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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 Pfynwald (Switzerland): I. Feeding ecology

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In the steppe area Rottensand at Pfynwald (CH), a severe flood in 1993 created differently influenced steppe habitats and early successional stages of bare gravel. GROSSRIEDER & ZETTEL (1999) showed that the pioneer *Formica selysi* was the dominant ant species in all of these zonation types. By studying the feeding ecology of an abundant arthropod predator such as *F. selysi*, we would enhance the understanding of the ecological processes during succession starting from a pioneer river bank.
From June to September 1998, we examined the prey items and the liquid food collected by *F. selysi* workers at one nest in the gravel area and one in the steppe. To assess the availability of food in the two habitats, the number of aphid colonies within the home ranges of the two study nests was determined once a month.
At both colonies, aphids, parasitic wasps, ants, beetles and Heteroptera were the most commonly collected insects. The prey composition was similar at both nests. More than half of the workers returned with honeydew in their crops, whereas proteins were found only rarely. The density of aphid colonies was higher in the gravel area than in the steppe, and the number of infested, woody plants (poplar) remained constant throughout the season. In the steppe habitat, the number of aphid colonies declined to an extremely low level in July due to the drying out of the herbaceous vegetation. These results suggest that, in dry steppe habitats, the nutritional situation for species depending on continuous food supply from spring through autumn deteriorates with the successional age of an area.

Keywords: Hymenoptera, Formicidae, Aphidina, zonation, steppe, alluvial area, feeding ecology, crop content analysis.

INTRODUCTION

Ants are the most important consumers among ground-dwelling insects in many ecosystems (SEIFERT 1996). In order to meet their large energy requirements, they are generalists feeding on a variety of invertebrates as well as on honeydew collected from aphids (DUMPERT 1994). By studying the feeding ecology of such a generalist predator with high energy demands, we can contribute to the understanding of the availability of various kinds of food in different habitats. In the present study, we compared the feeding ecology of two colonies of *Formica selysi* BONDROIT in two habitats representing different stages in the succession from a young alluvial area to a dry steppe.

Our study area, the Pfynwald, is located in the inner alpine dry zone of the central Valais, Switzerland and comprises the last remaining steppe area in the valley bottom of the Valais, the Rottensand (BILLE & WERNER 1986). During a high water in September 1993, a dyke broke and the river Rhone flooded parts of the Rottensand and covered approximately 5 ha of the steppe area with gravel and sand

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deposit, thus providing a unique opportunity to study invertebrate communities in habitats of different successional age. 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 different zonation types have been examined as part of a long-term project. GROSSRIEDER & ZETTEL (1999) showed that the ant fauna in all habitats at the Rottensand was dominated by *Formica (Serviformica) selysi* (Hymenoptera, Formicidae), a species which is known as a common pioneer in alluvial areas in the Alps (SEIFERT 1996). At the Rottensand, the density of *F. selysi* nests was higher in the non-flooded steppe than in the gravel area (GROSSRIEDER & ZETTEL 1999). We hypothesized that this difference in nest densities could be caused by the lower availability of food in the gravel area which would lead to differences in the diet of the two study nests. Furthermore, we expected that the density of aphid colonies would be lower in the open gravel area than in the steppe with its dense vegetation. The present study and a more detailed investigation of the habitat use of *F. selysi* in the two zonation types (KELLER & ZETTEL 2001) were carried out as a diploma thesis (KELLER 1999), and are part of the long term research project mentioned above.

MATERIAL AND METHODS

Study area and nests

The present study was carried out from June through September 1998 at the Rottensand in Pfynwald which is located between Susten and Sierre in central Valais, Switzerland. The area is characterized by a continental climate with dry and hot summers and cold winters. The arthropod fauna at the Rottensand is very diverse and contains many thermophilic species (BILLE & WERNER 1986). The steppe vegetation at the Rottensand is dominated by the grass *Stipa pennata* but also comprises rare species of eastern or Mediterranean origin. During the last decades, the tree cover (mainly *Pinus sylvestris*) in the Rottensand has increased due to the lack of occasional floods after the construction of a dam along the Rhone. In September 1993, this dyke broke during an exceptional high water, and the Rhone covered approximately 5 ha of the steppe area with sand and gravel deposit. A more detailed description of the study area is given by ZEHNDER & ZETTEL (1999).

