

High surface temperatures select for individual foraging in ants

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Natural selection favors signals, receptors, and signaling behavior that maximize the received signal relative to background noise and that minimize signal degradation. The physical properties of the environment affect rates of attenuation and degradation of the signal, and thus temperature may influence the evolution and maintenance of volatile chemical signals. We tested this hypothesis in ants, where nest mate recruitment to a food source by laying trail pheromones on a surface is a common phenomenon. We collected data on maximal soil surface temperatures during the ants' activity and mode of foraging (recruitment or solitary). By using two different comparative methodologies, we demonstrated a relationship between maximal soil temperature at which species are active and recruitment behavior (which is hypothesized to be related to the presence or absence of chemical signals). The species that were active at lower temperatures proved to be those that used chemical signals to recruit nest mates during foraging. This is also the case when comparing sympatric species and thereby controlling for other environmental factors. Moreover, all seven nonrecruiter species developed from recruiter ancestries, which is consistent with our hypothesis because ample evidence suggests a forest and tropical origin for ants. Thus, contrary to previous hypotheses, species that forage individually cannot be categorically considered primitive, but rather appear to be derived from recruiter species. Therefore, we conclude that temperature influences the evolution and/or stability of chemical signals in ants by determining the recruitment of nest mates. *Key words*: ants, chemical-signal evolution, foraging systems, Formicidae, surface temperature, trail pheromones. [*Behav Ecol* 11:396–404 (2000)]

Natural selection favors signals, receptors, and signaling behavior that maximize the received signal relative to background noise and that minimize signal degradation (Ender, 1992). The environment is spatially and temporally heterogeneous, and its physical properties affect rates of attenuation and degradation of the signal (Ender, 1986, 1990; Haliday and Slater, 1983; Lythgoe, 1979; Ryan, 1985, 1988; Wiley and Richards, 1982). Signals should depend on habitat, as has been reported concerning color pattern in fish (Levine and MacNichol, 1979; Lythgoe, 1979). This relationship should also be important in the evolution and maintenance of chemical signals, mostly in those that have to act for a long time, because most signaling chemical components are temperature dependent. For example, Markow and Toolson (1990) found that two different populations of *Drosophila mojavensis* showed different combinations of epicuticular dienes (used as pheromone to affect mate choice) varying in volatility in relation to the mean temperature of the two sites.

In ants, chemical signals allowing recruitment to exploit a food resource is a well-known phenomenon. Some ant species mark the way to food by laying a pheromone trail that is followed by nest mates (Hölldobler and Wilson, 1990). The use of pheromone trails in ants is considered an adaptive trait because (1) recruitment species are more efficient than individual-foraging species (Baroni-Urbani, 1989; Jaffe and Deneubourg, 1992); (2) the use of pheromone trails reduces the cost of nest defense because individual defense of territory is more costly than mass defense (Hölldobler, 1974); (3) the individual foraging system is considered the ancestral state of the different foraging behaviors in ants (Baroni-Urbani, 1993); and (4) it has been suggested that the complexity of

the foraging system in ants reflects an evolutionary gradient in the phylogeny of Formicidae (see, e.g., Baroni-Urbani, 1993; Dumpert, 1978; Fresneau, 1985; Hölldobler and Wilson, 1990).

Several ecological factors have been proposed as influences on ant foraging systems (Ayre, 1958; Crist and MacMahon, 1991; García-Pérez et al., 1994), such as vegetation structure (Fewell, 1988), food availability (Ayre, 1958), food abundance (Brown et al., 1979; Davidson, 1977; Steinberger et al., 1991), and food predictability (Sundström, 1993) and distribution (Bernstein, 1975; Whitford, 1978). Temperature has been proposed as a major factor influencing prey-size selection (Traniello et al., 1984) and foraging behavior in ants (Cerdá et al., 1998b; Crist and MacMahon, 1991; Crist and Williams, 1999). The relationship between recruitment behavior and soil temperature has been previously suspected (Carroll and Janzen, 1973; Cerdá et al., 1989; Marsh, 1988; Sundström, 1993; Traniello, 1989), but was not considered to be a rule because there are species that forage individually at cold (*Nothomyrmecia macrops*, Hölldobler and Taylor, 1983) or warm temperatures (*Pachycondyla apicalis*, Fresneau, 1985).

In response to this environmental variation, many ant species can change their foraging strategies from collective to individual (Crist and MacMahon, 1991; Detrain et al., 1990; Traniello, 1989). For instance, individual foraging can be as efficient as recruitment, or more so, at low prey densities (Calenbuhr and Deneubourg, 1992; Crist and Haefner, 1994) and therefore would be associated with scattered and unstable food sources (Bernstein, 1975; Carroll and Janzen, 1973; Cerdá et al., 1989; Fewell, 1988; Sundström, 1993; Wehner et al., 1983; Whitford, 1978). However, the optimal foraging strategy for a colony is best evaluated only in terms of its effect on colony fitness and should not be confused with the sum of optimal foraging by individuals (Carroll and Janzen, 1973; Fewell, 1988; Rissing and Pollock, 1984). In this sense, there are no comparisons available between species that forage individually and species that are able to recruit nest mates.

