

# Intraguild interactions between spiders and ants and top-down control in a grassland food web

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**Abstract** In most terrestrial ecosystems ants (Formicidae) as eusocial insects and spiders (Araneida) as solitary trappers and hunters are key predators. To study the role of predation by these generalist predators in a dry grassland, we manipulated densities of ants and spiders (natural and low density) in a two-factorial field experiment using fenced plots. The experiment revealed strong intraguild interactions between ants and spiders. Higher densities of ants negatively affected the abundance and biomass of web-building spiders. The density of Linyphiidae was threefold higher in plots without ant colonies. The abundance of *Formica cunicularia* workers was significantly higher in spider-removal plots. Also, population size of springtails (Collembola) was negatively affected by the presence of wandering spiders. Ants reduced the density of Lepidoptera larvae. In contrast, the abundance of coccids (Ortheziidae) was positively correlated with densities of ants. To gain a better understanding of the position of spiders, ants and other dominant invertebrate groups in the studied food web and important trophic links, we used a stable isotope analysis ( $^{15}\text{N}$  and  $^{13}\text{C}$ ). Adult wandering spiders were more enriched in  $^{15}\text{N}$  relative to  $^{14}\text{N}$  than juveniles, indicating a shift to

predatory prey groups. Juvenile wandering and web-building spiders showed  $\delta^{15}\text{N}$  ratios just one trophic level above those of Collembola, and they had similar  $\delta^{13}\text{C}$  values, indicating that Collembola are an important prey group for ground living spiders. The effects of spiders demonstrated in the field experiment support this result. We conclude that the food resource of spiders in our study system is largely based on the detrital food web and that their effects on herbivores are weak. The effects of ants are not clear-cut and include predation as well as mutualism with herbivores. Within this diverse predator guild, intraguild interactions are important structuring forces.

**Keywords** Field experiment · Collembola · Generalist predators · Stable isotopes ·  $\delta^{15}\text{N}/\delta^{13}\text{C}$

## Introduction

In terrestrial ecosystems, spiders and ants are ubiquitous and diverse generalist predators (Wise 1993; Hölldobler and Wilson 1995). Most Central European ant species are omnivores, being able to prey on a wide range of other invertebrates as well as to take up nutrients from plants indirectly by trophobiosis with phloem-feeding insects (Seifert 1996). Spiders and ants are potential competitors and mutual predators. Intraguild predation, i.e. the feeding on species of the same guild, is common in natural communities (Polis et al. 1989) and enhances the reticulate nature of a food web. Further, intraguild predation has been characterised as an important feature structuring arthropod communities (Wise 1993).

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Studies have reported high rates of predation by ants on spiders (Petal and Breymeyer 1969; Kajak et al. 1972), but there is a lack of evidence for these effects demonstrated by field experiments (Wise 1993). Halaj et al. (1997) tested the effect of ants foraging on a spider assemblage in Douglas-fir canopies. The abundance of hunting spiders increased significantly following ant exclusion. However, the authors concluded that not direct predation but the disturbance of spiders by ants was important. In contrast, such effects could not be demonstrated in other studies (Otto 1965; van der Aart and de Wit 1971; Brüning 1991; Gibb 2003; Lenoir et al. 2003). Brüning (1991) tested the effects of *Formica polycytena* on spiders in a forest ecosystem without finding any difference in the density or composition of the spider community neither inside nor outside the hunting area of ants.

In the current study, we manipulated densities of spiders and ants in a field experiment and tested their effects as predators in a diverse arthropod community. Additionally, we used a stable isotope analysis to gain a better understanding of trophic links in the food web. Stable isotope analysis of ratios of  $^{15}\text{N}/^{14}\text{N}$  and  $^{13}\text{C}/^{12}\text{C}$  is a promising tool for food web studies (De Niro and Epstein 1981; Wada et al. 1991; Kling et al. 1992; Ponsard and Arditi 2000). Values of  $\delta^{13}\text{C}$  are largely conserved in food chains and provide information about the identity of the resource base (DeNiro and Epstein 1978; Petelle et al. 1979; Magnusson et al. 1999; Van der Zanden and Rasmussen 1999), whereas  $\delta^{15}\text{N}$  values can be used as a trophic level indicator (Ponsard and Arditi 2000; Post 2002; Vanderklift and Ponsard 2003).

## Materials and methods

### Study site

The experiment was conducted on a limestone hillside (51°22'N, 9°50'E) with a southern exposure that is close to Witzenhausen (Hesse, Germany). The long-term mean temperatures are 0°C in January and 18°C in July, and the annual precipitation amounts to approximately 650 mm (Stein 1996). The experimental area comprised a dry grassland (Mesobromion) and a meadow (Arrhenatheretum) and had not been in use as pastureland throughout the last 10 years (for details of vegetation see Appendix 1). The experimental area was located 180–200 m a.s.l. adjacent to a mixed beech and pine forest and was surrounded by bushes. The density and height of the herb layer increased downhill from the area of the dry grassland to the meadow.

We found 72 spider species, with wolf spiders and web-building spiders such as linyphiids and araneids being most abundant. Among the 18 species of ants in the study site, the most abundant were *Myrmica sabuleti* Meinert, *Lasius alienus* Förster and the subterranean species *Lasius flavus* (Fabricius), with medium worker densities of all species combined outside the stricter nest areas of 500–700 individuals/m<sup>2</sup>. Nest distribution of less abundant species was very patchy. The herbivorous guild in the grassland was a diverse mixture of species consisting mainly of grasshoppers, planthoppers, leafhoppers, beetles, heteropteran bugs and aphids.

