

Nestmate recognition in the unicolonial ant *Formica paralugubris*

Michel Chapuisat, Christian Bernasconi, Sophie Hoehn, and Max Reuter

Department of Ecology and Evolution, Biology Building, University of Lausanne,
1015 Lausanne, Switzerland

In unicolonial populations of ants, individuals can mix freely within large networks of nests that contain many queens. It has been proposed that the absence of aggression in unicolonial populations stems from a loss of nest mate recognition, but few studies have tested this hypothesis. We investigated patterns of aggression and nest mate recognition in the unicolonial wood ant, *Formica paralugubris*. Little aggression occurred, even between workers from nests separated by up to 5 km. However, when aggression took place, it was directed toward non-nest mates rather than nest mates. Trophallaxis (exchange of liquid food) occurred very frequently, and surprisingly, workers performed significantly more trophallaxis with non-nest mates than with nest mates (bias 2.4:1). Hence, workers are able to discriminate nest mates from non-nest mates. Higher rates of trophallaxis between non-nest mates may serve to homogenize the colony odor or may be an appeasement mechanism. Trophallaxis rate and aggression level were not correlated with geographical distance and did not differ within and between two populations separated by several kilometers. Hence, these populations do not represent differentiated supercolonies with clear-cut behavioral boundaries. Overall, the data demonstrate that unicoloniality can evolve despite well-developed nest mate recognition. Reduced levels of aggression might have been favored by the low rate of interactions with foreign workers, high cost of erroneously rejecting nest mates, and low cost of accepting foreign workers. *Key words*: aggression, discrimination, kin recognition, unicoloniality. [*Behav Ecol*]

Recognizing kin from nonkin, and directing altruistic behavior toward the former, is an essential component of kin selection (Agrawal, 2001; Hamilton, 1964, 1987). Social insect colonies are composed of family groups, and nest mates are usually related (Crozier and Pamilo, 1996). In most social insect species, individuals recognize nest mates from non-nest mates and aggressively reject the latter, which maintains the colony integrity and ensures that altruism is directed toward relatives (Crozier and Pamilo, 1996; Wilson, 1971). The discrimination of nest mates is generally based on olfactory cues, which can be genetically determined or acquired from the environment (Beye et al., 1998; Crozier and Pamilo, 1996; Downs and Ratnieks, 1999; Giraud et al., 2002; Silverman and Liang, 2001).

Some species of ants have an extraordinary social system, called unicoloniality, which is characterized by very large aggregations of interconnected and mutually tolerant nests containing many queens (Hölldobler and Wilson, 1977; Queller and Strassmann, 1998). In unicolonial populations, individuals can move between nests without eliciting aggression, and colony boundaries become blurred (Bourke and Franks, 1995; Crozier and Pamilo, 1996; Hölldobler and Wilson, 1977). The absence of aggression permits the formation of huge cooperative units comprising large numbers of individuals at high density, which explains much of the tremendous ecological success of unicolonial species (Chapman and Bourke, 2001; Holway et al., 2002; Tsutsui and Suarez, 2003). However, the maintenance of unicoloniality is a potential challenge to kin selection theory, because altruism

occurs among nest mates whose relatedness may approach zero (Bourke and Franks, 1995; Crozier and Pamilo, 1996; Queller and Strassmann, 1998).

A major hypothesis to explain the evolution of unicoloniality is that a loss of genetic variation at recognition cues resulted in a loss of the ability to discriminate nest mates from non-nest mates (Chapman and Bourke, 2001; Giraud et al., 2002; Tsutsui et al., 2000, 2003). In particular, unicolonial populations of several invasive species are the result of recent introduction events. During the introduction and establishment, populations often pass through a bottleneck, and the loss of alleles at loci coding for recognition cues might result in a loss of recognition abilities (Tsutsui et al., 2000). In addition to the random loss of recognition alleles, selection may result in the fixation of common recognition alleles in the population if the colonies sharing the most frequent recognition alleles have a competitive advantage over colonies with rare alleles (Giraud et al., 2002; Tsutsui et al., 2003).

