EVOLUTION OF TERRITORIALITY AND NESTMATE RECOGNITION SYSTEMS IN ANTS

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Summary. Data on chemical signals used by ants in territorial behavior and nestmate recognition are reviewed and ordered according to their complexity and/or negentropy content. The evolutionary trends observed suggest: a) No relationship between polygyny and nestmate recognition systems. b) A relationship between territorial recognition and nestmate recognition systems. c) A trend towards simplification of recognition signals. d) The existence of analogous evolution in agonistic behavior. It is proposed that ants actually use a home-environment recognition system rather than separate recognition systems for territory and nestmates. A hypothesis for this new recognition system is developed. On the other hand, certain behavioral features such as ritualized intraspecific aggression, seem to hint at the existence of long-term forces such as selection at the community and/or population level.

Introduction

Nestmate recognition systems have been studied extensively in relation to kin-recognition, as a way of testing kin-selection theory (see review in CROZIER and DIX, 1979; HOlldobler and Michener, 1980; Getz, 1981, 1982; Holmes and Sherman, 1983; Gadagkar, 1985). In spite of this, much of the experimental data does not fit the theory (e.g. Gadagkar, 1985; Tsuji and Ito, 1986; West-Eberhard, 1986). Thus, other selective forces may have
helped in shaping nestmate recognition systems in social species and have to be taken into account when studying the evolution of recognition systems in these species.

On the other hand, the concept of territory in ethology, as applied to social organisms, is still controversial (WILSON, 1971; BARONI-URBANI, 1979; JAFFE, 1984b). Definitions of territory have been developed, mainly for solitary or sub-social species, although it is also a common feature in most social organisms. Following the generally accepted definition of territory given by Hölldobler (1979) for social insects, a territory is that part of the home range which is used 'exclusively' and defended against intra-specific intruders. In accordance with this definition, very few of the social insect species studied that mark their territory would qualify as truly territorial, as evidence for fighting related to the territorial mark cannot always be obtained. We believe that his definition, although theoretically reasonable, is not useful in practice. A lack of exclusive use of a territory does not necessarily mean a lack of partition of available space.

Lack of observed aggressive defence of a territory does not exclude the existence of a territory. As nobody will deny, front gardens of residential housings in any village or city are considered as part of the home territory of the inhabitant. Still, it is very difficult, if not impossible, to observe physically aggressive expulsion of unwanted intruders from front gardens. Verbal communication and social instruction seem to be sufficient in most cases for territorial defence in Homo sapiens. Ant societies in many cases, seem to have an equivalent ritualized system for territorial defence. The chemical marking of territories seems to be sufficient to ensure territory ownership, avoiding actual fighting between conspecifics. Although this type of 'active defence' is not normally considered sufficient for defining territories in contemporary ethology, common sense suggests that it is. Thus the error may lie in the current definition of territory. Nearly all behavior, even of the most subtle kind, will in the long-term produce a non-random spatial distribution of foragers of different colonies, if dependent on a colony specific mark on the territory. This is thought to be the consequence of territoriality (DAVIES, 1978). Thus, I think that a functional definition of territory, such as that given in JAFFE and PUCHE (1984), is more useful in the study of social
insects. That is: colony specific recognition of the territory and
differential use of it by workers of different colonies through a colony
dependent variation in behavioral reactions towards it, defines its
existence. Social insects may have evolved more subtle mechanisms for the
partitioning of a territory, which minimize energy expenditure and loss of
workers, than those implied by an active defence of an exclusively used area,
making a revision of the concept of territory necessary (see also
BARONI URBANI, 1979). Marking the territory can be considered to be an active
defence if it gives an advantage to the marking colony (JAFFE and PUCHE,
1984), such as an increased activity of workers on a territory or decreased
alarm behavior compared to a conspecific intruder.

A look into the evolution of the different territorial systems
should give some insight into its significance. Ant societies (all eusocial)
are excellent models for this purpose because of the diversity of their
social behavior. In order to look for the existing trends in the evolution of
territorial behavior and of nestmate recognition systems, this paper reviews
the existing data in the literature. Based on these trends, a reevaluation of
the concept of territory and nestmate recognition is undertaken.