### Experiment

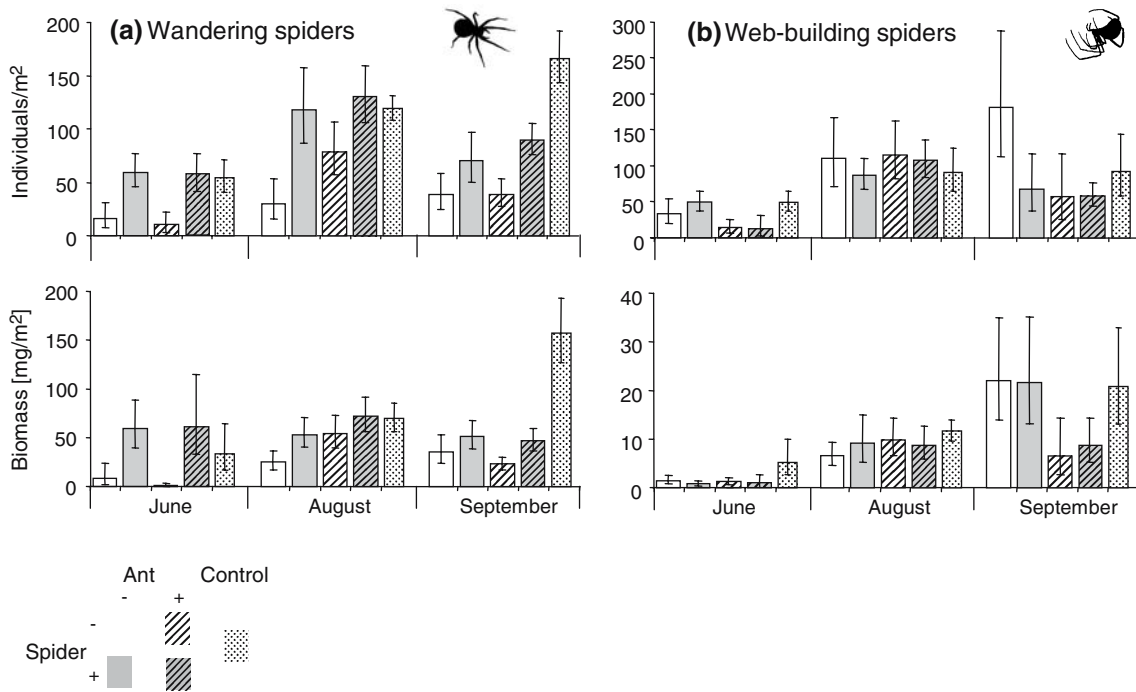
The basic experimental unit was a 2-m<sup>2</sup> area enclosed by a 30-cm high plastic fence. The fence surrounding these plots was buried 10 cm deep into the ground and was covered on both sides with slippery barriers of silicon gel: on the inner side of the fence to reduce emigration from non-removal-plots and on the outside to prohibit immigration of spiders and ants in removal plots (Orazé and Grigarick 1989). The experiment ran from May until September 2002 and was set up in a two-factorial design with two levels of spider and ant density (natural and low), resulting in four treatment combinations. Each combination was replicated five times in blocks, giving a total of 20 plots. The five blocks formed a transect from the top to the bottom of the hillside, each being located in different vegetation in the gradient of the dry grassland down to the meadow (see Appendix 1).

The low predator-density treatment was achieved indirectly by placing slippery barriers on the outside of the rings and by removing spiders manually and excluding ant colonies. Spider populations and ant colonies that became re-established in the removal plots were removed twice a week during the 4 months of the experiment. One person searched each plot for spiders and ant colonies for 10 min. Ant colonies that were detected in these plots were excavated and replaced by soil cores without ants from outside the plots. In ant plots with only one colony a supplementary colony of *Lasius* or *Myrmica* that was excavated outside the plots was added to achieve a comparable ant nest density. On average, three to six spiders per plot were removed from low spider-density treatments on each sampling occasion and released to the remaining non-removal plots in the same block. To assess the effect of enclosures, for each of the five blocks one sample was taken outside the plots in similar vegetation. A comparison with the control samples suggested that spider densities

and biomass and ant biomass reached a natural level in non-removal plots (see Figs. 1, 2a). Both wandering and web-building spiders were removed, but we achieved no reduction of web-building spider density in the removal plots (see Results).

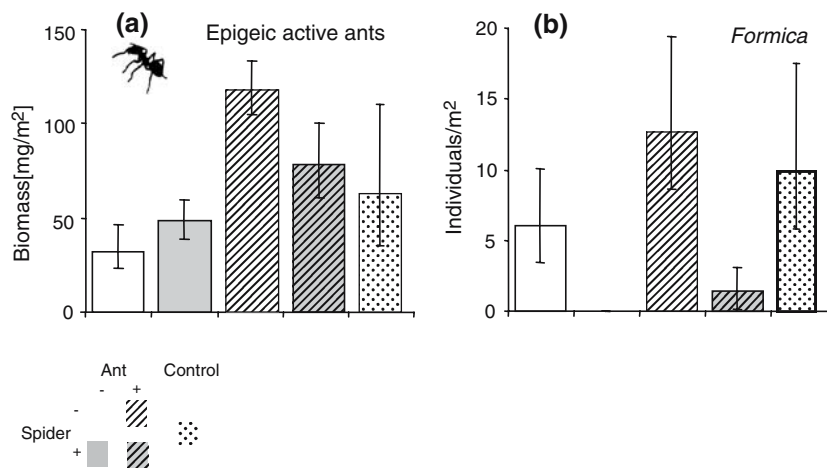
Sampling

The fauna was sampled in June, August and September 2002 with a suction sampler (Stihl SH 85, Germany; 10 s/sample using a 0.036-m<sup>2</sup> sampling cylinder) and



**Fig. 1** Mean abundance and biomass of wandering spiders (a) and web-building spiders (b) in suction-samples from the four different treatment combinations with natural and reduced ant and spider density and in control samples outside the plots. *Open bars* Plots with reduced spiders and ant density, *shaded bars* plots

with natural spider density, *hatched bars* plots with natural ant density, *dotted bars* controls from outside the plots. *Bars* represent geometrical means ( $n=5$ ), *error bars* are back-transformed standard errors of the mean ignoring the block effect. For statistical analyses see text and Table 1



**Fig. 2** a Biomass of epigeic active ants (geometrical means of total biomass of all epigeic ant species sampled per plot), b abundance of *Formica cunicularia* and *F. fusca* (suction samples from August) in the four different treatment combinations with natural and reduced ant and spider density and in control samples outside the plots. *Open bars* Plots with reduced spiders and ant density,

*shaded bars* plots with natural spider density, *hatched bars* plots with natural ant density, *dotted bars* controls from outside the plots. *Bars* represent geometrical means ( $n = 5$ ), *error bars* are back-transformed standard errors of the mean ignoring the block effect. For statistical analyses see Table 2

additionally on two occasions (June and September) by heat extraction from 0.036-m<sup>2</sup> soil cores (Kempson 1963; Schauermaun 1982). One sample per plot was taken on each occasion. Spiders, ants, planthoppers and leafhoppers were identified to the species level, while other arthropods were assigned to higher-ranking taxa. Spiders were separated into two functional groups: web-building spiders and wandering spiders. All spiders and ants found in the samples were dried for 72 h at a temperature of 60°C and the dry weights of ants and spiders were measured. On two occasions, in June and August, the number of spider webs in the plots was counted to assess the activity of web-building spiders.

### Data analyses

The effects of the spider and ant treatment and the response of the diverse arthropod community were analysed by a repeated measures two-factor analysis of variance (rmANOVA) (Ende 1993). For large-sized Collembola and for Lepidoptera larvae with data for only one sampling occasion we performed a two-factor ANOVA. For ants, the sum of all soil and suction samples was analysed because suction samples on their own were insufficient to record the abundance of ground-living ants. All abundance and biomass data were log-transformed to meet assumptions of normality and homogeneity of variances.