Another hypothesis is that unicoloniality is selected for by habitat saturation (Chapman and Bourke, 2001; Chapuisat and Keller, 1999; Hölldobler and Wilson, 1977; Ross and Keller, 1995). As the density of colonies increases, independent colony founding by queens becomes increasingly difficult. This favors the reacceptance of queens in the maternal colony and the establishment of new nests by budding, a process whereby queens and workers depart from their natal nest to found a new nest in the vicinity. Ultimately, this process may lead to the emergence of large networks of nests comprising many queens and monopolizing entire patches of habitat (Chapuisat and Keller, 1999; Hölldobler and Wilson, 1977).

A better understanding of the causes of unicoloniality requires studies of both aggression and recognition at various spatial scales and in a diverse range of species. In particular, it is important to assess if the absence of aggression is owing to a lack of recognition, or if unicoloniality can evolve despite well-developed nest mate recognition. Empirical data suggest that a complete lack of recognition indeed prevails in some

Address correspondence to M. Chapuisat. E-mail: michel.chapuisat@unil.ch. S. Hoehn is now at Institute of Environmental Sciences, University of Zürich, 8057 Zürich, Switzerland. M. Reuter is now at Department of Biology, University College London, London NW1 2HE, UK.

Received 7 November 2003; revised 10 May 2004; accepted 18 May 2004.

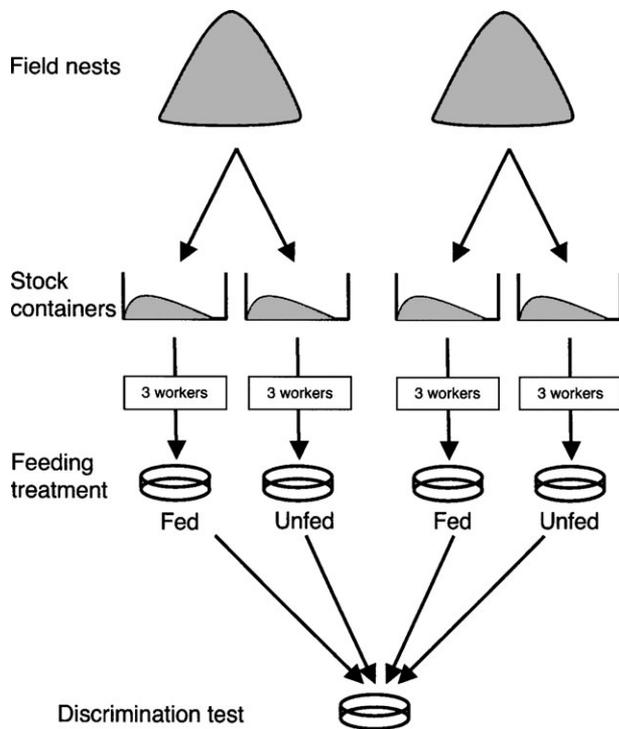


Figure 1
Diagram of the experimental design.

unicolonial populations of invasive ants. For example, in European populations of the Argentine ant, *Linepithema humile*, the frequency of antennation did not differ between workers from the same nest and workers sampled up to 6000 km apart (Giraud et al., 2002). In contrast, the recognition ability of noninvasive unicolonial species has not been tested experimentally.

In the present study, we investigated patterns of aggression and nest mate recognition in the wood ant, *Formica paralugubris*. This species forms unicolonial populations comprising many nests connected by a dense network of trails (Chapuisat and Keller, 1999; Chapuisat et al., 1997; Cherix, 1980). We staged experimental discrimination tests in which workers were simultaneously confronted with nest mates and non-nest mates. Two distinct behavioral traits were measured. First, we recorded all aggressive interactions. Second, we quantified the rate of trophallaxis, that is, oral exchange of liquid food between individuals. This second measure might reveal more subtle manifestations of nest mate recognition than those detectable by scoring aggressive behavior (Moritz and Hillesheim, 1990; Wilson, 1971). Patterns of aggression and recognition were studied within and between two populations separated by several kilometers. We first tested if workers are able to discriminate nest mates from non-nest mates. We then examined if aggression or discrimination ability increases with geographical distance between nests. Finally, we examined if the two sampled populations have distinct behavioral boundaries by testing if belonging to the same or to different populations had an effect on the level of aggression or trophallaxis.

