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Spatial and temporal niche partitioning in grassland ants

Abstract Species coexistence can reflect niche partitioning at several spatial and temporal scales. We measured patterns of spatial and temporal niche overlap in an Oklahoma grassland ant assemblage. Ant species foraging on a 400-m^2 grid of 25 tuna-fish baits were censused hourly for one 24-h period each month for 1 year. We used partial correlations to analyze pairwise associations of the four commonest species, and a null model analysis to quantify niche overlap among all seven species present. On a seasonal (monthly) time scale, niche overlap and pairwise species associations were random or aggregated, probably due to thermal constraints on ectotherms foraging in a seasonal environment. Within the warmer months of the year, there was some evidence of diurnal (24 h) niche partitioning: the variance in niche overlap was often greater than expected, and common species displayed both negative and positive associations with each other and with ambient air temperature. The strongest evidence for niche partitioning was at the spatial scale of individual baits. Species occurrences at baits were dynamic, with considerable turnover in composition and significantly less spatial niche overlap than expected by chance. These results are consistent with other studies suggesting that ant species partition resources at fine spatial and temporal scales.

Keywords Formicidae · Competition · Null model · Spatial patterns · Temporal patterns

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Introduction

Competitive interactions are an important mechanism structuring natural communities. Although evidence for competitive effects in many vertebrate assemblages is still controversial (Strong et al. 1984; Wiens 1989), there is broad consensus that ant assemblages are highly structured by competition (Hölldobler and Wilson 1990). Evidence for competition in ant assemblages includes behavioral dominance hierarchies (Perfecto 1994; Vepsäläinen and Pisarski 1982), territoriality (Fox et al. 1985), chemical defense (Andersen et al. 1991), spatial mosaics (Jackson 1984; Ryti and Case 1984, 1992), dominance-diversity relationships (Andersen 1992), competition-colonization trade-offs (Holway 1999), and the dramatic collapse of native ant communities in the presence of introduced species that are superior competitors (Porter and Savignano 1990; Human and Gordon 1997; Holway 1999).

Nevertheless, there are still many aspects of coexistence in ant communities that remain to be studied. One important question is: how do coexisting species partition spatial and temporal resources? Although food and space are the major resource axes for niche partitioning (Schoener 1974), time is also a resource axis that can be partitioned on both diel and seasonal scales (Case and Gilpin 1974; Carothers and Jaksic 1984). Partitioning on a diel temporal scale is likely to involve interference competition (Carothers and Jaksic 1984), whereas partitioning on an annual temporal scale may require differences in the time scales of consumer and resource dynamics (Loreau 1989).

The issues we address are much broader than the temporal patterns of niche overlap in prairie ant assemblages. A major source of controversy in community ecology has been the establishment of assembly rules based on strong species interactions (Cody and Diamond 1975; Weiher and Keddy 1999). Diamond (1975) first suggested that interspecific competition and niche adjustment lead to discernible assembly rules in the co-occurrence of species. Connor and Simberloff (1979) asked what co-

occurrence patterns would look like in the absence of competition and compared the structure of real communities to those generated by null model simulations. These exchanges touched off a debate in community ecology that continues today (Strong et al. 1984; Gotelli and Graves 1996; Weiher and Keddy 1999). In the context of niche overlap, the question is: how much overlap would be expected if species used resource states randomly with respect to one another? Schoener (1974) thought that real communities overlapped less than would be expected in the null case. Statistical methods for null model analysis of niche overlap have now been well developed (Sale 1974; Inger and Colwell 1977; Winemuller and Pianka 1990), but the patterns have not been tested in very many natural assemblages (Gotelli and Graves 1996).

Temporal activity cycles in ants have been documented on both seasonal time scales (Schumacher 1976; Whitford et al. 1981; Lynch et al. 1980; Fellers 1989; Suarez et al. 1998) and diel time scales (Talbot 1946; Bernstein 1979; Lynch et al. 1980; Herbers 1989; McCluskey and Neal 1990). However, studies of activity patterns of entire ant assemblages are uncommon (but see Whitford et al. 1981; Fellers 1989). Moreover, most studies of ant activity patterns extend for only part of the annual cycle. Although Hölldobler and Wilson (1990) suggested that annual activity patterns may be important in structuring ant communities, only Fellers (1989) has documented foraging patterns with surveys that extend through all seasons. Finally, most studies of temporal patterns of ant foraging have not compared patterns to those expected in a "null community" in which species forage independently of one another (Gotelli and Graves 1996).

