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Contribution to the autecology of *Formica selysi* BONDROIT, 1918 (Hymenoptera, Formicidae) in a mature steppe and a newly created alluvial zone at Pfywald (Switzerland): II. Habitat use

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In the inner alpine dry steppe area of Rottensand at Pfywald (CH), which was partly influenced by a severe flood in 1993, *Formica selysi* is the dominant ant species (GROSSRIEDER & ZETTEL 1999); it attains maximum nest densities in the steppe with low or no influence of the flood. Within the framework of a diploma thesis, we compared several habitat use parameters in two zonation types. We confirmed that the density of *F. selysi* nests was higher in the steppe than in the gravel area, but the nests were generally smaller and the dynamic density of foragers was significantly lower. Furthermore, the foraging distances were much smaller, and the foraging areas tended to overlap less between nearest-neighbour nests in the steppe than in the gravel area. Detailed studies at one nest per zonation type suggested that *F. selysi* showed a clear preference for foraging in sectors of the home range containing trees or saplings with aphid colonies throughout the entire observation period.

Keywords: Hymenoptera, Formicidae, zonation, steppe, alluvial area, pioneer species, nest density, dynamic density, foraging area.

INTRODUCTION

The Pfywald is located in the inner alpine dry zone of the central Valais (Switzerland) and includes one of the largest pine forests in Central Europe and the last remaining steppe area in the valley bottom of the Valais, the Rottensand. The steppe vegetation is dominated by the grass *Stipa pennata* but also comprises rare species of eastern or Mediterranean origin. The insect fauna is equally diverse, containing many thermophilic species (e.g. BILLE & WERNER 1986).

During an exceptional high water in 1993, the River Rhone flooded parts of the Rottensand and covered approximately 5 ha of the steppe area with sand and gravel deposit. This provided a unique opportunity to follow the recolonization of an alluvial area by arthropods and to compare different zonation types of a dry steppe habitat. In a long term project, we are monitoring the recolonization of the gravel area by different groups of insects. So far, the abundances of bees (LOEFFEL et al. 1999), digger wasps (ZEHNDER & ZETTEL 1999), grasshoppers (MÜLLER & ZETTEL 1999) and ants (GROSSRIEDER & ZETTEL 1999) in habitats of varying successional age have been studied. GROSSRIEDER & ZETTEL (1999) showed that the ant fauna in all zonation types was dominated by *Formica (Serviformica) selysi* (Hymenoptera, Formicidae) which is a common species in alpine alluvial zones (KUTTER 1977; SEIFERT 1996; LUDE et al. 1999). The density of *F. selysi* nests was higher in the non-flooded steppe than in the gravel area.

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These results suggested that the spatial organisation of *F. selysi* changes during the course of succession and that the older steppes are more intensively used by the species. In the present study, the habitat use of this species in the two zonation types was examined. At the same time, the feeding ecology of *F. selysi* was investigated (KELLER 1999; KELLER & ZETTEL 2001).

MATERIALS AND METHODS

Study area

The present study was carried out from May to September 1998 at the Rottensand in the Pfynwald, a dry steppe area located between Susten and Sierre in the central Valais. A detailed description of the study area is given by ZEHNDER & ZETTEL (1999).

For comparison, we chose two study sites in different zonation types (Fig. 1). Plot GR (= gravel) was 40x50 m in size and was located in an area where the top soil had been washed away and replaced by sand and gravel deposited during a flood in September 1993. In 1998, the vegetation consisted mainly of ca. 1 m high saplings of pioneer trees such as poplar (*Populus nigra*) and willow (*Salix eleagnos* and *S. purpurea*) at a density of ca. 1 plant / m². Study site ST (= steppe) was 45x30 m in area and was situated in mature steppe which had not been affected by the flood. The vegetation was dominated by herbaceous plants and small groups of pine (*Pinus sylvestris*). The plots were of unequal size but contained a similar number of nests, and both were subdivided with a 5x5 m grid, whose corners were marked with small posts to allow for easy orientation.

Nest density and colony size

At the two study sites, all nests of *F. selysi* were mapped by following ant foragers from tuna baits placed on the ground at 5 m intervals. According to GROSS-RIEDER & ZETTEL (1999) the use of tuna baits at a density of 5 m is a reliable method to find nests of large and agile ant species such as *F. selysi*. The medians of the number of nests per 25 m² were compared between the two study sites with a MANN-WHITNEY-U-test.