METHODS

Study organism

The wood ant, *Formica paralugubris*, is common in the western Alpine region, and several unicolonial nest aggregations occur in the Swiss Jura (Cherix, 1980; Gris and Cherix,

1977). Preliminary experiments revealed little aggression within nest aggregations, but did have strong and immediate aggressive behavior toward the sibling species *F. lugubris*, with severe biting, leg pulling, and spraying of formic acid. We sampled ants from two populations separated by approximately 3.5 km and located at the ‘‘Chalet à Roch’’ (6°11’30’’ E, 46°32’30’’ N, altitude 1380 m) and the ‘‘Grande Rolat’’ (6°14’15’’ E, 46°33’30’’ N, altitude 1350 m), respectively. The Chalet à Roch population is a very large network of approximately 1200 nests containing many queens, on which detailed ecological and genetic data are available (Chapuisat, 1998; Chapuisat and Keller, 1999; Chapuisat et al., 1997; Cherix, 1980). Genetic differentiation between nests increases with geographical distance and distant nests do not share recent common ancestry (Chapuisat et al., 1997). The genetic data suggest that new nests within populations are mostly formed by budding, and that the effective dispersal of both queens and males is restricted (Chapuisat and Keller, 1999; Chapuisat et al., 1997). The Grande Rolat population contains approximately 100 nests. Apart from smaller size, the Grande Rolat population appears to be similar to the Chalet à Roch population with respect to habitat and spatial organization, but no genetic data are available for this site.

Sampling

In the Chalet à Roch population, eight nests were sampled along a 900-m long transect, taking care to sample both closely located nests (less than 50 m apart) and distant nests (more than 200 m apart). In the Grande Rolat, five nests were sampled in a similar way. The position of each nest was recorded with a differential geographical positioning system (D-GPS; Garmin Ltd.). Overall, nests from the same population were separated by 20–900 m, whereas nests from different populations were separated by 3.6–5.0 km.

Approximately 1000 workers and 1 l of nest material were collected from each of the 13 nests. Each sample was divided in two equal parts and stored in large stock containers. The stock containers were kept at 20°C under a 12-h light/12-h dark cycle. The ants were provided with 8% sugar solution ad libitum and with sliced mealworms once per week.

Behavioral assays

In the discrimination tests, we recorded the behavior of workers toward nest mate and non-nest mate workers. Each test included 12 ants, six originating from one nest and six from the other. To control for the effect of isolation in stock containers, half of the ants from a nest came from one stock container and the other half came from the other stock container (Figure 1).

To increase the frequency of trophallaxis, we manipulated the feeding status of individuals before the start of the discrimination test. For each colony, three ants originating from one of the two stock containers were isolated for 2 h and fed ad libitum with 8% sugar solution, and three ants originating from the other stock container were isolated for 2 h without food (Figure 1). Hence, half of the ants were well fed before the start of the discrimination test, whereas the other half were food deprived. To recognize each colony and treatment group, the ants were marked on the thorax with a small dot of paint used for labeling honeybees (Kutex, Rithner Apiculture). For each test, colors were randomly attributed to treatment groups.

The discrimination tests started when all 12 ants were assembled in an arena consisting of a 13.5-cm Petri dish coated on the sides with fluron and with a thin layer of clean sand on the bottom. All aggressive and trophallactic

interactions were recorded for 20 min. Aggressive interactions consisted of biting and pulling the legs or antennae, with an additional spraying of formic acid on rare occasions. Trophallaxis is a very characteristic behavior. After prolonged antennal contacts, one worker places its mandibles between the ones of the other individual and a droplet of liquid is exchanged (Hölldobler and Wilson, 1990).

All pairwise combinations of nests were tested in three replicates. The tests were conducted blind (observers had no knowledge of the nest of origin and treatment of the ants being observed) and in a randomized order.

Statistics

Before statistical analysis, the data were corrected for differences in encounter probability. Specifically, a focal individual can interact with two other individuals belonging to its own treatment group (same nest of origin, stock container, and feeding treatment), as opposed to three individuals belonging to any other treatment group (Figure 1). To correct for this difference in encounter probability, we multiplied by 3/2 the number of interactions (aggression or trophallaxis) occurring among ants belonging to the same treatment group.

After this correction, the data were aggregated in discrimination indices which measure whether aggression or trophallaxis are biased toward nest mates or non-nest mates. Discrimination indices consisted of the number of interactions (aggression or trophallaxis) between non-nest mates minus the number of interactions between nest mates, summed over the three replicated discrimination tests. The value of the discrimination indices is positive if interactions occur more often between non-nest mates than between nest mates, negative in the opposite case, and close to zero if interactions occur randomly.