Our study nest GR (= gravel) was located in an area where the top soil had been washed away and replaced by sand and gravel during the flood in 1993. In 1998, the vegetation in the vicinity of the nest was dominated by ca. 1 m high saplings of poplar (*Populus nigra*) and willow (*Salix elaeagnos* and *S. purpurea*) at a density of ca. 1 plant / m^2. Nest ST (= steppe) was situated in a steppe area which had not been affected by the flood. Its surrounding vegetation was dominated by herbaceous plants (vegetation type Stipo-Poion carniolicae), but the foraging area of the colony also comprised one pine tree (*Pinus sylvestris*). The choice of the two study nests had been based on two factors. Firstly, relatively level ground was required in order to erect a fence around the nests. Secondly, the colonies had to be monodomous. Thus, we were sure that the ants did not have access to food items collected by workers from other nests. Monodomy was ascertained by releasing workers from all nearby colonies next to an entrance of the possible study nest and observing whether they were attacked.

Arthropod prey

We used a fence to collect the prey items brought back to the nest by the foragers. The fencing method commonly used for research on the nutritional ecology of red ants *Formica* s. str. L. (CHAUVIN 1966) was altered, as it does not work well for species with relatively low densities of returning foragers such as *Serviformica* FOREL sp. (D. CHERIX, pers. com.). The entire nest area was enclosed with a 20 cm high plastic fence, which could be secured in a raised position to allow free access of the ants or closed when required. At its base, the fence was sealed up with sand. Five plastic cups (diameter 7 cm) were buried to ground level at regular intervals directly outside the fence and were used as pitfall traps. The inside of the cups was covered with Fluon to prevent the trapped ants from escaping.

In order to catch the foragers returning to the nest, the fence was closed and the pitfall traps were opened for 10 min. After that period, the traps were removed and the fence raised again. The sampling was carried out every two weeks on sunny days between June and September on a total of 7 days per study nest. During each sampling day, eight prey samples were taken at regular intervals during the main foraging activity which varied depending on the ground surface temperature. As a first step, we determined the proportion of ant foragers carrying prey items. Then the traps were cooled on ice which caused the ants to drop their prey. The prey items were conserved in 70% ethanol, and the workers were released back into the nest area. The ants collected as prey and the intact specimens of Chalcidoidea (80% of the total number of individuals) were determined to species level, all other arthropods to order level. Only few insect and spider fragments could not be determined. Since it was not possible to weigh the prey items in the field with sufficient accuracy, their dry weight was determined in the lab later on. Individual prey items were dried at 80° C for 24 h and weighed on Sartorius supermicro scales to the µg. The average dry weight of the prey items was compared between the two study nests with a MANN-WHITNEY-U-test.

Crop content

Ant samples for crop content analysis were collected by using the fence method described above. Once a month from June to September, at least 75 returning *F. selysi* foragers were collected during the afternoon activity peak. Directly after capture, the ants were placed on ice to stop their activity and prevent trophallaxis. The animals were killed by freezing as soon as possible and stored frozen.

In the laboratory, the ants were dissected, their crops removed and emptied onto Whatman No. 1 chromatography paper. As controls, we applied 0.5 µl of a protein solution (5 mg BSA / ml) and 0.5 µl of a sugar solution (0.2 g D-fructose / ml) onto the chromatography paper. The amount and the concentrations of these controls were based on values published for *F. polyctena* FÖRSTER (HORSTMANN 1970). Then, the chromatography paper was stained with silver nitrate (TREVELYAN et al. 1950; DEDONDER 1952 cit. in PEACH & TRACEY 1955) with modifications, which allowed the detection of reducing sugars with a sensitivity of 2 µg. Instead of spraying the paper with a silver nitrate solution (see DEDONDER 1952 cit. in PEACH & TRACEY 1955), we rapidly passed the chromatography strip through a staining bath (0.43 g $AgNO_3$ in 0.2 ml H_2O added to 20 ml acetone, followed by sufficient drops of water to dissolve the precipitated salt). Amido black staining was used for protein detection (FINE & ROPARTZ 1968). This method is not sensitive to free amino acids solved in honeydew, and therefore allows the unequivocal identification of animal remains. The protein detection was not affected by the silver nitrate staining applied to the same paper strip before (CHERIX 1987, and own preliminary tests).

