

Ritualized Combat and Intercolony Communication in Ants

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(Received 23 February 1982, and in revised form 8 June 1982)

Colonies of the honey ant *Myrmecocystus mimicus* engage each other in elaborate display tournaments. Hundreds of ants are often involved, but almost no physical fights occur. Instead, opponents confront one another in highly aggressive displays, during which they walk on stilt legs while raising their abdomens and heads. The tournaments serve as temporary spatial borders within which food gathering occurs. In this study we develop the hypothesis that tournaments are a mechanism of intercolony communication, which opposing colonies use to gauge each other's strength. Models are proposed for the behavioral procedures that seem most likely to underly this capacity. For the first time it is possible to ascertain and compare the properties of such models in relation to a body of test data. It appears probable to us that intercolony communication in this species of ant may depend upon a novel capacity for integrative information harvesting by individual workers.

1. Introduction

Although all-out fights between members of the same species, resulting in injuries or even death, are more frequent than previously thought (for reviews see Wilson, 1975; Geist, 1978), ritualized fights or display tournaments are common features in animal contests. Ethologists long accepted group selection as the reason for the evolution of antagonistic display behavior and convention in intraspecific combat, arguing that inhibiting mechanisms and threat displays are beneficial to the survival of the species (Lorenz, 1963, 1978; Wynne-Edwards, 1962; Eibl-Eibesfeldt, 1975). Since all-out contests would militate against the survival of the species, the

hypothesis was that ritualizations of acts of fighting and intention movements of attack have replaced injurious behavior. "That is, show replaced force" (Geist, 1978).

From his detailed field observations of antagonistic behavior of mountain sheep and mountain goats, Geist (1966, 1967, 1968, 1971) came to a different conclusion: injury during intraspecific combat is reduced "less by inhibitions against using weapons than by skillful uses of defense strategies, behaviors, and morphological adaptations". According to Geist (1978), a "ritual consists of postures, stances and motions that increase the severity of blows, that maximize the chances of inflicting injury on the opponent and that minimize the chance of the opponent succeeding in his attack". Geist argued that for any given system of armament only a limited number of strategies will maximize the efficiency of attack and defence, and the interaction of these strategies gives rise to the ritualized, species-specific fighting pattern. He further argued that the rare instances of fighting in species with effective weapons and poor defences can be explained as a consequence of the possibility of retaliation. An animal might respond to an escalated attack by counter-attacking, inflicting injury or even death on the aggressor. The aggressor's chances of successful reproduction would be seriously jeopardized. Thus ritualized combat as well as the relatively infrequent occurrences of fatal fighting between members of the same species could now be explained by selection at the individual level.

Subsequently, and independently from Geist's considerations, Maynard Smith & Price (1973), Maynard Smith (1974) and later Maynard Smith & Parker (1976) developed a number of models of the evolution of behavioral strategies in contest situations, showing that ritualized fighting can evolve so as to maximize individual fitness. To reach these conclusions, Maynard Smith and his co-workers introduced the notion of an evolutionarily stable strategy (ESS) to describe a behavioral activity sequence that, within a specified range of evolutionary options, could not be displaced by an alternative algorithm for interacting with competitors. Their combination of game-theoretic reasoning and ESS concepts has since been used to explain many forms of ritual, bluff and display (Maynard Smith, 1976; Caryl, 1981).

In contrast to most animals however, social insects (particularly ants) regularly stage territorial combats that are not ritualized display. Intense physical fighting takes place, resulting in the death of many participants (Hölldobler, 1976a, 1979; Hölldobler & Wilson, 1978; Mabelis, 1979 and others). However, territories of ant societies are defended cooperatively by the usually sterile worker castes, and because of the division of labor between reproductive individuals and the workers, fatalities caused by

territorial defence have a different qualitative significance for social insects as compared to solitary animals. The death of a sterile worker represents an energy and labor debit, rather than destruction of a reproductive agent. In fact, worker death might more than offset its costs by bringing or maintaining resources and colony security.

Nevertheless, ritualized combat is also known to exist in a few ant species. Its ecological significance has recently been analyzed in the honey ant *Myrmecocystus mimicus* (Hölldobler 1976b, 1982; Hölldobler & Lumsden, 1980). These ants conduct tournaments in which hundreds of ants are often involved, but almost no physical fights occur. Instead, individual ants engage each other in highly stereotyped aggressive displays. During these tournaments spatiotemporal territories are defended, and simultaneously opposing colonies seem to assess each others' strength. Depending on the outcome of this mutual assessment the opponents either continue to fight a ritualized combat or one colony, which is considerably stronger than the other one, will escalate the contest into the raiding and enslavement of the weaker colony.

