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The competition for food and circadian succession in the ant fauna of a representative Anatolian semi-steppic environment

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Food exploitation has been studied in a representative semi-steppic environment in Central Anatolia. Practically only ants have been observed: 13 species were alternatively continuously active in exploiting lipidic, protidic and glucidic baits randomly distributed during day and night.

These ants do not appear to belong to a peculiar steppic fauna, but just to particularly resistent species surviving even in a steppic environment and which mainly adapted their feeding preferences to the available food sources. The exploitation of the baits by the ant population is $>99.9\%$ and practically no other invertebrates can compete with them.

The 13 observed species can be arranged in a 13 x 13 symmetric matrix showing 78 possible individual species pairs. Among them, 75 pairs have been observed to have a direct spatial and/or temporal vicariation or avoidance behaviour, while just one pair shows direct competitive behaviour.

It is argued that such biota are in a very stable equilibrium and that eventual new immigrants could hardly establish themselves.

Arid and semi-arid regions are of great interest to the ecologist both for practical and theoretical reasons. In fact, such areas contain several future potentially exploitable lands and their ecosystems are relatively poor in species, in a stable equilibrium, and, consequently, easier to study and to understand. Unfortunately, the information we have on several aspects of these environments is rather poor and incomplete. It is known that, among invertebrates, ants play a big role in the arid ecosystems, but most of the information we have on their relative impact on biocenosis is of purely descriptive nature. A few papers have recently dealt with different quantitative aspects of some desert ants and are worth mentioning here: Délye (1968) studied the Saharan fauna, mostly from the point of view of water retention and temperature tolerance; Dlussky (1974 *a, b*) and Dlussky & Sataplıev (1975) described the microdistribution and some behavioural aspects of ant biocenoses of some Russian desert. In America research concentrated mostly on the seed-harvesting species (see Whitford, 1978, for a review). But very limited information is available on the capacity of exploiting food sources in natural situations by most of the less spectacular xerophylous species with low colony populations.

SELECTED AREA AND METHOD OF STUDY

Our field work has been conducted in October 1977 in Southern Anatolia near to the village of Köprübaşi, 5 km S of Sarayköy (Denizli Region) at an altitude of 260 m. The environment we chose (fig. 1) was a grazed semi-steppe that spread widely into all the surrounding area. The vegetation consisted mostly of

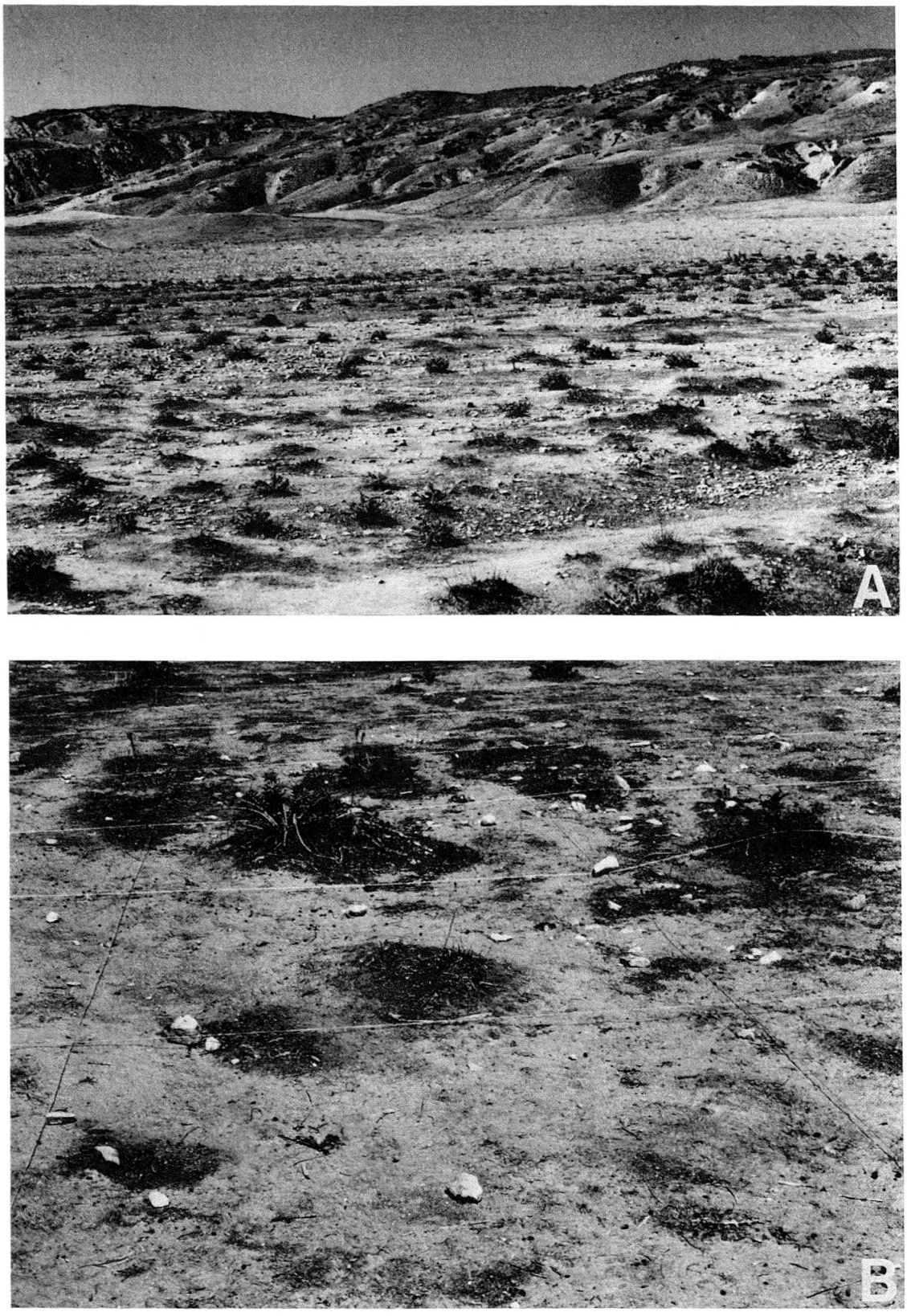


Fig. 1: Köprübaşi (Sarayköy) (A). General view of the steppe type widespread in S. Anatolia and studied in the present paper. Close view (B) of some of the 2 x 2 m quadrats representing the sample units used for this investigation.

Euphorbia, Verbascum, Carpina, Capparis spinosa, and Boraginaceae. The soil was calcareous and moderately stony. The study area consisted of a 60 x 16 m particularly homogeneous rectangle divided into 240 quadrats of 2 x 2 m each. Six quadrats had been selected by means of a table of random numbers and all our observations have been carried out on them. We intentionally excluded from our field all the large mammals such as camels and sheep which were crossing the area daily. On the other hand, small vertebrates, like birds and mice have been disturbed by our presence, and we did not observe a single lizard within nor around the study area.

A PRIORI PROBABILITY OF FOOD DISCOVERY

Before placing the baits in our randomly chosen quadrats, we always counted the number of ants crossing the diagonal of such quadrats during an interval time of 20 min. We assume that this quantity is a function of the probability of discovering randomly distributed food in our sample field. If the same ant crossed e. g. 3 times the diagonal, we counted it as 3 ants because, of course, it had 3 more chances to find food than an ant crossing the diagonal only once. The results of 27 sets of such observations between 7:40 a. m. and 4:00 p. m. ([1]) are reported in fig. 2. The a priori probability of discovering the food is equivalent to the specific density in the background which we define as

$$n_{S,B} = \frac{N_{S,B}}{\sum_{s,B}^{i} N_{S,B}} \leqq 1 \qquad (1)$$

where $N_{S,B}$ is the number of individuals of each species recorded in the background observations.