### Stable isotopes

Ratios of <sup>13</sup>C and <sup>15</sup>N were estimated by a coupled system consisting of an elemental analyser (model NA 2500; Carlo Erba, Milan, Italy) and a gas isotope mass spectrometer (Finnigan Delta<sup>plus</sup>, San Jose, Calif.). The system is computer-controlled and allows the measurement of <sup>13</sup>C and <sup>15</sup>N (Reineking et al. 1993). Isotopic contents were expressed in δ units as the relative difference between sample and conventional standards with  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  (‰) =  $(R_{\text{Sample}} - R_{\text{Standard}})/R_{\text{Standard}} \times 1,000$ , where  $R$  is the ratio of <sup>15</sup>N/<sup>14</sup>N or <sup>13</sup>C/<sup>12</sup>C content, respectively. The conventional standard for <sup>15</sup>N is atmospheric nitrogen and for <sup>13</sup>C PD-belemnite (PDB) carbonate (Ponsard and Arditì 2000). Acetanilide (C<sub>8</sub>H<sub>9</sub>NO; Merck, Darmstadt, Germany) served for internal calibration with a mean standard deviation of samples <0.1‰. Between 500 and 1800 µg of dry biomass of the dried samples was weighed into tin capsules and stored in a desiccator until measurement. For the large spider genera *Alopecosa*, *Pisaura* and *Atypus*, it was necessary to use only parts of the body (prosoma), while small individuals of juvenile spiders and springtails were combined into one sample. Albers

(2002) analysed parts of the body of arthropods and found no significant differences in their δ<sup>15</sup>N values. If possible, replicate measurements were made. We analysed spiders and ants, their potential prey and plants. Plants from the soil cores were separated into herbs, grasses and mosses, and samples of these groups were replicated six times. Stable isotope data were analysed by performing a general linear model (GLM) due to the different sizes of the samples. All statistical analyses were performed with SAS (ver. 8: PROC GLM and PROC ANOVA; SAS, Cary, N.C.). *Aulonia albimana* (Lycosidae), which was one of the most abundant spiders and present in all samples, was used for the comparison of possible block- and treatment-specific differences in stable isotope ratios. No such differences between the five blocks and treatments, including non-fenced controls, were found (δ<sup>13</sup>C: for treatment  $F_{4,16}=1.35$ ,  $p=0.29$ ; block  $F_{4,13}=0.93$ ,  $p=0.48$ ; δ<sup>15</sup>N: for treatment  $F_{4,16}=0.59$ ,  $p=0.68$  and block  $F_{4,13}=1.72$ ,  $p=0.20$ ; GLM).

## Results

### Manipulation of spider and ant density

During the experiment 964 spiders were captured and removed in the spider-removal plots (about 700 wandering spiders, 260 web-building spiders). There was a significant effect of spider removal on the total abundance and biomass of wandering spiders (Fig. 1a; Table 1). Biomass and density of wandering spiders was 2.4-fold lower in spider removal-plots. The effect on the biomass tended to be more pronounced in June than in August and September (Fig. 1a; Table 1). In contrast, biomass and density of web-building spiders were not affected by the manipulation (Fig. 1b; Table 1).

The total biomass of all epigeic active ants was successfully manipulated (Fig. 2a; Table 2). The biomass of ants and wandering spiders in non-removal plots was not significantly different from the biomass values in the control samples outside the plots (ant biomass:  $F_{1,8}=0.13$ ,  $p=0.72$  for the effect of treatment in a one-factor ANOVA; spider biomass:  $F_{1,8}=0.17$ ,  $p=0.69$  for the effect of treatment in a rmANOVA).

### Interactions between ants and spiders

The presence of ant colonies had a negative impact on web-building spider abundance in June (Fig. 1b;  $F_{1,12}=7.72$ ,  $p=0.017$ ; for ANOVA). Biomass of web-building spiders in suction-samples showed a negative

**Table 1** Response of wandering and web-building spiders to the treatments. Data were log-transformed ( $\log 10X + 1$ )

	<i>df</i> <sup>a</sup>	Wandering spiders (abundance)		Wandering spiders (biomass)		Web-building spiders (abundance)		Web-building spiders (biomass)	
		<i>F</i> <sup>b</sup>	<i>p</i>	<i>F</i> <sup>b</sup>	<i>p</i>	<i>F</i> <sup>b</sup>	<i>p</i>	<i>F</i> <sup>b</sup>	<i>p</i>
Ant (A)	1, 12	0.14	0.7180	0.21	0.6582	3.47	0.0873	0.91	0.3581
Spider (S)	1, 12	10.90	0.0063*	17.46	0.0013*	0.48	0.5022	0.00	0.9816
A × S	1, 12	0.01	0.9444	0.54	0.4760	0.26	0.6218	0.00	0.9597
Block (Bl)	4, 12	0.57	0.6866	1.99	0.1604	2.83	0.0730	2.89	0.0690
Time (T)	2, 11	6.79	0.0120*	4.82	0.0314*	9.27	0.0044*	35.48	<0.0001*
T × A	2, 11	1.08	0.3727	2.69	0.1117	3.31	0.0750	3.88	0.0531
T × S	2, 11	0.65	0.5392	4.14	0.0458*	0.66	0.5368	0.31	0.7419
T × A × S	2, 11	1.18	0.3425	1.18	0.3424	0.99	0.4012	0.35	0.7103
T × Bl	8, 24	1.09	0.4038	1.18	0.3517	1.85	0.1165	1.07	0.4132

\* $p < 0.05$ , indicating statistical significance

<sup>a</sup> *df* = degrees of freedom (Nom, Den)

<sup>b</sup> *F* values are given for a repeated measures ANOVA for suction samples from June, August and September; for the within-effects, *F* values for Pillai's Trace are given

**Table 2** Response of ants (sum of all epigeic species and abundance of *Formica cunicularia* and *F. fusca* workers from suction-samples), Collembola and Lepidoptera larvae (from soil samples), using a two-way ANOVA. Data were log-transformed ( $\log 10X + 1$ )

	<i>df</i>	Epigeic ants (biomass; sum of samples)		<i>Formica</i> (worker-abundance; August)		Collembola >1mm (abundance; June)		Lepidoptera larvae (abundance; September)	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Model	7, 12	4.83	0.0085*	3.23	0.0361*	1.53	0.2457	1.78	0.1818
Ant (A)	1, 12	19.03	0.0009*	2.28	0.1569	0.44	0.5174	6.84	0.0226*
Spider (S)	1, 12	0.003	0.9607	13.60	0.0031*	5.58	0.0359*	0.01	0.9109
A × S	1, 12	3.87	0.0727	0.45	0.5170	0.00	0.9691	1.06	0.3228
Block	4, 12	2.73	0.0792	1.57	0.2448	1.18	0.3692	1.13	0.3866