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In agreement with hypotheses suggesting that foraging patterns in ants constitute adaptations by individual species to particular conditions in their environment (Hölldobler, 1978; Jaffe, 1984), it has been shown that different foraging patterns can appear or disappear in the phylogenetic tree in a completely random manner (Baroni-Urbani, 1989; Beckers et al., 1989) and that the distribution of foraging patterns in the Formicidae taxa do not fit any conceivable phylogeny (Hölldobler, 1978; Jaffe, 1984).

Pheromones in ants are hydrocarbons and fatty acids, which are volatile components depending on the temperature (Morgan, 1984), and their production should be costly. Moreover, it is known that the duration of a pheromone trail is crucial for its effectiveness as a signal (Hölldobler and Wilson, 1990). However, although different hypotheses have been proposed (see review by Baroni-Urbani, 1993) for the evolution of recruitment systems (directly related to ant species being able to lay a pheromone trail), environmental temperature has never been seen as a factor influencing evolution of recruitment systems or associated pheromones. In this article, we hypothesize that environmental temperature should influence the evolution or maintenance of this chemical signal because the life span of the pheromone trail is likely to depend on the environmental temperature.

In any case, environmental factors such as those described above are also related to environmental temperature because it is known that temperature influences vegetation distribution, as well as food availability and distribution, in different habitats (Begon et al., 1987). Therefore, at the level of species, the hypothesis that temperature could influence the evolution and maintenance of signals, related to the ability of recruitment to be used in exploiting food resources, would be as plausible as others related to environmental factors.

Because pheromones deposited on the soil are highly volatile (Billen and Morgan, 1998), a high soil-surface temperature would reduce the coefficient of diffusion (Bossert and Wilson, 1963) and therefore would diminish the usefulness of these chemical signals. In the present study, we assessed whether species' ability to use chemical trails (estimated as the ability to recruit nest mates) is effectively correlated with soil temperature. Thus, we predict (prediction 1) that species active at high soil temperatures do not use chemical signals for nest mate recruitment because these signals are inefficient and are therefore counter-selected.

Because temperature is related to other environmental factors (see above), it is difficult to isolate the temperature effect. However, species that exploit the same resources in the same habitats, but at different times of day, and thereby at different surface temperatures when they forage, can be used to test the importance of temperature in the foraging strategy independently of other environmental conditions. We predict (prediction 2) that for sympatric species those foraging at higher temperature should not use chemical recruitment because pheromones are not effective.

One of the points supporting the idea that the use of different foraging strategies is related to environmental conditions is that foraging strategies occur apparently randomly in the ant phylogenetic tree (Baroni-Urbani, 1993). However, most of the described foraging strategies use pheromones to recruit nest mates (see Materials and Methods), and only those foraging solitarily do not use pheromones and thus do not recruit nest mates. Therefore, if we classify foraging strategies in two categories, using or not using pheromones, under the hypothesis presented above, we predict (prediction 3a) that pheromone use to recruit nest mates does not appear at random in the phylogenetic tree but is related to temperature. Moreover, ample evidence suggests a forest and tropical origin for ants (e.g., Baroni-Urbani, 1995), and therefore the

colonization of temperate and arid zones must have been a later event in the evolution of the ants. We then predict that the common ancestry may have used pheromones to recruit nest mates but derived groups foraging in high-temperature habitats should not (prediction 3b).

MATERIALS AND METHODS

Focusing on the evolution and maintenance of chemical signals that enable ants to recruit nest mates, we classified ant species according to those able to recruit nest mates (recruiters) and those never detected recruiting nest mates (solitary). We assume that while recruiter species produce chemical signals for recruitment, solitary species do not, or that such signals are ineffective.

Data collection

We collected data from the literature for all ant species for which information was available on maximal soil-surface temperatures during the ants' activity and mode of foraging (recruitment or solitary). We considered recruiter species those using recruitment systems such as group recruitment, mass recruitment, and trail and trunk-trail species. We have limited our comparison to species in Formicinae and Myrmicinae, for which ample ecological and behavioral information is available. We have omitted species that use tandem running and tandem calling because this recruitment is not based exclusively on the use of chemical signals, or they do not deposit the signals on the soil (Hölldobler and Wilson, 1990; Jaffe, 1984). We analyzed 50 ant species (Table 1) that met the following conditions: (1) maximal surface temperatures during activity on the soil are known, although these ants could also forage in other habitats (this condition excludes most tree-dwelling and tropical species); and (2) diurnal species in which activity patterns can be influenced by temperature fluctuation. This latter condition enables us to examine the possible effects of higher temperatures on ant activity and on possible deposited chemical signals. We did not use the soil temperature corresponding to the optimum activity range because such data are scant, and therefore we assumed that species active at high maximal temperatures in general have high optimal temperatures for activity.