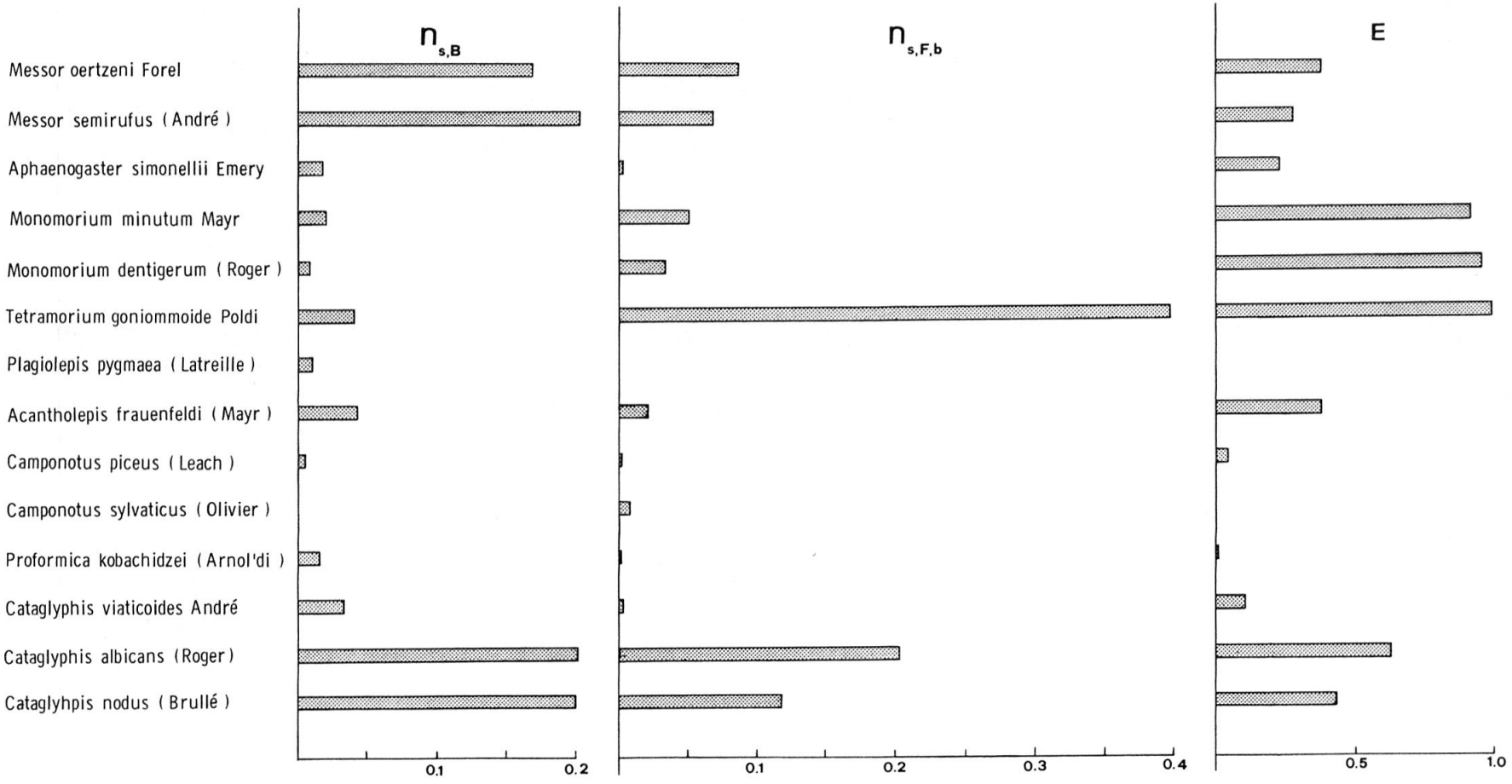
From the figure, one can easily see that practically four species *(Messor oertzeni* FOREL, *M. semirufus* [ANDRÉ], *Cataglyphis nodus* [BRULLÉ] and *C. albicans* [ROGER]) largely dominate, at least numerically, the environment and the remaining 9 species observed are much more reduced in numbers and are only seldom observed. All four numerically dominant species are typical steppe inhabitants, with high xeric requirements and they have in common a low efficiency in column foraging. Both *Cataglyphis* species, but to a minor extent, also *Messor,* never or seldom forage on trails. Even when trails are used, they appear much more disorderly and less efficient than for other ants.

ACTUAL FOOD EXPLOITATION

After placing the baits, the number of ants feeding on them has been recorded at 30 minute intervals for a total of 361 times on the same days in which the background situations were recorded and within the same interval between 7:40 a. m. and 4:00 p. m. Fig. 2 shows this type of result expressed as the ratio between

[1] Turkey, in October, still uses summer time, but the hours reported here always refer to solar time.

Fig. 2: A priori probability of food discovery ($n_{S,B}$), actual food exploitation ($n_{S,F,B}$), and feeding efficiency (E) among the 14 ant species observed. For further explanations, see text.



the number of ants per species observed and the total number of ants observed on the baits. That is, the number of feeding ants per species on the baits ($N_{S,F,b}$) is weighted as

$$n_{S,F,B} = \frac{N_{S,F,b}}{\sum_{s,F}^{i} N_{S,F,b}} \leqq 1 \qquad (2)$$

One can immediately see that, in most instances, the actual food exploitation is quite different from what one could expect on the basis of the background observations, i. e. there is no simple relation between $n_{S,B}$ and $n_{S,F,b}$. *Tetramorium goniommoide* POLDI (39.9% of the feeding ants) is by far the dominant species, while it represents only 4% of the ants observed in the background. *Cataglyphis nodus* is the second in order of frequency on the baits, as it was in the counts without food because it is present exactly in the same proportion in the two sets of observations. We regard this only in part as a surprising coincidence because it seems evident that this ant, at least in the environment we studied, is essentially an isolated forager which never recruits other comrades to the food sources. Moreover, we observed that, despite of its high walking speed and powerful mandibles, the recognition of food and eventual attempts of recruitment are easily disturbed by chemical or mechanical defenses exhibited by other ants like *Monomorium, Tetramorium, Acantholepis,* and even its own congeneric *C. albicans.* In spite of this, between these two species, the type of disturbance exercised and the consequent reactions are largely comparable, provided that the number of individuals involved remains comparable too. For the other species, the histograms of fig. 2 are self explanatory and we would like only to underline that 9 species out of 14 were less abundant on the baits than in the background observations, while 4 *(Monomorium minutum* MAYR, *M. dentigerum* ROGER, *Tetramorium goniommoide* and *Camponotus sylvaticus* (OLIVIER) increased in a considerable way their frequency after the baits had been placed. The case of one of these species *(C. sylvaticus),* might not be comparable to the one of the others because it is a rigorous nocturnal forager (see later) and we never observed it during daytime but only in the early morning and on some baits placed at night and always exploited by it before sunrise. The reverse is true for *Plagiolepis pygmaea* (LATREILLE) which represented 1.4% of the ants counted in the background and which was entirely missing from all the 565 subsequent observations we made on the baits.

From all the previous information, one can easily derive a measure of the feeding efficiency for each species. In order to have this quantity normalized between 0 and 1, we define here the feeding efficiency *(E)* as

$$E = 1 - e^{-\frac{n_{S,F,b}}{n_{S,B}}} \qquad (3)$$

The most efficient species is clearly *Tetramorium goniommoide* (fig. 2), but the other two largest E values *(Monomorium minutum* and *M. dentigerum)* do not correspond to the highest $n_{S,F,b}$ values. We explain this difference by the much more efficient recruiting mechanism of the three involved species.

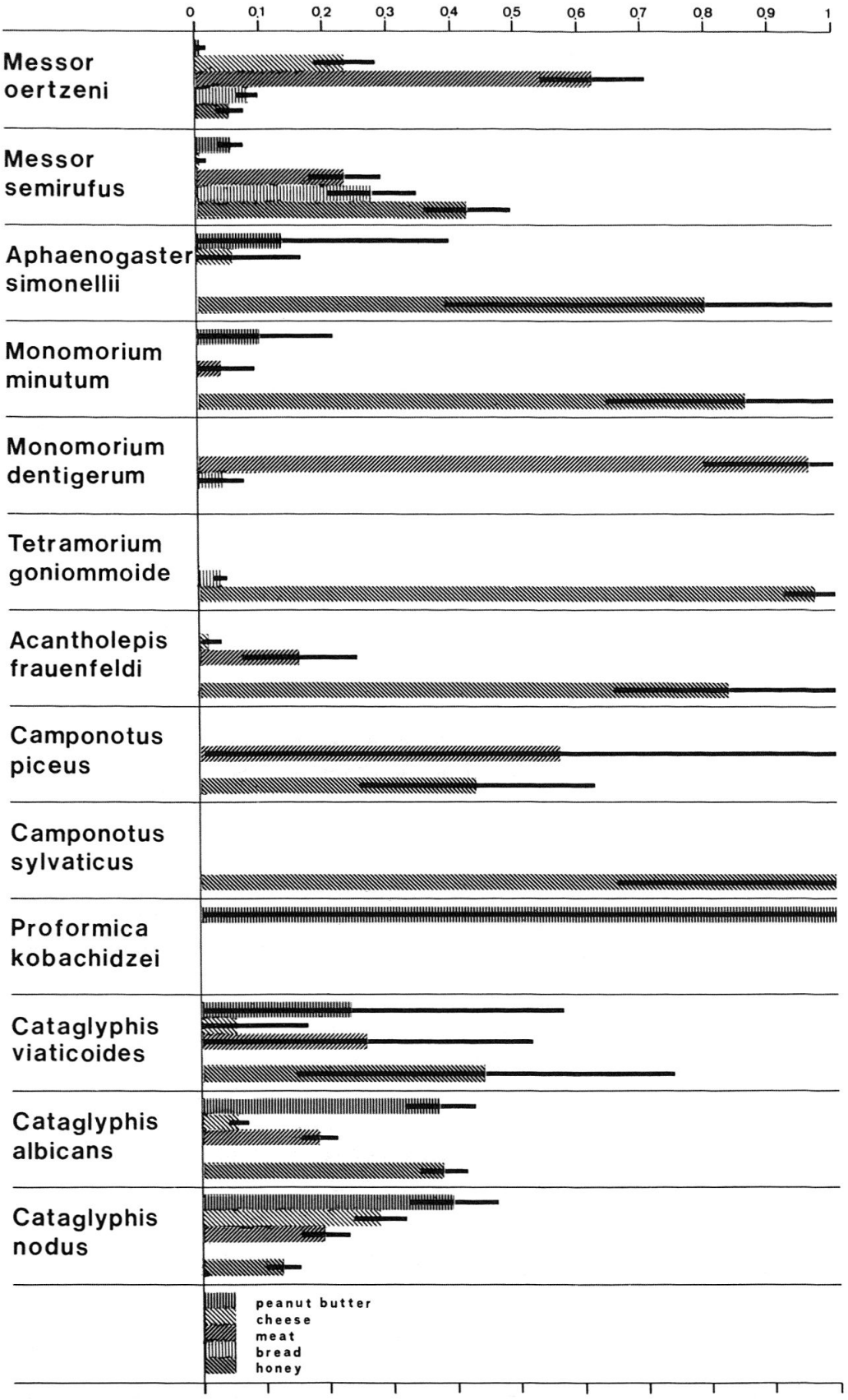


Fig. 3: Food preference as shown by exploitation of five different bait types by 13 steppe ant species. The black solid line superimposed to the histograms represents 99% confidence intervals.