The number of nest entrances was counted as a measure of colony size after placing a tuna bait in the centre of each nest area. Thus, high foraging activity could be induced, which facilitated the location of the often inconspicuous nest entrances. We tested for significant differences of the medians between the two study sites with a MANN-WHITNEY-U-test.

Dynamic density

The average dynamic density of ant foragers was determined on a 20x25 m plot at each study site. Within these two plots, 25x25 cm observation squares were established at 5 m intervals, which produced a grid of 30 such squares. The corners of these squares were marked with inconspicuous dots of paint, which did not influence the behaviour of the foragers. As a measure of dynamic density, we counted the number of workers entering each observation square during 4 min. The counts were carried out in random order on sunny days during the morning peak of activity (9 to 11 a.m. from July 17 to August 20, and 10 to 12 a.m. from August 28 to

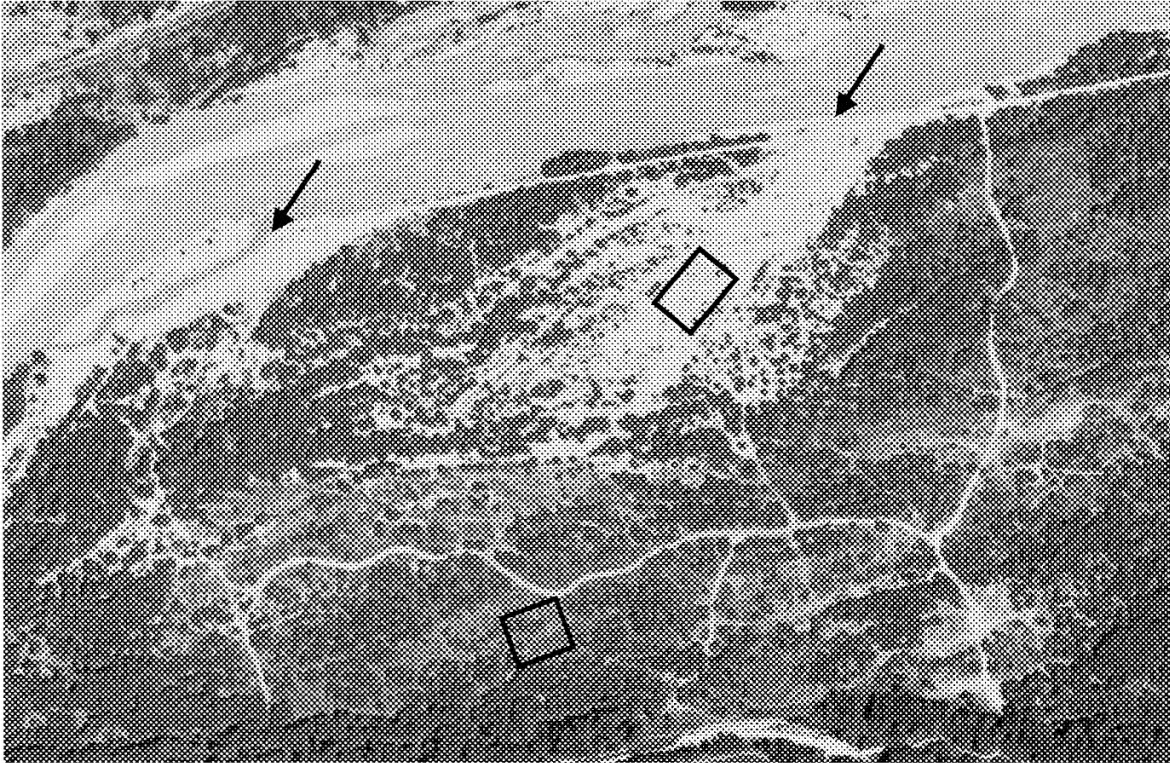


Fig. 1: Aerial photograph of the study area in the Pfynwald. The arrows indicate the breaches in the Rhone dam caused by the high water level in 1993. Upper rectangle = area GR (gravel). Lower rectangle = area ST (steppe). Photograph by Bundesamt für Landestopographie.