Despite their remarkable properties and their significance to the subject of behavioral ecology (Hölldobler & Lumsden, 1980), the ethological processes underlying these tournaments have received little attention from the analytic point of view. In the following we present a theoretical study of the behavioral mechanisms that we believe are likely to be involved in the mutual assessment of strength of opposing colonies during ritualized combat in *Myrmecocystus mimicus*. Analysis of this species in terms of the ultimate adaptive rationale of its territorial behavior is begun elsewhere (Hölldobler & Lumsden, 1980) and still involves many opportunities for quantitative game-theoretic modelling.

2. Natural History of Territoriality in *Myrmecocystus mimicus*

The results of the behavior-ecological analysis of territoriality of *M. mimicus* has been previously reported in Hölldobler (1976a, 1982) and Hölldobler & Lumsden (1980). In the following we briefly summarize these findings.

TERRITORIAL STRATEGY

Myrmecocystus mimicus uses termites as a major food source. The temporal and spatial distribution of termite galleries is highly unpredictable. Since there is little point in defending an area that is unlikely to provide adequate food in a given time, *Myrmecocystus* does not establish fixed

territorial borders around its foraging range, in contrast for example to the situation in the weaver ant *Oecophylla* (Hölldobler, 1979; Hölldobler & Lumsden, 1980). Since there are no well established territorial borders, aggressive mass confrontations with conspecific competitors are much more frequent in *M. mimicus* than in many other ant species, in which neighboring conspecific colonies establish and maintain separate foraging territories. Although fighting in the latter group can at certain times be heavy and costly, once the territorial borders are established the physical confrontations decline sharply. If the frequent massive aggressive interferences between neighboring colonies of *M. mimicus* were as violent as the physical combat in some of the other territorial species, they would result in a constant and heavy drain on the worker force. Thus, the display fight tournaments seem to be the much more economical strategy for defending spatiotemporal territories. Only when one colony is considerably weaker does it risk being overrun by the adjacent stronger colony, having its queen killed, and its workers being either killed or enslaved by the stronger colony.

THE DISPLAY BEHAVIOR

During the tournament contests the ants walk on stilt legs while raising the gaster and head. When two hostile workers meet, they initially turn to confront each other head on. Subsequently they engage in a more prolonged lateral display, during which they raise the gaster even higher and bend it toward the opponent (Fig. 1). Simultaneously they drum intensively with their antennae on and around each other's abdomen, and frequently kick with their legs against the opponent. This is almost the only physical contact, although each ant seems to push sideways as if trying to dislodge the other. After a few seconds one of the ants usually yields and the encounter ends. The ants continue to move on stilt legs, soon meet other opponents, and the whole ceremony is repeated.

In a tournament situation encounters with nestmates lasted only 1–2 seconds and were terminated by a brief jerking movement of the body. They usually did not develop into a lateral display. The duration of the individual encounters between opponents can vary considerably. In the initial phase of a tournament the display activity was usually very hectic. The display encounters lasted only 1–3 seconds and could escalate into a real physical biting fight. An intermediate level of escalation was characterized by sham attack behavior, where after a brief lateral display one ant lunged with open mandibles towards the yielding opponent without actually physically attacking it; but in a more stabilized tournament situation, for example in tournaments where both colonies were represented by approxi-

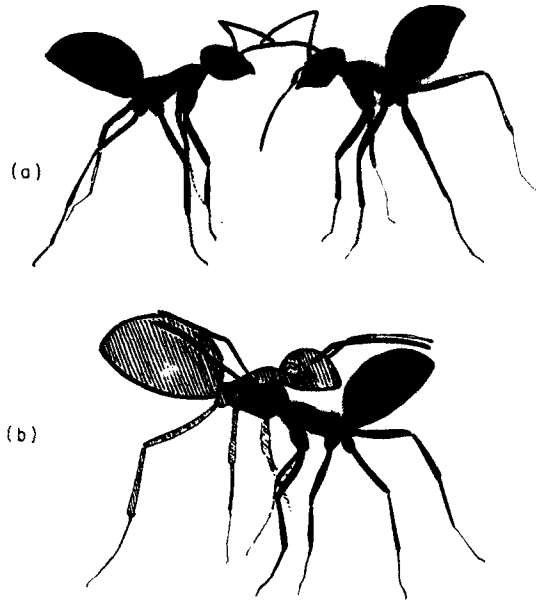


FIG. 1. The opponents in a *Myrmecocystus mimicus* display fight adopt highly stereotyped postures. (a) All such interactions begin with head-on displays. If the participants are nestmates, the display breaks off at this stage, usually with a jerking motion. If the workers are from different nests, the interaction develops into a sequence of lateral displays (b).

mately the same number of workers, individual display encounters were often considerably longer (up to 30 seconds), and sham attacks as well as biting fights were extremely rare.

