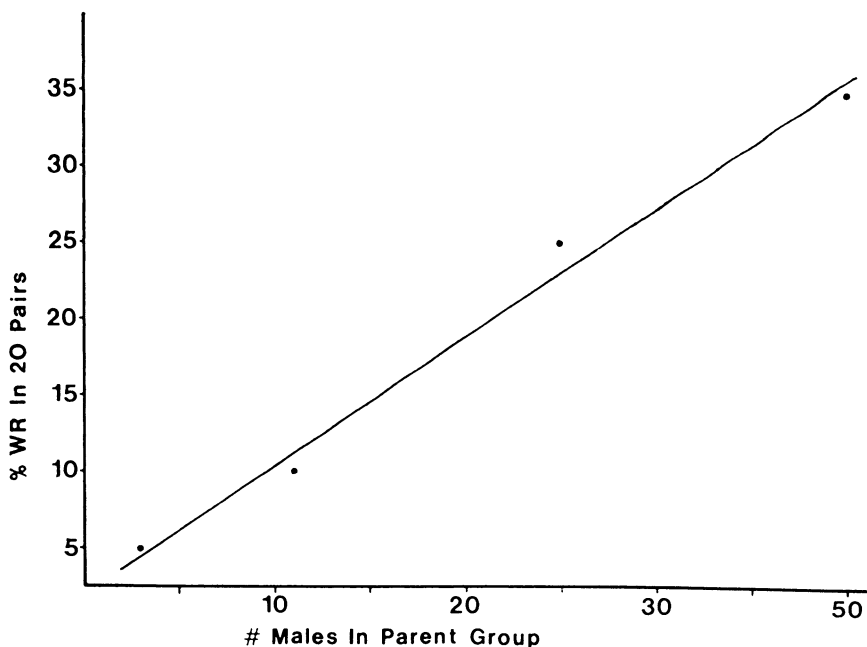


Fig. 2: Correlation between incidence of wing-raising and size of colony from which paired males were removed. Correlation coefficient, $r = 0.9947$, $P < .001$.

Fig. 2: Corrélation entre l'incidence du soulèvement des ailes et la grosseur de la colonie de laquelle les mâles appariés ont été prélevés. Coefficient de corrélation, $r = 0.9947$,

male impregnated with female odour and displays to him. However, a male from an all male colony elicits few WR. These results and the data reported above argue that sexual recognition is well developed in older *Nauphoeta* males. But, is sexual recognition of younger individuals as keen?

The dominant male in a pair displays to either teneral males (see table I) or females (see section 7), but not to teneral nymphs. Hence,

Table III: Effects of female odour on frequency of wing-raising by dominant males.

Tableau III: Effets de l'odeur des femelles sur la fréquence du soulèvement des ailes chez des mâles dominants.

	Source of introduced cockroach *		
	Female from cage of females	Male from cage of males and females	Males from cage of males
Frequency of WR per min $\bar{x} \pm$ S.E.M. (n)	21.14 ± 2.76 (7)	22.57 ± 2.24 (7)	6.14 ± 1.03 (7)

* The subordinate male in a pair was replaced by an introduced cockroach. WR frequency was recorded for 5 min.

either tactile and/or chemical releasers must be altered during adult ecdysis, establishing a mimicry complex between receptive females and young males.

4. EFFECTS OF PHYSICAL SIZE OF INDIVIDUALS

In many vertebrate and invertebrate agonistic contests, body size is the critical factor determining the outcome of the encounter. In *Nauphoeta*, body size, as determined by the length ($t = 0.1274$, NS) and width ($t = 0.2697$, NS) of the pronotum, and the length of the hind femur ($t = 0.5603$, NS) and tibia ($t = 0.8083$, NS) did not correlate with the outcome of the encounter ($N = 14$). Also, dominance did not correlate with the relative body weights measured before pairing. Ewing (1967) showed a 10% body weight loss in subordinates, but this outcome followed a stable hierarchy and might only contribute to the maintenance of the rank order.

5. EFFECT OF SOCIAL EXPERIENCES

All of the experiments presented thus far deal with males isolated when teneral, or dominant males whose history of social experience was known. In this section we attempt to elucidate some of the more common social experiences which affect the dominance hierarchy.

A 13 day old male was placed in a cage and one teneral male was added on each alternate night. When seven males were present in the cage (day 11) the dominant male was removed on successive nights until a pair of males remained in the cage. The first phase of this procedure was designed to examine the effect of teneral males on a stable rank order and to approximate natural situations in which newly ecdysed adults are incorporated into existing hierarchies.