Others factors besides the temperature, such as vegetation structure, resource availability, resource abundance, and resource predictability, have also been suggested to influence foraging systems in ants (see introductory section). However, humidity, as well as temperature, determines these ecological factors (Begon et al., 1987), and it is difficult to distinguish between the effect of such factors and temperature in the foraging system used by ants. One way to distinguish between the effects of temperature and other environmental factors is to experimentally manipulate soil temperature. However, if the ability to recruit nest mates is a fixed character in ant species and nonrecruiter species have lost the ability to produce pheromones for recruitment, interspecific experiments will not clarify the evolution of this character, and thus comparative methodology is the only feasible way to study the factors influencing the evolution of recruitment. A second possibility is to compare foraging behavior of sympatric species that share the same habitat and thus habitat structure, food availability, and other variables but that have different activity patterns at different temperatures. In these cases we recorded data on time of maximum activity in summer of several sympatric ant species and temperature at which ants reach the highest activity, or percentage of ants active at maximal temperatures.

Table 1
Species used to compare foraging system with maximum surface temperature during active period of each species of ant

Species	Max temp	CR/IF	Reference
Myrmicinae			
<i>Acromyrmex versicolor</i>	44	CR	Gamboa (1976)
<i>Aphaenogaster cockerelli</i>	40	CR	Hölldobler and Wilson (1990)
<i>Aphaenogaster senilis</i>	50	CR	Crós (1995)
<i>Atta texana</i>	30	CR	Hölldobler and Wilson (1990)
<i>Crematogaster scutellaris</i>	44	CR	Hölldobler and Wilson (1990)
<i>Messor aegyptiacus</i>	39	CR	Hölldobler and Wilson (1990)
<i>Messor barbarus</i>	46	CR	Cerdá et al. (1998a)
<i>Messor bouvieri</i>	46	CR	Cerdá et al. (1998a)
<i>Messor capitatus</i>	46	CR	Cerdá et al. (1998a)
<i>Messor denticornis</i>	39	CR	Marsh (1988)
<i>Messor ebeninus</i>	32	CR	Heatwole and Muir (1989)
<i>Messor pergandei</i>	39	CR	Hölldobler and Wilson (1990)
<i>Monomorium alamarum</i>	46	IF	Marsh (1988)
<i>Monomorium minimum</i>	40	CR	Hölldobler and Wilson (1990)
<i>Monomorium vatranum</i>	46	IF	Marsh (1988)
<i>Ocymyrmex barbiger</i>	67	IF	Marsh (1985)
<i>Ocymyrmex robustior</i>	50	IF	Marsh (1988)
<i>Pheidole gilvescens</i>	29	CR	Hölldobler and Wilson (1990)
<i>Pheidole megacephala</i>	28.6	CR	Heatwole and Muir (1989)
<i>Pheidole militica</i>	33	CR	Hölldobler and Wilson (1990)
<i>Pheidole pallidula</i>	46	CR	Crós (1995)
<i>Pheidole tenuinodis</i>	41	CR	Hölldobler and Wilson (1990)
<i>Pheidole xerophila</i>	33	CR	Hölldobler and Wilson (1990)
<i>Pogonomyrmex barbatus</i>	46	CR	García-Pérez et al. (1994)
<i>Pogonomyrmex californicus</i>	60	CR	Hölldobler and Wilson (1990)
<i>Pogonomyrmex desertorum</i>	52	CR	Hölldobler and Wilson (1990)
<i>Pogonomyrmex occidentalis</i>	50	CR	Hölldobler and Wilson (1990)
<i>Pogonomyrmex rugosus</i>	46	CR	Hölldobler and Wilson (1990)
<i>Solenopsis invicta</i> (= <i>wagneri</i>)	43	CR	Hölldobler and Wilson (1990)
<i>Solenopsis xyloni</i>	41	CR	Hölldobler and Wilson (1990)
<i>Tetramorium caespitum</i>	40	CR	Hölldobler and Wilson (1990)
<i>Tetramorium semilaeve</i>	44	CR	Crós (1995)
<i>Tetramorium sericeiventris</i>	46	IF	Marsh (1988)
<i>Trachymyrmex smithi</i>	48	CR	Hölldobler and Wilson (1990)
Formicinae			
<i>Camponotus cruentatus</i>	48	CR	Crós (1995)
<i>Camponotus detritus</i>	55	IF	Marsh (1985)
<i>Cataglyphis auratus</i>	52.3	IF	Heatwole and Muir (1989)
<i>Cataglyphis bombycinus</i>	60	IF	Wehner et al. (1992)
<i>Cataglyphis cursor</i>	53	IF	Cerdá et al. (1989)
<i>Cataglyphis ibericus</i>	56	IF	Crós (1995)
<i>Cataglyphis velox</i>	50	IF	Cerdá et al. (1998b)
<i>Formica ravidia</i>	40	CR	MacKay and MacKay (1984)
<i>Formica subrufa</i>	51	IF	Caviá-Miralles (1988)
<i>Lasius neoniger</i>	36	CR	Hölldobler and Wilson (1990)
<i>Melophorus bagoti</i>	70	IF	Christian and Morton (1992)
<i>Myrmecocystus depilis</i>	60	CR	Kay and Whitford (1978)
<i>Myrmecocystus mimicus</i>	60	CR	Kay and Whitford (1978)
<i>Polyergus breviceps</i>	42	CR	Topoff et al. (1985)
<i>Proformica longiseta</i>	50	IF	Fernández-Escudero and Tinaut (1998)
<i>Rossomyrmex minuchae</i>	40	IF	Ruano and Tinaut (1999)

CR, chemical recruitment; IF, individual foraging.