The hypothesis that workers discriminate between nest mates and non-nest mates was tested with Fisher's one-sample randomization test on 1000 resamples (Manly, 1997). For each resample, six independent pairs of nests were drawn at random with the proviso that no nest occurred in more than one pair. A test statistic was calculated as the mean discrimination index (aggression or trophallaxis) across these six nests, minus the mean discrimination index after randomizing signs (each of the six values changed sign with a probability of 50%, as expected under the null hypothesis that workers do not discriminate between nest mates and non-nest mates). The significance of a bias toward nest mates (respectively, non-nest mates) was estimated as the proportion of resamples which had a test statistic greater (respectively smaller) or equal to zero.

The statistical significance of the correlation between aggression and trophallaxis indices was determined with a Mantel test (Manly, 1997). Mantel tests were also used to examine the correlation between geographical distance and each index of discrimination (aggression or trophallaxis). Finally, we tested if belonging to the same or to different populations (Chalet à Roch or Grande Rolat, respectively) had an effect on the discrimination indices. For this aim, we constructed a matrix containing "1" for pairs of nests belonging to the same population and "0" for pairs of nests belonging to different populations, and examined the correlation of this matrix with each of the two matrices of discrimination in Mantel tests. All Mantel tests involved 2000 permutations of the rows and columns in one matrix.

RESULTS

Little aggression occurred in our experiments. During the 234 discrimination tests involving 12 ants each and summing up to

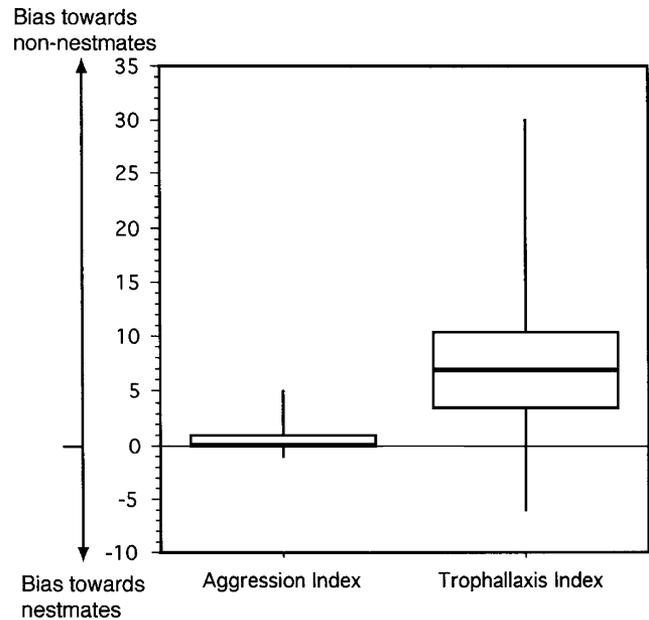


Figure 2
Distribution of the discrimination indices for all pairs of nests ($N = 78$). The aggression or trophallaxis indices consist in the number of interactions (aggression or trophallaxis, respectively) between non-nest mates minus the number of interactions between nest mates, summed over three replicates. The medians (dark lines), lower and upper quartiles (boxes), and ranges (vertical bars) are indicated.

a total 78 h of observation, only 60 cases of leg or antenna biting were recorded. Moreover, no aggression occurred in 83% of the tests and in 63% of all pairs of nests. Because many pairs of nests showed no aggression, the bias toward non-nest mates was not statistically significant when Fisher's one-sample randomization test was applied on resampled pairs of nests ($p = .3$) (Figure 2). However, when aggression occurred, it was directed against non-nest mates rather than nest mates (58 and 2 cases, respectively; binomial test, $p < .001$). The feeding status of ants had little impact on the frequency of aggressive behavior. Aggression between non-nest mates occurred between a fed and a food-deprived individual in 33 cases, two fed ants in 13 cases, and two food-deprived ones in 12 cases, which is not significantly different from the numbers expected given the probabilities of encounter ($\chi^2 = 1.14$, $df = 2$, $p = .57$).