In this study, we documented the temporal and spatial patterns of foraging activity in a guild of ground-foraging grassland ants. We used monthly 24-h surveys at bait stations to document the occurrence and abundance of ant species in an Oklahoma grassland. We compared the observed patterns to those expected under the null hypothesis of independent random occurrence of species.

Materials and methods

Study site

The study site was grassland habitat in a small sandstone canyon in Caddo County, Oklahoma. The canyons in this area of central Oklahoma are Permian sandstone, typically less than 2 km× 0.5 km, and are approximately 25 m deep. The canyon floors are cooler and more mesic than the surrounding uplands (Rice 1960). The site has not been under cultivation or heavy grazing for more than 30 years. The major vegetation present consists of Indian (*Sorghastrum nutans*), redtop (*Agrostis stolonifera*), little bluestem (*Schizachyrium scoparium*), and cheat grasses (*Bromus tectorum*), with vetch (*Vicia* spp.) and mullein (*Verbascum thapsus*) in lower areas.

Census methods

The study plot was a permanent 20 m×20 m square oriented north-south. Each month, 25 bait stations were placed in a grid pattern at

5-m intervals. Approximately 50 g of canned tuna fish were placed at each station on an impermeable 7.5 cm×12 cm card at 1300 hours. The number and species of ants at each bait was then recorded each hour for 24 hours. The ambient air temperature was also recorded each hour. Surveys were completed on a warm day of each month for 12 consecutive months (November 1991–October 1992). Surveys were repeated if there was precipitation. To eliminate residual chemical cues, we cleaned baits cards with hot, soapy water and air-dried them after each census.

Preliminary surveys showed that the abundance and identity of ant species that foraged at tuna fish baits were similar to those that foraged at insect carrion, the most abundant natural protein source at this site. Also, ant species composition at tuna fish, jelly, and seed bait stations were similar, but abundances were much higher at tuna fish baits (M. Albrecht and N.J. Gotelli, personal observations). As in other studies (e.g., Porter and Savignano 1990), the rank abundance of different ant species was similar for bait observations, pitfall catches, and nest-entrance census (Albrecht 1995). Specialized seed foragers (e.g., *Pogonomyrmex* spp.) were uncommon at this site, and did not nest within the study grid.

Although we minimized disturbances to foraging ants, we did collect representative specimens by aspiration for identification. Voucher specimens have been deposited in the Oklahoma State University, Department of Entomology invertebrate collection.

Null model analyses

The data consist of the bait occupancy patterns for each species, measured over 24-h periods for 12 months. We used these data to examine three distinct patterns of niche overlap:

1. Temporal niche overlap on an annual time scale. For this analysis, each row of the data matrix represented a species and each column represented a month of the year. The entries in the matrix consisted of the number of bait occurrences for each species, summed over the 24-h observation period each month. The number of bait occurrences could range from a minimum of 0 for a species that never occurred during a month, to a maximum of 25×24=600 for a species that occupied all 25 baits for each hour of the 24-h censuses.
2. Temporal niche overlap on a diurnal time scale. For this analysis, each row of the data matrix represented a species and each column represented a different hour of the day. The entries in the matrix consisted of the number of bait occurrences of each species at a particular hour. The data for each month were analyzed separately. For each hour of the survey, the number of bait occurrences ranged from a minimum of 0 for a species that never occurred, to a maximum of 25 for a species that occupied every bait. Only species that occurred at least once during a particular month were included in this analysis. Diurnal niche overlap analyses could not be conducted for the months of November, December, and January because there were only 0 or 1 species present during these months.
3. Spatial niche overlap. For this analysis, each row of the data matrix represented a species and each column represented a different bait station. The entries in the matrix consisted of the abundance of each species measured at each of the 25 baits for a particular survey. The data for each hour of a 24-h survey were analyzed separately. Only species that occurred on at least one of the baits during a particular census were included in this analysis.

To quantify patterns of niche overlap between a given pair of species, we calculated the Czechanowski index of niche overlap between each pair of species (Feinsinger et al. 1981):

$$O_{12} = O_{21} = 1.0 - 0.5 \sum_{i=1}^{n} |P_{i1} - P_{12}| \qquad (1)$$

where O_{12} is the overlap of species 1 on species 2, and p_{i1} is the fraction of bait observations for species 1 that occurred in resource state i. For example, in the analysis of seasonal overlap, the resource states represent the different months of the year, and p_{i1} is

136

the fraction of the total bait occurrences for a species that were found in month *i*.