Statistical analyses

To avoid biased analyses due to the fact that two species may share common ancestry and thus have many characters in common, we used available comparative methodologies that account for the effect of common phylogenetic ancestry when studying possible relationships between two different characters. First, we used the pairwise comparative method (Møller and Birkhead, 1992) between pairs of species from the same genus that differ in the variable expected to influence the variable of interest (soil temperature and presence or absence of recruitment, respectively). For polytomies in a genus, we

used mean soil temperature values for recruiter and solitary foraging species in the polytomy. Second, we used a comparative methodology based on Felsenstein's (1985) logic, modified to search for correlated evolution between a continuous trait, *Y* (maximal soil temperature at which species are active), and one independent trait, *X*, occurring only in two discrete states: presence or absence of recruitment, assigned 1 or 0, respectively (categorical variable). This methodology was applied using a computer program (CAIC 2.0.0) written by Purvis and Rambaut (1995), which finds a set of independent, pairwise differences or contrasts, assuming that changes along

the branches of the phylogeny can be modeled by a Brownian motion process (successive changes are independent of one another) and that the expected total change (i.e., the sum of many independent changes) is zero (Harvey and Pagel, 1991). In this case, we assumed a punctuational model of evolution. We could not use Grafen's method, which assumes that the ages of taxa are proportional to the number of species they contain (Purvis and Rambaut, 1995), because the number of species we could use in the analysis depends on the available information pertaining to recruitment and activity rhythm. The computer program CAIC performs the analyses reasonably well, even with grossly inaccurate branch lengths, and certainly performs much better than any method that treats species values as independent (Purvis et al., 1994).

We have reconstructed a phylogeny based on Agosti (1991), Agosti and Bolton (1990), Tinaut and Ruano (1998), and Hasegawa et al. (unpublished manuscript) for the subfamily Formicinae. The reconstructed phylogeny of subfamily Myrmicinae was derived largely from Shultz and Meier (1995), but the location of tribes Crematogastrini, Solenopsidini, and Tetramorini, as well as the genus *Messor* were from Bolton (1976, 1982, 1987). The phylogeny was based almost exclusively on morphological characters, and therefore we have no data on branch lengths. Therefore, we set all branch lengths equal to 1. This means that the dichotomous character (presence or absence of chemical signals for recruitment) can be modeled by a process that allows the character to change from one state to the other with a specified probability per unit of time. The probability of a change is therefore assumed to be the same in all branches of the phylogeny (Harvey and Pagel, 1991).

To reconstruct character states of hypothetical ancestors throughout the phylogenetic tree (character evolution), we used the MacClade (3.0) computer program written by Maddison and Maddison (1992) that uses parsimony. We assume unordered change and interpret polytomies as uncertainties in resolution (soft polytomies).

RESULTS

Maximal soil temperature and nest mate recruitment

In agreement with prediction 1, species foraging individually are active at a statistically significant higher mean maximal soil temperature (mean = 52.6°C, SE = 1.9) compared to species that use chemical recruitment (mean = 42.4°C, SE = 1.3; Mann-Whitney *U* test, $Z = 3.68$, $N_1 = 35$, $N_2 = 15$, $p = .00023$). However, this result could be confounded by phylogeny because we treat species as independent data points (see Materials and Methods). To solve this possible phylogenetic drawback, we took into account the phylogenetic tree of the group and used two different comparative methodologies.

The 50 ant species analyzed (Table 1) provide a phylogenetic tree with 80 branches (Figure 1). Some species belonging to the same genus had different foraging systems (Table 1). This occurred in four different genera: (1) *Tetramorium* (*T. sericeiventris* forages individually, whereas *T. caespitum* and *T. semilaeve* lay chemical signals on the soil), (2) *Monomorium* (*M. alamarum* and *M. vatranum* forage individually and *M. minimum* uses pheromones), (3) *Camponotus* (*C. cruentatus* uses chemical recruitment and *C. detritus* forages individually), and (4) *Formica* (*F. subrufa* forages individually and *F. ravidata* uses chemical recruitment). In these four genera, species that forage individually do so at higher temperatures than do species using pheromones for recruitment [pairwise comparisons (Møller and Birkhead, 1992), paired *t* test, differences in soil temperatures between recruiter and nonrecruiter pairs of species = -7.0, $t = 4.76$, $df = 3$, $p = .018$]. Moreover, species that forage individually are typical of desert or arid