September 22) and were repeated four to five times per square. We calculated the mean dynamic density for each observation square and tested for significant differences between the two study plots with a MANN-WHITNEY-U-test. Before each observation, we recorded the temperature of the soil surface with a digital thermometer Metrawatt M4013 (diameter of the probe 0.5 mm). At the end of the season, the distance between each observation square and the nearest nest of *F. selysi* was measured. We used MANN-WHITNEY-U-tests to compare these two factors between the study sites.

Size and overlap of foraging areas

To determine the maximum foraging distance of workers from one nest towards the closest conspecific colony, we randomly chose eight pairs of nearest-neighbour nests at each study site. We defined the foraging range of a nest as the area in which the ants are able to locate profitable food sources quickly and recruit nest mates to them. It is, however, clear that individual foragers may venture much farther from the nest during their foraging trips. To establish the boundaries of the foraging ranges, a tuna bait was placed in the middle between two nests, and foragers were followed on their way back from the food. A bait was considered to be outside the foraging areas of the two nests, if it had not been found within an hour after placement. The baits were moved 0.5 m at a time from the centre toward each nest until the boundaries of the foraging areas became apparent. In the steppe, the

limits of the foraging areas were determined with an accuracy of 0.25 m, to make allowance for the fact, that the average distance between the nests was approximately half of that in the gravel habitat. We waited for at least an hour before placing another bait between the same two nests to ensure that the number of foragers in the area was not higher than it would be under normal circumstances. We randomly selected one nest from each nearest-neighbour-pair to calculate the average maximum foraging distance. The medians of the two study sites were compared with a MANN-WHITNEY-U-test. The overlap of foraging areas between the nest pairs was calculated as a percentage of the distance between the two colonies, and compared between the two study sites with a MANN-WHITNEY-U-test.

Use of foraging areas

The use of different sectors of the foraging area by ant workers was investigated at one nest per study site. We counted the number of ants entering the nest area across four observation lines (A-D) which were placed 1 m from the centre of the nest. Each of these lines measured 30 cm and was set perpendicularly to the direction of the nest. The position of the first observation line was chosen arbitrarily, and the three remaining lines were placed at 90° angles to each other. Each nest was observed from 9 a.m. to 6 p.m. on five days between the middle of July and the middle of September. Three times per hour, the numbers of returning ants crossing each of the four lines during 2 min. were counted. FRIEDMAN two-way analysis of variance was used to test for significant differences between the four lines at each nest. Individual medians were compared with a WILCOXON-WILCOX-test.

RESULTS

Nest density and colony size

In the steppe (ST), the average nest density was significantly higher than in the gravel area (GR) ($P < 0.01$, Tab. 1). The average number of entrances per nest was significantly higher in GR than in ST ($P < 0.05$, Tab. 1).

Dynamic density

The average dynamic density of individuals was significantly higher in area GR than in area ST ($P < 0.01$, Tab. 1). The number of foragers entering the observation squares during 4 min was generally low in ST, and in 40 % of the observation periods the squares were not used by ants at all, which occurred in only 7% of the

	GR	N	ST	N	Sign.
Nest density (nests 25m ⁻²)	0 (0.36)	80	1 (0.72)	50	**
Number of nest entrances	4	25	3	33	*
Activity density (ants dm ⁻² min ⁻¹)	0.29	30	0.07	30	**
Foraging distance (m)	6	8	2	8	*

Tab. 1: Parameters of habitat use by *Formica selysi* at the Rottensand. GR = gravel area. ST = non-flooded steppe. Significance of differences between the medians: ** $P < 0.01$, * $P < 0.05$ (MANN-WHITNEY-U-test). The arithmetic mean of nest densities is given in parentheses.

cases in GR. The mean distance between the observation squares and the nearest nest of *F. selysi* was significantly higher in area GR (4.1 m) than in area ST (2.4 m) ($P < 0.05$). The average surface temperature during the observations was 34.2°C in ST, which was significantly higher than the 29.5°C measured in GR ($P < 0.01$).

Size and overlap of foraging areas

Foraging distances were significantly larger in GR than in ST ($P < 0.05$, Tab. 1). Furthermore, the overlap of the foraging areas between two nearest-neighbour nests tended to be larger in GR ($0.1 > P > 0.05$). Five out of the eight studied nest pairs in ST had clearly separated zones of activity, whereas all nest pairs in GR showed overlapping foraging areas (Fig. 2).