The Czechanowski index is a symmetric index of niche overlap, such that $O_{12}=O_{21}$. The index approaches 0 for species that share no resource states and approaches 1.0 for species pairs that have identical resource utilization distributions. To characterize the niche overlap patterns of the entire assemblage, we calculated the mean and variance of niche overlap among all unique pairs of species in the assemblage (Inger and Colwell 1977).

Next, we determined the statistical significance of the niche overlap patterns by comparing them with an appropriate null model, in which the observed utilization data were randomized among species. The data for each null model consists of a matrix in which the rows are species and the columns are resource states (months of the year, hours of the day, or individual bait stations within an hour). The entries in the matrix are the utilization of each resource state by each species. We used two kinds of randomization algorithms (RA) to test for non-random niche overlap patterns. Winemiller and Pianka (1990) have extensively analyzed these niche overlap models and have evaluated their performance on idealized data sets. For consistency, we used the same labels for the algorithms as Winemiller and Pianka (1990):

1. RA3. In this algorithm, the entries in each row of the utilization matrix were randomly reshuffled. This procedure retains the observed niche breadth of the species, but it allows utilization of any of the possible resource states. We used this algorithm for the analysis of spatial niche overlap. Although we used this algorithm in a preliminary analysis of temporal overlap, we do not believe that all resource states (different hours of a day or different months of a year) could necessarily be used by all species, even in the absence of species interactions.

Therefore it is not an appropriate null model for patterns of temporal niche overlap (see also Tokeshi 1986; Loreau 1989).

2. RA4. In this algorithm, only the non-zero entries in each row of the utilization matrix were randomly reshuffled. This procedure retains both the niche breadth of the species and the pattern of zero states. We used RA4 to analyze seasonal and diel patterns of niche overlap. Although RA4 is a somewhat conservative algorithm (Winemiller and Pianka 1990), it tended to produce higher expected niche overlap values with our data than did other alternative algorithms (RA1, RA2, RA3). Consequently, RA4 had the greatest chance of revealing significant patterns of reduced niche overlap.

For each data set, we randomized the utilization data according to algorithm RA3 or RA4 and created 1000 null assemblages. From these, we calculated the mean niche overlap of all possible species pairs and compared the observed mean to the distribution of simulated means. From these, we calculated the mean niche overlap of all possible species pairs as a community-level index of niche overlap. We compared this index to the histogram of 1000 indices that were calculated from the randomized data sets. We calculated the two-tailed probability values by tabulating the number of simulated niche overlaps that were greater or less than the observed overlap. Interspecific competition should cause mean niche overlap to be less than expected by chance, whereas abiotic constraints on activity, such as air temperature, might cause all species to have similar foraging patterns, so that observed niche overlap would be greater than expected.

We also tested for patterns in the variance, as well as the mean, of niche overlap. Inger and Colwell (1977) showed that if there is guild organization within the species assemblage, the variance in niche overlap will be greater than expected: species pairs within a

Fig. 1 Seasonal occurrence patterns of the four most abundant ant species. The maximum possible number of bait occurrences for each census was 625 (25 baits×24 h). Average temperature over the 24-h census period for each month is plotted on the *right-hand y-axis*
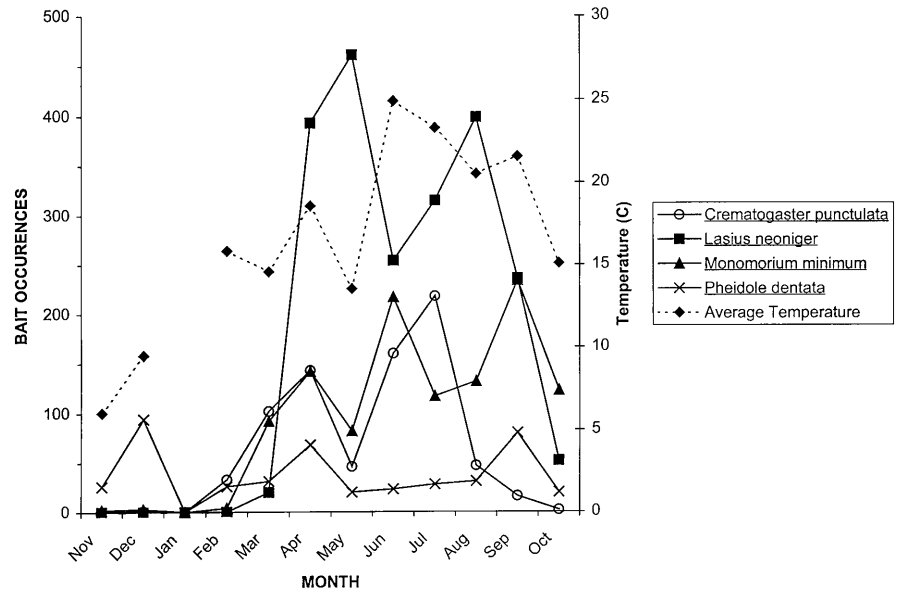
Table 1 Observed and expected mean and variance of niche overlap measured on a seasonal basis. The expected value is calculated from niche overlap indices for 1000 randomly assembled communities. See text for description of the randomization algorithms (RA3, RA4)