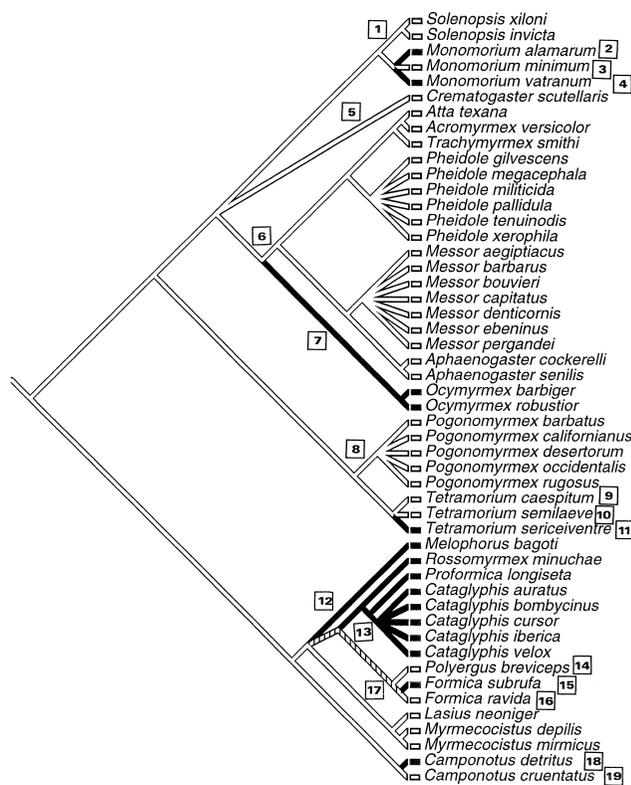


Figure 1

Character state reconstruction in the phylogenetic tree used in the comparative analyses. Open and filled bars represent recruitment and solitary foraging systems, respectively. Hatched bars represent nonresolved character state. Numbers represent clades where no change occurs.

habitats (Marsh, 1988). There are other genera with an absence of chemical recruitment (e.g., *Melophorus*, *Ocymyrmex*, and *Cataglyphis*; Table 1). Most of these taxa that forage individually have two traits in common: they typically live in arid environments and show higher maximal temperature of activity than do related species from different genera, which use chemical signals for recruitment.

When using phylogenetic independent-contrast methodology, we obtained seven negative, independent, standardized linear contrasts and zero positives. Among the taxa being contrasted, higher values of the maximal soil temperatures at which the species are active were consistently found in those that forage individually (two-tailed sign test, $p = .0156$).

However, temperature is related to other environmental factors, and thus previous results could be the consequence of these relationships. To isolate temperature effects on recruitment behavior in ants, we collected information from the literature on foraging behavior, as well as variables related to temperature during maximal activity in several sympatric ant species. We found three studies with this kind of information (see Table 2). In accordance with prediction 2, in the first study (Crós et al., 1997), the only solitary foraging species (*Cataglyphis cursor*) differs from the other recruiter species. Maximal activity of the solitary species spanned from 1200 h to 1500 h, when temperature reached its maximum. Moreover, more than 90% of the individuals detected over the entire day were found at this time. This difference between the solitary and the recruiter species in foraging activity was statistically significant (Wilcoxon test, $t = 0$, $N = 7$, $p = .018$; Table 2). Data from the second study (Heatwole and Muir, 1989) demonstrated that solitary ant species (*Cataglyphis bom-*

Table 2

Information from three different studies on foraging strategy, maximum activity period during the day, percentage of individuals active during the maximal temperature period (1200–1500 h), and temperature when maximal activity occurs for different sympatric ant species during summer

Species	CR/IF	Maximum activity	Activity 1200–1500 h	Highest activity temperature (°C)
From Crós et al. (1997)				
<i>Cataglyphis cursor</i>	IF	12–15 h	>90%	
<i>Camponotus foreli</i>	CR	10 h, 16 h	<10%	
<i>Aphaenogaster senilis</i>	CR	10 h, 16–17 h	<10%	
<i>Messor bouvieri</i>	CR	8 h, 19 h	0%	
<i>Messor capitatus</i>	CR	8 h, 18 h	0%	
<i>Camponotus cruentatus</i>	CR	9 h, 18 h	<20%	
<i>Pheidole pallidula</i>	CR	8 h, 20 h	<10%	
<i>Tetramorium semilaeve</i>	CR	7 h, 17 h	<5%	
From Heatwole and Muir (1989)				
<i>Cataglyphis bombycina</i>	IF	12–16 h		53.3
<i>Cataglyphis aurata</i>	IF	8–11 h, 14–17 h		52.3
<i>Messor aegyptiacus</i>	CR	20–7 h		37.7
<i>Plagiolepis schmitzi</i>	CR	16–20 h		36.3
<i>Monomorium salomonis</i>	CR	20–7 h		42.1
<i>Messor arenarius</i>	CR	6–7 h		32.6
<i>Pheidole megacephala</i>	CR			28.6
<i>Camponotus martensii</i>	CR	20–7 h		27.2
From Marsh (1988)				
<i>Messor denticornis</i>	CR	19–02 h		21.5
<i>Monomorium almarum</i>	IF	16–17 h		37.5
<i>Monomorium vatrannum</i>	IF	7–9 h, 15–16 h		40.5
<i>Pheidole tenuinodis</i>	CR	17–02 h, 08 h		21
<i>Tetramorium sericeiventris</i>	IF	8–9 h, 15–19 h		40
<i>Ocymyrmex robustior</i>	IF	10–16 h		47