In the previously reported observations we used different baits such as peanut butter, honey, bread, meat and cheese which should have, respectively, a predominant content of lipids, glucids, carbohydrates and proteins. It is obvious that each species is likely to be attracted differently or not attracted at all by each different type of bait. In order to have evidence of the specific food preference, in fig. 3 we reported the relative frequency of ants observed on the different baits. Moreover, we assumed that the frequencies of feeding ants could be approximated by a Poisson distribution and we also represented the 99% confidence intervals for each frequency observed. From the figure, one can easily see that only one species *(Cataglyphis albicans)* shows a marked and statistically demonstrable preference for peanut butter, while this type of bait is the only one on which we observed *Proformica kobachidzei* ARNOLDI, although in too small quantities to allow a statistical confirmation of this preference. 8 species out of 14 fed on peanut butter, but only *Cataglyphis viaticoides* ANDRÉ and *C. nodus* were in relatively large numbers (24% and 38% of the foragers observed for each species respectively). Nonetheless both species were found more frequent on honey and *C. viaticoides* even on meat.

Only 7 species fed on cheese and none of them in a predominant way although it accounted for 25% of the feeding *M. oertzeni* and 28% of *C. albicans.* For both of these species and only for them this type of food appears to be the second in order of preference.

Meat, with 9 species observed feeding on it, appears to be the second favourite food of ants. It is the most frequently visited by *M. oertzeni* and *C. piceus* (LEACH), although for the latter species this preference is not statistically proved. None of the species studied showed a preference for bread and only 4 of them fed on it. This is quite astonishing if one considers that our investigation included two

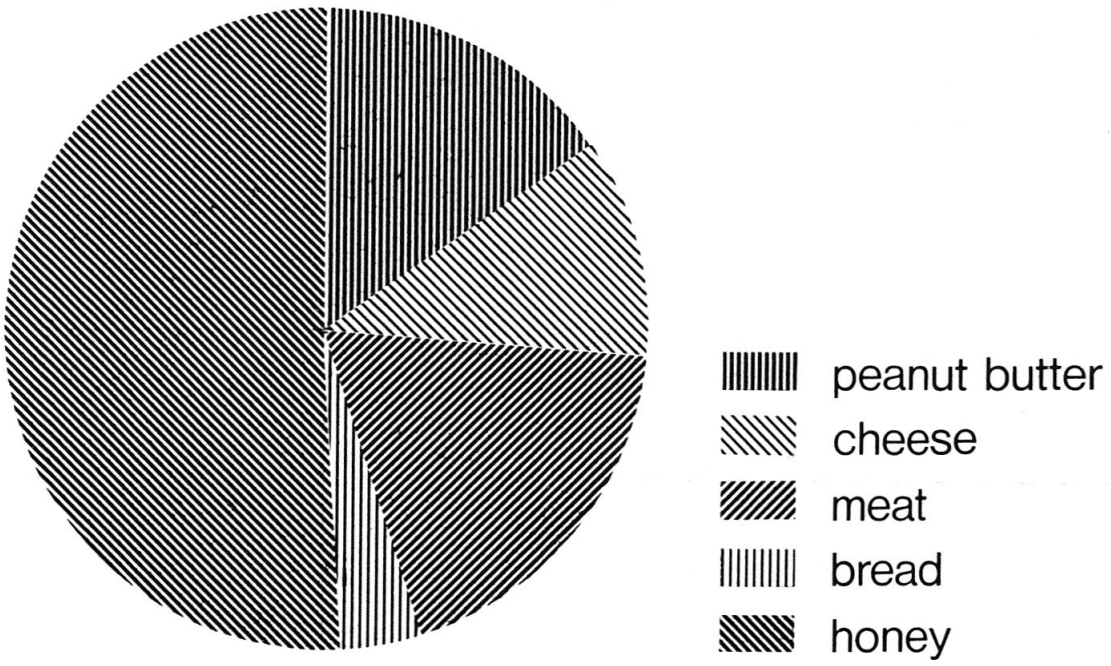
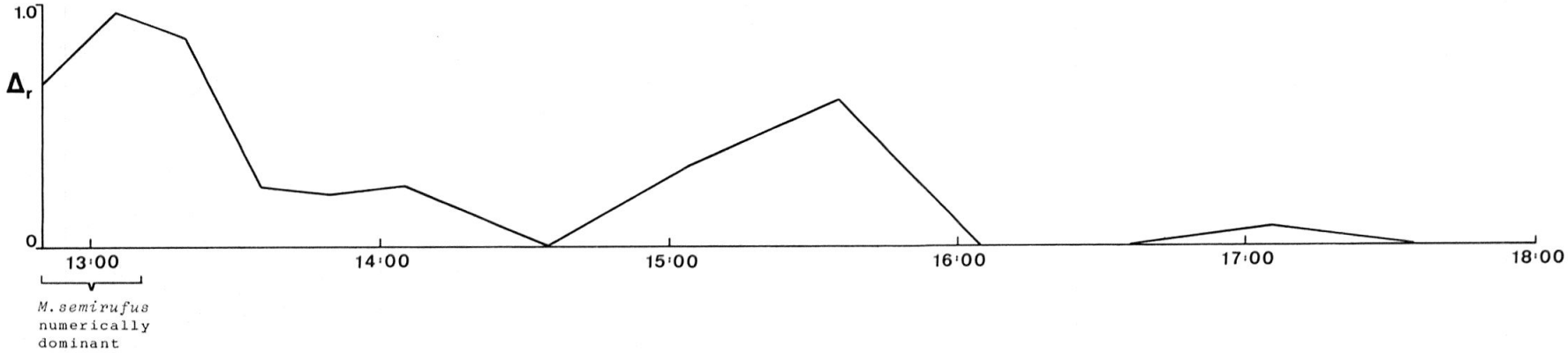


Fig. 4: Proportional exploitation of 5 bait types by the whole ant community under investigation.

Fig. 5: Variation of the relative importance of interspecific competition (Δ_r) on a meat bait. After an initial phase in which *Messor semirufus* is numerically dominant, continuously arriving *Cataglyphis nodus* foragers succeed in monopolizing the food source. After the recruitment mechanism of *M. semirufus* is definitely broken by *C. nodus* attacks, Δ_r values drop to 0 and the latter species feeds undisturbed.



supposed typically granivorous species such as *M. oertzeni,* which preferred meat and cheese to bread in a statistically significant quantity, and *M. semirufus,* which preferred honey in a statistically significant quantity. The other two species which fed on bread, but in much lower proportions, are *Tetramorium goniommoide* (3%) and, quite unexpectedly, *Monomorium dentigerum* (4%).

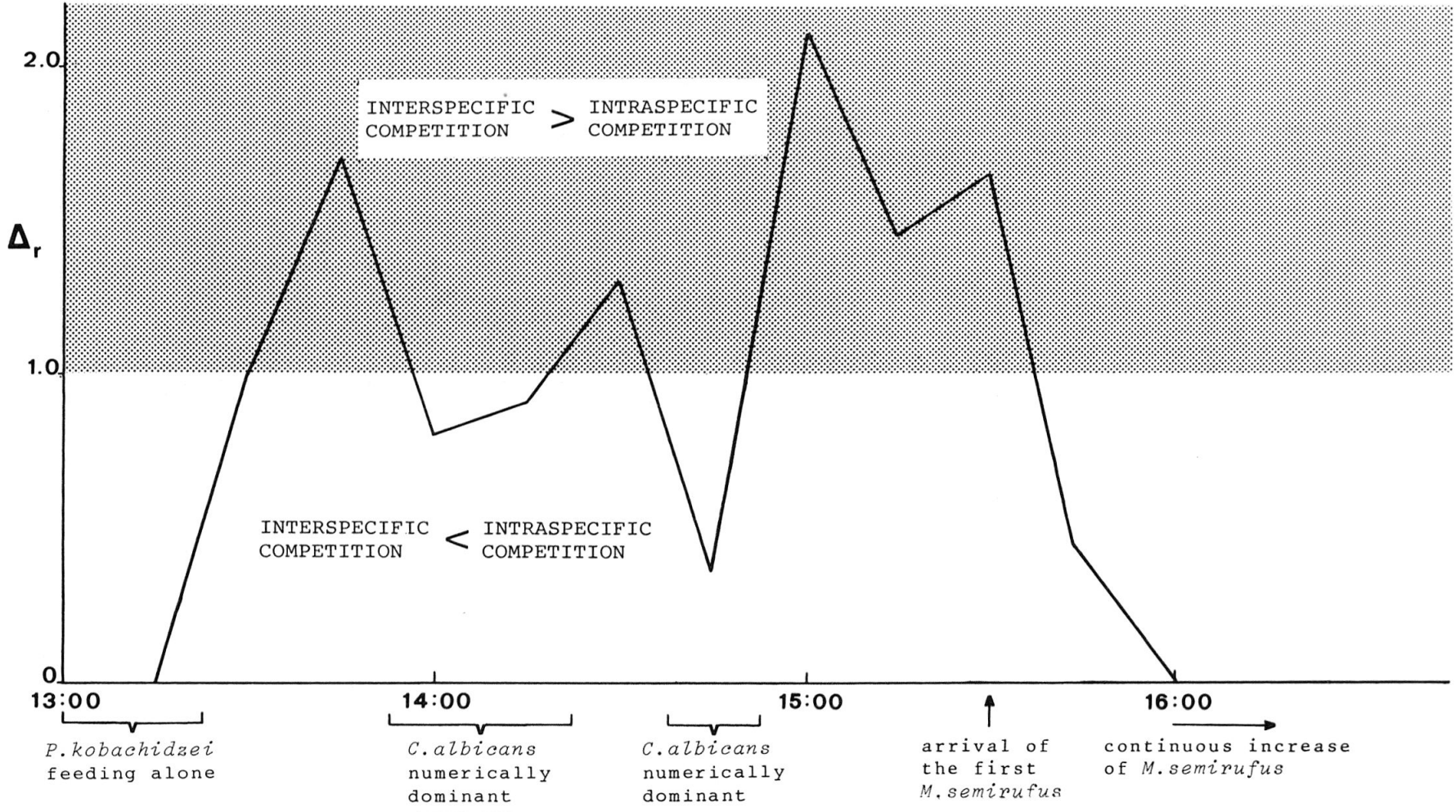
This species is one of the few *Monomorium* which developed a «soldier» caste with large heads and powerful mandibles, very similar to those of *Pheidole.* We were quite surprised to observe no *Pheidole* in our study area, but apparently, *M. dentigerum* which shows a convergent morphology, can play the same role of partial seed eater in this ecosystem and is likely to entirely substitute *Pheidole* under certain circumstances.