In a group of males, as in pairs, the majority of sexual displays were directed toward young males (*fig. 3* and *table IV*). This experiment presents an interesting situation in which to examine the shift in behavioural acts from WR to L. *Figure 3 B* shows the percentage of young males (< 6 days old) in the population resulting from adding day 0 males or removing dominant males (*fig. 3 A*). The greatest absolute frequency of WR would be expected to occur when the percentage of young males in the population is greatest, i.e. day 5 (3 young, 1 older male). In the experimental cases ($N = 3$) WR peaks on days 5-7 (*fig. 3 C*). As more males become mature (older than 6 to 7 days) lunging becomes more common; WR is completely replaced by L by day 16. If lunging and WR are taken as mutually exclusive acts in the ontogeny of aggression and percent WR is taken as

$$\frac{\text{WR}}{\text{L} + \text{WR}} \times 100$$

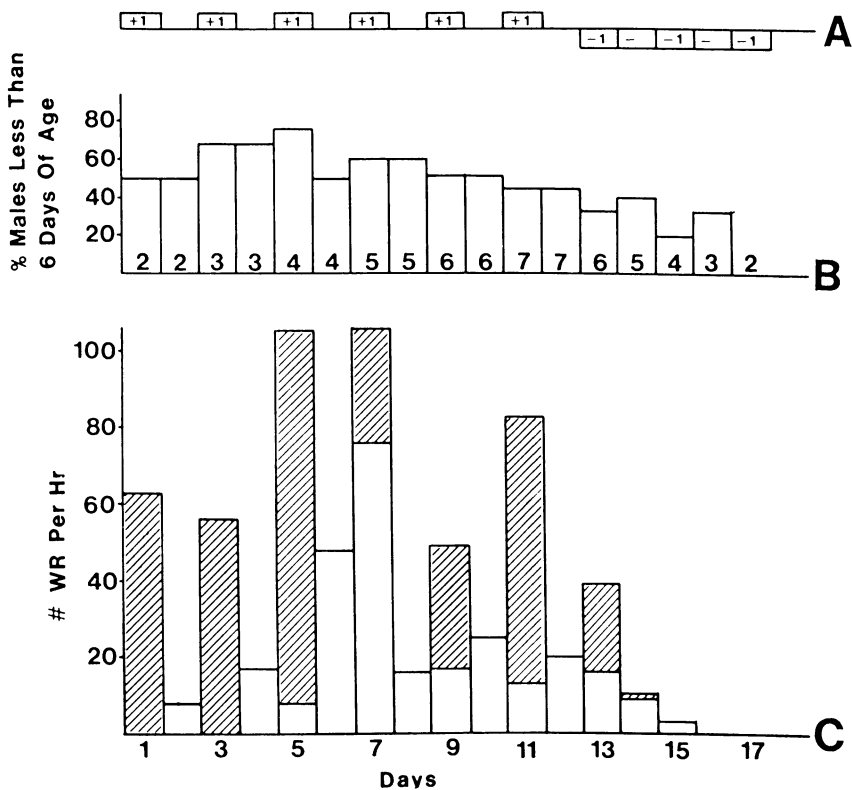


Fig. 3: Effects of relative numbers of young males on frequency of wing-raising. (A) On day 1, a teneral male was added to a cage containing an older (13 days) male; additional teneral males were added on days 3, 5, 7, 9 and 11 (+1). The dominant male was removed on days 13, 14, 15, 16 and 17 (-1). (B) Percent of males in the group less than 6 days of age; values indicate actual numbers of males. (C) Incidence of wing-raising per hour prior to (open bar) or after (hatched bar) adding or removing a male.

Fig. 3: Effets des nombres relatifs de jeunes mâles sur la fréquence du soulèvement des ailes. (A) Au jour 1, un mâle nouvellement mué a été ajouté à une cage contenant un mâle plus âgé (13 jours); des mâles nouvellement mués additionnels ont été ajoutés aux jours 3, 5, 7, 9, et 11 (+1). Le mâle dominant a été enlevé aux jours 13, 14, 15, 16 et 17 (-1). (B) Pourcentage de mâles dans le groupe âgés de moins de 6 jours; les valeurs indiquent les nombres actuels de mâles. (C) Incidence du soulèvement des ailes par heure antérieurement (barre ouverte) et après (barre hachurée) l'addition ou la suppression d'un mâle.

then WR constitutes 100 % of the acts for the first 6-7 days and decreases to 0 % by day 16 (fig. 3 C).

