Carabid adaptation to a collembolan diet: hunting efficiency and nutritional value

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Abstract. 1. Collembola are an important potential food source for carnivorous arthropods living on the soil surface. Nevertheless, due to their effective evasive manoeuvres, Collembola are not an easy prey. Several carabid groups, however, have evolved morphological specialisations to overcome this otherwise effective defence strategy. The adaptive value of this specialisation is still unclear, since some generalist carabids also consume collembolans.

2. Feeding experiments with the collembolan specialist *Notiophilus biguttatus* and four generalist carnivorous carabids revealed that the specialised species are more efficient in hunting Collembola than the generalist species.

3. A comparison between specialised and generalist carabid species subjected to a pure collembolan diet further suggests that Collembola are only a dietary supplement for generalists: the generalist carnivore *Bembidion lampros* decreased in weight and had a higher mortality rate when fed exclusively with collembolans.

4. Analogously, a third experiment shows that edaphic mites or other non-collembolan soil arthropods are just a nutritional supplement for *N. biguttatus*, since mortality increased when they were fed exclusively with these groups. The adaptation toward Collembola as prey, in contrast, does not constrain *N. biguttatus*, since they even increased in weight when fed with drosophila.

5. The enhanced hunting efficiency of *N. biguttatus* on Collembola compared to generalist species supports the hypothesis that the convergent evolution of mandibles in all collembolan specialist carabids is highly adaptive. The advantage of specialisation most probably is reinforced by the fact that generalist carabids are not real competitors for specialists, due to their poor efficiency in utilising collembolans.

Key words. *Bembidion*, Collembola specialists, feeding behaviour, food specialisation, mandible morphology, *Notiophilus*.

Introduction

Collembolans are an important and abundant prey for various arthropod groups (Gomez-Polo *et al.*, 2016). Due to the effective evasive manoeuvres of epigeic and many hemiedaphic species that use tail-like appendages to fling themselves into the air, however, collembolans are no easy prey. Therefore, several morphological specialisations for capturing collembolans have evolved in different arthropod groups (Yin *et al.*, 2017).

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Ground beetles are among the most abundant carnivorous predatory arthropods and many species feed on collembolans (Ribera *et al.*, 1999b, 2001; Kotze *et al.*, 2011; Homburg *et al.*, 2014; Šerić Jeleska *et al.*, 2014). Most of them are generalist carnivores that only occasionally use this food source, such as members of the genera *Bembidion*, *Poecilus*, *Pterostichus*, and *Asaphidion*. Only a few species are specialists with a well-documented high hunting efficiency on collembolans, such as members of the genera *Leistus*, *Loricera*, and *Notiophilus* (Ernsting & Jansen, 1978; Bauer, 1981, 1985a). Morphological adaptations seem crucial as a specialisation toward a primary diet on collembolans. Other coleopteran taxa, such as species from the family Staphylinidae, evolved a protrusible labium to hunt Collembola (Bauer & Pfeiffer, 1991). In carabids, these adaptations include setal traps

in the genera *Leistus* and *Loricera* (Bauer, 1985a; Hintzpeter & Bauer, 1986), which mostly hunt at night using olfactorial cues. Species of the genus *Notiophilus*, in contrast, do not possess comparable morphological adaptations, but hunt during the day aided by their highly enlarged eyes. However, common to all species of the genera *Loricera*, *Leistus*, and *Notiophilus* is a convergently evolved specialised mandible shape as an adaptation to hunting collembolans (Baulechner *et al.*, 2020). Compared to generalist carabids, Collembola specialists show a smaller primary mandibular joint, a more delicate and pointed incisor tooth and lack retinacular ridges (Baulechner *et al.*, 2020). While these adaptations are most likely responsible for an increased hunting efficiency towards elusive and delicate prey, they hinder consumption of food items requiring high mandible pressure (such as 'hard' arthropods or seeds). Specialists like *Notiophilus* may nevertheless also feed on other small prey to some extent (Hengeveld, 1979, 1980).

