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ESCALATION OF AGGRESSION IN *LEPTOTHORAX* ANTS

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SUMMARY

The spatial pattern of escalated aggression is examined in the ant *Leptothorax allardycei*. A total of 973 aggressive interactions were observed, categorized according to the level of aggression achieved and the type of nearby brood. Aggression is more likely to occur in the presence of brood, and escalated aggression is most likely to occur in the presence of the eggs. A model for the decision involved in the initiation of aggression and its subsequent escalation is presented.

RESUME

Escalade de l'agression chez les fourmis Leptothorax

On étudie le modèle spatial de l'escalade de l'agression chez la Fourmi *Leptothorax allardycei*. 973 interactions agressives furent observées, puis classées en fonction du niveau d'agression et en rapport avec les types de couvain présent. L'agression est plus probable en présence du couvain qu'en l'absence de celui-ci, et une escalade de l'agression se montre encore plus probable en présence des œufs. Un schéma présente l'enchaînement des décisions impliquées dans le commencement de l'agression et dans son escalade consécutive.

INTRODUCTION

In an agonistic encounter between two individuals, the aggression is often ritualized. The aggressive action of one individual may, however, be escalated. Escalation of conflict may occur in response to the escalated response of the other individual, as a consequence of asymetries in the value of a resource to the participants or due to asymetries in the abilities of the participants to defend a resource (PARKER, 1984).

Conflicts also arise in a social context. Here the outcome of an agonistic

encounter may be modified depending upon the relatedness of the participants and upon the type of resource under contention. Social hierarchies are well known in wasps (PARDI, 1948 ; WEST-EBERHAR, 1969, 1975, JEANNE, 1972), bees (FREE, 1955) and in ants (COLE, 1981, 1986, 1988). An agonistic encounter may be very brief and ritualized, or it may escalate to higher aggressive levels.

When an aggressive interaction takes place between closely related individuals, the rules of escalation may change. Any potential cost due to monopolizing a resource by another individual must be weighted against the value of the resource to that relative and devalued by the degree of relatedness. Any potential benefit that may be gained by monopolizing a resource through escalation may be devalued by the cost to a close relative.

There is relatively little information concerning the circumstances under which aggressive encounters are escalated, and especially the circumstances under which these interactions are escalated among the members of colonies of social insects. The purpose of this paper is to examine the escalation of aggressive encounters between workers of the myrmicine ant, *Leptothorax allardycei* (Mann). The workers within queenright colonies of this species are arranged into dominance hierarchies based on routine aggressive encounters between individual workers. A fuller description of the social behavior of this species is found in COLE (1981, 1986a, 1986b). It is already known that encounters between the alpha and the beta worker are much more likely to be escalated than encounters between the alpha and the gamma worker (COLE, 1988). In this study I ask under what circumstances, or in what portions of the nest are aggressive interactions escalated ?

MATERIALS AND METHODS

The data were collected during 23 one-half hour observation periods from nine colonies of *Leptothorax allardycei.* Colonies were collected from Sugarloaf Key in the Florida Keys and were maintained in laboratory observation nests. The nests were constructed of glass plates (40 mm × 33 mm) held apart by a balsa wood partition (1.5 mm thickness). Nests were housed in plastic boxes which contain a water source and source of honey-water. Colonies were observed under a dissecting microscope after allowing the colony to acclimate for approximately twenty minutes. The inside of the nest (approximately 20 mm × 16 mm) was divided into a 2 mm × 2 mm grid. The number of eggs, larvae and pupae was recorded in each grid square as well as the position of the queen and of any sexuals.

The data consist of 973 interactions which were scored as to the level of aggression. The grid square in which the aggressive interaction took place was also recorded. The interactions were scored as level one (involving antennal drumming only), level two (in addition, involving tugging with the forelegs), level three (in addition, moving onto the subordinate with the second pair of legs), level four (in addition, moving completely onto the subordinate). Escalation of aggression in the form of biting of legs, thorax, etc. or full-blown fights were not observed in this study. Aggressive levels one through

four represent a hierarchy of escalation in that level four is always preceeded by level three; level three by level two and level two by level one. The highest level of aggression in an interaction was recorded.