Availability of aphid colonies

Before the counting of aphid colonies, the home ranges of the two study nests were mapped. We determined the maximum foraging distance by following workers on their return to the colony from tuna baits placed between each study nest and its four nearest-neighbours. The baits were moved 0.5 m at a time from the centre towards each nest until the boundaries of the foraging areas became apparent. The home ranges of the two colonies were defined as the area encompassed by straight lines connecting these four observed boundary points.

Once every month from June to September, all above-ground parts of the plants within the home ranges were carefully searched for aphid colonies. On the small pine tree in the foraging area of nest ST, the search for aphid colonies was restricted to the branches below 2 m.

RESULTS

Arthropod prey

The median dry weight of the collected arthropods did not differ significantly between nest GR (37 µg) and nest ST (41 µg)($P>0.6$). 79% of the prey items caught in the traps at GR and 67% at ST were lighter than 100 µg and could be carried by individual foragers; the average dry weight of *F. selysi* workers was 923 µg ($N=16$). Thus, foragers carried prey items that weighed on average 4% of their own body weight. Collective foraging was only observed on the rare occasion when heavy arthropods had to be carried back to the nest. The heaviest individual insect collected by *F. selysi* during our sampling was another ant (*Camponotus vagus* SCOPOLI, 8245 µg).

The proportion of ants carrying a prey item when caught in the pitfall traps was similar at both nests, averaging 22% at nest GR and 18% at nest ST.

There were no fundamental differences in the prey taxa collected by the foragers at the two study nests (Tab. 1a). In both cases, aphids constituted one of the largest groups of prey items with respect to the number of individuals. In terms of dry weight, however, the Homoptera lose importance due to their small size. Dead ants made up approximately half of the total dry weight of prey items. At nest ST, one third of the ants collected as prey was *F. selysi*, whereas at nest GR only one fifth were conspecifics. At both colonies, slightly more than 25% of the collected ants were sexuals of various species. The foragers especially at GR collected a large number of parasitic wasps (mainly Chalcidoidea). 85% of the determinable individuals belonged to the three species *Psilonotus adamas* WALKER (Pteromalidae), *Aprostocetus escherichi* SZELÉNYI and *A. pallipes* DALMAN (Eulophidae). All three wasps are parasitoids of *Semudobia betulae* WINNERTZ, a cecidomyiid (Diptera) causing galls in birch seeds. In terms of dry weight, Heteroptera (mainly Lygaeidae and Tingidae) were important at GR, and Coleoptera at ST. The diet of the two nests also comprised small numbers of e.g. Araneae, Acari (especially at GR), Collembola, Cicadina, Thysanoptera (especially at ST) and Diptera. Most of the more common taxa were present in the prey of *F. selysi* throughout the entire season (frequency in Tab. 1a). The number of collected prey items, however, decreased continuously during the observation period (Tab. 1b), with a stronger decline at the steppe.

Tab. 1a: Percentage of arthropod taxa in prey collected by *Formica selysi*, ranked after total abundance of individuals. GR = nest in gravel area (N = 504), ST = nest at non-flooded steppe (N = 204). The most abundant taxa are shaded. Frequency = number of days on which the taxa were collected by the ants (maximum = 7).

	individuals		dry weight		frequency	
	GR	ST	GR	ST	GR	ST
Homoptera, Aphidina	19.7	21.6	4.6	8.1	7	7
Homoptera, others	1.9	6.8	2.1	6.9	6	4
Hymenoptera, Formicidae	14.2	14.2	48	45.1	7	6
Hymenoptera, Terebrantes	19.6	3.9	5.7	0.8	6	4
Hymenoptera, others	0.6	1.5	0.8	0.5	2	2
Diptera	4.2	8.8	2.4	1.6	5	5
Heteroptera	9.7	2	26.3	6.3	7	3
Acari	6.9	3.4	1.6	1	7	4
Coleoptera	1.6	6.4	1	22	5	5
Araneae	3.4	4.4	4	4.1	6	4
Thysanoptera	0	5.9	0	0.4	0	5
Collembola	1	2.5	0.2	0.2	3	3
Saltatoria	0	0.5	0	1.2	0	1
Chilopoda	0.2	0	0.1	0	1	0
Neuroptera	0.2	0	0.5	0	1	0
Psocoptera	0.2	0	0.2	0	1	0
Arthropod fragments	16.5	18.2	2.5	1.9	7	6