A comparative analysis of the behavioral patterns of intraspecific fighting in several formicine species strongly suggests that the threat display between two opponents of *M. mimicus* evolved from intention movements of attack. We have recorded similar behavioral patterns in the initial phase of physical fighting in several other *Myrmecocystus* species, in *Oecophylla*, and in *Camponotus* (Hölldobler & Wilson, 1978; Hölldobler, unpublished data).

Finally, one other feature appears to be important during the display tournament, and that is the size of the individual ants. If a large and a small ant were matched in a display encounter, usually the smaller ant yielded. In fact, measuring the width of the head and length of the thorax of the ants we found that the tournamenting ants were usually larger on the average than the foragers of the colony. Frequently we observed that displaying ants not only walked with their legs in a stilt-like position while simultaneously raising their gasters and heads, but in addition some of

them even seemed to inflate their gasters, so that the tergites were raised and the whole gaster appeared to be considerably larger.

During the tournaments scout ants repeatedly return to their nest, where they recruit reinforcements of 100 or more workers to the tournament area. Usually the recruitment of a new major army by one colony is countered by a similar action of the opposing party. The relative sizes of the opposing forces thus tend to reflect the relative sizes of the two colonies. If the colonies are markedly different in size, so that one has a significant majority of the ants engaged in tournament interactions, the tournament is shifted more and more toward the nest of the weaker colony. When one of the opposing colonies is still an incipient colony and therefore unable to summon a large defending worker force, the tournaments end quickly and the weaker colony is raided by the mature colony. During these raids the foreign workers invade the nest, the queen of the resident colony is killed or driven off, and the larvae, pupae, and callow workers are carried or dragged to the nest of the raiders. There, some of the captives may be killed and eaten, but many are enslaved and integrated into the worker force of the victors' colony.

3. Mechanisms of Intercolony Communication

On the basis of these observations we hypothesize that opposing colonies might be able to assess each other's strength during tournament interactions. We postulate that numerous threat displays between individual workers are integrated into a massive group display between opposing colonies. In parallel to solitary animals, the groups' "strategic decisions" to retreat, to recruit, to continue to fight by display or convention, or to launch an escalated attack depend on information about the strength of the opposing colony, obtained during the ritualized combats at the tournament site.

Although the mechanisms by which the information is gathered and transmitted cannot yet be identified uniquely, the available data permit us to suggest a narrow range of possibilities. At present three mechanisms appear to us to be especially likely, and thus to merit more explicit formulation: (1) behavior in which worker ants estimate the proportion of nestmates versus opponents on the tournament site ("head counting"); (2) behavior in which individual ants sample the sizes of opponents ("caste polling"), obtaining information about the stage of development of the opponent colony; and (3) behavior in which workers respond not to collectivities of sampled encounters, but instead modulate tournament behavior by acting on more local conditions, such as the presence of opponents uninvolved in display fights.

HEAD COUNTING

A tournament involving N participants from two colonies, say C_1 and C_2 , contains n_1 workers from C_1 and n_2 from C_2 such that $n_1 + n_2 = N$. As a combatant moves through the tournament it progresses through a sequence composed of both display fights with members of the opposing colony and signal interactions with nestmates. A worker has probability $p = n_1/N$ of encountering a member of colony C_1 and $(1 - p)$ of encountering a member of colony C_2 , provided that the successive confrontations are essentially independent of each other.

The assumption of probabilistically independent encounters is an accurate approximation if there exists sufficient activity in the tournament to re-randomize the participants after every encounter. Real tournaments between colonies of *Myrmecocystus mimicus* are undoubtedly characterized by inter-encounter correlations due, for example, to the finite mobility of the worker ants. However, our qualitative visual inspections of many cine film records of tournaments suggest to us that intra-tournament movement is often hectic, especially in the initial phase, with each participant covering much of the tournament site in a relatively short time. Thus the assumption of probabilistic independence appears to be a useful first approximation.