Results

Table I summarizes the existing data on agonistic communication
(where the kind of recognition signal is known) and some important social
features of ant species. Each feature is ranked in accordance to its
complexity, i.e. in accordance to its negentropy content (JAFFE, 1984a)
measured as the amount of transferred information in the case of
communication systems, and in accordance with its absolute value of
complexity if possible (number of individuals per colony for example). In
some cases only descriptions of the type of behavior are given, because no
relation to complexity of the behavior is evident. This is the case of the
decision-making system used by workers during recruitment (JAFFE et al.,
1985). Recruitment communication is considered to be more complex, the more
the three possible kinds of information (presence of food, location of food,
quality of food) are transmitted by workers during food recruitment (JAFFE,
1984a).
Table I. Communication systems of some Formicidae.

<table>
<thead>
<tr>
<th>Species</th>
<th>Recr</th>
<th>Territ</th>
<th>Recog</th>
<th>Alarm</th>
<th>Col</th>
<th>Queen</th>
<th>Caste</th>
<th>References</th>
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<tr>
<td>Atta laevigata</td>
<td>IV A</td>
<td>XQM s</td>
<td>A m</td>
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<td>7</td>
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<td>4</td>
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<td>XQ?</td>
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<td>m</td>
<td>4</td>
<td>M</td>
<td>3</td>
<td>JAFFE and NAVARRO, 1985</td>
</tr>
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<td>X-</td>
<td>NS</td>
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<td>3</td>
<td>M</td>
<td>1</td>
<td>JAFFE and VILLEGAS, 1985</td>
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<td>-</td>
<td>-</td>
<td>?</td>
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<td>M</td>
<td>1</td>
<td>VILLEGAS, 1984</td>
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<td>-</td>
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<td>XQM t</td>
<td>A m-g</td>
<td>m-g</td>
<td>6</td>
<td>M</td>
<td>2</td>
<td>JAFFE and PUCHE, 1984</td>
</tr>
<tr>
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<td>XQM t</td>
<td>A m-g</td>
<td>m-g</td>
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<td>XQM d</td>
<td>A d</td>
<td>m-d</td>
<td>4</td>
<td>P</td>
<td>1</td>
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<td>M</td>
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<td>XQ</td>
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<td>-</td>
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<td>P</td>
<td>1</td>
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<td>X?</td>
<td>NS</td>
<td>m</td>
<td>2</td>
<td>M</td>
<td>1</td>
<td>GOLDSTEIN and TOOFF, 1985</td>
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<td>XQ</td>
<td>A m-g</td>
<td>m-g</td>
<td>3</td>
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<td>1</td>
<td>JAFFE and MARQUEZ, 1987</td>
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<td>XQ</td>
<td>NS</td>
<td>m</td>
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<td>NS</td>
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<td>m-g</td>
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<td>A m</td>
<td>m-g</td>
<td>4</td>
<td>M</td>
<td>1</td>
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<td></td>
<td>XQ?</td>
<td>NS</td>
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<td>FORMICINAE</td>
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<td>m</td>
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<td>g</td>
<td>A m</td>
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<td>Formica rufa</td>
<td>II</td>
<td></td>
<td>X?</td>
<td>?</td>
<td>m</td>
<td>1</td>
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<td>1</td>
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<tr>
<td>Gigantopus destructor</td>
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<td>Azteca foreli</td>
<td>IV</td>
<td>DOLICHODERINAE</td>
<td>XQM</td>
<td>t</td>
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<td>m-g</td>
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<td>m-g</td>
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<td>m-g</td>
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</table>

Territorial behavior is classified into three categories:

1) Presence of territorial behavior, where workers use no odor cues, but use for example visual cues for territory recognition.
2) Recognition of their territory using (in addition to visual cues) chemical cues;
3) Territorial marking with a specific pheromone.

Nestmate recognition is thought to be of two possible kinds:
1) Advanced if a specific signal (in all cases the alarm pheromone) is used [A in Table I]; and
2) Less advanced if non-specific signals (NS), i.e. different signals from those described in 1) (sometimes in addition to alarm pheromones) are used for nestmate recognition. These 'different signals' could include environmental odors adsorbed on the cuticle, cuticular hydrocarbons, or mixtures of various pheromone complexes. In this case, negentropy is related to specificity and not to the number of signals.

Alarm communication is only described in accordance to the known sources of the pheromone, because any indication of the complexity of the signal is lacking in the literature, with the sole exception of the alarm communication in Decophylla longinoda (BRADSHAW et al., 1975).