RESULTS

Of 973 interactions, 515 (53 %) were escalated to levels two through four. 368 interactions (38 %) were escalated to level two; 108 (11 %) were escalated to level three; 39 (4 %) were escalated to level four.

Table I. — The total number of squares that were counted which contained a particular brood type in relation to the fraction of encounters that occur within each type of square. Encounters occur significantly more frequently in egg, larval and pupal squares than expected and significantly less frequently in squares without brood.

Tableau I. — Nombre total de secteurs carrés de la grille contenant un certain type de couvain en fonction de la fraction de rencontres se produisant pour chaque type de secteur. Les rencontres se produisent significativement plus souvent dans les secteurs à œufs, larves ou pupes et significativement moins souvent dans les secteurs sans couvain.

	Eggs	Larvae	Pupae	No Brood	Total
Number of Squares	79	608	97	1167	1951
Fraction	.040	.312	.050	.598	
Fraction of encounters	.098	.362	.109	.432	N = 973

Aggressive interactions, both escalated and non-escalated, are significantly more likely to take place in the presence of the brood. *Table I* shows the total number of squares with eggs, larvae, pupae and no brood which were counted during this study. The fraction of interactions that take place in each type of square differs significantly from the fraction of that type of square (percentage test, $p < 0.05$ in all cases). For squares with eggs, larvae or pupae, interactions take place more frequently. For squares with no brood in them, interactions take place less frequently. However, there is no effect of brood, *per se*, on the probability of escalation of aggression. When the data are classified as taking place in a brood square or a non-brood square (*table II*) there is no difference in the probability of escalation (Chi-square 2.54, df = 1 $p > .1$).

There was an effect of the presence of the particular type of brood on the probability of escalation of aggression. *Table III* shows the association between the aggressive level that was achieved in an interaction and the presence of the various categories of brood. In a G test there is an interaction between the category of brood and the level of aggression ($G = 22.2$, df = 9, $p < 0.01$).

Table II. — Escalated encounters classified as to whether they take place in brood or non-brood squares. There is no significantly greater tendency for encounters to escalate in brood squares in general.

Tableau II. — Rencontres en escalade d'agression classées en fonction de l'endroit où elles interviennent : dans les secteurs à couvain ou dans les secteurs sans couvain. Il n'y a pas de tendance significativement plus élevée à la réalisation d'esclalades d'agression dans les secteurs à couvain en général.

	Brood Square	Non-Brood Square	Total
Non-Escalated	248	210	458
Escalated	305	210	515
Total	553	420	973

Chi-square = 2.54, $p > 0.1$.

Table III. — The distribution of the level of aggression in relation to the type of brood found within a square. The entries refer to the number of aggressive acts within a square which contained such a brood type. There is significant heterogeneity in this table.

Tableau III. — Distribution du niveau d'agression en fonction du type de couvain trouvé dans un secteur de la grille. Les entrées du tableau se rapportent au nombre d'actes d'agression dans un secteur contenant un certain type de couvain. Il y a une hétérogénéité significative dans ce tableau.

Aggressive Level	Eggs	Larvae	Pupae	No Brood	Total
1	28	161	59	210	458
2	50	137	37	144	368
3	11	41	9	47	108
4	6	13	1	19	39
Total	95	352	106	420	973

$G = 22.2$, $p < 0.01$.

There seems to be little effect, however, beyond the categorization into escalated versus non-escalated encounters. Splitting the aggressive interactions into levels two, three and four does not appear to give greater insight. *Table IV* shows the data categorized as either non-escalated (level one), or escalated (levels two through four). In a G test there is an obvious relationship between escalation of aggression and neighboring brood ($G = 17.1$, $df = 3$, $p < 0.01$).