Tables IV and V summarize the distribution of lunging and WR expressed as number of acts per hour. In most cases, males lunge only at younger males with most lunging directed at the male next youngest to the aggressive male. In those cases where a younger male directed more lunges at an older male than directed at him (e.g. males 5 and 3), the

Table IV : Incidence (acts per hr) of lunging (a) and wing-raising (b) in groups of male *Nauphoeta cinerea*.

Tableau IV : Incidence (actes par heure) des sauts en avant (a) et du soulèvement des ailes (b) dans des groupes de mâles *Nauphoeta cinerea*.

(a)		Individual toward which lunge is directed *						
		0	1	3	5	7	9	11
Individual lunging	0	—	26.0	30.0	12.0	8.0	8.0	0.0
	1	0.0	—	8.8	6.0	1.2	1.6	0.0
	3	0.0	0.0	—	1.6	1.2	1.6	0.0
	5	0.0	0.0	2.2	—	2.0	2.2	2.4
	7	0.0	0.0	0.0	0.0	—	0.4	0.6
	9	0.0	0.0	5.6	2.8	5.0	—	4.2
	11	0.0	0.0	0.0	0.0	0.4	0.0	—
(b)		Individual toward which wing-raise is directed *						
		0	1	3	5	7	9	11
Individual wing-raising	0	—	6.0	3.8	5.0	5.2	19.0	2.4
	1	3.6	—	2.0	4.4	6.2	1.6	6.6
	3	1.6	0.8	—	1.4	2.4	3.0	1.6
	5	0.0	0.0	0.0	—	1.6	0.8	1.2
	7	0.0	0.0	0.0	0.0	—	0.0	0.0
	9	0.0	0.0	0.0	0.0	0.0	—	1.2
	11	0.0	0.0	0.0	0.0	0.0	0.0	—

* 0, first male placed in cage, older than 13 days post-ecdysis; 1-11, day on which a teneral male was added to the cage (refer to Fig. 3). Male age decreases to the right and down in each data set.

older male directed a larger percentage of his lunges at this young male (*table V a*). In the case represented in *table IV a*, male number 9 preceded number 7 in gaining dominance when the old male and males 1, 3 and 5 were removed.

For WR, the situation is even more clear. Males wing-raise only to younger males with most WR directed at the youngest male in the group (*tables IV b and V b*). Here, again it is apparent that WR is important in the establishment of dominance. L maintains and reinforces the dominant status. In the presence of young males, both adding and removing individuals causes an increase in WR (*fig. 3 C*).

Age can again be examined in the second phase of this experiment, but its effects may be somewhat masked by the effects of social experience. When the dominant male (oldest) was removed, the next two oldest males engaged in much lunging and occasional grappling. Usually the older of the two emerged as dominant, although in some cases one age group was surpassed and the next oldest male became dominant. This strengthens the argument that age is the most important determinant, as most aggressive acts by the dominant male were directed toward the next oldest male (*table IV a*) and yet the latter emerged as the alpha male in the absence of the previously dominant male.

Table V : Incidence of lunging (a) and wing-raising (b) expressed as a percent of total acts of an individual.

Tableau V : Incidence des sauts en avant (a) et du soulèvement des ailes (b) exprimée en tant que pourcentage des actes totaux d'un individu.

(a)		Individual toward which lunge is directed *						
		0	1	3	5	7	9	11
Individual lunging	0	—	31	36	14	10	10	0
	1	0	—	45	31	6	18	0
	3	0	0	—	36	27	36	0
	5	0	0	25	—	23	25	27
	7	0	0	0	0	—	40	60
	9	0	0	32	16	28	—	24
	11	0	0	0	0	0	0	—

(b)		Individual toward which wing-raise is directed *						
		0	1	3	5	7	9	11
Individual wing-raising	0	—	10	6	8	8	30	38
	1	15	—	8	18	25	6	7
	3	15	7	—	13	22	28	15
	5	0	0	0	—	44	22	33
	7	0	0	0	0	—	0	0
	9	0	0	0	0	0	—	100
	11	0	0	0	0	0	0	—

* 0, first male placed in cage, older than 13 days post-ecdysis ; 1-11, day on which a general male was added to the cage (refer to Fig. 3). Male age decreases to the right and down in each data set.