A sequence of M ritualized encounters in such a tournament is a Bernoulli process with density

$$\rho(m_1) = \binom{M}{m_1} p^{m_1} (1-p)^{(M-m_1)} \quad (3.1)$$

where p is the ratio n_1/N and m_1 is the number of interactions with workers from colony C_1 . Because a display fight rarely escalates into an altercation causing injury or death to any of its participants, as a potential information-gathering mechanism a sequence of ritualized encounters is equivalent to sampling with replacement. The sample contains information about the strengths of the colonies as they are represented on the tournament site

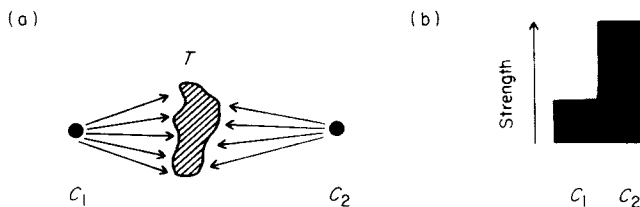


FIG. 2. (a) Two colonies, C_1 and C_2 , dispatch workers to a tournament site T . The number n_1 of workers from colony C_1 is that nest's strength in T ; n_2 is the strength of C_2 . (b) Through tournaments, colonies have the opportunity to obtain information about their comparative strengths.

(Fig. 2). This information can be harvested if tallies of encounters with nestmates and with opponents are maintained by the workers. It can then be used to determine subsequent patterns of behavior, such as recruitment of additional armies and group attack or retreat.

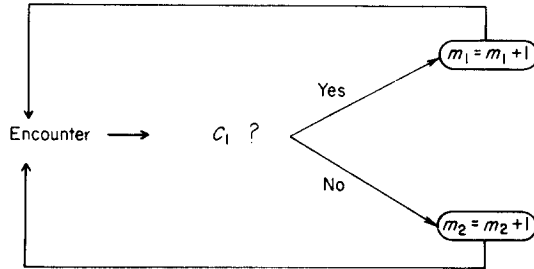


FIG. 3. Computational organization of the head-counting mechanism. m_1 = number of workers encountered from colony C_1 ; m_2 = number of workers encountered from colony C_2 . See text for discussion.

At first sight it might appear that such an integrative capacity (Fig. 3) is beyond the evolutionary reach of these animals, whose nervous systems contain $\approx 10^5$ neurons. There is evidence that such a conclusion would be premature. Certain species of Hymenoptera, particularly among the ants and the social bees, are now known to have a capacity to handle considerable information. The information load transmitted in systems used by social insects for recruitment to food and nest sites can amount to 2 to 4 bits (Haldane & Spurway, 1954; Wilson, 1962; Wilson, 1975, pp. 194–200). A sequence of M ritualized encounters in a *Myrmecocystus* tournament has $M + 1$ possible states of colony strength information, corresponding to 0, 1, 2, ..., M encounters with workers from colony C_1 . Thus even in sequences 100 to 1000 encounters long the gathered information amounts to 7 to 10 bits, near the range of known values and well within the theoretical storage capacity of brains endowed with the size and complexity of Hymenopteran nervous systems (Lumsden & Wilson, 1981, p. 335).

There is further pertinent evidence. In a series of remarkable studies on nest site selection in the honey bee *Apis mellifera*, Seeley (1977) has established that scout bees can integrate information about the linear dimensions of tree cavities into estimates of volume. Moreover, the numerous experimental studies on the orientation and communication behavior in honeybees have revealed several other examples of complex integrative capacities in the Hymenoptera. While not bearing directly on the existence of a capacity for integrative sampling in *Myrmecocystus*

mimicus, these findings suggest that its presence would not be entirely without precedent. We conclude that it is fruitful to more fully develop models based on the assumptions of head-counting and other mechanisms of integrative learning.

It is possible to work out the information-gathering requirements of the head-counting strategy. If the probability is to be $1 - \alpha$ that a worker will estimate the colony strength parameter $p \in [0, 1]$ to within $\pm\beta$ of its true value, then application of the central limit theorem to the process (3.1) leads at once to the conclusion that the minimum number of encounters required is

$$M = p(1-p)(Z_{\alpha/2})^2/\beta^2 \quad (3.2)$$

where

$$\int_{Z_{\alpha/2}}^{\infty} N(x) dx = \alpha/2 \quad (3.3)$$

and $N(x)$ is the standard normal density for the probability variate x (Hamburg, 1977, p. 250). In these equations, $Z_{\alpha/2}$ is that value of x for which the total area under each tail, $[-\infty, Z_{\alpha/2}]$ and $[Z_{\alpha/2}, \infty]$, of $N(x)$ is equal to $\alpha/2$.