Honey is by far the preferred food of ants. 11 species have been observed to feed on it and 8 of them in a preferential manner. For 5 species ecologically and taxonomically disparate such as *Messor semirufus, Monomorium minutum, Tetramorium goniommoide, Acantholepis frauenfeldi* (MAYR) and *Camponotus sylvaticus,* this preference is statistically significant and *C. sylvaticus* has been observed feeding only on it.

Up to now we have dealt with the relative specific frequency of ants on the different food sources, but, however, it might be interesting to know how many ants exploited a given food source as a whole. The number of ants on each bait has been normalized according to the number of observations on that bait type and the results are given in fig. 4. From this figure it appears very clearly that most of the ants in the studied steppe (51.2%) prefer honey, while meat, peanut butter and cheese follow in this order of preference and less than 4% of the ants fed on bread. We do not think that these differences in exploiting our baits can even roughly correspond to the frequency of comparable food sources in the field. For instance, we observed no Aphids at all in our sample plot, although some might surely be tended by the ants on the grass roots. We believe that, in natural conditions, the sugar supply is much lower than what one could expect judging only by the strong preference for it shown by the population under examination. We can therefore conclude that these steppe ants as a whole did not develop a diet particularly adapted to the environment where they live. On the contrary, at least a numerically dominant part of the population is composed by species with large niche breadth capable of surviving even in a steppic environment. From these considerations one can suppose that there should be a strong competition between different species to exploit preferred and rare food sources.

In fact, we observed direct competition quite often, but, only in a relatively few instances one species succeeded in entirely monopolizing a food source for a given period. During the daytime *Cataglyphis nodus* appears to be by far the dominant species: it succeeded in monopolizing 4 times a food source (3 times peanut butter, 1 time meat). Each of the following five species monopolized a food source at once: *Cataglyphis albicans* (peanut butter), *Monomorium dentigerum* (meat), *M. minutum* (cheese), *Tetramorium goniommoide* (honey) and *Messor semirufus* (meat). Another eleven sets of observations never ended with a clear supremacy of only one species over the others. If we are allowed to attempt some generalizations on the monopolization of a food source by the different species, one big difference between *C. nodus* and all the other species appears immediately. The success in exploiting a given food source obviously depends on several environmental factors such as distance from the nest, temperature, natural density of ants in the area, etc.; but, in all the four instances we observed *C. nodus* to be

Fig. 6: Multiple exploitation of a meat bait giving a succession of three consecutive dominant feeders. The first random foragers *Proformica kobachidzei),* after disturbance from other species, give the way to *Cataglyphis albicans* in less than 40 min. *C. albicans* maintains at least one forager on the bait for more than 90 min., when the bait is entirely monopolized by *Messor semirufus.* A total of 7 ant species fed more or less regularly on this bait before *M. semirufus* kept the supremacy. In fact, values of $\Delta_r > 1.0$ imply the direct competition of more than 2 species on the bait.



successful, it arrived first on the bait and continuously held the position without allowing an efficient quantity of alien individuals to feed. All the other ants we observed, arrived early or late on the bait, but they succeeded in monopolizing it after an initial period in which other species, sometimes in high numbers, were capable of exploiting the same food source. To visualize these observations, we calculated the relative importance of interspecific competition (Δ_r) on our baits at regular time intervals (according to HURLBERT, 1971, slightly modified), as

$$\Delta_r = \frac{\Delta_2}{1 - \Delta_2} \tag{4}$$

where,

$$\Delta_2 = 1 - \sum_{i=1}^{m} \left(\frac{n_{S,t}}{N_t} \right)^2 \tag{5}$$

and, $n_{S,t}$ = number of individuals of the i-th species observed $N_t = \Sigma_i \, n_{S,t}$ = total number of individual observed m = number of species observed.

Among the numerous cases observed, we report here as representative in fig. 5 the exploitation of a meat bait by *C. nodus* on our square 240 and in fig. 6 the late monopolization of another meat bait on square 35 by *M. semirufus*. One can easily see that, after some initial difficulty, *C. nodus* exploited the bait always in increasing numbers and never allowing other ants to establish themselves in a profitable manner on the bait. On the other hand, in the square 240, a total of seven species competed for the food exploitation for more than three hours. In this time interval, two species *(P. kobachidzei* and *C. albicans)* succeeded in reducing the interspecific competition for at least two consecutive observations, but have been overwhelmed by continuously recruited alien foragers. *M. semirufus* arrived last because of the disturbance effect exerted by other ants around the bait. Despite of this it easily succeeded in overcoming all the competitors due to the short distance between the nest and the bait. It is interesting to note that the three species which monopolized the meat bait 240, succeeded in monopolizing the bait for a while in an order directly proportional to their specific walking speed.

THE CIRCADIAN SUCCESSION OF FOOD EXPLOITATION

Let $n_{S,t}$ be the total number of individuals of one species observed at one time on the baits and $n_S = \sum_{i=0}^{r} n_{S,t}$ (r = number of observations), the total number of individuals of one species observed.

Then we have $N_t = \sum_{i=0}^{m} n_{S,t}$ (m = number of species), the total number of observed at a given time and $N_T = \sum_{i=0}^{m} N_t$ the total number of ants observed on the baits.

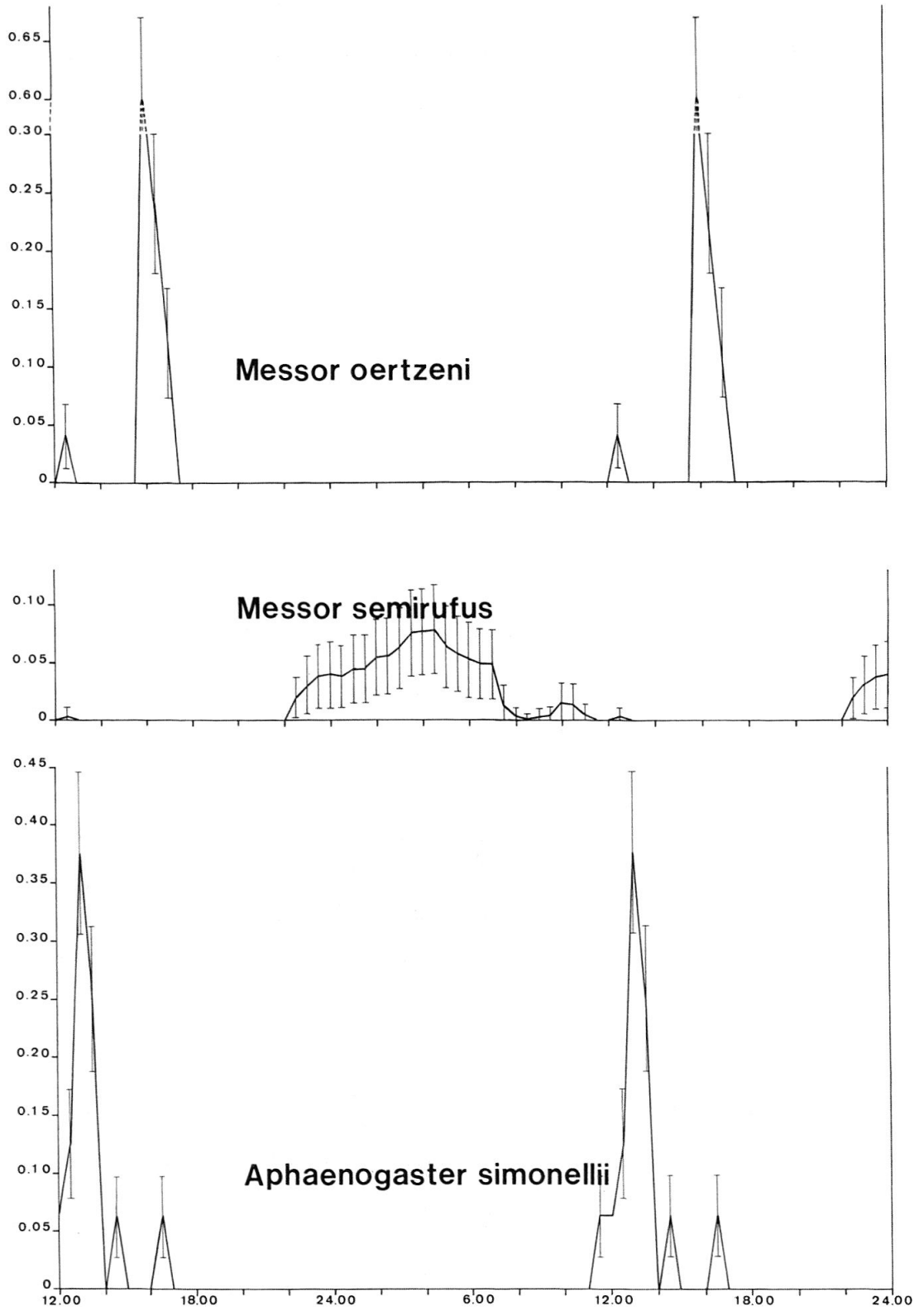
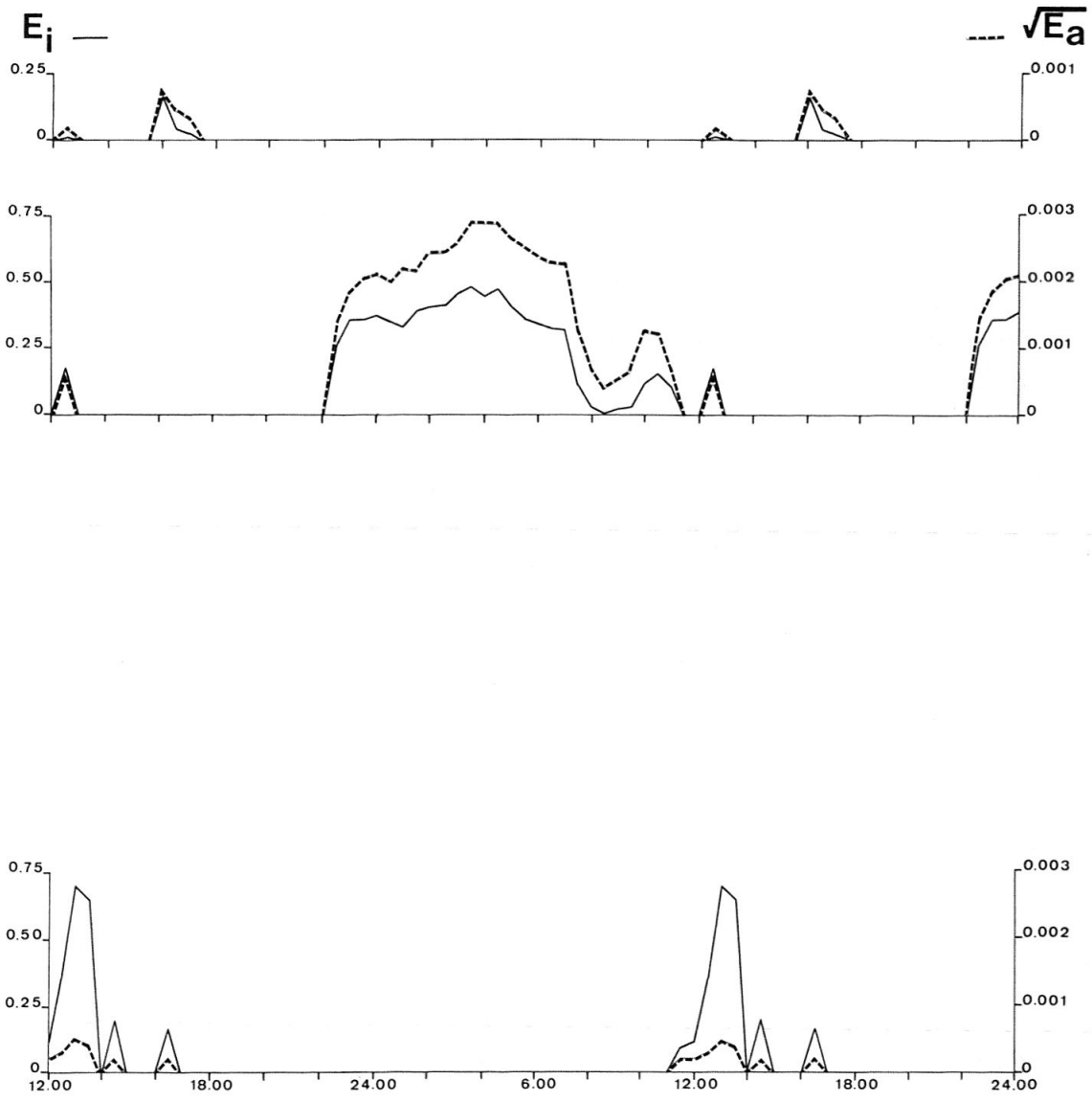