Although the general pattern of *figure 3 C* agrees with that predicted on the basis of age, there are major differences in the relative levels of WR on different days. Males 6 days of age or older wing-raise to younger males and L at males that are 6 days old or older. However, males younger than 6 days may wing-raise to younger males. For instance, on day 7 we would predict a decrease in lunging from day 5, as there are 3 young and 2 older males. However, both the 4-day old and 2 day old males may wing-raise to the introduced male on day 7, making the effective group of wing-raisers 4 rather than 2 as implied by age alone. Hence, the occurrence of more WR than predicted.

In 5 pairs of males in which one was 13 days or older and the other a general adult, lunging took place only after the younger male was at least 6-7 days old (7 ± 0.55 days ; $x \pm \text{SEM}$). Here, however, the dominant male initiated lunging at a newly introduced general male earlier as the size of the group increased (*table VI*). It is not known whether this is due to spontaneous changes in the dominant male or to different stimuli emanating from the introduced male as the frequency of social contacts increases.

Table VI: Number of days before lunging towards introduced newly emerged males occurs in groups of males.

Tableau VI: Nombre de jours avant l'apparition de sauts en avant vers les mâles nouvellement émergés présentés, chez des groupes de mâles.

	Number of males in the group at the time the newly emerged male is introduced				
	1	2	3	4	5
Cage 1	5	4	4	2	1
Cage 2	4	3	4	1	1
Cage 3	5	4	3	2	1

6. PHYSIOLOGICAL CORRELATES

Cook, Cuesta and Pomonis (1969) and Ewing and Ewing (1973) investigated the role of Factor S, a neuro-muscular excitant, in stressed cockroaches. In order to examine the possibility of a haemolymph mediated factor in the development or maintenance of subordinate behaviour, we transfused blood between dominant and subordinate individuals. A donor pair was used to transfuse blood from a dominant to a recipient and blood from a subordinate to another recipient (N = 13 pairs). The recipients were paired after a 3 day recovery period. This procedure did not override the effects of age in the establishment of a rank order.

Although insect testes are not known to actively secrete materials into the haemolymph, they may mediate other neural or secretory processes. Hence, we tested their role in the ontogeny of hierarchies in *Nauphoeta* males. Newly ecdysed males were castrated and isolated for 10 days. In all cases (N = 10 pairs), agonistic behavior was manifested normally in the establishment of hierarchies. Similar results were obtained with males castrated as last instar nymphs.

Little is known about the role of the corpora allata (CA) in the physiology and behaviour of adult male insects. Since odours are involved in male and female recognition and the production of some pheromones is controlled by the CA (Barth, 1968), we tested for possible effects of CA hormones on agonistic interactions in males. Newly emerged males were allatectomized surgically and allowed to recover for 10 days in isolation. We recorded the incidence of wing-raising, lunging, and mutual antennation in pairs of allatectomized males. In 100% of the pairs (N = 8 pairs) lunging and grappling dominated the initial encounters. No WR was observed. Hence, the CA do not directly influence the ontogeny of agonism in *Nauphoeta* males.

In the above three experiments, only naive insects were tested. As shown by Ewing and Ewing (1973), surgeries and carbon dioxide or cold narcoses of dominants and subordinâtes caused reversals in rank which could not be separated from the effects of other experimental manipu-

lations. We therefore did not analyze the effects of transfusions, allatectomies or gonadectomies on stable rank orders.

7. MATING SUCCESS VS. REVERSALS

We used three procedures to test for differential matings by dominant and subordinate males and the effects of females on the rank order. In the simplest case a receptive female was introduced to a pair of males. In 25 of 31 cases (80.6 %) the dominant male copulated successfully after engaging in frequent WR toward the female and L toward the subordinate male. In a second set of experiments we allowed the subordinate male to court an unreceptive female for 24 hrs, placed him back in his cage (with the dominant male), and introduced a receptive female. Reversals occurred in 46.7 % of the cases (7 of 15) and the new dominant males copulated successfully in 6 of the 7 cases (85.7 %) where reversals occurred. In the remaining 8 cages 7 dominant and one subordinate male mated successfully. A reversal followed in the latter cage the next night. Interestingly, the results indicate that it is difficult to force successive reversals on a pair of males by repeatedly introducing females. Following a reversal the new dominant male maintains his rank (and enhanced mating success) for several days even if the subordinate male is preferentially isolated with females and engages the dominant male in grappling bouts when they are paired again.