\* $p < 0.05$ , indicating statistical significance

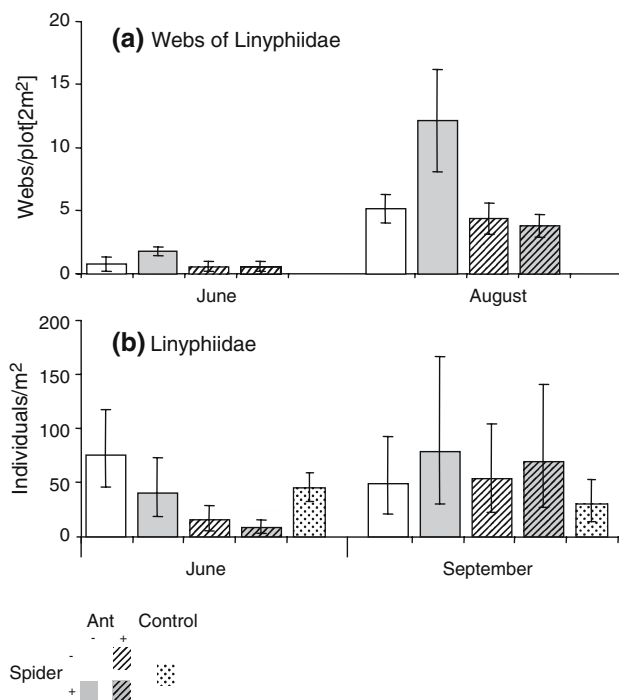
response to higher ant densities only in September ( $F_{1,12}=5.50$ ,  $p = 0.037$ ; for rmANOVA including interaction ant × time; see Table 1). Samples taken by heat extraction from soil cores revealed a negative effect of ants on web-building spiders, most of which belonged to the Linyphiidae (Fig. 3b, Table 3). Higher ant densities also significantly decreased the number of established linyphiid webs (Fig. 3a, Table 3). In June, the density of web-building spiders was 2.5-fold higher and in September threefold higher in ant-removal plots (samples taken by suction trap; Fig. 1b). The mean number of web-building spiders in the ant and spider-removal plots in September was 180 individuals/m<sup>2</sup> compared to 60 individuals/m<sup>2</sup> in non-removal plots of spiders and ants, but these effects of ants and wandering spiders on the abundance of web-building spiders were not significant (Table 1). The abundance and biomass of wandering spiders were not affected by the presence of ants (Fig. 1a, Table 1).

In August, the abundance of *Formica cunicularia* Latreille and *F. fusca* L. workers reached higher densi-

ties in spider-removal plots (Fig. 2b, Table 2). *Formica* colonies were not present inside the plots; abundance ranged from 7 to 13 individuals of *Formica*/m<sup>2</sup> in plots excluding wandering spiders.

#### Effects of ants and spiders on the arthropod community

Higher densities of wandering spiders had a negative effect on the density of epigeic Collembola. In June, wandering spiders negatively affected the abundance of Collembola species larger than 1 mm (Fig. 4a, Table 2) but not the abundance of all Collembola (Fig. 4b, Table 3). The density of Collembola increased by 37% in ant-removal plots compared to that in natural-ant density plots in June, but the difference was only marginally significant ( $F_{1,12}=3.97$ ,  $p=0.0696$ ), whereas the abundance of larvae of Lepidoptera responded negatively to the presence of ants in September (Fig. 4c, Table 3). We found no effects of spiders on planthoppers and leafhoppers (Fig. 4d, Table 3) nor did we find



**Fig. 3** Mean numbers of spider webs (a) and linyphiids (samples from soil cores) (b) in the four different treatment combinations with natural and reduced ant and spider density and in control samples outside the plots. *Open bars* Plots with reduced spider and ant density, *shaded bars* plots with natural spider density, *hatched bars* plots with natural ant density, *dotted bars* controls from outside the plots. For webs (a), the arithmetic means are given ( $n=5$ ), and *error bars* are standard errors of the mean; for Linyphiidae (b), geometrical means are given ( $n=5$ ), and *error bars* are back-transformed standard errors of the mean. Both ignore the block effect. For statistical analyses, see Table 3

any effect on the total number of Isopoda, Julidae, Geophilidae, Lithobiidae, Heteroptera, aphids, beetles, dipterans.

The phloem-feeding Ortheziidae (coccids) showed a positive response to higher densities of ants (Fig. 4e, Table 3). The abundance of Ortheziidae increased significantly from June to September (Table 3). Thysanoptera (thrips) showed a similar negative response to ant removal (Fig. 4f); however, the response was only significant in September ( $F_{1,12}=6.90$ ,  $p=0.0221$ ; for ANOVA). This effect was dependent on spider treatment and time (significant time  $\times$  ant interaction  $\times$  spider interaction; Table 3).

#### Analysis of stable isotopes

The plant groups had  $\delta^{13}\text{C}$  values of  $-28.5$  to  $-30\%$  and  $\delta^{15}\text{N}$  values of  $-5$  to  $-3\%$  (Fig. 5). Most herbivorous insects, such as planthoppers, leafhoppers, Ortheziidae and aphids, showed  $\delta^{15}\text{N}$  values very similar to those of plants. The Alticinae (Chrysomelidae) were

more enriched in  $^{15}\text{N}$ , with a  $\delta^{15}\text{N}$  value of  $-2.2\%$ . Detritivorous and fungi-feeding arthropods, such as Julidae, Isopoda and Collembola, with a  $\delta^{15}\text{N}$  value of  $-1.84\%$ , had higher  $\delta^{13}\text{C}$  values than plants.

Wandering spiders, consisting of *Aulonia albimana* (Walckenaer) and juvenile spiders of the genus *Zora*, *Tibellus*, *Pardosa* and *Clubiona*, were 2–3‰ more enriched in  $^{15}\text{N}$  than Collembola ( $F_{1,53}=55.78$ ,  $p<0.001$ , for GLM). Both groups had similar  $\delta^{13}\text{C}$  values ( $F_{1,53}=0.32$ ,  $p=0.57$ , for GLM; Fig. 5a). Juvenile web-building spiders and adult *Tenuiphantes tenuis* (Blackwell) (Fig. 5b) were also more enriched in  $\delta^{15}\text{N}$  than Collembola ( $F_{1,13}=19.88$ ,  $p<0.001$ , for GLM) and had similar  $\delta^{13}\text{C}$  values ( $F_{1,13}=0.21$ ,  $p=0.66$ , for GLM). *Walckenaeria acuminata* Blackwell, *Atypus piceus* (Sulzer), *Alopecosa trabalis* (Clerck), *Pisaura mirabilis* (Clerck) and *Tibellus oblongus* (Walckenaer) were more enriched in  $\delta^{15}\text{N}$  with values 4–5‰ higher than those of Collembola. Among all spiders, *Atypus* was most enriched in  $\delta^{13}\text{C}$ .

The spiders most enriched in  $^{15}\text{N}$  were the web-building species *Argiope bruennichi* (Scopuli), *Mangora acalypha* (Walckenaer) and the wolf spiders *Arctosa lutetiana* (Simon) and *Pardosa lugubris* (Walckenaer) with  $\delta^{15}\text{N}$  values higher than 4.  $^{15}\text{N}/^{14}\text{N}$  ratios in adult wandering spiders (*Pisaura*, *Pardosa*, *Tibellus*) were generally significantly higher than in juveniles (Fig. 5a;  $F_{1,9}=8.63$ ,  $p=0.016$ , for GLM).

Among the ant species, *Lasius flavus* and *L. alienus* had lower  $^{15}\text{N}/^{14}\text{N}$  ratios than *Myrmica sabuleti*, *Formica cunicularia* and *Ponera coarctata* (Latreille) (Fig. 5c).  $\delta^{13}\text{C}$  values of the *Lasius* species had a higher variance in comparison to *Formica* and *Myrmica*. Among the generalist predators, adult wolf spiders and *Atypus* contained higher values of  $\delta^{15}\text{N}$  (Fig. 5d) than most web-building spiders and ants ( $F_{1,79}=46.32$ ,  $p<0.001$ , for GLM). Values of all arthropods analysed can be found in the Appendix 2. Diptera of the family Sphaeroceridae were most enriched in  $^{15}\text{N}$  with  $\delta^{15}\text{N}$  values of 5.74.