Tab. 1b: Number of animals of the most abundant prey taxa and total number of prey items collected on individual sampling days. The numbers after the months refer to the first and the second half of the month respectively.

	steppe						
	Jun2	Jul1	Jul2	Aug1	Aug2	Sep1	Sep2
Homoptera, Aphidina	19	10	2	9	1	1	1
Hymenoptera, Formicidae	9	5	4	6	1	4	0
Hymenoptera, Terebrantes	1	2	4	1	0	0	0
Total	**65**	**53**	**26**	**36**	**2**	**15**	**7**
	gravel area						
Homoptera, Aphidina	26	13	7	11	6	17	13
Hymenoptera, Formicidae	13	8	8	11	11	16	5
Hymenoptera, Terebrantes	15	39	30	7	7	1	0
Total	**100**	**116**	**79**	**53**	**64**	**51**	**40**

Crop content

At both nests, more than half of the foragers returned to the colony with detectable crop content (Tab. 2). In the sample taken in August, 72% of the foragers from ST had empty crops as opposed to only 12% at nest GR. In all the other samples, the number of animals with no detectable crop content was similar at the two nests. 97.5% (GR) and 90% (ST), respectively, of the workers with crop content carried sugar solutions. Protein was found in the crops of 4 individuals at GR and 19 at ST. In most cases it was mixed with sugars.

Availability of aphid colonies

The density of plants with aphids was higher within the foraging area of the gravel nest than within the home range of the steppe nest. The number of infested plants remained constant throughout the season in area GR, whereas in area ST, it dropped to a very low level in midsummer (Tab. 3).

Tab. 2: Crop contents of returning foragers at two *Formica selysi* nests (in %). GR = nest in gravel area (N = 285), ST = nest at non-flooded steppe (N = 296).

	GR	ST
sugars	75.8	56.1
proteins	0.4	0.7
sugars & proteins	1.1	5.7
others (e.g. water)	0.7	0.0
crop empty	22.0	37.5

Tab. 3: Density of aphid colonies (number of infested plants / 25 m^2) within the foraging areas of two *Formica selysi* nests. GR = nest in gravel area, ST = nest at non-flooded steppe.

Nest	Host plants	June	July	Aug.	Sept.
GR	*Populus nigra*	5.1	6.1	5.5	5.5
ST	*Astragalus onobrychis*	1.3	0	0	0
	Pinus sylvestris	0.3	0.3	0	0.3

DISCUSSION

Arthropod prey

The vast majority of arthropods collected by *F. selysi* was lighter than 100 µg, which can mainly be explained by the abundance of different size classes in nature. Generally, small organisms are much more common than large ones (ODUM 1980; BEGON et al. 1990). Large arthropods may also be able to escape more easily when attacked by ants. However, we also observed groups of *F. selysi* workers carrying aggressive arthropods such as live wasps (*Vespula* THOMSON sp., Vespidae) not contained in our prey samples.

F. selysi is a generalist predator, like almost all ant species in Central Europe (DUMPERT 1994). Its prey belongs to many different taxa and several trophic levels. Several prey taxa occurred in very small numbers and were detected by chance only. Other groups may have been overlooked entirely due to the relatively short sampling times (80 min per study day). SKINNER (1980) found for *F. rufa* L. that these rare prey taxa could be important in terms of biomass because they were usually rather large, in our case this could be true e.g. for Saltatoria and Neuroptera.

At both study nests, the foragers collected a large number of Aphidina (approximately 20% of individuals, Tab. 1a), but at all aphid colonies within the home ranges, we also observed ant workers tending the aphids. This indicates that these aphids were used both as prey and as a source of honeydew. The same situation was reported for *F. lugubris* ZETTERSTEDT and *Lasius niger* L. (CHERIX 1981; SAKATA 1995). In these two species, predation was strictly regulated in order to prevent the complete destruction of aphid colonies. The proportion of aphids in the diet of red wood ants (*Formica* s. str.) varied between 5 and 80% in various studies (WELLENSTEIN 1952; CHAUVIN 1966; HORSTMANN 1970; SKINNER 1980; CHERIX 1981). CHERIX (1981) suggested that aphids might be more intensively preyed on in poor habitats where alternative sources of protein are scarce.