If we analyze the data in Table I, we find that in the Ponerinae, the species with no recruitment communication, Odontomachus bauri, has also the simplest territorial behavior. It bases its nestmate recognition system on signals which are different from the alarm pheromones. Neoponera apicalis with an incipient recruitment communication system, uses chemical information for regulating territorial behavior, but has a nestmate recognition system apparently not based on a specific signal. Ectatomma ruidum transmits more information in recruitment, has a nestmate recognition system based on signals from the alarm pheromones and its territorial behavior is similar to that of N. apicalis. Therefore, we may order these three species in a gradient of increasing complexity.

If we now observe the situation in the Pseudomyrmecinae, we find that Pseudomyrmex termitarius, with no detectable recruitment communication, with terrestrial habits, and which forms relatively small colonies among Pseudomyrmex species, is the one with a territorial behavior and nestmate recognition system equivalent to Neoponera. P. triplarinus, a symbiotic species which forms large colonies, uses a specific pheromone to mark its
territory and uses the alarm pheromone as signal for its nestmate recognition system.

A similar gradient can be observed among the Dolichoderinae, the Myrmicinae, and especially among the Attini. Here, the recruitment systems seem to be equivalent in complexity, but the colony size and the degree of polymorphism could indicate the societies' complexity.

Again, the primitive species has an agonistic behavior comparable to the Ponerinae, whereas the species forming more complex societies have an agonistic behavior similar to that of *P. triplarinus*.

**Discussion**

**Gestalt odor vs individual odor**

Polygyny does not seem to influence the pattern of agonistic behavior, as is shown by the examples of *Crematogaster* and *Azteca*. This contradicts the suggestion of CROZIER and DIX (1979) and HÜLLEDOBLER and MICHENER (1980), who proposed that polygynic species should use a kind of gestalt odor in order to recognize their nestmates. This does not seem to be the case for these two species, as only alarm pheromones are used as a recognition signal. The chemical composition of pheromones is very probably genetically fixed, and learning of the colony-odor (i.e. the odor of the nestmates) is required in order to recognize nestmates. Thus, a kind of pattern recognition of chemicals from the alarm pheromone (SMITH et al., 1985) is probably used by the workers for nestmate recognition.

**Relation between nestmate recognition and territorial recognition systems**

It is evident from Table I that territorial behavior, nestmate recognition systems and alarm communication, but not recruitment communication, are related. Primitive species, lacking territorial marking behavior, although not necessarily the capacity for territorial recognition, have nestmate recognition systems based on many cues. The more socially advanced species actively mark their territory with chemical signals and use specific pheromones, i.e. alarm pheromones for nestmate recognition. Relative amounts of the different chemicals of a pheromone are characteristic of the colony (e.g. JAFFE and MARCUSE, 1983). Species not advertising their
territory with a pheromone are more sensitive in recognizing foreign conspecific ants, as many different odor signals, i.e. redundant information, are used as nestmate recognition signals. An explanation of the relationship between nestmate recognition mechanisms and territorial behavior could be that ants that do not advertise their territory lack a mechanism for an efficient partition of the available space. Therefore interspecific intercolony contacts are more probable. Thus selective pressure will act on sensitive recognition systems (i.e. redundant recognition signals). In contrast, ants that advertise their territory diminish the probability of random intercolony encounters. They require intraspecific recognition only in intraspecific combats, where alarm pheromones play the main role in organizing the fight. From the aforementioned arguments, I propose that recognition systems based on alarm pheromones should be favored by evolution only in those species having territorial marking behavior. This hypothesis proposes that colonies of socially advanced species, which are generally very large, would need to develop territorial behavior in order to diminish intraspecific competition. Territorial behavior would then force the evolution of the appropriate nestmate recognition system.