The heterogeneity of the response of aggressive escalation to the presence of any type of brood is due to the effects of the eggs to the effects of the pupae. Total aggression occurred with disproportionately high frequency in egg squares as compared to larval or pupal squares. In *table V* is given the

Table IV. — Aggressive encounters classified strictly as to whether the aggression esca lated or non-escalated. Various brood squares differ in the tendency for aggression to be escalated.

Tableau IV. — Rencontres agressives classées selon qu'elles se sont produites avec ou sans escalade. Plusieurs secteurs de couvain diffèrent en fonction de la tendance de l'agression à y être exprimée en escalade.

	Eggs	Larvae	Pupae	No Brood	Total
Non-escalated	28	161	59	210	458
Escalated	67	191	47	210	515

$G = 17.1$, $p < 0.01$.

Table V. — Within brood squares, aggression is more likely to occur in a square with eggs or pupae than in squares with larvae only.

Tableau V. — Parmi les secteurs à couvain, l'agression a plus tendance à apparaître dans un secteur avec œufs ou pupes que dans les secteurs avec uniquement des larves.

	Eggs	Larvae	Pupae	Total
Number of Squares	79	608	97	784
Numbers of Encounters	95	352	106	553
Total	174	960	203	1337

$G = 30.86$, $p < 0.001$.

frequency of aggressive encounters in egg square in comparison to larval and pupal squares. Aggression occurs more frequently in egg squares than in pupal squares than in larval squares (*table V*, $G = 30.9$, $p < 0.001$).

DISCUSSION

The above results suggest a model for the " decision-making " process involved in initiating an aggressive interaction and the subsequent escalation of aggression. This model is outlined as a flow chart in *figure 1*. For the decision aggression : no aggression or the decision escalation : no escalation, there is a large stochastic element. Escalated aggression may occur under any set of local conditions, however the nature of local conditions alters the probability of various outcomes. The probability of engaging in an aggressive act depends upon the presence of brood. The probability of escalating the aggressive action depends on the specific kind of brood. The level to which the aggression is escalated does not appear to bear any relation to local conditions (*tables II and III*). The ultimate level of an aggressive interaction

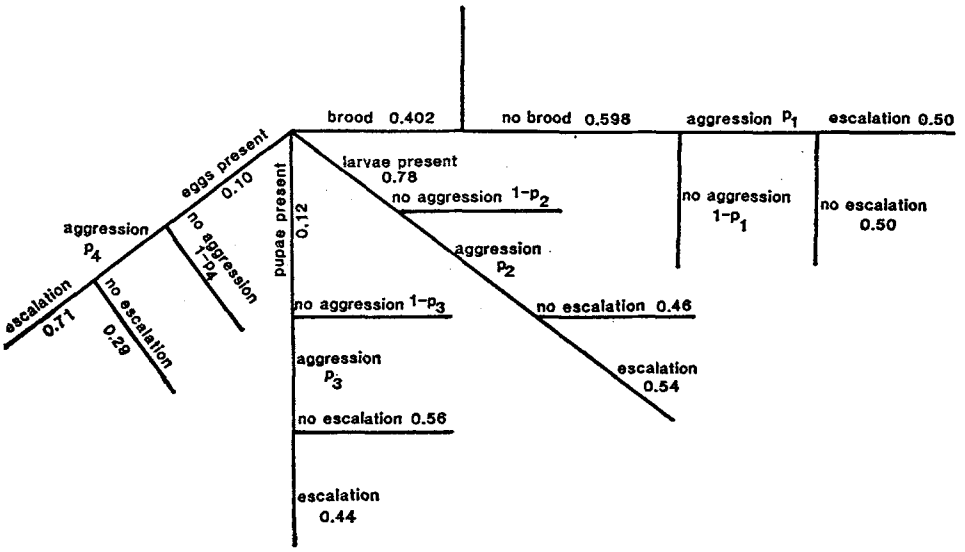

Fig. 1. — Flow chart for decisions involved in aggression and subsequent escalation.