Fig. 7: Circadian patterns of the specific feeding efficiency (E_a), actual feeding efficiency, i. e. compared with the whole ant population (E_a), and instantaneous feeding efficiency (E_i) for the 10 commonest species observed. Instead of the actual values of E_a, the values of $\sqrt{E_a}$ have been mapped for purely practical reasons.


E_i —
---- $\sqrt{E_a}$
0.25
0
0.001
0
0.75
0.50
0.25
0
0.003
0.002
0.001
0
0.75
0.50
0.25
0
0.003
0.002
0.001
0
12.00
18.00
24.00
6.00
12.00
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24.00

Fig. 7 (cont.).

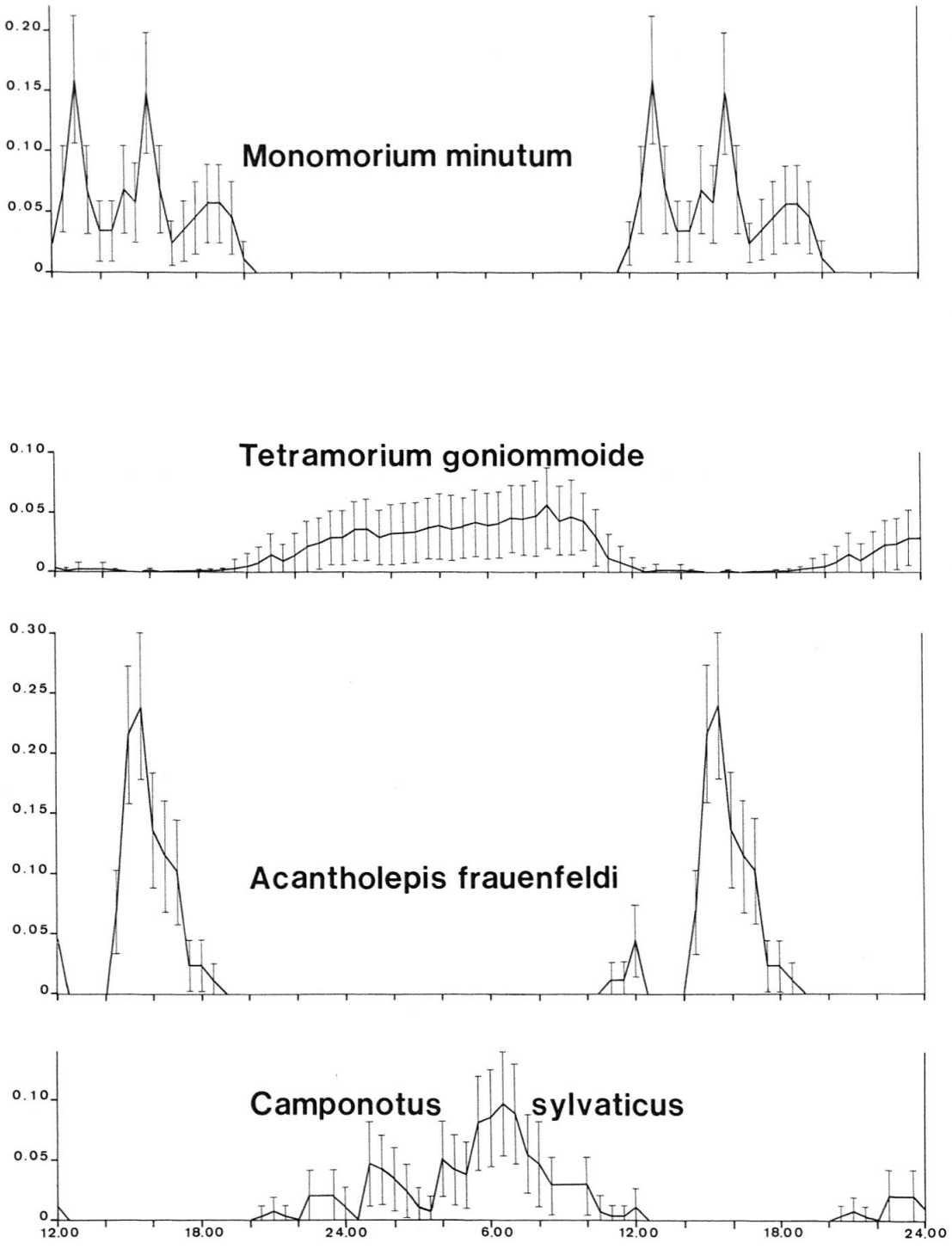

Fig. 7 (cont.).

We define the feeding of one species at a given time as

$$E_a = n_{S,t}/n_S \tag{6}$$

The actual feeding efficiency of one species (E_a) per time unit is given by

$$E_a = n_{S,t}/N_T \tag{7}$$

We suppose that, at least in some instances, one species, although usually foraging in low numbers, might be particularly efficient in food exploiting because