In contrast to aggression, trophallaxis occurred very frequently and between all pairs of nests. A total of 1431 trophallactic exchanges were recorded during the experiments. The feeding treatment promoted trophallaxis: 910 instances of trophallaxis occurred between a fed and a food-deprived individual, 299 between two fed ants, and 222 between two food-deprived ones, which significantly differs from the numbers expected given the probabilities of encounter ($\chi^2 = 56.03$, $df = 2$, $p < .001$).

Trophallaxis was strongly biased toward non-nest mates (Figure 2). In the raw data, 72.6% of all trophallaxis involved workers from different nests. After correcting for encounter probability, trophallaxis between non-nest mates was on average 2.4 times more likely than trophallaxis between nest mates (70.8% versus 29.2%, respectively). Concurrently, the discrimination index had a mean of 7.8 and was significantly greater than zero (Fisher's one-sample randomization test on resampled pairs of nests, $p = .028$) (Figure 2), which demonstrates that trophallaxis was directed toward non-nest

mates. Moreover, trophallaxis was biased toward non-nest mates in 77% of the tests and in 95% of the pairs of nests. Indices of aggression and trophallaxis were positively correlated (Mantel test, matrix correlation = 0.56, $p = .0005$), indicating that when workers were more aggressive toward individuals from different nests, trophallaxis was also more biased toward non-nest mates.

Neither aggression nor trophallaxis was significantly associated with geographical distance between nests. We found no significant correlation between discrimination indices and distance either when analyzing all nests (Mantel tests; aggression: matrix correlation = 0.09, $p = .4$; trophallaxis: matrix correlation = 0.01, $P = 0.9$) or when restricting the analysis to nests within the Chalet à Roch population (aggression: matrix correlation = 0.11, $p = .6$; trophallaxis: matrix correlation = 0.17, $p = .4$). Furthermore, no difference in aggression or trophallaxis was detected between pairs of nests belonging to the same or to different populations (aggression: matrix correlation = -0.07 , $p = .6$; trophallaxis: matrix correlation = 0.03, $p = .8$).

DISCUSSION

The evolution of unicoloniality is still poorly understood. In some invasive ant populations, there is a complete lack of nest mate recognition ability within very large populations (Giraud et al., 2002; Tsutsui et al., 2000, 2003). In contrast, the present study provides clear evidence that workers of the wood ant, *F. paralogubris*, are able to discriminate nest mates from non-nest mates. In symmetrical discrimination tests, the rate of trophallaxis between nest mates differed strikingly from that between individuals from different nests, and the rare cases of aggression were preferentially directed toward non-nest mates.

The differences in nest mate recognition ability among locally unicolonial species support the hypothesis that unicoloniality can arise by different evolutionary processes (Chapman and Bourke, 2001; Chapuisat and Keller, 1999; Hölldobler and Wilson, 1977). In *L. humile* and other introduced pest ants, a loss of nest mate discrimination ability might be the cause of the evolution of unicoloniality, in association with the ecological release from predators, parasites and competitors that follows the invasion of a new habitat (Chapman and Bourke, 2001; Holway et al., 2002; Tsutsui and Suarez, 2003). In *F. paralogubris* and other wood ants, locally unicolonial populations probably arose through progressive saturation and monopolization of stable habitat patches, leading to restricted migration and high numbers of queens coexisting in long-lived nests (Bourke and Franks, 1995; Chapuisat et al., 1997; Chapuisat and Keller, 1999; Hölldobler and Wilson, 1977). The present study suggests that this process can be associated with a lack of aggression between nests that does not require or necessarily entail a total loss of nest mate recognition ability.

The strength of discrimination between non-nest mates did not vary with the geographical distance between nests. Individuals from neighboring nests were not treated differently from those originating from nests up to 5 km away. This suggests that genetic cues do not play a major role for nest mate recognition within the Chalet à Roch population, in which neighboring nests are genetically very similar and genetic differentiation between nests increases with geographical distance (Chapuisat et al., 1997). Moreover, workers did not behave more aggressively or perform less trophallaxis with workers from the other population than with workers from other nests in their own population. As far as behavior is concerned, and over the geographical scale investigated, the two sampled populations of *F. paralogubris* do not exhibit

clear-cut boundaries and seem to merely represent dense aggregations of nests rather than mutually aggressive supercolonies.