Generalist carnivores, which occasionally feed on collembolans, lack these mandible adaptations and should, therefore, be less efficient predators. To our knowledge, however, this hypothesis has never been validated experimentally. Moreover, the nutritional value and thus the ecological relevance of collembolans in the diet of generalist carnivores has yet to be proven. Physiological factors may play a role in this context. For example egg production and adult body weight of *Bembidion lampros* (Herbst, 1784) are adversely affected when larvae are fed with a single collembolan species only (Bilde *et al.*, 2000). It remains unclear, however, whether a mixed diet, including collembolans as alternative prey is more suitable for generalists (Bilde *et al.*, 2000). In this study, we compare the value of collembolans as a main food source between generalist and specialist species. We aim to test the hypotheses that morphological adaptations increase hunting efficiency in Collembola specialists compared to generalist carnivores (H1), and that a pure collembolan-based diet benefits Collembola specialists but not generalist carnivores (H2). Moreover, we hypothesise that the morphological specialisation does not necessarily lead to the exclusion of other prey and does not result in a strict ecological specialisation toward collembolans (H3). Since the value of alternative prey items such as mites and other soil organism is not well documented for Collembola specialists, this aspect is also evaluated.

Materials and methods

Specimen and prey collection

Carabids of the species *Notiophilus biguttatus* (Fabricius, 1779), a collembolan specialist, and the generalist carnivores *B. lampros* (Herbst, 1784), *Asaphidion flavipes* (Linnaeus, 1761), *Poecilus versicolor* (Sturm, 1824), and *Pterostichus melanarius* (Illiger, 1798) were captured with pitfall traps or by hand in central Hessen in close proximity to the city of Giessen. Prey items were hand-collected or extracted from soil cores obtained from the same locality where the beetles were captured, using a modified Macfadyen extractor (Macfadyen, 1961). The collection tubes were equipped with wet tissue paper to provide enough humidity. The extraction was carried out at 40 °C

for 4 days and animals were removed from the collection tubes every day. Soil and litter organisms were sorted into Collembola, mites, and 'others' (mainly insect larvae, dipterans, spiders, and staphylinid beetles). As collembolan prey, we include epigeic species of the families Isotomidae and Entomobryidae. Since living collembolans could not be determined to species level, they were instead classified as small (<2 mm), medium (2–3.5 mm), and large (4–6 mm). Size class of collembolans initially entered analyses as a confounding factor but was ultimately dropped because it did not improve or affect any statistical result. Flightless *Drosophila melanogaster* (Meigen, 1830) was obtained from a pet shop.

Feeding experiment 1 – Hunting efficiency

The experiments were conducted in 2018 and 2019, between June and August. For each of the five species included (*N. biguttatus*, *B. lampros*, *A. flavipes*, *P. versicolor*, *P. melanarius*), 13 to 35 individuals per species were used in a total of 212 experimental trials (110 individuals in total). Accordingly, approx. half of the individuals entered one trial, the remaining individuals entered multiple trials, which were conducted at least 2 days apart (see Table 1 for number of trials per species). Until the start of each trial, each individual was kept in a separate plastic container with a diameter of 10 cm. The bottom was covered with cellulose filter paper and water was sprayed in the container each day to increase humidity. Folded tissue paper as refuges and a small cup with water were provided. Before each experimental trial, carabids were kept without food for 2 days. For each experimental trial, carabids were placed in a new container at room temperature (18 °C), avoiding direct light and observer shadow and left for 5 min to resume normal behaviour. The ground was covered with cellulose filter paper so that the beetles had sufficient grip but no refuges when hunting. One collembolan was placed in the middle of the container and the number of capture attempts was recorded until the prey was successfully captured. Experiments were aborted after 15 min if no attempt was successful. From this data, two parameters were calculated: (i) overall hunting success per species (percentage of trials that resulted in captured prey, regardless of the number of attempts); (ii) Average hunting success of a species (percentage of attempts that resulted in captured prey). If a specimen failed to capture the prey within 15 min, the average hunting success rate was set at 0%, irrespective of the number of attempts. We also provide the total amount of capture attempts and the mean number of attempts for successful and unsuccessful experiments.

Feeding experiment 2 – Effect of collembolans as prey on body weight and survival

Individuals of the collembolan specialist *N. biguttatus* ($n = 23$) and the generalist carnivore *B. lampros* ($n = 18$) were kept separately for up to 19 days in 2018, with collembolan prey items in plastic containers (diameter 15 cm). To provide sufficient moisture, the container floor was covered with plaster and watered daily. In addition, a small plastic cup with water was provided.

Table 1. Total number of trials and attempts to capture prey, overall hunting success rate and mean successful and unsuccessful attempts per experiment.