Ants are very often the most dangerous enemies of other ants (SEIFERT 1996), and these actually were the most important prey taxon with respect to dry weight at both nests (Tab.1a). Several studies have shown that the diet of red wood ants (*Formica* s. str.) also contains varying amounts of ant prey (WELLENSTEIN 1952; CHAUVIN 1966; HORSTMANN 1970; SKINNER 1980; CHERIX 1981). At the Rottensand, the species most frequently brought back to the nest was *F. selysi* itself, which is a direct consequence of its dominance in all zonation types (GROSSRIEDER & ZETTEL 1999). However, we are not able to say whether these ants were hunted or collected as dead animals. At both study nests, sexuals of various ant species were collected. It is known that the majority of virgin queens die within hours of leaving the mother nest, with predation by birds and ants being the most important causes of death. Many foundress queens are killed by conspecific workers from established nests, which may be considered as intraspecific competition (HÖLLDOBLER & WILSON 1990). At our two colonies, no sexuals of *F. selysi* were brought back to the nests during the sampling periods. This can be explained by the fact that the swarming peaks of the species occurred in the middle of June before we started the study. During these main swarming periods, we often observed *F. selysi* workers carrying conspecific queens and males. Thus, queen predation by foragers from established colonies appears to be quite important for the regulation of nest densities in *F. selysi*.

It is striking that the three Chalcidoidea species most commonly collected by the ants were all parasitoids of *Semudobia betulae*, a cecidomyiid causing galls in birch seeds. The birch trees (*Betula pendula*) in the vicinity of the two study nests were clearly outside the foraging areas of the colonies (pers. obs.), but we commonly found birch seeds on the ground within the home ranges of the nests. The fully grown larvae of *S. betulae* remain inside the seeds when these fall to the ground in autumn and emerge in spring (M. SKUHRAVA, pers. com.). Therefore, we expect that the Chalcidoidea may also hibernate in seeds on the ground as M. SKUHRAVA (pers. com.) observed under laboratory conditions, and could be caught by the ants upon hatching. An alternative explanation could be that the parasitoids were collected during food intake. If the three wasp species also feed on aphid honeydew, as do several species of both the Pteromalidae and the Eulophidae (SEDLAG 1959; IDOINE & FERRO 1988), they would have been easily accessible to ants visiting aphid colonies. However, this hypothesis does not explain the prevalence of parasitoids of *S. betulae*.

In our study on arthropod prey, there were no fundamental differences between the diets of nests ST and GR. To a large extent, this may be due to the fact that the availability of food in the gravel area appears to be much higher than expected, due to the high density of aphid colonies (see below), which in turn attract honeydew collectors, invertebrate predators and parasitoids. In order to substantiate possible differences between the two zonation types, it would be necessary to examine several nests per site, which was not possible in the present study due to time constraints. However, we expect that the diet of other nests would be similar, since the vegetation is quite homogeneous within each zonation type.

The number of prey items collected by the foragers decreased continuously during the observation period (Tab. 1b), with a stronger decline in the steppe. We assume that the availability of arthropod prey deteriorates during summer due to the drying out of the vegetation or the prey phenology. This hypothesis is supported by our results concerning the availability of aphid colonies (see below). The difference between the two nests can be explained by the prevalence of herbaceous plants in ST, which are more strongly affected by the drought than the saplings in GR (pers. obs.).

Crop content

The proportion of *F. selysi* workers returning to the nest with full crops is comparable to the range of 40–80 % obtained for red wood ants *Formica* s. str. by SKINNER (1980) and CHERIX (1981). The composition of the crop contents, however, varies considerably between different studies. Similarly to *F. selysi*, the majority of *F. lugubris* and *F. rufa* workers carried honeydew in their crops (MÜLLER 1961; CHERIX 1981). In another study on *F. rufa*, the proportion of protein solutions in the crops of ant workers was as high as 60% (GÖSSWALD & KLOFT 1956), and in *F. polyctena* about 30% of the prey volume was transported in the crops (HORSTMANN 1974). Thus the tendency of the workers to ingest arthropod prey and carry it back to the nest internally appears to vary greatly between different *Formica* species or even different colonies of the same species.

The proportion of workers with empty crops was similar at the two colonies on three of the four sampling days. In August, however, the percentage of workers with empty crops was much higher in ST than in GR, as a result of the scarcity of aphids in the dry steppe vegetation (see below).