Model	Observed mean niche overlap	Expected mean niche overlap	Tail probability
RA3	0.205	0.139	0.012
RA4	0.205	0.193	0.236
Model	Observed niche overlap variance	Expected niche overlap variance	Tail probability
RA3	0.055	0.042	0.151
RA4	0.055	0.058	0.441

guild will have unusually low niche overlap, whereas species pairs in different guilds will have unusually high niche overlap, leading to a large variance in niche overlap. In our data, these patterns might arise if there were a guild of night-foraging and day-foraging species, or if there were a guild of early-season and late-season foragers.

All simulations were carried out with EcoSim software (N.J. Gotelli and G.L. Entsminger, 1999, EcoSim: null model software for ecology, version 3.0, Aquired Intelligence Inc. and Kesey-Bear, http://homepages.together.net/~gentsmin/ecosim.htm). Although we used a two-tailed statistical test, we did not use any further adjustments such as a Bonferonni correction (Sokal and Rohlf 1981) for multiple tests because were interested in the overall pattern of which data sets showed significance and which did not.

Species associations

We examined pairwise Pearson product-moment correlations among species occurrences on both seasonal and diurnal time scales. We restricted this analysis to the four most abundant species (*Crematogaster punctulata*, *Lasius neoniger*, *Monomorium minimum*, and *Pheidole dentata*) so that there would be enough observations to make the statistical tests meaningful. Diel tests were restricted to the three warmest months (June, July, and August 1991) because these months had the highest ant abundances. We used partial correlation calculations to remove the effects of other species for each species pair tested. We also included ambient air temperature in the model to distinguish statistical associations of species with one another from associations of each species with ambient air temperature.

Results

Seasonal overlap

We recorded the presence of seven species during the year-long study, 4 of which were common (Fig. 1). In the unrestricted analysis of these data (RA3), seasonal niche overlap was significantly greater than expected, with few species foraging in the cooler months of the year. When the analysis was restricted to the months in which species were actually present (RA4), there was no evidence of non-random seasonal niche overlap. The variance of seasonal niche overlap also did not differ significantly from expected for RA3 and RA4 (Table 1).

Diurnal overlap

On a 24-h time scale, there were three months (December, March, and October) in which diel niche overlap was significantly greater than expected, and one month (July) in which niche overlap was significantly less than expected (Fig. 2a). In all months except June, the variance of diel niche overlap was greater than expected, and the pattern was statistically significant in May, July, August, and September (Fig. 2b).

Spatial overlap

Both expected and observed overlap in spatial niches varied greatly among months and among hours of the

day within a month (Fig. 3). Out of 216 (24 h×9 months) null model tests, 64 were significant at *P*=0.05, whereas the number expected by chance was only 10.8. Of these 64 significant tests, in 57 cases spatial niche overlap was less than expected, and in only 7 cases was spatial niche overlap greater than expected. In most months, and at most times of day, spatial niche overlap was less than expected.