The minimum number of encounters M varies inversely with β^2 in equation (3.2), suggesting that the load on the information integrating mechanism is a sensitive function of its precision. For example, to narrow the window of uncertainty around p from $\beta = \pm 0.1$ to $\beta = \pm 0.01$ requires M to increase by a factor of 100. Contours of $M(p|\beta)$ are plotted in Figure 4 for different values of the precision parameter β , where for the purposes of illustration we have selected the reliability, $1 - \alpha$, to equal 0.95, that is, 95% of the workers estimate colony strength to within the precision specified. Empirical estimates of $Z_{\alpha/2}$ are not yet available, but the 0.95 value is likely to err in the conservative direction relative to M , overestimating rather than underestimating the required number of ritualized encounters.

The function $M(p)$ attains maximal values when the two colonies are most evenly matched. Relatively long chains of ritualized combat are then required to assess colony strength, numbering in the thousands of interactions for high levels of precision. In contrast, when one colony greatly outnumbers the other relative proportions can be assessed with high precision using much shorter sequences of ritualized encounters. Thus precise head counting and the associated responses of recruitment or raiding will take comparatively longer when the opposing forces are more or less equally matched. The equivalent information can be obtained more quickly when the match is very uneven.

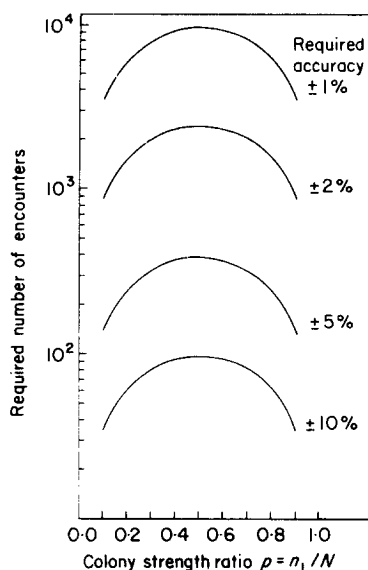


FIG. 4. The number M of ritualized encounters required by a head counting mechanism in order to estimate the relative colony strength p with a given precision $p \pm \beta$. Contours of $M(p|\beta)$ are illustrated for the case in which the head-counting mechanism is 95% reliable.

Our data are in rough accord with this pattern. Tournaments between colonies of similar strength can last for days, with relatively infrequent recruitment to each day's tournament site. Contests between grossly unmatched forces are more likely to escalate quickly, with workers from the weaker side leaving the site frequently to recruit additional armies. When the colony is too small to equalize an initial disparity, the tournament itself is likely to end quickly, culminating in a raid on the weaker colony.

Equation (3.2) for $M(p)$ presupposes that the tournaments are sufficiently large that the sample M does not exhaust N ; it is accurate for $M \geq 20N$ and implies tournaments requiring hundreds of workers for lower levels of precision (for example $\pm 10\%$) and thousands of workers for higher precision (for example, $\pm 1\%$). Fully-developed tournaments between *M. mimicus* colonies usually involve hundreds of ants, an observation suggesting that if head counting is carried out by members of this species, then it may be performed at lower levels of precision. However, even at precision levels on the order of $\pm 10\%$, ratios p indicative of very unequal strengths (in the range 8:2 to 9:1) would not suffer qualitative distortion. The stronger colony could still be determined with near-certainty. When the colonies are much more evenly matched, precisions of $\pm 10\%$ more easily

lead to erroneous qualitative determinations of colony strength. Decision-making in such a circumstance therefore contains elements of greater risk and uncertainty.

Again we are struck with the similarities between this pattern and the natural history of these honey ants. We have found that when colonies are equally matched the tournaments are often prolonged and inconclusive, shifting back and forth in the region separating the colonies, and dying away only after one or both colonies have exhausted the food resources in the areas temporarily defended. When the strengths are very unequal and one force is ten or more times the size of the other, the tournaments more often end not only quickly but also decisively, with the stronger force mounting a raid on the other colony.