Surprisingly, trophallaxis was strongly biased toward non-nest mates. On average, 2.4 times more trophallaxis occurred between workers from different nests than between nest mates. This preference for non-nest mates stands in sharp contrast to the hypothesis that workers should preferentially allocate resources to their more related nest mates and discriminate against non-nest mates. Hence, it is likely that the trophallaxis observed here does not represent an altruistic sharing of resources. The elevated rate of trophallaxis between non-nest mates may have been influenced by the experimental conditions and might therefore have no adaptive significance. However, two functional hypotheses might also account for the bias in trophallaxis observed in our trials. First, increased rates of trophallaxis with unfamiliar workers might be a mechanism for scrambling the recognition cues among colony members in order to restrain nepotism and intracolony conflicts that negatively affect colony performance (Keller and Chapuisat, 1999). Trophallaxis results in a high rate of transfer of cuticular hydrocarbons, which are major discrimination cues (Boulay et al., 2000; Lahav et al., 1999; Lenoir et al., 2001; Soroker et al., 1995). In the ant *Camponotus fellah*, workers engaged in more trophallaxis when they were reintroduced in their natal colony after a short period of isolation during which they had developed a slightly different hydrocarbon profile (Boulay et al., 2000). Second, trophallaxis might be an appeasement mechanism. It has been observed that intercolonial and even interspecific trophallaxis often follows aggressive interactions in laboratory arenas or at baits in the field (Bhatkar and Kloft, 1977; Hölldobler and Wilson, 1990).

Despite the well-developed nest mate recognition during trophallaxis, our experiment and various field assays revealed few aggressive interactions between conspecific workers in *F. paralogubris*. This contrasts with the behavior of workers from most other ant species, which attack and reject workers from foreign colonies. The very low level of aggression despite nest mate recognition ability is difficult to reconcile with kin selection. One possibility is that workers do behave more agonistically toward non-nest mates when a higher fitness loss is at stake than in encounters between workers on neutral terrain. For example, workers may aggressively reject unrelated queens trying to join their nests or may compete with foreign workers for the control of specific resources. The theory predicts that unconditional acceptance of conspecifics should be favored when the proportion of interactions with desirable individuals is high, when the fitness cost of erroneously rejecting a desirable individual is high, and when the fitness cost of accepting an undesirable individual is low (Agrawal, 2001; Reeve, 1989). In *F. paralogubris*, encounters with nest mates or neighbors that are moderately related are probably much more frequent than are encounters with unrelated foreign workers, because most ants stay in or close to their natal nests and populations are genetically viscous (Chapuisat et al., 1997; Chapuisat and Keller, 1999). Moreover, rejecting nest mate workers decreases the nest's workforce, and accepting non-nest mate conspecific workers might have minimal costs as long as intruders have a limited ability to harm or selfishly exploit the host nest.

We thank Andrew Bourke, Sara Cahan, Philippe Christe, Barbara Holzer, Laurent Keller, Laurent Lehmann, and two anonymous referees for comments on the manuscript. We also thank Arnaud Maeder for information and help in the field. This study was supported by the Swiss National Science Foundation (grant 31-61934.00 to M.C.).