	Overall			Mean attempts per experiment	
	Trials	Success rate (%)	Attempts	Successful	Unsuccessful
Notiophilus biguttatus	86	77	178	2.3	1.4 (1–8)
Bembidion lampros	80	19	293	5.8	3.2 (1–17)
Asaphidion flavipes	34	35	105	4.8	2.2 (1–11)
Poecilus versicolor	36	14	262	9.2	7.0 (1–35)
Pterostichus melanarius	16	31	52	2.6	3.5 (3–7)

Trials are the number of repetitions performed for each species. Overall success rate is the percentage of trials resulting in successful capture of the prey.

Food was provided *ad libitum*, ensuring that there were at least five Collembola per container each day. Dead collembolan prey was removed. Prior to these trials, carabids were starved for 2 days within the same containers. Carabids that died within 2 days were excluded from the experiment and are not included in the analyses. To rule out a higher mortality rate under laboratory conditions we kept 10 individuals of *B. lampros* in a 30 cm container with forest soil and litter from the same location where the beetles were collected. We added fresh forest soil and litter every few days to provide enough soil and litter fauna as food. We checked for survival every 2 to 3 days until the end of all experiments.

Feeding experiment 3 – Effect of alternative prey on body weight and survival

Similar to feeding experiment 2, feeding experiment 3 was set up for 15 days in the summer of 2019 to evaluate the performance of the collembolan specialist *N. biguttatus* on alternative prey taxa. A total of 29 individuals of *N. biguttatus* were kept separately in plastic containers and fed *ad libitum* with one of three prey item treatments: at least five mites ($n = 9$), at least five drosophila ($n = 11$), or a randomly distributed assortment of soil arthropods ($n = 9$). Feeding started 2 days after the carabids were placed into the containers. Dead and partly consumed prey was replaced daily. As a reference, we used the same data of collembolans fed to *N. biguttatus* as described above.

Measurements and statistical analyses

For Experiment 1, descriptive statistics reporting the successful and unsuccessful hunting attempts were used to calculate the overall and mean and median hunting success rate. To account for multiple trials of individual carabids, we compared the linear mixed effect model with beetle identity as a random factor against a simple model without random factors (lmne-function of the R package lmne version 3.1; Pinheiro *et al.*, 2020). Both models showed comparable Akaike information criterion (AIC) and Bayesian information criterion (BIC) (Table S1) and we thus used the simpler generalized least squares (gls) model for subsequent analyses of hunting efficiency.

In feeding experiments 2 and 3, the body weight of each beetle was measured with a Sartorius 0.01 mg half-microbalance every second or third day until the end of the experiment or until the beetle died. Weight gain or loss over the course of the experiment was calculated in percent of the first day of the experiment. We calculated the proportion of experiments in which individuals did not survive until the end of the experiment as the mortality rate. Further, we calculated the mean number of days a species survived in the experiment. We tested the correlation between body weight and time for the feeding experiments by fitting a linear mixed model with beetle ID as a random variable and tested for autocorrelation between day and ID using the lmne function of the R package lmne version 3.1 (Pinheiro *et al.*, 2020). These models reached a higher AIC and BIC value than models without temporal autocorrelation and without ID as random variables and were, therefore, used for subsequent analyses (Tables S2–S5). For feeding experiment 2 with collembolans fed to *N. biguttatus* and *B. lampros*, we used species as a factor and day (of experiment) as a continuous predictor variable as well as the interaction between these two parameters. For feeding experiment 3 with different prey items fed to *N. biguttatus*, we used prey item as a categorical and day (of experiment) as continuous independent predictor variables and as interaction terms. Models were fitted with a restricted maximum likelihood estimation. Residuals were analysed for normal distribution. To evaluate the effect of time, species, and the interaction of the two, we used the analysis of variance function from the R package car 3.0–8 (Fox & Weisberg, 2019) to calculate Wald-chi-square tests for fixed effects. We conducted a post-hoc test for multiple comparisons with a Tukey adjustment using the R Package multcomp 1.4-13 (Hothorn *et al.*, 2008) and lsmeans 2.30-0 (Lenth, 2016).