Limits to precision of approximately $\pm 10\%$ would roughly divide the range of p into a small number of coarse-grained intervals of width ≥ 0.1 . The information transmission capacity of such a system is 2–3 bits, a range in accord with the capacities found in other social insects, (Haldane & Spurway, 1954; Wilson, 1962, 1975).

We can estimate how long it takes a head counter to assess the strengths of the colonies. Let the probability per unit time be λ that an encounter will take place, such that the likelihood of an encounter within any time interval δt is $\lambda \delta t$, and the probability of an encounter involving more than two workers is negligible. Many-participant encounters do occur in *Myrmecocystus mimicus*, but their number relative to binary encounters is usually small. If $P(m, t)$ is the likelihood that a worker's total number of ritualized encounters by time t is equal to m given that it was zero at some arbitrary time $t = 0$, then

$$P(m, t) = \begin{cases} e^{-\lambda t} (\lambda t)^m / m! & m \geq 0 \\ 0 & m < 0 \end{cases} \quad (3.4)$$

(Lumsden & Wilson, 1981, p. 32) such that the rate of growth of the expected value \bar{m} is

$$\frac{d\bar{m}}{dt} = \lambda. \quad (3.5)$$

The interval required for m to equal M has duration M/λ . In a fully-developed *Myrmecocystus mimicus* tournament workers encounter one another every few seconds. If λ is on the order of one per second, the tournament duration expected on the basis of these simple estimates is on the order of minutes to hours between very unequal colonies (the M required for reliable information gathering can be small—recall Fig. 4), and hours to days when colony strengths are more equally matched (the

M required is then considerably larger). This order of time scales is similar to that found in real tournaments (Hölldobler, 1982).

POLLING THE CASTE DISTRIBUTION

During individual display fights the contestants appear to gauge each other's size. We noted in section 2 that during the encounters an opponent's abdominal region is antennated extensively over much of its surface while simultaneously the contestants push and kick each other. One or both fighters are often dislodged during these procedures. Even deceit appears to play a role in the interactions. The combatants often seem to pretend to be larger than they are by walking high on stilt legs, by inflating their gasters, and by surmounting small pebbles. How can this microstrategy between individual workers contribute to the macrostrategy of territorial competition among colonies?

It appears that in *Myrmecocystus mimicus* the larger worker type is especially effective in tournaments (Hölldobler, 1982). Because of its size it is usually the victor in a display fight with a smaller opponent. On the other hand from the standpoint of harvestable information, the mere presence of such workers represents a sign of colony size and strength. Our reasoning is as follows. The caste systems of ants usually consist only of smaller workers during the early stages of colony development, when the colony itself is still small. Larger workers are manufactured later, when the colony has entered a more mature state of development and is able to sustain the greater ergonomic costs involved in their production. Thus the presence of larger workers on a tournament site can act as a cue, indicating that their nest has achieved a certain range of probable sizes. If this capacity to recognize large workers is enhanced with the capability of a worker to determine the proportion of a colony's larger workers on the site (Fig. 5),

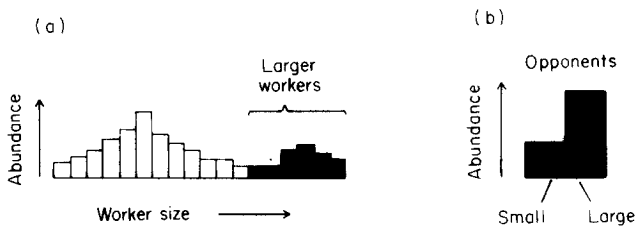


FIG. 5. (a) Because of their relatively high ergonomic cost, larger workers are in general produced only when a colony has surpassed a certain minimum size. (b) Detection of large opponents in a tournament can therefore transmit information about the probable strength of their colony.

then a crude, coarse-grained image of the opponent colony's caste system is harvested, transmitting more accurately than contact with a single larger worker information about colony size.

Such information could be subtly related to the head-counting process described earlier. *A priori* a worker will not have information about the colony strength parameter p , and the regulation of M will be problematical. The conservative response to this situation would take the worst case and regulate M according to $p \approx 0.5$. The sequences of ritualized encounters so produced would be larger than necessary for the determination of high or low values of p , but would achieve this function while maintaining some precision for more equally matched colonies. Signals corresponding to the detection of large workers would allow M to be regulated more efficiently by providing initial estimates of p , which could then be used to determine a suitable length for the encounter sequences (recall equation (3.2)).