## Discussion

### Manipulation of spider and ant densities

We successfully manipulated densities and biomass of wandering spiders and ants. Natural spider density treatment was achieved by the addition of spiders to the non-removal plots because the enclosures seemed to have had a negative effect on spider populations. Wandering spider density and biomass in non-removal plots was similar to control samples in June and

**Table 3** Response<sup>a</sup> of members of the arthropod community from soil and litter layer (heat extraction of soil cores) to the biomass manipulation of ants and wandering spiders. Data were log-transformed (log 10*X* + 1)

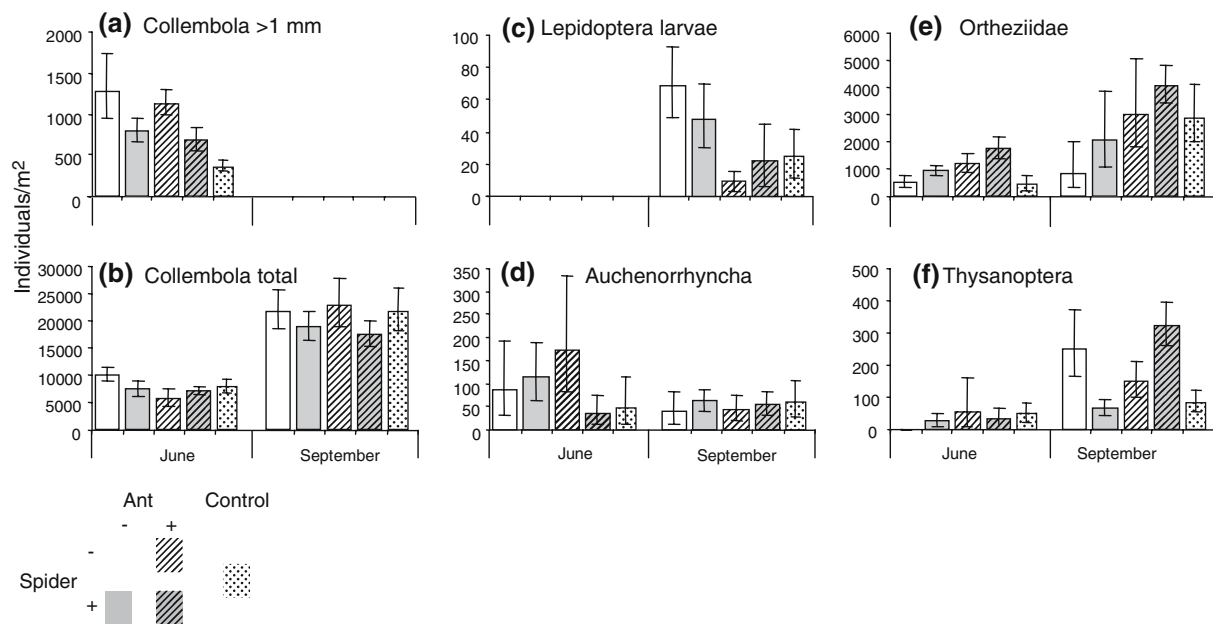
	<i>df</i> <sup>b</sup>	Linyphiidae (abundance)		Linyphiidae webs		Collembola (total)		Auchenorrhyncha		Ortheziidae		Thysanoptera	
		<i>F</i> <sup>c</sup>	<i>p</i>	<i>F</i> <sup>c</sup>	<i>p</i>	<i>F</i> <sup>c</sup>	<i>p</i>	<i>F</i> <sup>c</sup>	<i>p</i>	<i>F</i> <sup>c</sup>	<i>p</i>	<i>F</i> <sup>c</sup>	<i>p</i>
Ant (A)	1, 12	7.49	0.0180*	5.63	0.0352*	1.90	0.1935	0.02	0.8969	5.20	0.0416*	4.11	0.0655
Spider (S)	1, 12	0.03	0.8593	2.74	0.1235	1.04	0.3287	0.02	0.8969	2.17	0.1665	0.01	0.9310
A × S	1, 12	0.01	0.9234	3.71	0.0783	0.85	0.3753	0.66	0.4310	0.32	0.5823	0.51	0.4886
Block (Bl)	4, 12	6.31	0.0057*	1.40	0.2920	2.28	0.1207	1.64	0.2274	1.62	0.2326	2.77	0.0770
Time (T)	2, 11	2.44	0.1446	26.72	0.0002*	137.04	<0.0001*	7.24	0.0196*	13.10	0.0035*	46.70	<0.0001*
T × A	2, 11	1.70	0.2167	3.42	0.0892	3.02	0.1078	0.46	0.5104	0.34	0.5700	0.19	0.6717
T × S	2, 11	0.90	0.3612	1.64	0.2246	0.91	0.3595	0.94	0.3505	0.04	0.8412	0.83	0.3813
T × A × S	2, 11	0.16	0.6953	2.45	0.1436	3.77	0.0760	1.19	0.2968	0.20	0.6655	13.10	0.0035*
T × Bl	8, 24	0.80	0.5452	2.49	0.0993	3.00	0.0622	4.23	0.0230*	3.15	0.0549	4.29	0.0220*

\**p*<0.05, indicating statistical significance

<sup>a</sup> All comparisons were made using a two-way repeated measures ANOVA for data from June and September

<sup>b</sup> *df*= degrees of freedom (Nom, Den)

<sup>c</sup> For the within-effects, *F* values for Pillai's Trace are given



**Fig. 4** Mean abundance of Collembola larger than 1 mm (a), of all Collembola (b), of Lepidoptera larvae (c), of Auchenorrhyncha (d), of Ortheziidae (e) and of Thysanoptera (f) in samples from soil cores taken in the four different treatment combinations with natural and reduced ant and spider density and in control samples outside the plots. *Open bars* Plots with reduced spiders