On the other hand, recognition systems based on a few signals (one pheromone complex only) require less memory and therefore should optimize the limited capabilities of the insect nervous system. This is specially important for large colonies, where individual odors are impossible to memorize and thus a more 'anonymous' recognition system based on a simple signal is more efficient. Primitive species with small colonies do not appear to be subjected to this selective pressure. Individuals that grow up in the same colony are recognized as nestmates, even if they have different odors. This has been shown for primitively social bees (BARROWS et al., 1975; BUCKLE and GREENBERG, 1981). This also seems to be the case for many ant species, as experiments on imprinting of nestmate odor (JAISSON, 1980) and experiments with mixed colonies (LE MASNE, 1952; PROVOST, 1979; LE MOLT et al., 1982; ERRARD and JAISSON, 1984; ERRARD, 1985) have shown. This hypothesis proposes that species with large colonies need to develop a simple nestmate recognition system. Therefore, they are also forced to develop territorial marking behavior in order to assure the cohesion of the society. In nature probably both hypothetical selective pressures work together, complementing each other.
Home-environment recognition

It is proposed to combine territory with nestmate recognition defining a home-environment recognition (based on various recognition cues) which includes the recognition of individuals and of the actively announced territory. This home-environment recognition system is subjected to the pressure of evolution through the outcome of agonistic interactions. In this context, trends made evident in Table I are self-explanatory if the following hypotheses are assumed:

Aliens and not nestmates are recognized. That is, the presence of an unfamiliar odor is taken as unusual and thus as alien. This system can be taken as an extension of the 'Foreign-label rejection' hypothesis of Getz (1981, 1982); though in our case, both intrinsic and extrinsic cues or 'discriminator substances' in the sense of Hülldobler and Michener (1980) could be part of the odor. The odors of nestmates are learned or imprinted (Jaisson, 1980; Errard 1985) by the worker just after or before its eclosion to the adult state and thus are taken as familiar. A similar situation occurs with the territory. Familiar odors are experienced near or around the nest, and an unfamiliar odor in the home-environment may induce aggression. Odors of a non-familiar home-environment will induce escape behavior or other kinds of cryptic behavior. A typical case can be found with Acromyrmex landolti. Workers on a strange territory will assume nymphal postures and the owners of the territory will pick them up and carry them a distance away from the nest entrance and finally drop them. The cryptic posture is only displayed if in addition to being in a foreign territory, workers of this colony are present (Jaffe and Navarro, 1985). Thus, when two workers meet, the worker experiencing the unfamiliar environment will have a disadvantage as it will tend to escape, whereas the one on a familiar environment will engage in aggressive encounters. An illustrative example can be found in Atta cephalotes where a worker placed on the foraging ground of a foreign colony will immediately show alarm behavior, making, itself evident to the workers which will start attacking it (Jaffe, 1983).

In more advanced species the different odors begin to have specific meanings. More signals are used for communication, and thus more genetic or ontogenetic memory is used for this purpose. The ants should become more efficient in using information making odors less redundant as signals. Evolution probably will tend to use the same signal for different
purposes if the signals always appear concomitantly. Savings in memory and a
more efficient use of the limited neuronal capabilities should be important
in focusing evolution in organisms which do not show a trend to
macroencephalism (JAFFE, 1986). Thus, nestmate recognition signals and alarm
pheromones are fused, as the detection of an alien is always accompanied with
alarm communication. In turn the alien, if detecting unfamiliar odors on the
territory or on nestmates, will also start alarm communication. The alarm
pheromone seems to be the most evident signal for nestmate recognition. This
hypothesis predicts that social parasites have to evolve a capacity for
avoiding alarm communication or to dispense with alarm pheromones altogether.
I could not find any reference in the literature on this aspect, but it
should not be difficult to test experimentally.

Different types of territory or of home-environments may exist. One species could use many different pheromones for marking trunk trails,
nest entrances, food sources, etc., for agonistic advertisement. Also
individual recognition may be more complex. The use of alarm pheromones as a
nestmate recognition signal in agonistic encounters does not exclude that
ants use other signals for caste recognition, age recognition, etc.