REFERENCES

- Agrawal AF, 2001. Kin recognition and the evolution of altruism. *Proc R Soc Lond B* 268:1099–1104.
- Beye M, Neumann P, Chapuisat M, Pamilo P, Moritz RFA, 1998. Nestmate recognition and the genetic relatedness of nests in the ant *Formica pratensis*. *Behav Ecol Sociobiol* 43:67–72.
- Bhatkar AP, Kloft WJ, 1977. Evidence, using radioactive phosphorus, of interspecific food exchange in ants. *Nature* 265:140–142.
- Boulay R, Hefetz A, Soroker V, Lenoir A, 2000. *Camponotus fellah* colony integration: worker individuality necessitates frequent hydrocarbon exchanges. *Anim Behav* 59:1127–1133.
- Bourke AFG, Franks NR, 1995. Social evolution in ants. Princeton, New Jersey: Princeton University Press.
- Chapman RE, Bourke AFG, 2001. The influence of sociality on the conservation biology of social insects. *Ecol Lett* 4:650–662.
- Chapuisat M, 1998. Mating frequency of ant queens with alternative dispersal strategies, as revealed by microsatellite analysis of sperm. *Mol Ecol* 7:1097–1105.
- Chapuisat M, Goudet J, Keller L, 1997. Microsatellites reveal high population viscosity and limited dispersal in the ant *Formica paralugubris*. *Evolution* 51:475–482.
- Chapuisat M, Keller L, 1999. Extended family structure in the ant *Formica paralugubris*: the role of the breeding system. *Behav Ecol Sociobiol* 46:405–412.
- Cherix D, 1980. Note préliminaire sur la structure, la phénologie et le régime alimentaire d'une super-colonie de *Formica lugubris* Zett. *Ins Soc* 27:226–236.
- Crozier RH, Pamilo P, 1996. Evolution of social insect colonies: sex allocation and kin selection. Oxford: Oxford University Press.
- Downs SG, Ratnieks FLW, 1999. Recognition of conspecifics by honeybee guards uses nonheritable cues acquired in the adult stage. *Anim Behav* 58:643–648.
- Giraud T, Pedersen JS, Keller L, 2002. Evolution of supercolonies: the Argentine ants of southern Europe. *Proc Natl Acad Sci USA* 99:6075–6079.
- Gris G, Cherix D, 1977. Les grandes colonies de fourmis des bois du Jura (groupe *Formica rufa*). *Mitt Schweiz Ent Ges* 50:249–250.
- Hamilton WD, 1964. The genetical evolution of social behaviour. *J theor Biol* 7:1–52.
- Hamilton WD, 1987. Discriminating nepotism: expectable, common, overlooked. In: Kin recognition in animals (Fletcher DJC, Michener CD, eds). New York: John Wiley; 417–437.
- Hölldobler B, Wilson EO, 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64:8–15.
- Hölldobler B, Wilson EO, 1990. The ants. Berlin: Springer-Verlag.
- Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ, 2002. The causes and consequences of ant invasions. *Annu Rev Ecol Syst* 33:181–233.
- Keller L, Chapuisat M, 1999. Cooperation among selfish individuals in insect societies. *Bioscience* 49:899–909.
- Lahav S, Soroker V, Hefetz A, Vander Meer RK, 1999. Direct behavioral evidence for hydrocarbons as ant recognition discriminators. *Naturwissenschaften* 86:246–249.
- Lenoir A, Hefetz A, Simon T, Soroker V, 2001. Comparative dynamics of gestalt odour formation in two ant species *Camponotus fellah* and *Aphaenogaster senilis* (Hymenoptera : Formicidae). *Physiol Entomol* 26:275–283.
- Manly BFJ, 1997. Randomization, bootstrap and Monte Carlo methods in biology, 2nd ed. London: Chapman and Hall.
- Moritz RFA, Hillesheim E, 1990. Trophallaxis and genetic variance of kin recognition in honey-bees, *Apis mellifera* L. *Anim Behav* 40:641–647.
- Queller DC, Strassmann JE, 1998. Kin selection and social insects. *Bioscience* 48:165–175.
- Reeve HK, 1989. The evolution of conspecific acceptance thresholds. *Am Nat* 133:407–435.
- Ross KG, Keller L, 1995. Ecology and evolution of social organization: insights from fire ants and other highly eusocial insects. *Annu Rev Ecol Syst* 26:631–656.
- Silverman J, Liang D, 2001. Colony disassociation following diet partitioning in a unicolonial ant. *Naturwissenschaften* 88:73–77.
- Soroker V, Vienne C, Hefetz A, 1995. Hydrocarbon dynamics within and between nestmates in *Cataglyphis niger* (Hymenoptera, Formicidae). *J Chem Ecol* 21:365–378.
- Tsutsui ND, Suarez AV, 2003. The colony structure and population biology of invasive ants. *Conserv Biol* 17:48–58.
- Tsutsui ND, Suarez AV, Grosberg RK, 2003. Genetic diversity, asymmetrical aggression, and recognition in a widespread invasive species. *Proc Natl Acad Sci USA* 100:1078–1083.
- Tsutsui ND, Suarez AV, Holway DA, Case TJ, 2000. Reduced genetic variation and the success of an invasive species. *Proc Natl Acad Sci USA* 97:5948–5953.
- Wilson EO, 1971. The insect societies. Cambridge, Massachusetts: Harvard University Press.