CR, chemical recruitment; IF, individual foraging.

bycina and *Cataglyphis aurata*) are active at maximum temperatures, whereas recruiter species are not. Moreover, temperatures during maximal activity were significantly higher for solitary ant species (Mann-Whitney U test, $U = 0$, $N_1 = 2$, $N_2 = 6$, $p = .046$; Table 2). Finally, data from Marsh (1988) also supported prediction 2 because ant species foraging solitary were active at mid-day, and temperatures coinciding with maximal activity were higher for solitary species (Mann-Whitney U test, $U = 0$, $N_1 = 4$, $N_2 = 2$, $p = .06$; Table 2). Therefore, the hypothesis that temperature influences the use of chemical signals to recruit nest mates is supported by behavior of sympatric ant species, with solitary species being active at higher temperatures than recruiter species.

Reconstruction of nest mate recruitment in the phylogenetic tree

Reconstruction of character evolution using parsimony reveals that, notwithstanding two unresolved branches concerning the subfamily Formicidae, the ancestral state of foraging system is recruitment (Figure 1), in agreement with prediction 3b. Furthermore, when the number of branches in the tree was reduced according to the evolutionary changes detected in the foraging system, the ancestral state also proves to be recruitment, and no unresolved branches appear (Figure 2).

To test prediction 3b, we also used phylogenies from Baroni-Urbani (1993) studying the evolution of ant recruitment behavior, who concluded that the ancestral state of foraging systems in ants is solitary. However, he did not address the use of pheromones in nest mate recruitment, but rather in the evolution of the different types of foraging behavior, using different degrees of nest mate recruitment (trail laying, mass

recruitment, and army ant behavior) as independent discrete characters. When we classified species used by Baroni-Urbani (1993) into solitary or recruiter species (see Methods for criteria), using the same phylogenies that he used for reconstructing character evolution using parsimony, the resulting ancestral state in all six trees is recruitment (Figure 3). In other words, the common ancestor used pheromones to recruit nest mates.

Furthermore, in agreement with prediction 3a, the use of pheromones to recruit nest mates did not appear randomly in the phylogenetic trees. In all cases, regardless of the phylogenetic tree for reconstructing character evolution, all detected changes in foraging system were from nest mate recruitment to individual foraging (Figures 2 and 3). In addition, all calculated contrasts were negative. That is, a change in foraging system (from recruiter to solitary) corresponded to a significant increase in maximal soil temperature (see above).

DISCUSSION

In this study, we hypothesized that environmental temperature influences the evolution or maintenance of foraging systems by changing the effectiveness of the associated pheromones. We established two different groups of predictions, the first assessing whether species' ability to use chemical trails correlated with soil temperature (predictions 1 and 2), and the second related to the evolution of this character in the Formicidae phylogenetic tree (predictions 3a and 3b).

By using two different comparative methodologies, we have demonstrated a relationship between maximal temperature at which species are active and the presence or absence of nest

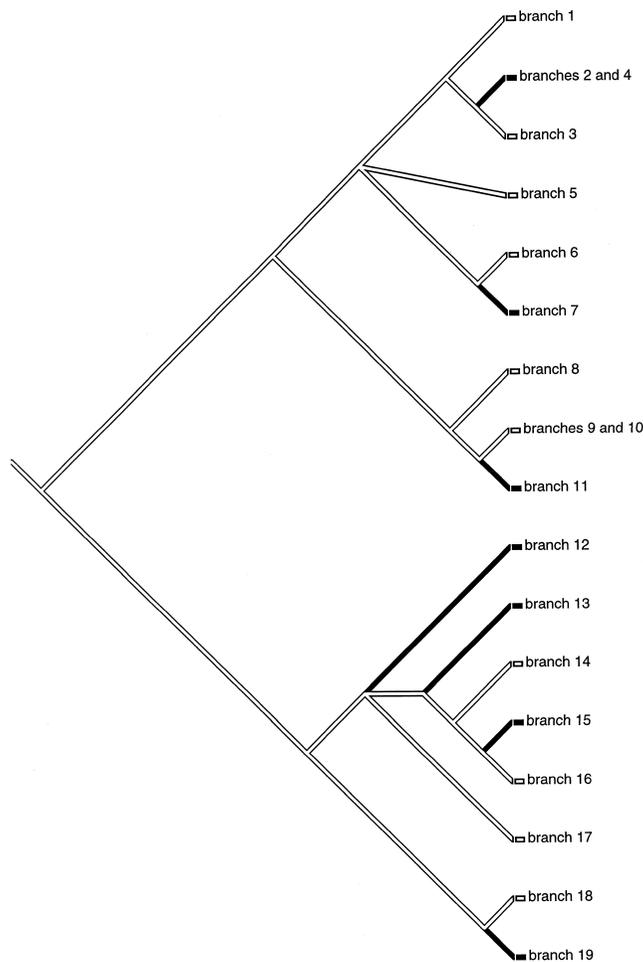


Figure 2

Character state reconstruction in phylogenetic tree of clades where no change occurs. Branch numbers match those in Figure 1. Open and filled bars represent recruitment and solitary foraging systems, respectively.