A simple computational structure for caste polling (Fig. 6) resembles the head-counting algorithm (Fig. 3), and by our previous arguments comprises an adaptive design that may not be overly complex. Its operation is described by equations (3.2) and (3.4), where now $p = n_L / (n_L + n_S)$, with n_L representing the number of larger opponent workers and n_S the number of smaller opponents on the site, and λ the probability per unit time of an encounter with an opponent.

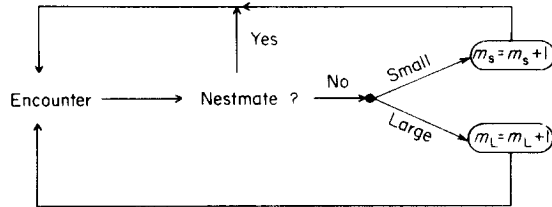


FIG. 6. Computational organization of the caste polling mechanism. m_L , number of larger opponent workers encountered; m_S , number of smaller opponent workers encountered. See text for discussion.

QUEUE FLOODING: A NULL HYPOTHESIS

Is it possible that the tournaments are not sites for integrative sampling, and that the group behaviors we have described are epiphenomena of a more minimal capacity for worker learning? We believe that the answer to this question is yes, and that it forms a proper null hypothesis against which models of intercolony communication based on integrative learning can be tested.

In order to obtain one formulation of such a null hypothesis, let us recall that many species of ants, including *Myrmecocystus mimicus*, use recruitment signals to bring groups of workers to food sites. The ethological mechanisms generating this mass behavior can be starkly simple. For example, in the fire ant *Solenopsis saevissima* (Wilson, 1962) a worker finding a rich new food source is very likely to recruit nestmates, using a combination of signals that includes the laying of a chemical trail. Recruits subsequently arriving at the food site are likely to add to this trail if they return home laden with booty. Volatile chemical deposits accumulate, causing a dramatic outflux of workers that dies away as the food source is covered by workers and progressively fewer returning workers emit recruitment signals. This impressive instance of group homeostasis appears to be created by the responses of the workers to their own foraging success, rather than by an ability to census the global or overall state of the food site.

Similarly in the tournaments of *Myrmecocystus mimicus*, workers might not engage in procedures of active, global harvesting of information, such as head counting and caste polling. Information about colony strength might instead take effect passively, with workers responding to more local cues produced by the mass dynamics of the tournament. For example, a worker “serves up” displays to its partners in encounters. If both colonies are equally matched then most workers will on the average be engaged in a display fight. When one side is outnumbered, “waiting lines” will exist on the stronger side, queues composed of workers unable to find free opponents. The detection of a supply of such unengaged workers might in itself be sufficient to release recruitment behavior. There is then no integrative procedure of large-scale sampling to tally the colony strengths, and the requirements for information storage and processing by workers are

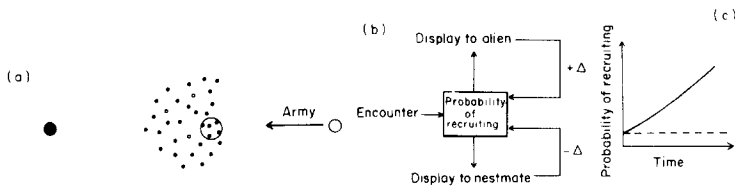


FIG. 7. (a) The detection of unengaged opponents (the circle overlaid on the tournament site) might be sufficient to make likely the recruitment of additional armies by workers on the weaker side. (b) Example of a simple ethological procedure that regulates the likelihood of recruitment in accord with local conditions in the tournament. Encountering a worker from the opponent colony raises the likelihood that a recruitment response will occur. Encountering a nestmate lowers this probability. (c) When a worker is outnumbered by opponents, the probability of recruitment tends to shift upward (solid line). When the forces are balanced, the probability drifts around a more constant value (dashed line). For clarity of rendition these random walks have been sketched as smooth curves.

less demanding (Fig. 7). However, the behavior brings recruits to the tournament when they are most needed (Fig. 8(a)). Equivalent numbers of opponents build up and the tournament stabilizes in structure (Fig. 8(b)), enlarging only more slowly through occasional bouts of bilateral recruitment. When the balance of power cannot be equilibrated, transformation into a raid on the weaker colony becomes likely as unengaged workers move into the alien territory (Fig. 8(c)).