Use of foraging areas

At the two nests where activity was studied in detail, the ant workers concentrated their foraging efforts on certain sectors of the home range. At nest GR, the number of ant foragers entering the nest area was highest at the observation lines B and C ($P < 0.01$, Fig. 3). The ants at nest ST showed a clear preference for foraging trips in sector C ($P < 0.01$, Fig. 3). These preferences were constant throughout the season.

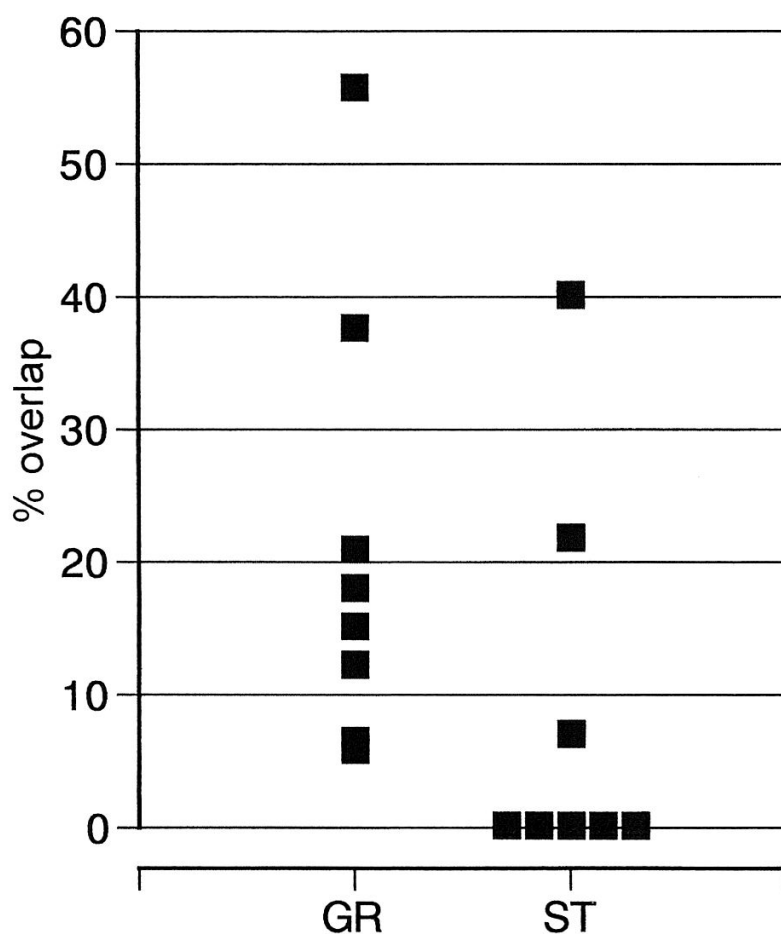


Fig. 2: Overlap of foraging areas expressed as percentage of total nest distance between nearest-neighbour nests of *Formica selysi* at two zonation types. GR = gravel area (median = 16.5%). ST = non-flooded steppe (median = 0%).