Analogous evolution

The communication systems developed by the most advanced
representatives of the different subfamilies are surprisingly very similar,
in spite of the fact that their complex social organization evolved
independently (WILSON, 1971; JAFFE, 1984a). This suggests either the
existence of similar selective pressures on communication systems, and thus
on social organization, i.e. similar needs in transferring information
(analogous evolution); or a common phylogenetic predisposition (limited
genotypic possibilities for example) of Formicidae, for certain types of
communication systems (homologous relations). The latter view is favored by
findings on the decision making systems used by ants (JAFFE et al., 1985),
where homologous relations are proposed at least for the Attini. However, the
two homologous different decision-making systems found do not correlate with
either the different recruitment systems or any other communication system
employed by the species. In addition, studies on termite recruitment (LUSCHER
and MÜLLER, 1960; STUART, 1969, 1970) show that the same communicational
devices are used by ants and termites, in spite of the fact that both groups
of insects evolved independently. Studies on nestmate recognition of
primitive social bees (BARROWS et al., 1975; BUCKLE and GREENBERG, 1981)
also show that both primitive bees and primitive ants tend to have similar
nestmate recognition systems. On the other hand, more socially complex bees
also use the mandibular alarm pheromone as a recognition signal (CREWE,
1982). Recognition systems in territorial birds also tend to be based on a
few recognition signals, contrary to that which occurs with non-territorial
birds where recognition signals are more elaborate (KOHWER, 1975). Even in
humans, the intraspecific recognition signals are mainly based on a few
features in only one part of the body, the face (EIBL-EIBESFELDT, 1984). This
would suggest that the first alternative is more likely, i.e. the evolution
of social behavior has many features which evolved analogously. It can be
concluded that the majority of arguments support the view that only a reduced
spectrum of solutions are available for the evolution of social organization.

Level of selection

The more advanced recognition system in Formicidae seem to be
related to kin recognition, as the specific composition of a pheromone is
probably genetically determined (JAFFE and MARCUSE, 1983). Thus kin
recognition is more plausible in those species not using the environmental
odors adsorbed on the cuticle or other non-specific recognition cues as
nestmate recognition signals, but which use intrinsically produced chemicals
for this purpose. As we see from Table I, this step has been made by all but
the more primitive ant species. On the other hand, ritualization in
intraspecific encounters indicates that selection of agonistic behavior acts
at the colony level or population or community level.

Nestmate recognition based on specific signals, which are
genetically determined, will establish a gradient in aggressive behavior
dependent on kin relations as could be observed in bees (GREENBERG, 1979),
ants (MINTZER and VINSON, 1985; JAFFE et al, 1986) and even in vertebrates
(HALPIN, 1980; QUINN and BUSACK, 1985).

In socially more primitive species the situation seems to be
different. Individuals use more environmental odors or non-specific signals
for nestmate recognition (Table I). Species living in the same environment
and thus learning similar odors through early experience, will accept a
neighbor rather than a genetically close relative, as seems to be the case
with the primitive Ponerinae and Myrmeciinae. Birds appear to be at this
degree of social evolution as they are also more dependent on the familiarity
of signals than on genetically determined signals (WELTY, 1970), and the same
is true for the raccoon and the red fox (BARASH, 1974).

These conclusions would place the theory of group selection
(HAMILTON, 1981) and kin selection (HAMILTON, 1964) at the same level of
importance for the evolution of societies. At different stages of evolution
one of them has a more important role, but both are at work and one might
provide the initial conditions for triggering the other, as appears to occur
in ants. First, group selection pressures for a more efficient agonistic
behavior system, which in turn sets the bases for kin selection, establishing
the relation between nestmate recognition and kin-relation.

The kind of agonistic behavior based on home-environment
recognition will not favor the individual colony as it does not allow for
intra-specific parasitism or 'spying', but protects the colony against it.
Spying seems to be a feature in the bee *Apis mellifera* (LINDAUER, 1961) but
has not been reported for ants or termites. This kind of behavior which
benefits the population or species as a whole has to be selected by long-term
evolutionary forces acting on whole populations, species or species groups.

On the other hand, population level selection and/or colony level selection
may be in opposition to kin selection, as discriminative behavior based on
kin recognition may result in a relative increase in the reproductive success
for some family groups but at the same time may result in a lower total
productivity of the population (PAGE, 1986). This could explain some
experimental findings showing lower than expected sister-sister relatedness
in ants (e.g. PAMILLO, 1982; PAMILLO and ROSENBERG, 1984). This suggests the
existence of another level of selective forces working in evolution, i.e.
population selection and/or community (LEWIN, 1985) selection. This would
include the evolution of interspecific recognition systems (e.g. WILSON,
1976; CARLIN and JOHNSTON, 1984). Here the unity of selection is a
population and/or the community. This implies that the chances of survival
not only depend on the species fitness, but also on the neighbors' characteristics, independently of genetic relationship. In the case of
population selection, the degree of genetic interchange between a population
could determine whether the emphasis is on kin rather than on group
selection.
REFERENCES