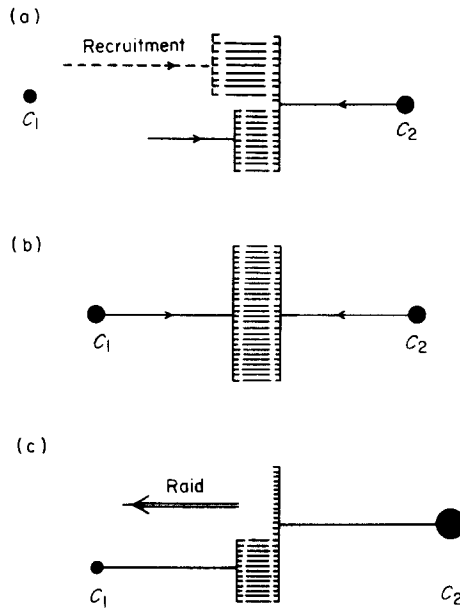


FIG. 8. Mass effects of queue flooding (a). A supply of unengaged opponents releases recruiting behavior, which tends to move the tournament toward equalized strengths (b). If the colony is too small to respond with additional armies, the tournament develops into a raid (c).

TESTING THE MODELS

At present, the available data are insufficient to test the alternatives of active, global procedures versus more passive, local strategies of strength determination. However, the kind of data required from future studies can be suggested. Detailed characterization of the paths followed by individual workers during a tournament will be particularly revealing. If movement is for the most part restricted to small regions within the tournament area, then the evidence will favor passive local procedures such as queue flooding and the detection of isolated pools of unengaged competitors. In the

head-counting and caste-polling mechanisms as developed here in simplest form, individual workers are postulated to cover much of the tournament area and sample many workers from both colonies during their excursions.

Differentiation between head counting and caste-polling might be conducted using artificially arranged or modified tournaments. Wilson (1980*a,b*) has shown that it is possible to modify the effective caste distribution of an ant colony by removing workers of specific size classes from the groups leaving the nest. By applying this "pseudo-mutant method" (Wilson, 1980*a,b*) to *Myrmecocystus mimicus*, data could be gathered from tournaments in which both the number and size of opponents were controlled. The head-counting mechanism will be called into question if normal recruitment and raid dynamics does not emerge when all combatants are the same size and the number from each colony unequal. Conversely, caste-polling will not be favored if normal tournamenting fails to appear when opposing forces are equal in size but very different in the proportion of large workers to small workers.

4. Discussion

Several features in the social insects, particularly in ants, make the behavioral organization of territoriality considerably more complex than that of solitary animals. The establishment and maintenance of territories are based on a division of labor and a complex communication system. The analyses of territorial strategies in ants comprise the study of the design and spatio-temporal structure of the territory as well as the social mechanisms through which the insect society pursues its territorial strategy.

In this study we have argued that intercolony communication is also a major feature of territorial behavior in ants. In fact, the insect society can be treated like a single organism (a superorganism) which, like any other territorial solitary animal, negotiates a territorial contract with its neighbour, employing a whole repertory of strategies in which strength is displayed. The success of these "negotiations" depends on the size of the colony. The possibility that insect societies engage in an economics of information exchange has previously been little explored.

The results of the behavioral ecological analysis of the foraging pattern and the spatiotemporal territories of the honey ant species *Myrmecocystus mimicus* strongly suggest that during territorial tournaments opposing colonies somehow assess each other's strength. The phenomenon can lead to intraspecific slavery or to a temporary dominance order among neighboring colonies. The underlying mechanisms of intercolony communication might be remarkably simple. Whereas tournaments involve many par-

ticipants and are the sites of rapidly shifting activity, structurally they are assemblages of similar components, the separate display fights. Pilot models based on this observation appear to be highly heuristic at the present stage of analysis. They are simple enough to make the possible mechanisms clear, but they also retain enough realism to suggest falsifiable hypotheses. At the present stage, however, it is not yet possible to decide whether this remarkable form of group behavior involves a capacity for integrative information harvesting by the workers, such as "head counting", or depends primarily upon responses in which workers utilize only more local conditions on the tournament site, such as the presence of unengaged opponents. These models comprise competing hypotheses. We believe that they are empirically testable, and that the resolution will be of great interest in understanding the mechanisms of territorial behavior in ants.

This work was supported by funds from the Harry Frank Guggenheim Foundation (CJL) and by grant BNS 80-02613 from the National Science Foundation (BH).

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