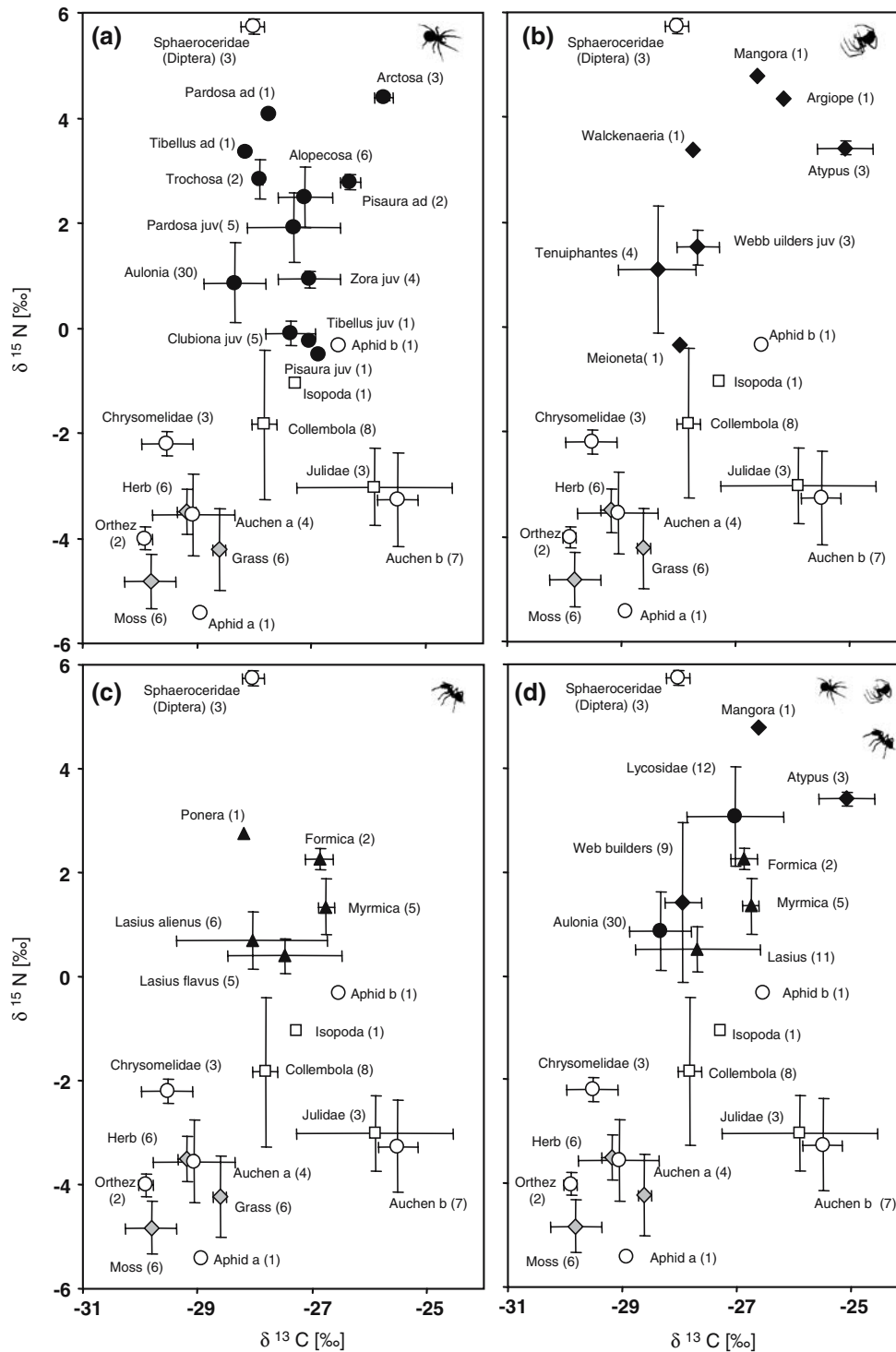
and ant density, *shaded bars* plots with natural spider density, *hatched bars* plots with natural ant density, *dotted bars* controls from outside the plots. *Bars* represent geometrical means (*n*=5), *error bars* are back-transformed standard errors of the mean ignoring the block effect. For statistical analyses, see Table 3

August, but tended to be lower in September. We assume that the barriers of the fence and silicon gel did not prevent all spiders from leaving the plots. An alternative explanation is an enhancement of cannibalism at higher spider densities. In most cases it seems to be impossible to achieve densities higher than the natural densities of spiders in a long-term experiment (Wise 1993). We were unable to reduce the density and bio-

mass of web-building spiders in the removal-plots, probably due to an increased survival in plots without wandering spiders.

**Intraguild interactions**

Intraguild predation has been identified as an important feature structuring terrestrial arthropod communities,



**Fig. 5**  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values ( $\pm\text{SD}$ ) of wandering spiders (a), web-building spiders (b), ants (c), their possible prey organisms (open circles) and plants (shaded diamond). Numbers of samples analysed are given in parentheses. A summary for the most important predatory groups is presented in d. Web builders: juv juvenile web-building spiders (Linyphiidae, Theridiidae, Tetragnathidae,

Araneidae), Auchen Auchenorrhyncha. Full names and values of the taxa referred to in this figure are given in Appendix 2. Filled circle Wandering spiders, filled diamond web-building spiders, filled triangle ants, open circle herbivores, open square detritivorous and fungivorous groups

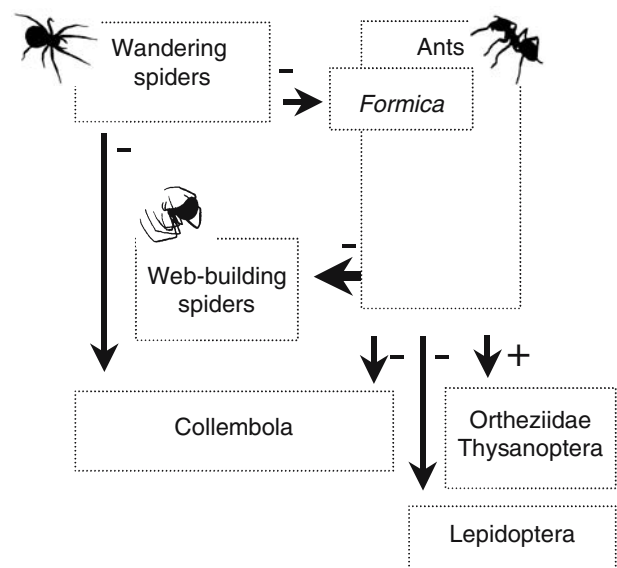


in particular if spiders are involved (Wise 1993). However, to date most studies have not provided any evidence of interactions between spiders and ants affecting population densities (Otto 1965; van der Aart and de Wit 1971; Brüning 1991; Lenoir et al. 2003; Gibb 2003).

Our results provide experimental evidence for negative interactions between ants and spiders in a grassland (Fig. 6). We observed a negative effect of ants on the abundance of web-building spiders. This effect was strong in June and September, with densities of web-building spiders being up to threefold higher in ant-removal plots. This coincides with periods of high predation by *Myrmica* in the time of intensive growth of ant larvae, as reported by Kajak et al. (1971). The density of spider webs in the herb layer was also significantly lower in plots with ant colonies, indicating a lower activity of web-building spiders. Lenoir et al. (2003) found a similar negative effect of *Formica rufa* on the activity of Linyphiidae on the forest floor after excluding ants from their usual food sources in the tree canopy and thus forcing them to forage on the ground. In our experiment the effects of ants on web-building spiders were stronger in samples from soil cores than in suction samples, indicating that ants had a greater impact on ground-dwelling spiders than on those in higher strata of the herb layer. The majority of web-building spiders were sheet-web weavers of the subfamilies Linyphiinae and Erigoninae. These spiders build their cryptic webs in the litter layer as juveniles and live within easy reach of foraging ants.

In August, higher densities of wandering spiders led to a decrease in the abundance of the ants *Formica cunicularia* and *F. fusca*. This effect could be substantiated only for ants away from their colonies, since no colonies were present within our plots. Both *Formica* species seem to be less aggressive than *Myrmica* spp. and *Lasius alienus* (Seifert 1996); foraging workers of *Formica* species probably avoid areas of higher densities of wandering spiders due to a higher disturbance rate. Such trait-mediated effects caused by a disturbance seem to be important in arthropod communities as recently demonstrated for spiders and other prey groups (e.g. grasshoppers, planthoppers and leafhoppers) (Schmitz 1998; Cronin et al. 2004). However, Brüning (1991) observed some species of Theridiidae, Amaurobiidae and Segestriidae preying upon workers of *Formica*. In our study, the feeding activity of the spiders was not directly assessed, but we observed a few individuals of Lycosidae and Thomisidae preying upon ants.