Pairwise correlations

Correlation analysis was restricted to the 4 most abundant species in the 3 warmest months (Fig. 4). Table 2
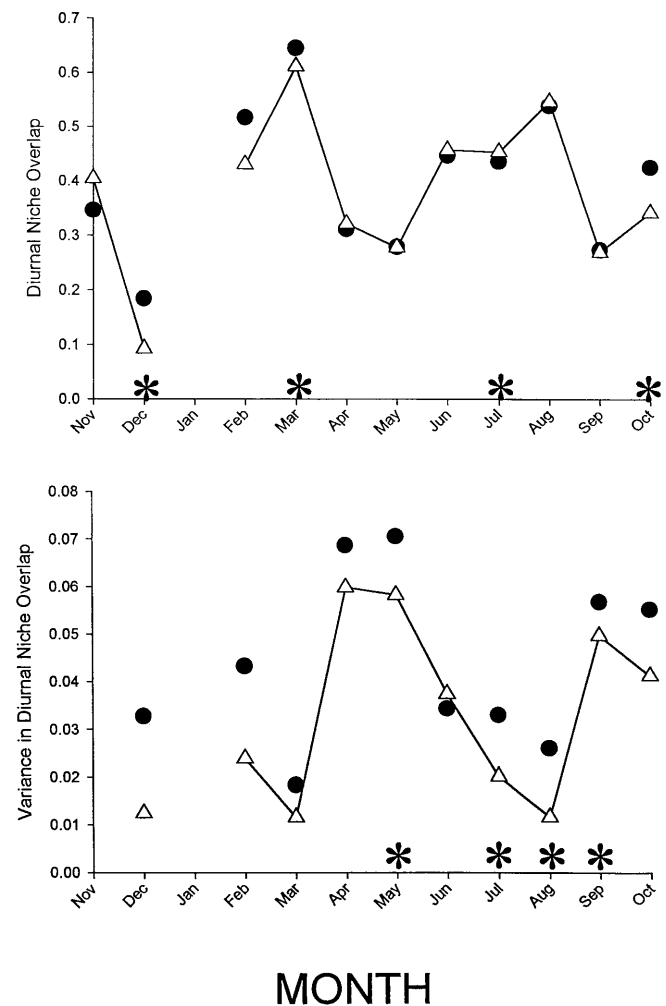

Fig. 2a,b Observed and expected diurnal niche overlap of ground-foraging ants. Each *pair of points* represents the diurnal niche overlap of foraging activity of ants recorded during a particular month. The *open triangle* is the expected niche overlap, calculated as the average niche overlap in 1000 randomized assemblages. The *solid circle* is the observed diurnal niche overlap in each month. An asterisk indicates an observed niche overlap that was significantly different from the null model (*P*<0.025). The *x*-axis indicates the month of the census. **a** Average pairwise niche overlap. Each *point* represents the average niche overlap of all unique pairs of species. **b** Variance in niche overlap. Each *point* represents the variance in pairwise niche overlap