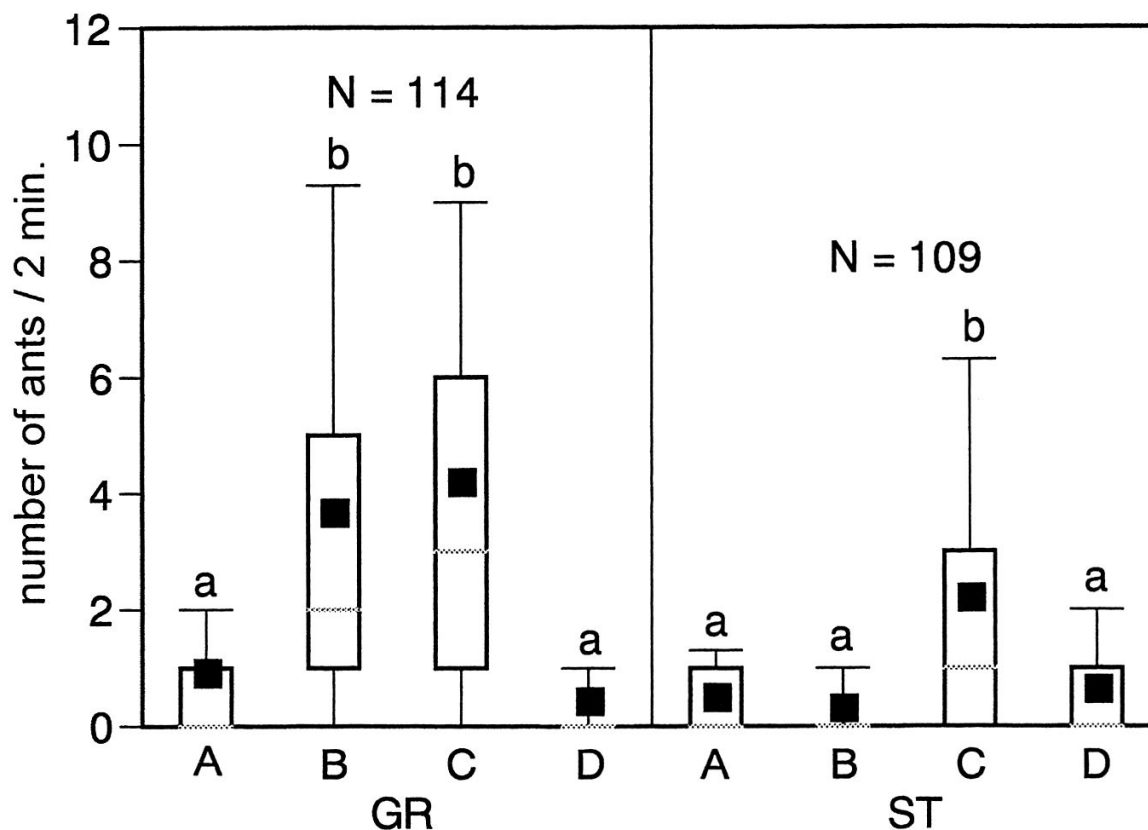


Fig. 3: Number of ants entering the nest area from four directions (A–D) at right angles to each other, pooled over the whole season. GR = nest in gravel area, ST = nest at non-flooded steppe. Different letters indicate significant differences of the medians (WILCOXON-WILCOX, $P < 0.01$).

DISCUSSION

Nest density and colony size

Our findings on colony density confirmed the results obtained by GROSSRIEDER & ZETTEL (1999) with a different method. In optimal habitats, the nest density of *F. selysi* can reach values five times higher than those observed at the Rottensand (SEIFERT, pers. com.). At GR, it is likely that the food resources available at such an early successional stage could not sustain a larger number of colonies. At the moment, all areas of GR are intensively covered by foraging ants which renders it difficult for young queens to found new colonies due to heavy predation by workers from established nests (pers. obs.). It is likely, however, that the number of colonies will increase as succession progresses and more food is available. At the steppe habitat, on the other hand, succession seems to be too advanced, and the nest density may have decreased from a maximum value which was reached at some intermediate successional stage as observed by GROSSRIEDER & ZETTEL (1999).

In the fire ant *Solenopsis invicta* BUREN, the number of nest entrances correlated with colony size (TSCHINKEL et al. 1995). The situation can be expected to be similar in *F. selysi*, since the number of ants required for maintenance work is likely to increase with the number of nest entrances. External factors such as soil struc-

ture probably only lead to small variations in the number of nest entrances. Therefore, it can be assumed that colonies in ST are generally smaller than those in GR.

Dynamic density

The lower dynamic density (individuals / dm² and min.) in area ST cannot be attributed entirely to differences in surface temperature or mean distance between the observation squares and the nearest nest of *F. selysi* between the two sites. The mean surface temperature in ST (34.2° C) was closer to the values of 35–40° C at which *F. selysi* showed the highest activity at the Rottensand (pers. obs.). Furthermore, the average distance between the observation squares and the nearest nest of *F. selysi* was smaller in ST than in GR. Therefore, it is likely that the observed difference in dynamic density would be even larger if these two parameters were the same at the two sites.

In August, the values for dynamic density were particularly low in ST, which could be due to the exceptional drought during that month (21% of the expected precipitation, Swiss Meteorological Institute 1998), since in 1996, under wetter conditions, no such decrease in foraging activity was observed (GROSSRIEDER, pers. com.). In several steppe nests, foraging stopped completely for several days, but was resumed immediately after a thunderstorm on August 18. Although the drought may have lowered the dynamic densities observed in ST, it was not responsible for the significant difference between the two sites. If we compare the dynamic density values obtained in July only, we also find a significant difference between the two study plots, although that month was not particularly dry (96% of the average precipitation).