We conclude that intraguild interactions were important forces for structuring the community. Web-



**Fig. 6** A model of important interactions between arthropod groups in the grassland food web. Effects were tested by ANOVA for strong effects ( $p < 0.05$ )

building spiders reached the highest densities in ant-removal plots, indicating a negative influence of ants (Fig. 6). Further, ants of the genus *Formica* were negatively affected by the presence of wandering spiders.

#### Top-down control

There is a growing body of evidence for an important role of ants and spiders as controlling forces for other grassland arthropods (Kajak et al. 1972; Wise 1993; Riechert and Lawrence 1997). In their study of the role of *Myrmica* in a meadow ecosystem, Kajak et al. (1972) reported high predation rates of ants on juvenile arthropods. In our study we observed a negative effect of ants on larvae of Lepidoptera and on Collembola, but a positive effect on Ortheziidae and Thysanoptera (Fig. 6). In contrast, for wandering spiders we observed only an effect on the abundance of large-sized Collembola, but not on any group of herbivorous arthropods. Lawrence and Wise (2000, 2004) and Wise (2004) demonstrated that experimental removal of wandering spiders in the field significantly increased the abundance of Collembola. Wolf spiders consume Collembola in amounts ranging between 8 and 40% of a total spider's diet (for reviews, see Nentwig 1986; Nyffeler 1999). In our study,  $\delta^{13}\text{C}$  values of Collembola and many ground-living spider species (wandering spiders and juvenile web builders) were similar, suggesting that these spiders feed on Collembola to a significant extent. Juvenile wandering and web-building spiders in our study showed  $^{15}\text{N}/^{14}\text{N}$  ratios just one trophic level

above those of Collembola, indicating that Collembola are an important prey group.

A comparison of our results with studies of agro-ecosystems (Sigsgaard 2002; Agusti et al. 2003) suggest that, in general, the food resource of ground-living spiders is based mainly on the components of the detrital food web (notably Collembola and other detritivores) and that effects on herbivore populations are often weak. In contrast, other studies found strong effects of spiders on pest species in agro-ecosystems (Riechert and Bishop 1990; Snyder and Wise 2001; Schmidt et al. 2003). However, in these latter studies the guild of herbivores only consisted of few pest species, whereas in our study the herbivore guild as well as the predator guild consisted of very diverse mixtures of many species from different taxa.

Attention must also be paid to the indirect effects of intraguild predation, which have recently been shown to reduce the strength of top-down effects (Finke and Denno 2003, 2004; Lang 2003; Denno et al. 2004) and, therefore, it may not be possible to demonstrate top-down effects on the herbivorous guild in highly diverse systems. Effects on herbivores and spiders in another recent ant exclusion experiment were not strong, probably due to a compensatory change in the composition of the invertebrate predator guild (Laakso and Setälä 2000). The removal of ants and wandering spiders in our experiment caused high web-building spider densities. The nearly constant presence of generalist predators in all treatments may result in a constant overall top-down control by these three different predator groups. This effect of a highly diverse predator guild may stabilize the whole system, as indicated by the weak overall effect when any single predator group was reduced.

#### Food web analysis

On average, the  $^{15}\text{N}/^{14}\text{N}$  ratio of predators is 3–4% higher than that of their prey (DeNiro and Epstein 1981; Minagawa and Wada 1984; Owens 1987; Peterson and Fry 1987; Cabana and Rasmussen 1994). However, within this general pattern, variation in consumer diet  $\delta^{15}\text{N}$  enrichment can be substantial (Vanderklift and Ponsard 2003). Our data indicate that the food web in the dry grassland may span three trophic levels (values between  $-5.4$  and  $+5.7\%$   $\delta^{15}\text{N}$ ). In spiders, values ranged from  $-0.5$  to  $+4.8\%$   $\delta^{15}\text{N}$ , with a high overlap and variance of  $^{15}\text{N}/^{14}\text{N}$  ratios. Hence, we could not assign spiders to a single trophic level. Adults were more enriched in  $^{15}\text{N}$  than juveniles, indicating different trophic positions in the food web. In contrast to  $^{15}\text{N}/^{14}\text{N}$  ratios,  $^{13}\text{C}/^{12}\text{C}$  ratios of plants tend to pass

along the food chain with little further fractionation and are only slightly enriched in higher trophic levels (DeNiro and Epstein 1978; Petelle et al. 1979; Macko et al. 1982; Minagawa and Wada 1984; Lajtha and Michener 1994). The  $^{13}\text{C}$  content in the tissue of predators resembles that of their food (DeNiro and Epstein 1978) and can be used to identify the food resource (Magnusson et al. 1999; Vander Zanden and Rasmussen 1999). Apparently, juvenile spiders in particular prey largely upon Collembola, as can be inferred from their very similar  $\delta^{13}\text{C}$  values. A similarly tight trophic connection between small spiders and Collembola was also found by McNabb et al. (2001) in an agro-ecosystem. In contrast, in adult individuals of *Pisaura* and wolf spiders,  $\delta^{15}\text{N}$  values more than one trophic level above Collembola indicate that they often feed on predatory arthropods, which probably include other spiders and members of their own species. As predators grow, the size range of utilised prey may change and may include smaller individuals of other predatory species (Rosenheim et al. 1993). However, Oelbermann and Scheu (2002) found a significantly lower  $^{15}\text{N}$  content in hatchlings of the wolf spiders *Pardosa lugubris* than in their mothers, indicating the existence of nitrogen pools with different  $^{15}\text{N}$  signatures in female *P. lugubris*. Among all spiders *Atypus piceus* showed the highest  $\delta^{13}\text{C}$  values and may, therefore, be more strongly connected to the soil food web. This species builds a silken tube reaching from belowground to the soil surface and is supposed to prey upon arthropods such as Julidae and Isopoda, which move over the tube. This interpretation is supported by the higher  $\delta^{13}\text{C}$  values of these two prey groups in comparison to other possible prey groups.

Ants that are mainly predatory, such as *Formica cunicularia* and *Ponera coarctata*, were more enriched in  $^{15}\text{N}$ . In contrast, *Lasius flavus* and *L. alienus* had a lower  $^{15}\text{N}/^{14}\text{N}$  ratio, probably due to higher rates of trophobiosis with aphids or coccids. A similar relationship has been demonstrated for a rainforest ant community (Blüthgen et al. 2003). The authors found that  $\delta^{15}\text{N}$  values for ant species that commonly forage for nectar were low, while predominantly predatory species showed high values. The positive effects of higher ant densities, especially of *Lasius flavus*, on the abundance of Ortheziidae are in accordance with known interactions between this ant species and other aphids of plant root groups (Seifert 1996).