mate recruitment (Figure 1), which is hypothesized to be related to the presence or absence of chemical signals for recruitment. Moreover, when comparing sympatric species from three different studies (Table 2), differences in foraging activity at maximum temperature appeared between recruiter and solitary species. However, it could also be that those chemical signals occur in species without recruitment, but, because temperature is negatively related to their effectiveness (Bossert and Wilson, 1963), chemical signals disappear quickly, not enabling recruitment at high soil temperatures. Hence, because soil temperature appears to determine the effectiveness of chemical signals (Billen and Morgan, 1998; Bossert and Wilson, 1963; Hölldobler, 1976, 1978), which in terms of resource allocation are costly to produce, it can be predicted that, for ants active with high soil temperature, natural selection should favor individuals that do not allocate resources in a noneffective chemical product. This should be the case in our data because species classified as nonrecruiters never have been detected foraging in groups (see Materials and Methods), and therefore it is likely that these species do not have the ability to produce chemical recruitment signals.

At high temperatures, the most efficient foraging system appears to be individual foraging because it offers certain advantages, such as reduced competition for resources with other mass-recruiter species (Cerdá et al., 1998a). We have found

cases of closely related species having opposite kinds of recruitment (see Table 1) but that are active at different maximal soil temperatures (see Results). Species with strict physiological impositions can adapt activity cycles to only the most favorable soil temperatures, their recruitment system being related to their optimal temperatures. This occurs, for example, in species belonging to the genus *Messor*, which lives in desert or subdesert habitats and invariably restricts its activity periods during the hot season to early morning and late afternoon (Baroni-Urbani and Aktaç, 1981; Delalande and Lenoir, 1984; Heatwole and Muir, 1989; Steinberger et al., 1991). All this confirms the relationship between temperature, foraging system, and guild, and thus it is not a coincidence that when temperatures rise, the foraging system changes.

Our hypothesis of temperature forcing the evolution or maintenance of foraging systems in ants on the basis of a temperature habitat for a Formicidae ancestry (see Introduction) predicted a recruiter ancestry because of the absence of high temperature. In insects, trail use has evolved twice among ground-dwelling social insects (ants and termites), and once in a species of bees (*Bombus transversalis*) (Cameron and Whitfield, 1996). Thus, trail use appears to be related to social behavior. In fact, a relationship has been suggested among colony size, communication, and foraging strategy in ants because ant species with solitary foraging have small colony sizes (Beckers et al., 1989). This is the case for *Myrmecia* (Jaffe, 1984; Wilson, 1971), *Neoponera* (Fresneau, 1985), and *Nothomyrmecia* species (Hölldobler and Taylor, 1983; Jaffe, 1984). Moreover, ant species with small colony sizes are considered more primitive than species with large colony sizes (Beckers et al., 1989) because of the hypothetical nonsocial ancestry of the true Formicidae group (Baroni-Urbani, 1989; Grimaldi et al. 1997). Based on these two assumptions, a prevalent view is that “primitive” ants (with small colony size) should be unable to recruit or able to recruit only a few individuals, whereas more advanced ant species should have developed pheromonal and anatomical means to enable the recruitment of larger numbers of individuals simultaneously (Baroni-Urbani, 1993, and references therein).

However, the association between colony size and foraging strategy in ants is not clear because several recruiter species (*Pogonomyrmex*, for instance) have smaller nest populations than do some solitary species (e.g., some *Cataglyphis* species with more than 2000 workers) (see other examples in Hölldobler and Wilson, 1990; Wehner et al., 1983). Moreover, modern ant phylogenies (Grimaldi et al., 1997; Schultz and Meier, 1995) do not support the interpretation of ant evolution reflecting the complexity of the foraging system, and it is not clear whether primitive species are in fact nonrecruiters with small colony sizes.

In our phylogenetic tree, the appearance of individual foraging in different tribes points to a nonphylogenetic explanation for the foraging systems in the majority of ants we studied (Figures 1–3). Furthermore, our results (Figure 3) demonstrate that, when reconstructing evolution of foraging systems (recruiter versus solitary), the ancestral state in ants is recruitment, and all seven cases of nonrecruiter species developed from recruiter ancestries. Thus, in accordance with our hypothesis, recruitment must have appeared very early in the ant phylogenetic tree, and it is the most parsimonious state of the ancestry of the true Formicidae groups in our phylogenetic trees (Figures 2 and 3).