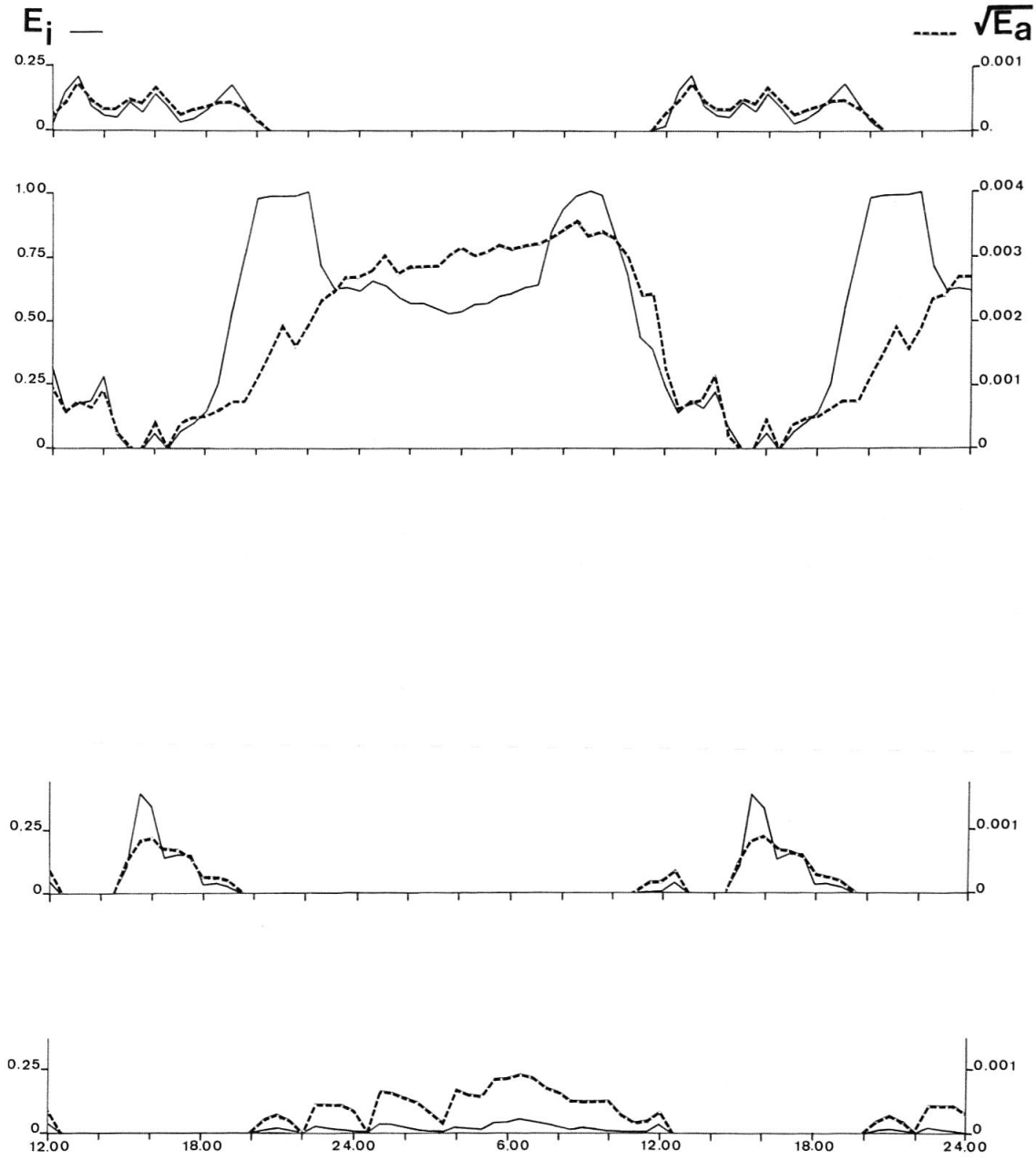

Fig. 7 (cont.).

of the lack of competitors. For this reason, we calculated also the instantaneous feeding efficiency of one species at a given time which we define as

$$E_i = n_{s,t}/N_t \tag{8}$$

All these three functions are normalized such as

$$\Sigma\, E_a \equiv \Sigma\, E_a \equiv \Sigma\, E_i \equiv 1.$$

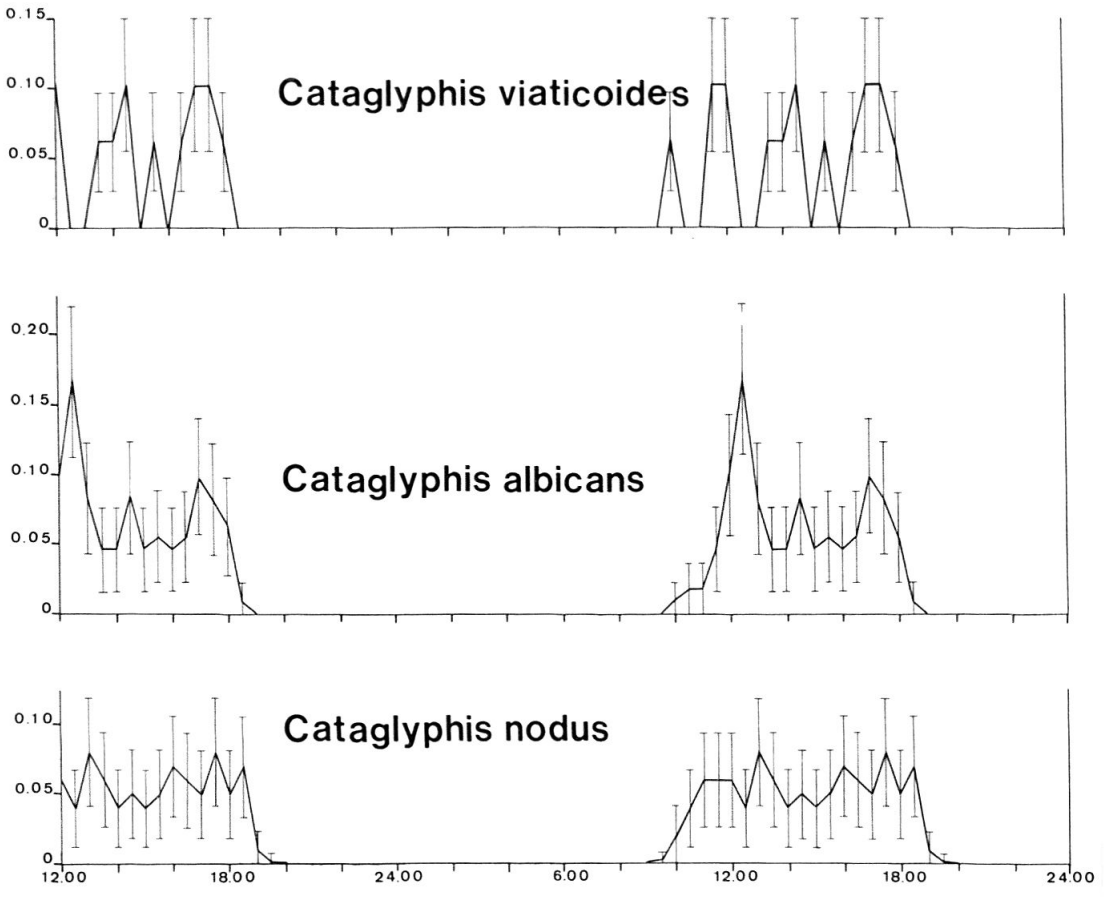

Fig. 7 (cont.).

Fig. 7 gives graphically the variation of E_a, E_i and E_a on a total of 144 observations on honey baits during 24 continuous hours. These observations had been made on honey baits because all but two of the studied species had been observed to feed on honey and for most of them this represented the obviously preferred food.

For each E_a value the 95% confidence interval has been calculated, while, to make the results visually more comparable, the curve of $\sqrt{E_a}$ has been drawn instead of the one derived from the actual values.

From the figure, one can easily see that only *M. semirufus, T. goniommoide* and *C. sylvaticus* are essentially nocturnal foragers, while all the remaining species are typically diurnal. It is noteworthy also that the two *Messor* species *(oertzeni* and *semirufus)* have complementary foraging activities even if their observed food preferences are only slightly overlapping (see fig. 3). The three *Cataglyphis* species show comparable rhythms with peaks between 12:00 a. m. and 2:00 p. m. and this obviously involves a good degree of competition because their feeding requirements are also very similar. The remaining species show also comparable feeding activities with maxima in the afternoon. Of the greatest interest is also the comparison between the E_a and E_i curves. A trivial remark is that none of them takes the shape of the E_a curve. Moreover, E_a shows regularly higher values than E_i, but it is among the three nocturnal species that E_a shows the greatest increase. This is obviously due to the lack of competition from most of the other species. On the

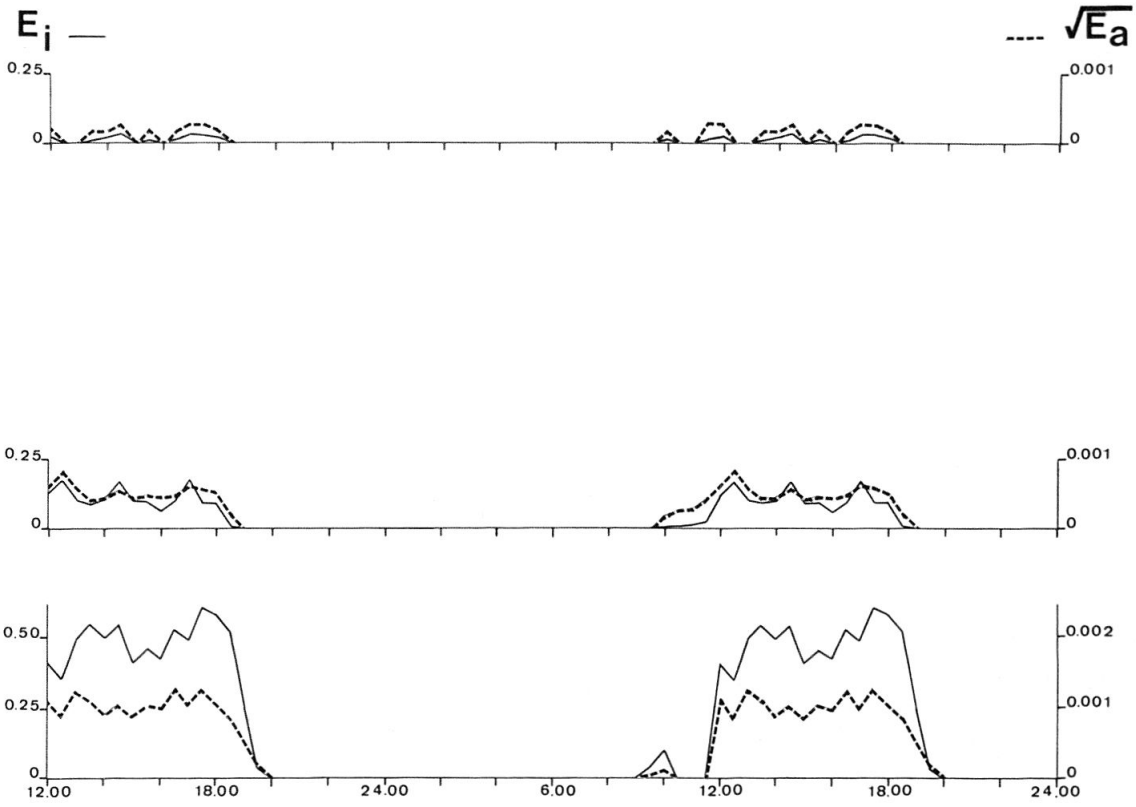

Fig. 7 (cont.).

contrary, the E_i curve has a much more irregular shape representing single instantaneous competitory successes of one or of another species feeding.