Among all of the arthropods studied, members of Diptera of the family Sphaeroceridae were the most enriched in  $^{15}\text{N}$ . Larvae of most Diptera species are known to feed on dung or other decaying matter of plants and animals (Pitkin 1988; Smith 1989). Consequently,

high  $\delta^{15}\text{N}$  values may result from dead animal material in their diet.

For juvenile wandering spiders and for ground living web-building spiders, Collembola were a key resource. This finding is supported by top-down effects revealed by the field experiment and the stable isotope analysis. Additionally, we found top-down effects of ants on Lepidoptera larvae and on Collembola. However, the effects of ants included predation as well as mutualism with sap-feeding herbivores. The food resource of most generalist predators in our study system is largely based on the detrital food web, at least temporarily.

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## Appendix 1

Phyto-sociological record of the five different blocks<sup>a</sup> in July 2002

Block (each consists of four plots)	Dry grassland–Meadow				
	1	2	3	4	5
<i>Sanguisorba minor</i> Scop.	2 <sup>b</sup>				
<i>Corylus avellana</i> L.	5				
<i>Agropyron repens</i> L.	2				
<i>Fragaria vesca</i> L.	2	2			
<i>Leucanthemum vulgare</i> (Lam.)	2	5	20		
<i>Lotus corniculatus</i> L.	6	1	5		
<i>Silene vulgaris</i> Garcke		2			
<i>Medicago lupulina</i> L.	10	4	10	20	10
<i>Clinopodium vulgare</i> L.	17	50	40	15	15
<i>Euphorbia cyparissias</i> L.	2	10			5
<i>Viola hirta</i> L.	4	10		5	10
<i>Hypericum perforatum</i> L.	2	1		4	4
<i>Poa pratensis</i> L.	7	2	2		4
<i>Bromus erectus</i> Huds.	2			5	
<i>Agrimonia eupatoria</i> L.	15	5	5	4	20
<i>Centaurea jacea</i> L.	1	4		2	
<i>Knautia arvensis</i> (L.) Coult	2	2	4		2
<i>Trisetum flavescens</i> (L.) P.Beauv.	1	3	4	2	2
<i>Cirsium arvense</i> Scop.	2				4
<i>Arrhenatherum elatius</i> (L.) P.Beauv.		2	5	5	2
<i>Brachypodium pinnatum</i> (L.) P.Beauv.		1	5	30	
<i>Anthriscus sylvestris</i> Hoffm.		4	5	2	5
<i>Tanacetum vulgare</i> L.			2		
<i>Astragalus</i> spec.			5	20	
<i>Galium album</i> Mill.				5	2
Height of herb layer (cm)	70	100	120	120	120
Height of shrub layer (cm)	50				110
Cover of herbs (%)	60	85	85	95	85
Cover of mosses (%)	30	60	70	40	60
Total vegetation cover (%)	80	100	95	100	100
Cover of litter (%)		10	50	60	60

<sup>a</sup> The five blocks were located along the hillside with each in different vegetation

<sup>b</sup> Values represent percentage for cover of single species

## Appendix 2

Arthropod taxa referred to in Fig. 4, with values and standard deviations of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$

	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	SD $\delta^{13}\text{C}$	SD $\delta^{15}\text{N}$	$n^a$
<b>Wandering spiders</b>					
<i>Alopecosa trabalis</i> (Clerck)	-27.1	2.5	0.5	0.6	6
<i>Arctosa lutetiana</i> (Simon)	-25.7	4.4	0.2	0.1	3
<i>Aulonia albimana</i> (Walckenaer)	-28.3	0.9	0.5	0.8	30
<i>Clubiona</i> juv	-27.4	-0.1	0.4	0.2	5
Lycosidae	-27.0	3.1	0.8	1.0	12
<i>Pardosa</i> juv	-27.3	1.9	0.8	0.7	5
<i>Pardosa lugubris</i> (Walckenaer)	-27.7	4.1			1
<i>Pisaura</i> juv	-26.9	-0.5			1
<i>Pisaura mirabilis</i> (Clerck)	-26.3	2.8	0.2	0.1	2
<i>Tibellus</i> juv	-27.0	-0.2			1
<i>Tibellus oblongus</i> (Walckenaer)	-28.2	3.3			1
<i>Trochosa terricola</i> Thorell	-27.9	2.8	0.1	0.4	1
<i>Zora sylvestris</i> Kulczynski	-27.0	0.9	0.5	0.2	1
<b>Web-building spiders</b>					
<i>Argiope bruennichi</i> (Scopoli)	-26.1	4.4			1
<i>Atypus piceus</i> (Sulzer)	-25.1	3.4	0.5	0.1	3
<i>Mangora acalypha</i> (Walckenaer)	-26.6	4.8			1
<i>Meioneta rurestris</i> (C.L.Koch)	-28.0	-0.4			1
<i>Tenuiphantes tenuis</i> (Blackwall)	-28.4	1.1	0.7	1.2	4
<i>Walckenaeria acuminata</i> Blackwall	-27.7	3.4			1
Web-builders	-27.9	1.4	0.3	1.5	9
Web-builders juv <sup>b</sup>	-27.7	1.5	0.4	0.3	3
<b>Ants</b>					
<i>Formica cunicularia</i> Latreille	-26.9	2.2	0.2	0.2	2
<i>Lasius alienus</i> Förster	-28.0	0.7	1.3	0.6	6
<i>Lasius flavus</i> (Fabricius)	-27.5	0.4	1.0	0.3	5
<i>Myrmica sabuleti</i> Meinert	-26.8	1.3	0.1	0.5	5
<i>Ponera coarctata</i> Latreille	-28.2	2.7			1
<b>Herbivores and detritivores</b>					
Aphidinae a	-29.0	-5.4			1
Aphidinae b	-26.5	-0.3			1
Auchenorrhyncha group a	-29.1	-3.6	0.7	0.8	4
<i>Arboridia parvula</i> (Boheman)	-29.4	-2.5			1
<i>Mocydiopsis attenuata</i> (Germar)	-28.4	-4.1			1
Auchenorrhyncha group b	-25.5	-3.3	0.3	0.9	7
<i>Adarrus multinotatus</i> (Boheman)	-25.4	-4.0			1
<i>Anoscopus albifrons</i> (Linnaeus)	-25.4	-3.6			1
<i>Aphrophora alni</i> (Fallén)	-25.8	-2.3	0.1	0.1	3
Chrysomelidae (Alticinae)	-29.5	-2.2	0.5	0.2	3
Collembola	-27.8	-1.8	0.2	1.4	8
Diptera (Sphaeroceridae)	-28.0	5.7	0.2	0.1	3
Isopoda	-27.3	-1.1			1
Julidae	-25.9	-3.0	1.4	0.7	3
Ortheziidae	-29.9	-4.0	0.1	0.2	2
<b>Plants</b>					
Grass	-28.6	-4.2	0.1	0.8	6
Herb	-29.2	-3.5	0.21	0.4	6
Moss	-29.8	-4.8		0.4	60.5

<sup>a</sup>  $n$ , Number of samples for analysis

<sup>b</sup> Juvenile web-building spiders (Linyphiidae, Theridiidae, Tetragnathidae, Araneidae)

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