DISCUSSION

DETERMINANTS OF RANK

The results presented here show that the rank of each male *Nauphoeta* can be predicted for an ensuing encounter with reasonable accuracy if the age and previous experience of each male is known. Certain behavioural acts are better predictors of an eventual dominant than others, and certain acts can be accurately predicted if the age and experience of the individuals are known. For example, once a rank order is established, grappling is replaced by lunging and submission. Wing-raising of males to females or teneral males increases the probability that grappling will occur upon pairing with other males. Individual isolation of older males also increases the probability that grappling will be employed in the early phases of agonism. Both age and wing-raising experience correlate well with dominance. In a socially naive pair, the older of the two is more likely to emerge as the dominant male; if one of the males is younger than 6-7 days, wing-raising by the older male indicates its eventual dominant status.

SEXUAL RECOGNITION

Wing-raising during male agonistic encounters poses an interesting problem. WR by males to other males may be explained either as an indication of a deficient sex recognition system or as a behaviour that

has dual function in both courtship and agonism. The correlation between dominant rank and WR, and the concurrent occurrence of WR with spontaneous rank reversals argue for the latter explanation. If an older male reinforces its dominant status with WR, why does it switch to L at a later time? The age-related shift suggests a deficient sex recognition system: an older male cannot distinguish females from young males and it courts both.

Courtship in males is released by a non-volatile chemical on the surface of females. Pieces of filter paper from cages of virgin females do not elicit sexual responses in males (Roth and Barth, 1967). Recent evidence regarding the female sex pheromone of *Nauphoeta* indicates that the WR stimulant is present mainly in the hydrocarbon fraction of the cuticular wax (Fukui and Takahashi, 1980; Takahashi and Fukui, 1980). Moreover, the chemical composition of this fraction is identical in both males and females. Since only teneral adults and older females elicit WR, there must be a mechanism which labels an older male and which develops sometime after the adult moult. Gautier (1974 a) reached a similar conclusion in his studies of *B. craniifer*. Our experiments with anaesthetized and freshly killed individuals indicate that recognition of male age classes is independent of behavioural releasers from the test insect, i.e. the recognition process does not depend on the sequential transition of behavioural acts between the two individuals. It is most probable that chemical rather than structural stimuli are involved, as few changes occur in the cuticular morphology after the adult moult.

Uebel, Sonnet, Miller and Beroza (1975) showed that both males and females of the face fly, *Musca autumnalis*, possess courtship releasers in their cuticular hydrocarbons. In the fly the ratio of saturated to unsaturated hydrocarbons is similar in both sexes, but five days after emergence males have a lower proportion of unsaturates and a higher level of saturated compounds. It was further shown that the activity of unsaturated hydrocarbons is attenuated by the presence of saturates. A similar system may operate in *Nauphoeta*. Fukui and Takahashi (1980) found that in addition to common cuticular hydrocarbons in both sexes, the female ether fraction has a second wing-raising releaser, whereas the benzene fraction of males has a wing-raising inhibitor. Males may use such cues to distinguish females from males.

We know of no studies which examine the changes in either the structure or the availability of these compounds during the moulting and tanning process in cockroaches, although in *P. americana* and *B. germanica* the total and relative quantities of principal hydrocarbons in the haemolymph are dependent on age (Acree, Turner, Smittle and Burden, 1965). In the flesh fly ecdysone stimulates hydrocarbon biosynthesis in the integument (Arnold and Regnier, 1975).

Wing-raising to newly emerged adults is more common in the Blaberidae than in the Blattidae and Blattellidae. In some cockroach species

the emission of a sex pheromone is age-dependent (Roth and Willis, 1952); sexual recognition is delayed for several days following the adult moult (e.g. *P. americana*, Hawkins, 1978). In other species teneral females are sexually receptive and may copulate immediately following ecdysis; a precopulatory period is eliminated. Hence, for a male to maximize its fitness it must search for teneral females. An odour associated with adult moulting fluids would constitute an important chemical signal in this process. If such were the case, then teneral adults of both sexes would elicit sexual behaviour in older males. Exposed cuticular releasers on the teneral adult would be expected somehow to be masked or altered during or shortly after the tanning process; the female then develops a new WR stimulant which may be identical to the teneral compound or may be an entirely different compound. Roth and Barth (1964) state that *Diploptera punctata* and *Neostylopyga rhombifolia* females mate when white and teneral. Their results are corroborated with field data for the former species (Woodhead, pers. comm.). *Eublaberus posticus* (Roth, 1970) and *Epilampra involucris* (Schal, unpublished) also mate just after leaving the nymphal cuticle. Virgin *Nauphoeta* females become sexually receptive at the age of four days. By the sixth day after emergence, more than 95 % of all females are receptive (Roth, 1964). *Nauphoeta*, as well as other Oxyhaloine species (e.g. *Leucophoea*) may represent intermediates between teneral matings (e.g. *Diploptera*) and matings which result from female age-related courtship releasers (e.g. *Periplaneta*). Interestingly, this continuum is not rigorously taxonomically dependent. *Neostylapyga* females, in the Blattidae, mate when teneral as do several Blaberid females.