One should also note, for instance, how rare and non aggressive species such as *A. simonellii* EMERY can easily have the highest instantaneous feeding efficiency for short periods, greater than that of the much more abundant and aggressive *C. nodus* which has a roughly similar foraging pattern and is the sole species present in comparable numbers on the baits during these short periods of *Aphaenogaster's* spectacular feeding efficiency.

We should probably mention, at this point, that HARKNESS (1977) reported slightly different circadian activities for *C. nodus* (under the name *C. bicolor)* in Greece. Besides the obvious environmental and seasonal differences among the two populations studied, HARKNESS recorded the number of ants going in and out of the nest. If we assume that the maximum external activity should fall between the two peaks of entries and exits recorded by HARKNESS, his curves appear perfectly comparable to ours.

THE DEGREE OF COEXISTENCE BETWEEN THE FEEDING SPECIES

By comparing the simultaneous presence of every possible pair of species on a bait during the previously quoted series of observations, and by using the Jaccard's association coefficient, one can easily calculate the degree of coexistence

on the baits for each possible species (table 1) and construct a coexistence polygon for all the species studied in this environment (fig. 8).

Jaccard's coefficient is as follows:

$$Q_J = C/(A+B+C) \quad (9)$$

Where A = number of samples in which only species A is present
B = number of samples in which only species B is present
C = number of samples in which both species A and B are present.

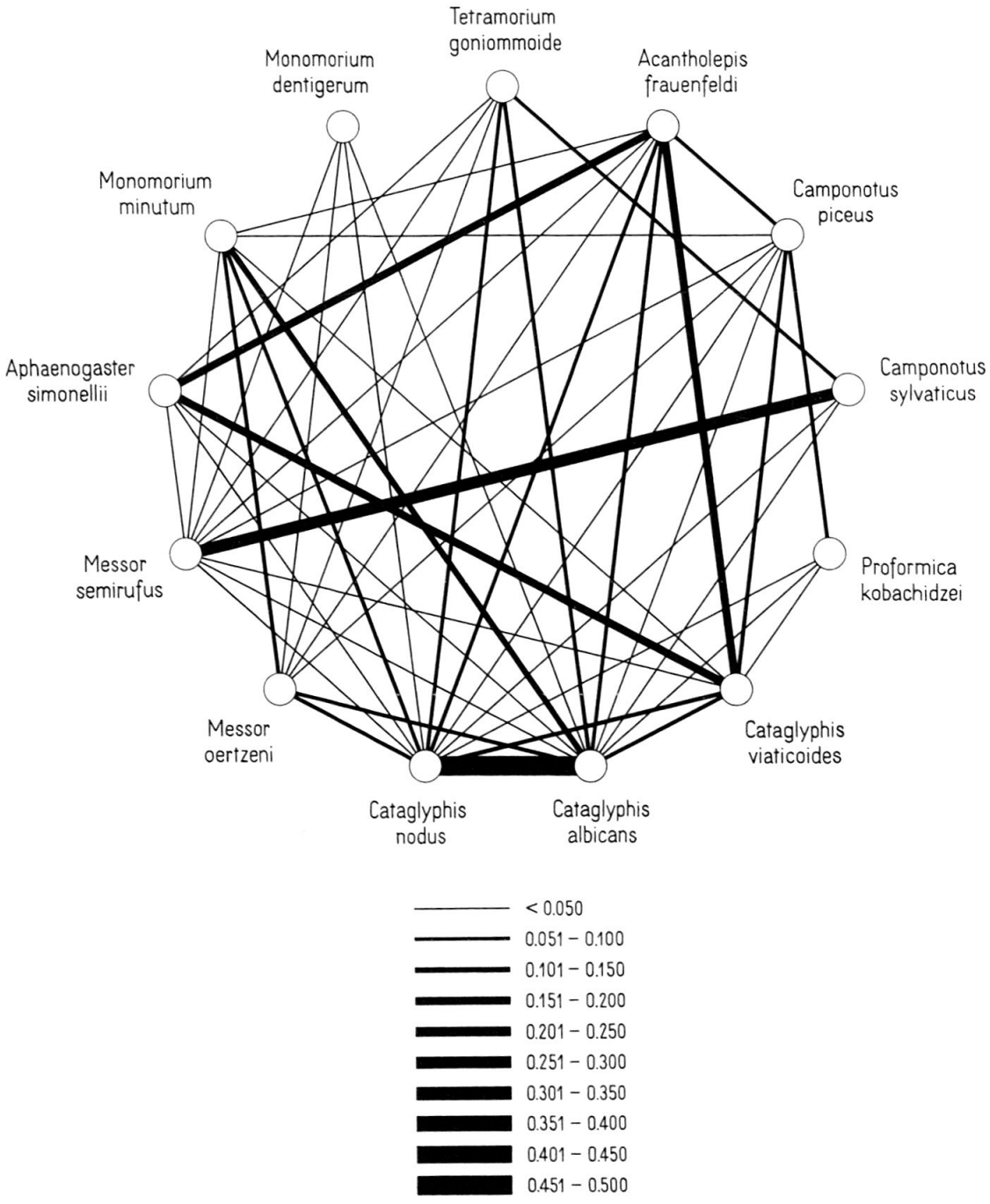

Fig. 8: Coexistence polygon for the 13 ant species observed on the baits. The thickness of the lines connecting specific vertices is proportional to the Q_J value. Note the great majority of narrow lines (i. e. avoidance behaviours) or the absolute lack of coexistence between several species pairs.

Its statistical significance has been obtained by comparing the QJ value with the values reported in the table prepared by BARONI URBANI (1980 b).

Both the table and the figure show statistically significant mutual exclusions between the great majority of species pairs. However, the mutual exclusion could be the product of a direct competitive activity of one or both involved species or can be just the result of different circadian activities as it has already been shown by BARONI URBANI (1969), STEBAEV & REZNIKOVA (1972), BARONI URBANI & KANNOWSKI (1974) and BARONI URBANI (1979).

In order to verify this hypothesis, we calculated the degree of nonoverlap between the specific frequencies of a priori probability of food discovery ($n_{S,B}$) for every species pair (1,2) as

$$D_{\text{circadian}} = \frac{\int | f_1(n_{S,B}) - f_2(n_{S,B}) | \, dn_{S,B}}{2} \qquad (10)$$

When $D_{\text{circadian}} > \cdot 5$ the rhythms are predominantly overlapping, and when $D_{\text{circadian}} < \cdot 5$ the rhythms are assumed to be or to tend to non-overlapping.

However, species having either similar or dissimilar circadian activities may further be separated by having similar or dissimilar feeding preferences.

The similarity in feeding preference for every species pair has been calculated on the same data of fig. 3 where the feeding preference for every species is given as a set of histograms $\{s_{1i}\}$, $\{s_{2i}\}$, etc.

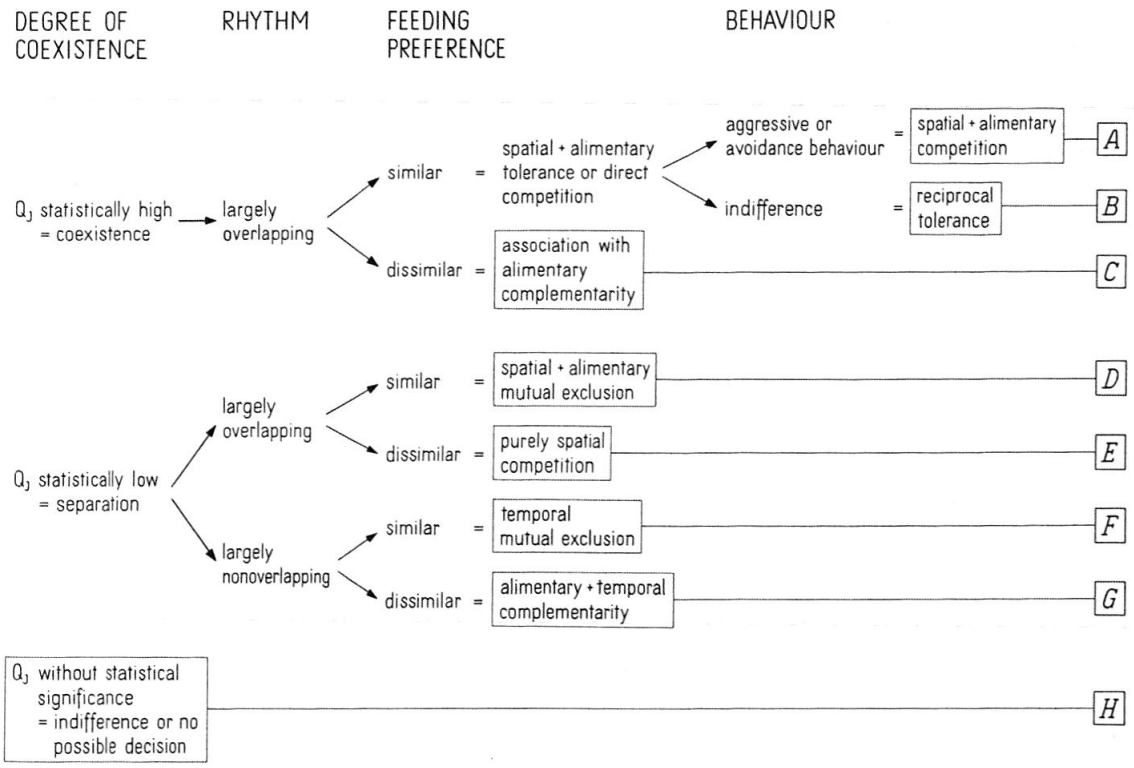

Fig. 9: Schematic diagram of the 8 possible interrelation types between any species pair. The main focus is on spatial, temporal and nutritional association or tolerance versus competition.