SPATIAL NICHE OVERLAP

HOUR

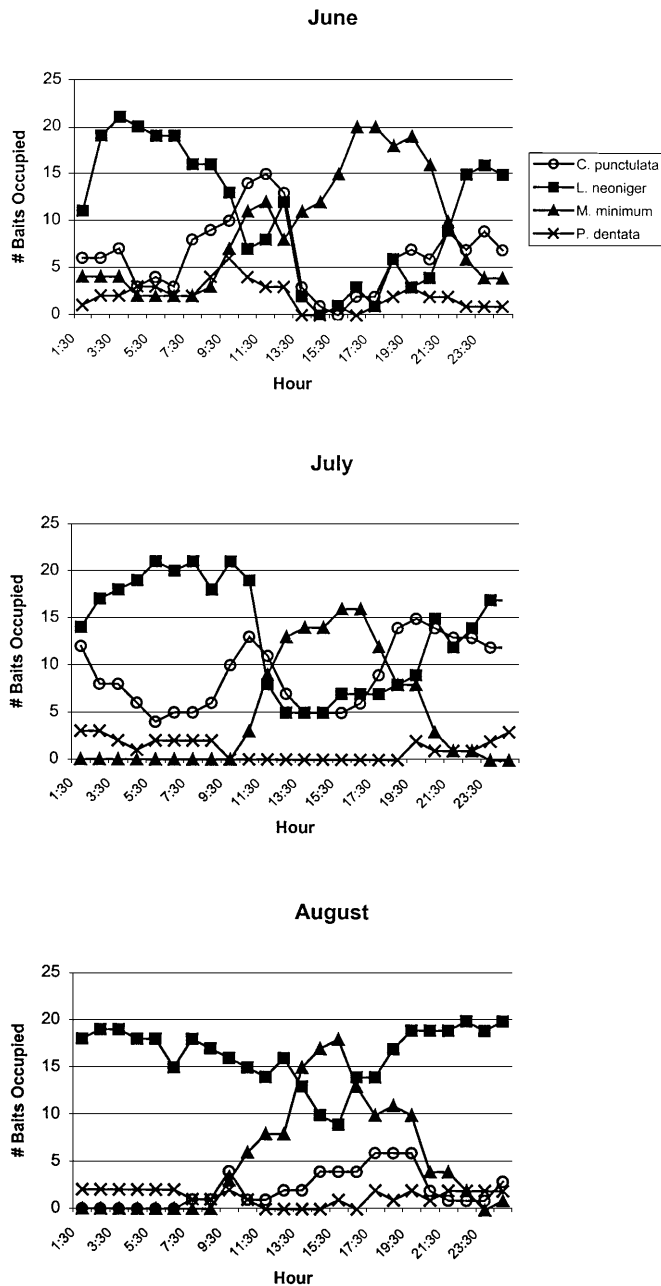## June

July

August
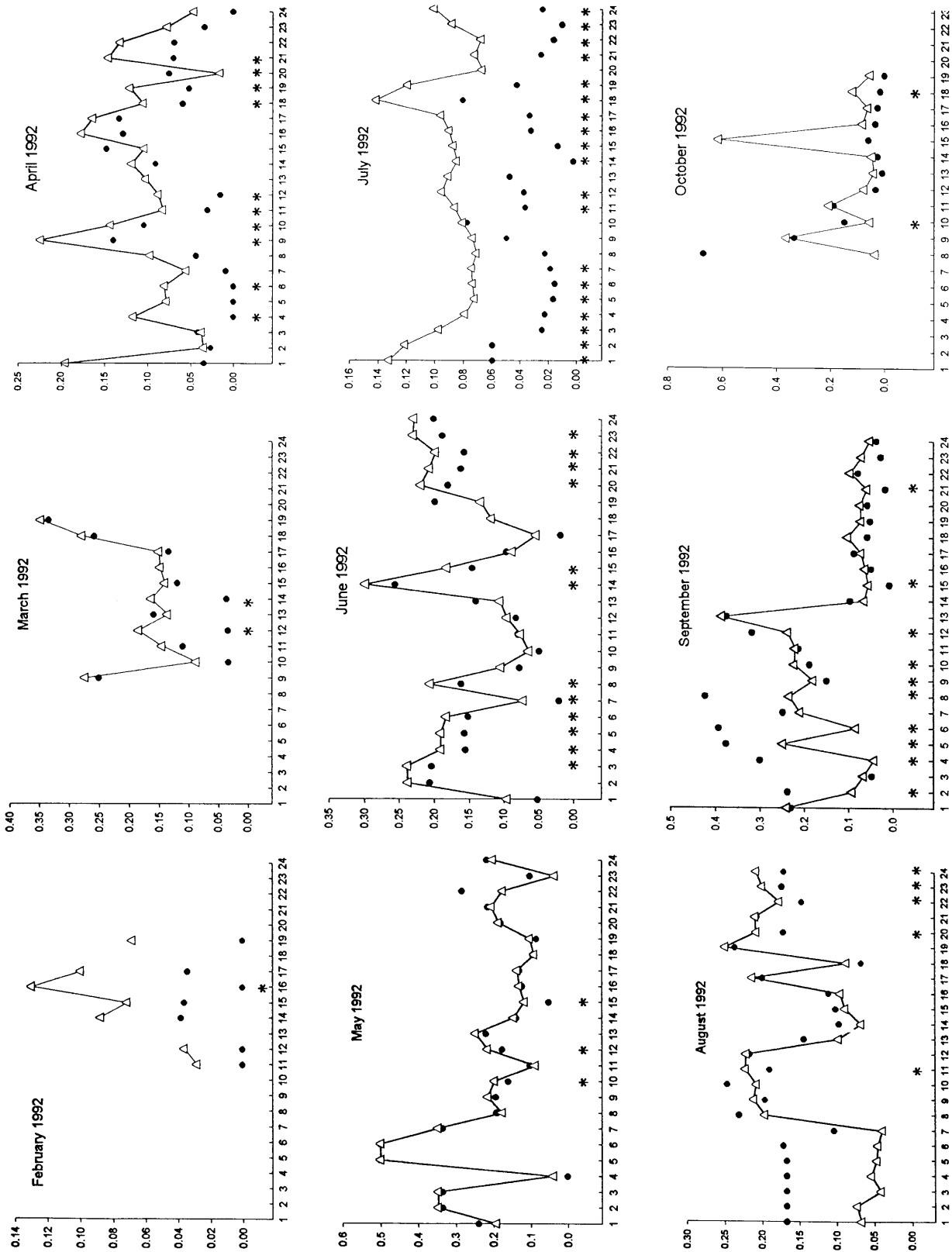
Fig. 4 Diel bait occupancy by the four most abundant species (*Crematogaster punctulata*, *Lasius neoniger*, *Monomorium minimum*, and *Pheidole dentata*). Each *point* represents the number of baits occupied by a species at each hour of the census. The maximum number of baits that could be occupied in each hour is 25