A nonadaptive explanation could also match our results. That is, solitary species may not have evolved from recruiter ancestries but, being better able to exploit resources under high temperature, could colonize desert environments. However, we have recorded no case where recruiter species appeared from nonrecruiter ancestry (Figures 1–3). Moreover,

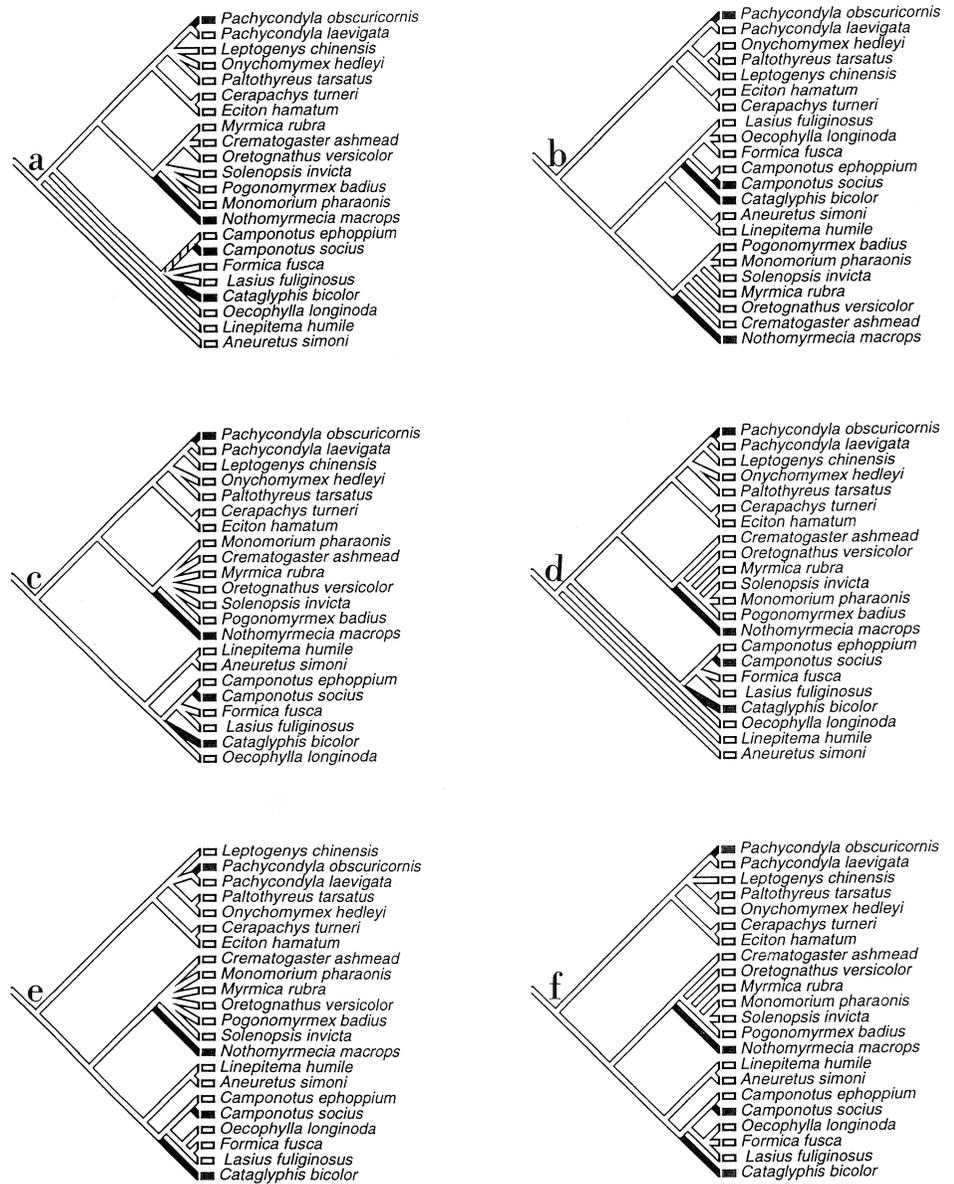


Figure 3
 Character state reconstruction in the phylogenetic trees from Baroni-Urbani (1993) using different methodologies (a–f; see Baroni-Urbani, 1993, for information on methodologies). Open and filled bars represent recruitment and solitary foraging systems, respectively. Hatched bars represent non-resolved character states.

desert environments harbor both recruiter and solitary species, and their activity correlates with the temperature, with solitary species being active at higher temperatures. Thus, it is unlikely that differences in the ability to colonize desert environments explains the relationship between maximal soil temperature and foraging behavior in the two groups of ants. From this perspective, species that forage individually cannot be categorically considered primitive but rather derived from recruiter species.

In conclusion, our results confirmed the hypothesis that temperature influences the evolution and maintenance of chemical signals related to the ability of recruitment to exploit food resources in ants. This is because (1) species active at high soil temperature do not recruit nest mates, even after controlling for environmental variables other than temperature; (2) the use of pheromones to recruit nest mates disappears in the phylogenetic tree in relation to temperature increases; and (3) recruitment is the ancestral state of solitary foraging. This temperature effect on pheromones represents another facet of the importance of temperature in the structure of the ant communities.

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