Results

Feeding experiment 1 – Hunting efficiency

N. biguttatus had the highest overall success rate (gls = $P = <0.001$, Table S2), effectively capturing collembolans in 77% of the trials. The generalist species had much lower success rates of 19–35% (Table 1). *N. biguttatus* also had the highest average hunting success (Fig. 1) and thus needed the fewest number of attempts to capture a collembolan. On average, 50% of the individuals were successful at the first attempt (median Fig. 1). Generalist carnivores were considerably less efficient: the median hunting success rate
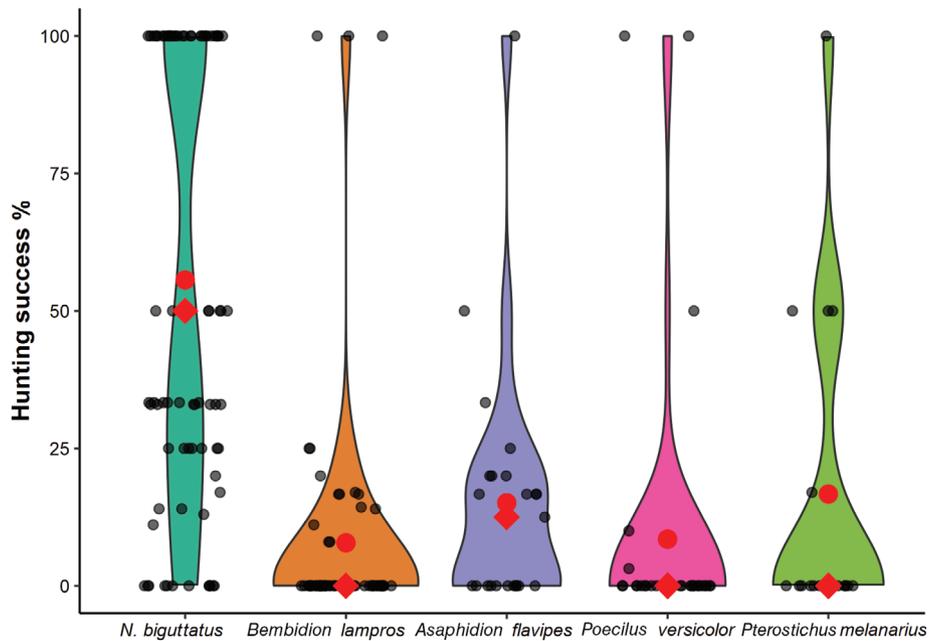
Fig. 1. Hunting success of the specialist *Notiophilus biguttatus* in percentage compared to the four-generalist species. Width of the violin-plot corresponds to the data distribution. Red circles indicate the mean, and red diamonds the median. Hunting success indicates how many attempts it takes an individual to successfully capture a collembolan (100% = 1 attempt, 50% = 2 attempts, etc).

was 0 and the mean hunting success rate was lower than 20% (5 attempts until success) for the generalist species *Bembidion tetracolum*, *P. melanarius*, and *P. versicolor*, while *A. flavipes* had a slightly higher mean and median hunting success rate than the other generalist species (Fig. 1). In experiments not resulting in the capture of the prey item, *N. biguttatus* abandoned the hunt after fewer attempts than the generalist carnivores and required fewer attempts in successful experiments (Table 1). In successful trials, *P. melanarius* required a similar number of attempts to *N. biguttatus*, but was successful in just 31% of the experiments and conducted more attempts in unsuccessful experiments (Table 1). *P. versicolor* had the highest mean number of attempts in unsuccessful and successful experiments (Table 1). On average, for all species, the number of attempts was lower in unsuccessful experiments than in successful experiments. However, specific individuals conducted a high number of attempts in unsuccessful experiments. For example *B. tetracolum* attempted to capture the prey between 10 and 17 times in 7 trials and *P. versicolor* between 20 and 35 times in 50% of the trials.

Feeding experiment 2 – Effect of collembolans as prey on body weight and survival

The final linear mixed effect model that best explained the changes in body weight based on the AIC and BIC values included the variables species, day and the interaction between the two fixed effects (Table S3). The interaction between species and day was highly significant (Pr > χ^2 = <0.001, Table S3). When fed only with collembolans, the weight of the

collembolan specialist *N. biguttatus* increased (Fig. 2). Only four *N. biguttatus* individuals did not survive until the end of the experiment, resulting in a mortality rate of 17.3%. In contrast, the weight of the generalist carnivore *B. tetracolum* decreased (Fig. 2). *B. tetracolum* showed a high mortality rate of 83% during the experiment and survived on average 9.6 days. In the control group fed with diverse microarthropods, however, 9 of 10 *B. tetracolum* individuals survived for more than 19 days (five individuals survived for 8 months), which rules out a higher mortality in captivity.