Tab. 1: Matrix of the QJ values and their relative statistical significance between all the species pairs observed on the baits.

	Messor semirufus	Aphaenogaster simonellii	Monomorium minutum	Monomorium dentigerum	Tetramorium goniommoide	Acantholepis frauenfeldi	Camponotus piceus	Camponotus sylvaticus	Proformica kobachidzei	Cataglyphis viaticoides	Cataglyphis albicans	Cataglyphis nodus
Messor oertzeni	0.0 p<<0.01	0.0 p<<0.01	0.057 p<<0.01	0.013 p<<0.01	0.030 p<<0.01	0.036 p<<0.01	0.013 p<<0.01	0.0 p<<0.01	0.0 p<<0.01	0.0 p<<0.01	0.093 p<<0.01	0.072 p<<0.01
Messor semirufus		0.009 p<<0.01	0.007 p<<0.01	0.009 p<<0.01	0.005 p<<0.01	0.008 p<<0.01	0.008 p<<0.01	0.280 p<0.01	0.0 p<<0.01	0.024 p<<0.01	0.040 p<<0.01	0.044 p<<0.01
Aphaenogaster simonellii			0.0 p<<0.01	0.0 p<<0.01	0.011 p<<0.01	0.167 p<0.10	0.0 p<0.01	0.0 p<<0.01	0.0 p<0.01	0.167. p<0.10	0.044 p<<0.01	0.043 p<<0.01
Monomorium minutum				0.0 p<<0.01	0.0 p<<0.01	0.016 p<<0.01	0.035 p<<0.01	0.0 p<<0.01	0.0 p<<0.01	0.008 p<<0.01	0.110 p<<0.01	0.075 p<<0.01
Monomorium dentigerum					0.0 p<<0.01	0.0 p<<0.01	0.0 p<<0.01	0.0 p<<0.01	0.0 p<<0.01	0.0 p<<0.01	0.024 p<<0.01	0.004 p<<0.01
Tetramorium goniommoide						0.0 p<<0.01	0.0 p<<0.01	0.061 p<<0.01	0.0 p<<0.01	0.0 p<<0.01	0.076 p<<0.01	0.083 p<<0.01
Acantholepis frauenfeldi							0.074 p<0.01	0.0 p<<0.01	0.0 p<<0.01	0.158 p<0.05	0.057 p<<0.01	0.057 p<<0.01
Camponotus piceus								0.0 p<<0.01	0.053 p<0.01	0.069 p<0.01	0.043 p<<0.01	0.040 p<<0.01
Camponotus sylvaticus									0.0 p<<0.01	0.0 p<<0.01	0.008 p<<0.01	0.003 p<<0.01
Proformica kobachidzei										0.034 p<0.01	0.039 p<<0.01	0.026 p<<0.01
Cataglyphis viaticoides											0.052 p<<0.01	0.084 p<<0.01
Cataglyphis albicans												0.489 p>>0.99

Tab. 2: Different interaction types observed between the 79 pairs of species attracted by the baits. For further explanations see text.

	Messor semirufus	Aphaenogaster simonellii	Monomorium minutum	Monomorium dentigerum	Tetramorium goniommoide	Acantholepis frauenfeldi	Camponotus piceus	Camponotus sylvaticus	Proformica kobachidzei	Cataglyphis viaticoides	Cataglyphis albicans	Cataglyphis nodus
Messor oertzeni	*G*	*G*	*E*	*F*	*G*	*E*	*F*	*G*	*G*	*G*	*E*	*D*
Messor semirufus		*G*	*F*	*F*	*D*	*F*	*F*	*D*	*G*	*F*	*G*	*G*
Aphaenogaster simonellii			*D*	*E*	*F*	*H*	*E*	*F*	*E*	*H*	*D*	*F*
Monomorium minutum				*E*	*F*	*F*	*D*	*F*	*E*	*D*	*D*	*E*
Monomorium dentigerum					*G*	*G*	*D*	*G*	*E*	*E*	*E*	*E*
Tetramorium goniommoide						*F*	*G*	*D*	*G*	*F*	*F*	*G*
Acantholepis frauenfeldi							*D*	*F*	*E*	*D*	*D*	*E*
Camponotus piceus								*G*	*E*	*D*	*D*	*D*
Camponotus sylvaticus									*G*	*F*	*F*	*G*
Proformica kobachidzei										*E*	*E*	*D*
Cataglyphis viaticoides											*D*	*D*
Cataglyphis albicans												*A*

The degree of similarity in food preference D_{feeding} has been calculated analogously with $D_{\text{circadian}}$ as

$$D_{\text{feeding}} = \frac{\sum_{i=1}^{n} |s_1 i - s_2 i|}{2} \tag{11}$$

for which also the same numerical values $\leqslant .5$ imply the same degree of overlap or of differentiation in the feeding habits.

Finally, also species regularly encountered together on the baits may tolerate each other or may be present in a more or less precarious equilibrium maintained only by continuous fights. In this eventuality, only the direct behavioural observation can clear this point.

Fig. 9 summarizes all the possible explanations for coexisting or competing species pairs which, in the following text, will be briefly coded als follows:

A = spatial + alimentary competition
B = reciprocal tolerance
C = association with alimentary complementarity
D = spatial + alimentary mutual exclusion
E = purely spatial competition
F = temporal mutual exclusion
G = alimentary + temporal complementarity
H = indifference or no statistically possible decision.

The 13 species included in the present research allow 78 different pair combinations and table 2 gives the type of interaction between every possible species pair according to the previously proposed schema and indicated by the letters *A-H*.

At first one can see that only two species pairs *(Aphaenogaster simonellii x Acantholepis frauenfeldi* and *A. simonellii x Cataglyphis viaticoides)* are underobserved, while all the other pairs allow a decision on their respective relationships. Just one pair of co-generic species *(Cataglyphis albicans x C. nodus)* show a high degree of coexistence coupled with similar circadian rhythms and feeding preferences. In this case, however, we so often observed individual fighting and reciprocal stealing of food particles in the field that we are obviously in presence of a case of spatial and alimentary competition.

The remaining 75 cases are all mutually exclusive pairs and represented practically in the same proportion al follows:

Type *D* = 19 pairs (24.4%)
Type *E* = 18 pairs (23.1%)
Type *F* = 19 pairs (24.4%)
Type *G* = 19 pairs (24.4%)

Hence, mutually exclusive competition seems to be by far the commonest situation in this ant association.

DISCUSSION

On the whole, 10 998 insects have been observed on our baits during the observation period and 10 991 of them were ants. Of the remaining 7, all beetles, 5 have been identified as *Tentyria rotundata* ssp. *mittrei* Solier (Tenebrionidae), observed 4 times on meat and one on cheese baits, 1 has been identified as *Calathus fuscipes* Gze. (Carabidae), observed once on meat, and the last is a single unidentified Curculionidae which we observed only once on honey.

Although the number of beetles present on the baits was too low to allow a serious study of their impact on the biocenosis, we must notice that these species should have a high feeding efficiency because none of them has been recorded in the background observations without baits.

Moreover, as far as we can tell, and at least until they are present in such low numbers, none of them seems to be seriously attacked nor affected in any other way by the ants.

However, the most important result of our investigation is that the ants represent 99.94% of the feeding animals observed and largely dominate both numerically and as predatory effect in this type of environment.

Despite of the good adaptation to the environment, none of the involved ant species appear to be a peculiar steppe inhabitant because they are all widespread also in many other biotopes with a much higher nutritional imput.

We believe that the Turkish steppe ant fauna is composed essentially by the most resistent indigenous Anatolian species which have been able to adapt themselves to this environment. It is intuitive that the whole population must be subject to a strong K selection and each species plays an important role in it. The case of *Monomorium dentigerum,* replacing the genus *Pheidole* with which it converges morphologically and behaviourally and which is astonishly absent in our environment, is, in our view, a further proof of such a severe selection and of the resulting habitat saturation (see BARONI URBANI, 1980 a). As a result, the ant population is capable of exploiting practically every type of food available, even if just a small amount of it is theoretically preferred.

The high number of multiple contemporaneous occurrences we observed on our baits clearly indicate that spatially separate territories are not very common, but they seem to be still more frequent than it was previously thought in the literature (BARONI URBANI, 1979), when one considers that type *D* and *E* competitions account for 47.5% of the observed species pairs. But temporal mutual exclusion is still a little more frequent than the spatial one (type *F* and *G* competition represent 48.8% of the species pairs). Both spatial and temporal mutual exclusion can be exerted when the feeding preference is similar or different in about the same proportion. This implies that a territory can be maintained by an ant species for purely antagonistic reasons only, without a direct competition in exploiting the food sources.

We did not observe a single case of pacifical coexistence or reciprocal tolerance among this Anatolian ant community. On the other hand, competition is practically the rule, but in the great majority of cases, such competition appears to be in an equilibrium state in which each species occupies a well delimited spatial and/or temporal niche. In fact we observed no intercolonial battles at all and very little individual true fights even on the baits.

The case of the two *Cataglyphis* species *(nodus* and *albicans)* is a remarkable exception because both species are present in comparable numbers, forage on large territories, and are purely diurnal animals. Individual fightings are relatively frequent, at least on the baits, and one species *(nodus)* seems to take advantage of its larger size and greater power in carrying a prey, while the second seems to be favoured perhaps even to a greater degree by a higher walking speed.

From superficial observations in other regions of Turkey, we suppose that this is a widespread situation and the resulting equilibrium should also be widespread and relatively stable, but such a stability is continuously adjusted by continuous small confrontations which never depass the tolerance thershold of one or the other species.

Finally, we did not observe a single case of intraspecific fight and we interpret this fact as an indirect proof that cospecific territories have always nonoverlapping boundaries.

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