Fig. 1. — Diagramme des successions impliquées dans l'agression et l'escalade consécutive.

is, perhaps, a function of the individual ants involved or other uncontrolled factors. The subsequent discussion will involve only escalated versus non-escalated conflict. The specific level of escalation will be regarded solely as stochastic.

At the first decision node the assessment is whether or not any brood are present. The fraction of squares with brood in the study nests is taken to be an estimate of the probability of the presence of brood and is known from *table I* to be .402. The fraction of squares with no brood was .598. The presence of brood alters the subsequent probability of aggression. If no brood is present, the probability of aggression is p_1. The probability of escalation of the aggression is known from the data (*table IV*) to be 0.50.

If brood are present, the probability of aggression changes depending upon whether the brood are eggs, larvae or pupae (*table V*). If there are larvae among the brood present, then the probability of aggression is p_2. The probability that there will be larvae is 0.78. The probability of escalation of the aggression is known from *table III* to be 0.54. The probability that there will be pupae is 0.12. If there are pupae present the probability of aggression is p_3. The probability of escalated conflict when there are pupae present is 0.44. The probability of escalation of conflict is the same when there are only larvae or pupae present as when there are no brood present. The probability that there will be eggs present given that there are brood present

is 0.10. If there are eggs present the probability of aggression is p_4. The probability that this aggression is escalated (from *table III*) is 0.71.

There are four unknowns in this model of the escalation of aggression, the probability of aggression in the presence of the eggs, of pupae, of larvae or in the presence of no brood. It is difficult to obtain an independent measure of p_1, p_2, p_3 and p_4. In order to obtain the observed probabilities of aggression, the ratio $p_1 : p_2 : p_3 : p_4$ must be 1 : 1.60 : 3.15 : 3.39. However, this still, allows an infinite number of possibilities because of the unknown fraction of times that aggression does not occur.

It is possible to estimate the total probability of non-aggression as the fraction of the time budget not involved in agonistic behavior. For *Leptothorax allardycei* this is 0.932 (COLE, 1986). If the overall probability of non-aggression is 0.932 the one can make the following estimates $p_1 = 0.049$, $p_2 = 0.078$, $p_3 = 0.154$, $p_4 = 0.166$. Since the estimate of the fraction of time involved in agonistic activity involves both aggressive and submissive behavior, these estimates represent upper bounds.

Some alternative models for the series of decisions involved in being aggressive and escalating aggression are not consistent with the observations. The decision aggression/no aggression must be made after an assessment has been made of the presence of the kinds of brood. The decision escalation/no escalation is made after assessing further the category of brood nearby. The data of *tables V and VI* indicate that the presence of various categories of brood changes the total number of aggressive interactions. The data indicate that the presence of brood is distinguished as : no brood, larvae, pupae, eggs.

The motivation for aggressive interaction among workers of *Leptothorax allardycei* is to establish, signal or maintain dominance hierarchy rank. High rank correlates with a higher amount of reproduction and a lower probability that eggs will be destroyed by lower-ranking nestmates. Asymetries in aggression can be associated with resource holding potential or with resource value (see PARKER, 1984 for review). In this situation the resource value seems the more relevant characteristic.

The need to signal dominance status should be higher in the vicinity of brood than when there are no brood present. Further, escalation should be more likely in the presence of the eggs because the value of the resource to the dominant is much higher than the value to the subordinate. Eggs are more likely to be the offspring of the dominant than the offspring of the subordinate. The dominant should have more to lose from egg destruction due to the presence of a subordinate in the vicinity of the eggs and, thus, should have a greater tendency to escalate aggression to higher levels.

The pattern of aggression observed within the colony is consistent with this interpretation. Aggression is more likely to occur in a square which contains brood (*table IV*). Non-escalated aggression is as likely to occur in

an egg square as in another brood square (*table VII*), however, escalated aggression is far more likely to occur in the vicinity of the eggs than in the vicinity of other brood (*table V* and *table VII*). The greater tendency for aggression in the vicinity of the pupae, does not fit easily into an interpretation based on the defense of reproductive output.

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