A pilot study carried out before the flood yielded similar results for activity density of ant workers at the Rottensand (Université de Neuchâtel 1993): The number of ant workers caught in pitfall traps was highest on the gravel banks of the Rhone and decreased with progressive successional age of an area. At two different sand dune habitats, on the other hand, the worker density of the pioneer species *Lasius niger* L. and *L. alienus* FÖRSTER respectively was relatively low in early successional stages and increased with the age of the site (BOOMSMA & VAN LOON 1982; GALLÉ 1991). The comparison between the alluvial GR at the Rottensand and the sand dune sites shows, that it is not possible to make a general statement on the dynamic densities of ant foragers at early successional stages, but that the situation varies between habitats due to differences in factors such as vegetation, availability of food or soil structure which shape the ant communities in different habitats.

The average value for dynamic density in area ST (0.07 ants / dm² and min.) is comparable to the 0.05 ants / dm² and min. which ZAKHAROV (1975) obtained for *Formica fusca* L.. Such low values are typical for species ranking low in the dominance hierarchy. Based on the competition hierarchy model proposed by VEPSÄLÄINEN & PISARSKI (1982), *F. selysi* would be in the lowest category, because the species only defends the immediate vicinity of the nest, but tolerates ants from other colonies within its foraging area or at profitable food sources (pers. obs.). The dynamic density of *F. selysi* is somewhat higher in GR than in ST, but the values are still considerably lower than those mentioned in the literature for more dominant species. Territorial ants such as species of the subgenus *Formica* s. str. which are at the top of the dominance hierarchy (VEPSÄLÄINEN & PISARSKI 1982), attain dynamic densities of at least 2 ants / dm² and min. (ZAKHAROV 1975). Our data show that in the absence of a behaviourally aggressive species, a submissive one such as *F. selysi* is able to dominate in a habitat. Our findings agree with observations in other alluvial areas along alpine rivers, where *F. selysi* was the most common ant species (KUT-

TER 1977; SEIFERT 1996; LUDE et al. 1999).

The results on dynamic density support the hypothesis that nests are generally larger in GR than in ST. It is unlikely that a higher percentage of workers leaves the nests to forage in GR, because we can expect a coarse correlation to exist between the size of the forager group and the total number of workers, as was shown by KRUK-DE BRUIN et al. (1977) for *Formica polyctena* FÖRSTER. In laboratory colonies of *Solenopsis invicta*, the proportion of foraging workers even declined with colony size (MIRENDA & VINSON 1981).

Size and overlap of foraging areas

It is unlikely that the observed difference in the foraging distances between ST and GR was caused by stronger prevailing winds in the relatively open gravel area, because the nests which were located downwind from the bait did not have consistently larger foraging areas than the ones situated upwind.

However, our results do not represent the true average foraging distance of workers, because it cannot be assumed that the foraging areas of *F. selysi* nests are circular. For this reason, more detailed information is required for each nest in order to compare the results with published values for the average territory radius in other ant species.

The foraging areas between two nearest-neighbour nests had a clear tendency to overlap more in GR than in ST, which supports the rest of our data on habitat use. The entire area GR appears to be intensively used, and the lower nest density does not lead to ant-free spaces between nests. This complete coverage of GR by foragers may be facilitated by the lower impediment to movement in the open gravel area.

It is known for *Solenopsis invicta* and *Tetramorium caespitum* L. that territory area correlates with colony size (BRIAN et al. 1965; TSCHINKEL et al. 1995). At the Rottensand, there also appears to be at least some correlation, with the smaller steppe nests having smaller foraging areas than the larger nests in the flooded area. In social insects, population size is limited by the biomass of animals and not the number of nests supported per unit area (ADAMS & LEVINGS 1987). At the Rottensand, this carrying capacity is very likely to vary between the two sites, due to the fact that the nutritional situation for *F. selysi* appears to be worse in ST (KELLER & ZETTEL 2001). The vegetation in ST dries out during the summer and is abandoned by most herbivores and other arthropods. Thus, it becomes increasingly difficult for the ants to find suitable foraging grounds. In GR, on the other hand, the tree saplings with their deep reaching roots provide aphid colonies and invertebrate prey throughout the season, which could make it possible for a higher number of ants to be supported per unit area.