summarizes monthly and diel correlations between species pairs and between species and ambient air temperature. On the monthly time scale, occurrences of all species but *C. punctulata* were positively correlated with average ambient temperature; correlations between all
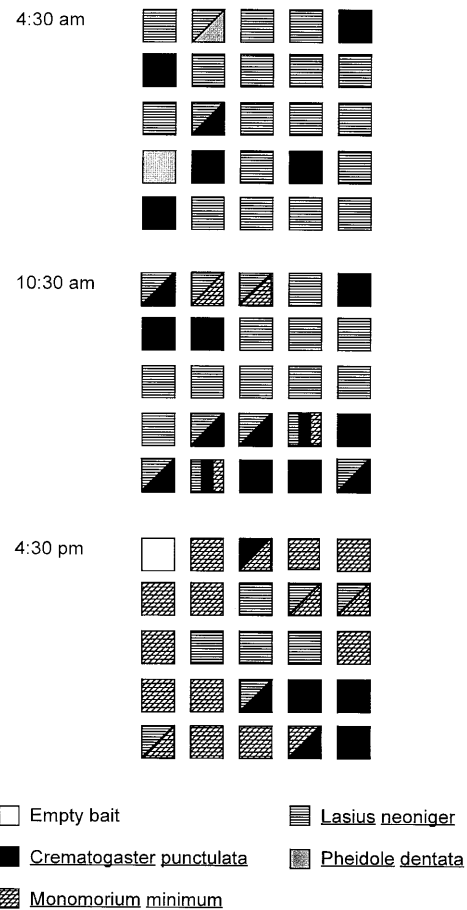
◀ **Fig. 3** Observed and expected spatial niche overlap of ground foraging ants. Each *panel* represents a different month of the year. *Points* represent the spatial overlap among baits calculated at different times of day. *Symbols* as in Fig. 2

Fig. 5 Each *square* represents a tuna fish bait in the 5 m×5 m grid, at three times of day during the July census. Modified from Gotelli and Graves (1996)

species pairs were non-significant. On the 24-h time scale the occurrences of *L. neoniger* and *P. dentata* were negatively correlated with ambient air temperature in all three months, whereas the occurrence of *M. minimum* was positively correlated with ambient air temperature. After partial correlation was used to remove the effects of air temperature and other species, there was a significant positive correlation between *P. dentata* and *L. neoniger*; also both species were negatively correlated with *M. minimum*. On the 24-h time scale, the occurrence of *C. punctulata* was uncorrelated with air temperature or the occurrence of other species.

Discussion

Niche partitioning in ant assemblages has been attributed to species temperature preferences (Talbot 1946; Lynch et al. 1980), humidity preferences (Talbot 1946; Levings and Traniello 1981), food availability (Bernstein 1979), and nest site availability (Herbers 1989), and competition (e.g., Davidson 1977; Hölldobler 1987; Human and Gordon 1996). The activity of one or two behaviorally dominant species may determine the activity patterns of less domi-

Table 2 Partial correlation analysis of species occurrences at baits on month and diel time scales. For each species pair, the occurrence of other species and ambient temperature were factored out. For the correlation between each species and temperature, the occurrences of the other three species were factored out. *Entries above the diagonal* indicate the partial correlation coefficient between each species pair and between each species and ambient air temperature measured monthly. *Entries below the diagonal* summarize partial correlation analyses conducted on a diel time scale (24 hourly measurements) for the months of June, July, and August 1991. Each *symbol* indicates the statistical significance and the direction of the correlation for each month (*0* non-significant correlation, + significant positive correlation at $P<0.05$, – significant negative correlation at $P<0.05$)

	Crematogaster punctulata	*Lasius neoniger*	*Monomorium minimum*	*Pheidole dentata*	Air Temperature
C. punctulata	X	0.449	0.398	–0.198	0.666*
L. neoniger	0 0 0	X	0.515	–0.085	0.577*
M. minimum	0 0 0	– – –	X	0.071	0.809**
P. dentata	0 0 0	+ + 0	– – 0	X	–0.088
Air temperature	0 0 0	– – –	+ + +	– – –	X

*$P<0.05$, **$P<0.01$

nant species (Lynch et al. 1980; Fellers 1989; Andersen 1992). In our study, temperature appears to be an important determinant of temporal activity patterns. The activity of the two most abundant species correlated significantly but negatively, suggesting differing physiological preferences of these species. Similar patterns have been described for woodland ant assemblages (Lynch et al. 1980).