Feeding experiment 3 – Effect of alternative prey on body weight and survival

All prey groups had a statistically different effect on body weight of the collembolan specialist *N. biguttatus* (adjusted *P* values of the Tukey HSD posthoc test; Tables S5 and S6). Body weight increased when fed with Drosophila or Collembola, but it increased more when fed with Drosophila (Fig. 3, Tables S5 and S6). Mortality rate was lowest when fed with Drosophila (0%), also compared to a collembolan diet (17.3%, see section above). When fed only with mites or other soil arthropods, body weight of *N. biguttatus* decreased in both cases (Fig. 3, Tables S6 and S7). Mites and a mixed arthropod diet both resulted in a high mortality rate of 77% (mean survival of 8.3 days when fed with mites and 6.8 days when fed with other arthropods). None of the *N. biguttatus* individuals fed with mites or mixed arthropods survived more than 13 days.
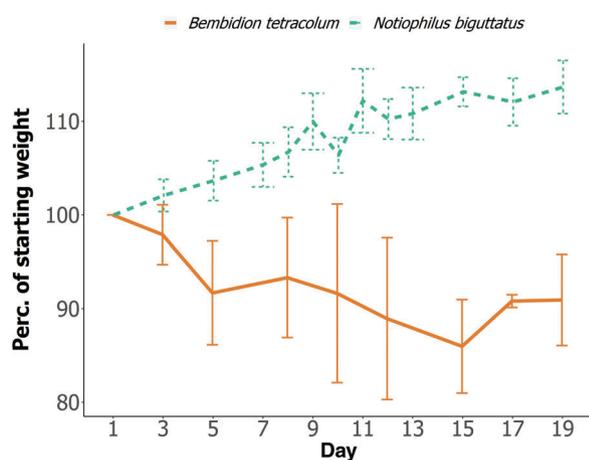
Fig. 2. Percentage changes in the weight of the generalist *Bembidion tetracolum* (solid line) and the specialist *Notiophilus biguttatus* (dotted line) when fed with pure collembolan diet. Mean values and standard error (vertical bars) are shown.
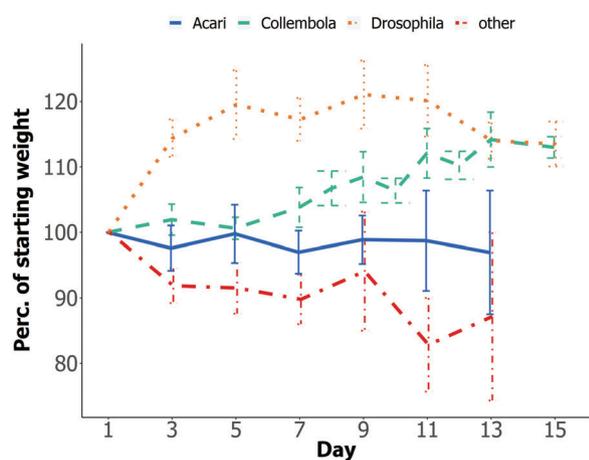
Fig. 3. Percentage changes in body weight of *Notiophilus biguttatus* when fed with different prey. Mean values and standard error (vertical bars) are shown. The term 'other' refers to a mixed diet of random soil arthropods.

Discussion

The role of Collembola as prey for many generalist carnivores has probably been overestimated. Our results suggest that highly evolved morphological specialisations are necessary to efficiently feed on collembolans. The generalist species in this study are known to feed, at least occasionally, on collembolans. We show, however, that they are inefficient hunters compared to the collembolan specialist *N. biguttatus*. Moreover, the generalist carnivore *B. lampros* had a high mortality rate and a significant decrease in body weight when fed solely with Collembola. This is most likely caused by the low hunting success rate and suggests that collembolans are not an essential food item for generalist carnivore carabids.