PHYSIOLOGICAL CORRELATES

The elevated frequency of wing-raising that occurs with spontaneous reversals seemed to indicate a possible hormonal effect in the recognition process. Our work with the corpora allata suggest that the presence of these glands is not requisite for the development of agonistic behaviour and sex recognition. Tobe, Musters and Stay (1979) reached similar conclusions with *D. punctata* males with regard to sexual maturation. To the best of our knowledge our study is the first analysis of the role of the corpus allatum in agonistic behaviour of adult male cockroaches. Gautier (1974 a) showed that the number of immobilisations in response to tactile stimuli increased in *B. craniifer* nymphs injected with corpora allata. We also confirmed previous reports (Ziegler, 1972) that the testes have no detectable effect on sexual or agonistic behaviour in males.

MALE STRATEGIES AND MATING SUCCESS

The correlation between mating success and rank in a dominance hierarchy will remain an open question until more is known of the ecology of *Nauphoeta*. Ewing (1972) found that under crowded condi-

tions (ten males, 49 cm²/male) rank and mating success did not correlate. Breed *et al.* (1980), working with groups of 4 males (63 cm²/male) reported that the alpha male mated successfully in 46 % of all matings. Here we report similar results for pairs of males (112 cm²/male). However, both of the latter studies suffer from several weaknesses. In both studies introductions of females during the active period resulted in temporary disruption of the male group, and increased activity (in this study and presumably in Breed *et al.*, 1980) due to the introduction of a foreign odour. High activity resulted in an advantage to the dominant male which was able to interfere in and interrupt subdominant courtship.

More importantly, Ewing (1973) found that receptive and unreceptive females formed a group, usually on a male occupied territory. Under very low density conditions (8 males, 4900 cm²/male) receptive females in a small female group mated with the territory holder; other males occupied adjoining territories. With larger female groups, males were attracted to the female site, thus effectively increasing the male density; a dominance hierarchy developed. Although no quantitative data are present on the subject, Ewing (1973) states that "under these circumstances the territory holder no longer has exclusive access to his property but... he does appear to have exclusive rights to his females".

If Ewing's (1973) description is a good approximation of the natural situation, then it may be advantageous for a male to control a group of adult females, regardless of their reproductive history or condition. Receptive females may be attracted to this group thus conferring increased fitness on the male. Also, if teneral males mimic female odour (older males court them) so that receptive females cannot discriminate them from other females, it may be advantageous for a territory holder to monopolize young males. By wing-raising he induces submissive behaviour and immobility in the young male. As the teneral male matures, he becomes a competitor and the dominant male lunges to drive him away.

Breed *et al.* (1980) present data showing that receptive females are olfactorily attracted to dominant males more often than to subdominants. These results are consistent with our predictions. The relative attractiveness of a receptive female to another female vs. to a dominant male will determine whether the male will employ a "harem" to attract other females (at the additional cost of chasing more males away) or adopt a dominant calling strategy. However, such comparisons have not been performed.

Little information is available regarding the subordinate male strategy(ies). Ewing (1973) showed that at low densities subdominant males might be tolerated on the dominant male's territory so long as they remain motionless. Teneral males may thus avoid the consequences of escalation to such overt aggressive acts as lunging and biting. When females were present on a male's territory, other males (beta rank) con-

verged on the site and established territories peripheral to the alpha males's range (Ewing, 1973). With a large female group, male dominance hierarchies were established on the alpha's territory. These observations suggest a conditional male strategy (Cade, 1980) where male strategic decisions are made on the basis of age and male and female population density and demography. Such alternate male reproductive strategies have been documented for a number of species (review : Cade, 1979).

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