Nest site availability is probably not limiting in this grassland because all species found are ground-nesting (Albrecht 1995). Instead, spatial and temporal niche partitioning of foraging activity may permit coexistence. On a monthly time scale, there was little evidence of seasonal niche partitioning: all species showed a common pattern of foraging more in the warmer months (Fig. 1), and niche overlap measured across the entire year was significantly greater than expected by chance (RA3; Table 1). A modified analysis that controlled for species absences (RA4) showed that seasonal niche overlap was not greater than expected by chance (Table 1). The partial correlation analysis also confirmed that the occurrences of the four common species were positively correlated with temperature, with no evidence of significant species associations. These results are probably typical for assemblages of ectotherms in thermally seasonal environments (Herbers 1989; Bernstein 1979; Herbers 1989). For ants, the foraging activity of many species increases in spring due to increased worker production after winter die-off (Hölldobler and Wilson 1990).

Foraging patterns measured on the diel time scale were less uniform, and provided some evidence of temporal niche partitioning. During some of the cooler months of the study (December, March, and October) temporal niche overlap was significantly greater than expected, probably reflecting foraging constraints of cool nighttime temperatures. In contrast, average niche overlap was significantly less then expected in July, when nighttime temperatures did not pose a physiological limit to foraging. In all months but June, the observed variance in niche overlap was greater than expected, suggesting the presence of two or more diel foraging guilds within the assemblage. These results are consistent with the correlation analyses during the three warmest months: the foraging activity of different species was positively (*M. minimum*), negatively

(*P. dentata*, *L. neoniger*), and randomly (*C. punctulata*) associated with ambient air temperature (Table 2).

Although it is difficult to disentangle the statistical correlations of foraging activity with temperature and with the presence of other species, the partial correlation analysis did reveal negative associations between the warm-foraging *M. minimum* and the cool-foraging *L. neoniger* and *P. dentata*. The presence of venomous alkaloid compounds that are used in competition by *M. minimum* (Andersen et al. 1991) may be the mechanistic basis for these negative associationsallow this species to dominate in foraging. Although *L. neoniger* was the most abundant species in this study, it does not possess a polymorphic worker caste or appear to employ chemical defenses. *L. neoniger* was active at cooler temperatures in the diel cycle and rarely encountered *M. minimum* at baits.

The strongest evidence for niche partitioning was the spatial analysis of bait occupancy at each hour of the survey. Although the patterns changed from hour to hour and month to month, niche overlap was often significantly less than expected by chance (Fig. 5). This result is consistent with abundant evidence for territoriality (Mercier et al. 1997; Grasso et al. 1994) and behavioral dominance hierarchies (Savolainen and Vepsäläinen 1988) that is expressed at relatively small spatial scales.

For the species in this assemblage, average foraging distances from nest entrances to food patches were typically less than 0.5 m (Albrecht 1996), whereas the bait stations were 5.0 m apart. Thus, the nonrandom patterns reflect the spatial segregation of different species as well as the spatial segregation of individual colonies within the study plot (Levings and Traniello 1981). However, it is not the case that particular species monopolized a bait and created static co-occurrence patterns that were repeated each hour. Instead, the pattern of bait occupancy was highly dynamic. There was a substantial amount of turnover in species composition as different species colonized, occupied, and abandoned baits over the 24-h census period (Fig. 5). Ward (1987) described a similar pattern of temporal niche partitioning in a California ant community invaded by the Argentine ant. Colonization-competition tradeoffs (Holway 1999) can also contribute to species coexistence under these circumstances.

In summary, we found little evidence of seasonal niche partitioning by ground-foraging ants. Instead, partitioning occurred on a diel time scale in which common species were active at different time of the day, and on a small spatial scale, in which species used food resources in a shifting spatial mosaic.

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