Availability of aphid colonies

The aphids found on poplar (*Populus nigra*) in GR appear to be monoecious and were available to the ants throughout the entire observation period. The poplar saplings are likely to be in contact with ground water, and were therefore little affected by the summer drought. Within the home range of nest ST, the availability of aphids and probably invertebrates in general decreased rapidly when the herbaceous vegetation became dry in midsummer. The only source of honeydew left for the ants was the aphid colony on the pine (*Pinus sylvestris*), which was probably continously available as indicated by aphids in the prey of nest ST (Tab. 1b). However, the exceptionally large number of animals with empty crops in August indicates that the density and/or the productivity of the aphids was very low at that time. It is probable that the pine strongly reduced the transport of nutrients in its conductive tissues in August, which was by far the driest month during the observation period (Swiss Meterological Institute 1998).

In June, when the availability of aphids was at its maximum in area ST, the density of infested plants was still much lower than within the home range of nest GR. This agrees with the general pattern in animal succession that sap suckers are the most abundant guild during early succession and decline in importance in later stages (BROWN & SOUTHWOOD 1987).

Conclusions

It is well established in successional theory that the abundance and the diversity of invertebrates is positively correlated with the structural complexity of a habitat (e.g. BOOMSMA & VAN LOON 1982). This was confirmed for the Rottensand, where the diversity of all taxa examined increased with successional age (GROSSRIEDER & ZETTEL 1999; LOEFFEL et al. 1999; MÜLLER & ZETTEL 1999; ZEHNDER & ZETTEL 1999). However, as a generalist predator, *F. selysi* does not depend as much on the diversity of its prey taxa as on the continuous availability of relatively large quantities of food. The energy demands of an ant colony are very high due to the large numbers of workers and larvae which have to be maintained. In consequence, the ants depend on profitable food resources throughout most of the year, especially since temperate grassland and forest species generally do not store food (VANDER WALL 1990). Further results showed that the nests of *F. selysi* were significantly larger in the gravel area than in the steppe habitat (KELLER & ZETTEL 2001) and support the idea that GR may be the more suitable habitat for this ant. Thus, a habitat such as the gravel area, which appears very extreme at first glance, may offer sufficient living conditions for some pioneer insect species.

ZUSAMMENFASSUNG

Durch ein schweres Hochwasser im Herbst 1993 entstand im Gebiet des Rottensandes im Pfynwald (CH) ein Mosaik aus unterschiedlich stark veränderten Trockensteppen und offenen Alluvialflächen, welche frühe Sukzessionsstadien darstellen. GROSSRIEDER & ZETTEL (1999) zeigten, dass die Pionierart *Formica selysi* die dominante Ameisenart in allen Zonationstypen war. Die Untersuchung der Nahrungsökologie dieser häufigen, räuberischen Arthropodenart ermöglichte es uns, zum besseren Verständnis der ökologischen Prozesse während der Sukzession ausgehend von offenen Kiesbänken beizutragen. Von Juni bis September 1998 untersuchten wir die Beutetiere und die flüssige Nahrung, welche von *F. selysi* auf der offenen Geröllfläche und in der Trockensteppe eingetragen wurden. Um das Nahrungsangebot in den zwei Habitaten beurteilen zu können, wurden monatliche Zählungen der Blattlauskolonien auf den Fouragierflächen der zwei Untersuchungsnester durchgeführt.

Bei beiden Kolonien wurden am häufigsten Blattläuse, Schlupfwespen, Ameisen, Käfer und Wanzen eingetragen. Das Beutespektrum war bei beiden Nestern ähnlich. Mehr als die Hälfte der zum Nest zurückkehrenden Arbeiterinnen transportierte Honigtau im Kropf, während Proteinlösungen nur selten gefunden wurden. Die Dichte von Blattlauskolonien war auf der Geröllfläche höher als in der Steppe. Zudem blieb die Anzahl befallener Pflanzen (v.a. Gehölze) während der ganzen Saison konstant, während sie in der Steppe im Juli sehr stark abnahm, da ein Grossteil der Krautvegetation austrocknete. Diese Resultate deuten darauf hin, dass sich in Trockensteppen die Bedingungen für Arten, die von Frühling bis Herbst auf ein beständiges Nahrungsangebot angewiesen sind, mit fortschreitender Sukzession verschlechtern.

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