Use of foraging areas

At the nests studied in detail, *F. selysi* showed a constant preference for certain sectors of its home range. In ST, this preferred foraging sector contained a pine (*Pinus sylvestris*). Repeated counts on one day showed that an average of 0.8 ants per minute crossed a 10 cm wide line on the trunk base and started to climb the tree. This indicates a regular flow of ant workers from the nest to the pine. Observations at tuna baits placed on the tree showed that all foragers returned to the same nest. It is known that species which are not normally territorial start to defend their home range if the dynamic density of ants is increased above a certain threshold (ZAKHAROV 1975). Thus, it is conceivable that *F. selysi* workers become territorial on a tree where the

encounter rates between foragers are likely to be higher than on the ground.

In GR, foragers preferred to leave the nest area in the direction of poplar saplings (*Populus nigra*) with a large number of aphid colonies. During one day, we repeatedly counted the number of ant workers tending aphids on a poplar located approximately 3 m south of the nest and obtained a mean value of 25 ants present. These observations indicate that trees have an important value as extended foraging areas for *F. selysi*. In an extensive study in different habitats, SEIFERT (1986) found that the closely related *F. cinerea* MAYR spent only 12% of its foraging time on trees and shrubs and concentrated on hunting on the ground. Under the arid conditions at the Rottensand, the ants appear to increase the amount of time spent foraging on woody plants. In GR, the aphid colonies on poplar and the insects attracted by the plantsuckers provide ample food for the ants in the middle of a gravel area where prey is likely to be scarce. In ST, the single pine may be the only suitable foraging ground left once the herbaceous plants become dry in midsummer.

Conclusions

The spatial organisation of *F. selysi* differs conspicuously between areas ST and GR, but future studies are needed to examine whether GR is truly the more suitable habitat for *F. selysi* or whether the observed differences were the result of two different, but equally successful strategies. There are quite a number of ant species which show extreme variation in their social organisation. In *F. cinerea*, e.g., some populations consist of monogynous colonies, others of polygynous ones (LINDSTRÖM et al. 1996), and such differences in social organisation could exist in *F. selysi* as well. In order to determine whether one of the two habitats is more advantageous for the species, it would be necessary to examine the production of sexuals which represents an exact measure of colony fitness (HÖLLDOBLER & WILSON 1990). However, our results on feeding ecology indicate that the availability of food is considerably better in GR than in ST (KELLER & ZETTEL 2001) and support the hypothesis that habitat quality is reduced for *F. selysi* as ecological succession progresses.

ZUSAMMENFASSUNG

Durch ein schweres Hochwasser im Herbst 1993 entstand im Rottensand (Pfywald, VS) ein Mosaik aus unterschiedlich stark beeinflussten Trockensteppen und offenen Geröllflächen. GROSSRIEDER & ZETTEL (1999) zeigten, dass die Ameisenfauna in allen untersuchten Zonationstypen von der Pionierart *Formica selysi* dominiert wurde. Die höchste Nestdichte erreichte *F. selysi* auf Steppenflächen, welche vom Hochwasser nur schwach oder gar nicht beeinflusst worden waren. In der vorliegenden Arbeit untersuchten wir mehrere Aspekte zur Raumnutzung der Art in der unbeeinflussten Steppe und der offenen Geröllfläche, um abzuklären, ob ältere Sukzessionsstadien von *F. selysi* intensiver genutzt werden.

Unsere Resultate bestätigten die höhere Nesterdichte von *F. selysi* in der Steppe im Vergleich zur Geröllfläche. Die Nester waren jedoch in der Steppe kleiner und die Aktivitätsdichte der Arbeiterinnen signifikant tiefer. Zudem waren die Foragierdistanzen geringer, und die zur Nahrungssuche genutzten Flächen überlappten zwischen benachbarten Nestern weniger. Detaillierte Untersuchungen an einem Nest pro Zonationstyp zeigten, dass *F. selysi* für die Nahrungssuche während der ganzen Beobachtungsperiode Flächen bevorzugte, welche einen Baum mit Blattlauskolonien enthielten.

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