Without any morphological specialisations for collembolan prey, generalist carnivores seem less well equipped to efficiently use collembolans as a primary food source. Several different complex morphological specialisations have evolved in various taxa to enable them to feed on collembolans, like saeta traps in *Leistus* and *Loricera*. *N. biguttatus* is lacking comparable morphological structures, but has evolved as a fast visual hunter with overlapping frontal vision (Ernsting & Jansen, 1978; Bauer, 1981; Ribera *et al.*, 1999a). *N. biguttatus* even outperformed *Asaphidion*, which has a comparable visual overlap (Bauer, 1985b), in terms of hunting efficiency. Consequently, mandible morphology appears to be the prevailing common trait evolved in carabid collembolan specialists (Baulechner *et al.*, 2020) and can be used to identify true feeding specialisations in carabids. This is consistent with the observation of a strong link between morphology and dietary specialisation in the animal kingdom (Grant & Grant, 1996; Aguirre *et al.*, 2002), although mismatches are also common (Bouton *et al.*, 1998; Ungar *et al.*, 2008; Brandl *et al.*, 2015; de Vries *et al.*, 2016). Our study confirms that the morphological specialisation to a certain food source does not necessarily imply the inability to use other prey items, since drosophila was a valuable alternative food resource for *Notiophilus* spp. and mites at least appeared not to be disadvantageous in terms of body weight change. Exploiting alternative resources is crucial for specialists when the preferred resource is scarce (Robinson & Wilson, 1998; Fontaine *et al.*, 2008; Ungar *et al.*, 2008). During droughts in summer, for example collembolan densities are exceptionally low (Pflug & Wolters, 2001), while mites are more drought-tolerant (Perdue & Crossley, 1989; Santonja *et al.*, 2017). When fed with mites only, however, mortality of *N. biguttatus* increased, probably due to a large share of oribatid mites, which were regularly approached and captured, but always released unharmed after a short handling between the mandibles. If at all, just non-oribatid mites should be considered additional food for *N. biguttatus*, which to our knowledge has never been specified in the literature. Therefore, classification as a Collembola specialists should be based on the fact that collembolans make a substantial contribution to the diet of a species, with morphological or behavioural adaptations confirming predominant use of the target prey. Gut content analyses or anecdotal observations alone, in contrast, may overestimate the occasional consumption of collembolans by scavengers or other generalists in carabids. The term specialist is often used subjectively, so it should be specified, which type of specialisation is present (e.g. ecological vs. adaptive specialist) and in which way or if at all it is constrained to a narrow range of food (Ferry-Graham *et al.*, 2002). This is even more important in the classification of generalist carnivores, since Collembola are regularly found in their diet.

Collembolans are not a valuable primary food source for generalist carnivorous carabids. Our results show that *Pterostichus*, *Poecilus*, and *Bembidion* have a very low and *Asaphidion* a low hunting success (Bauer, 1985b), which resulted in a high mortality rate. This finding is supported by the fact that generalist carnivores are able to consume dead rather than live Collembola (Mundy *et al.*, 2000), whereas *N. biguttatus* prefers live to dead collembolans (Mundy *et al.*, 2000). Accordingly, density-dependent relationships with Collembola

abundances in ecological studies should only be expected for true collembolan specialists, such as *Notiophilus* spp., *Leistus* spp., and *Loricera pilicornis*. For example when collembolan abundance is enhanced, the abundance of the collembolan specialist *Loricera pilicornis* increases, but not the overall carabid abundance (Birkhofer *et al.*, 2008). Similar reactions might be expected from *N. biguttatus* and other species of this genera, but evidence is lacking so far. Still, collembolans might serve as an additional food resource for generalist carnivorous carabid species when other prey is not available. In structurally complex organically managed wheat fields, collembolans might compensate for a temporal lack of aphid prey for *B. lampros* (Birkhofer *et al.*, 2011). The decreased egg production and larval development resulting in lower weight of adult *B. lampros*, however, suggests short-term effects only (Bilde *et al.*, 2000). Our results suggest that Collembola are only an additional food resource and is not valuable enough as an exclusive food.

Considering that Collembola were already widespread and abundant more than 200 million years before Coleoptera diversified (Whalley & Jarzembowski, 1981; Misof *et al.*, 2014; Yin *et al.*, 2017; Leo *et al.*, 2019), surface-dwelling Collembola had most likely developed their escape mechanisms long before carabids appeared as potential predators. The response of generalists in our feeding experiments shows that the efficiency of these mechanisms holds for most carabids up to the present day. However, the findings for *N. biguttatus* suggest that the ability to overcome this barrier opened a nutritional niche for certain carabid species that allowed them to successfully reduce food competition with other species, while still being able to use alternative food sources. The fact that the ability to use Collembola as preferred prey evolved independently in different genera of carabids and other taxa indicates the ecological relevance of this process. However, there are still many open questions concerning the density dependency between Collembola specialists and their prey, as well as the influence of land use, prey availability, and competition on prey choice.

Acknowledgements

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Document S1. Supplementary information.

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