

## Research



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## Animal behaviour

# Behaviour, morphology and microhabitat use: what drives individual niche variation?

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Generalist populations are often composed of individuals each specialized on only a subset of the resources exploited by the entire population. However, the traits underlying such niche variation remain underexplored. Classically, ecologists have focused on understanding why populations vary in their degree of intraspecific niche variation, with less attention paid to how individual-level traits lead to intraspecific differences in niches. We investigated how differences in behaviour, morphology and microhabitat affect niche variation between and within individuals in two species of spider *Anelosimus studiosus* and *Theridion murarium*. Our results convey that behaviour (i.e. individual aggressiveness) was a key driver of intraspecific trophic variation in both species. More aggressive individuals capture more prey, but particularly more Coleoptera, Hymenoptera and Diptera. These findings suggest that behavioural traits play a critical role in determining individuals' diet and that behaviour can be a powerful force in driving intraspecific niche variation.

## 1. Introduction

Any natural population is composed of ecologically heterogeneous individuals. Notably, generalist populations of diverse taxa are often, in fact, collections of individuals specialized on particular subsets of the resources exploited by the population [1]. This intraspecific niche diversity (i.e. individual specialization (IS)) has implications well beyond the structure of populations, affecting community assembly [2,3], ecological interactions [4,5] and eco-evolutionary dynamics [6]. Despite such broad relevance, only recently have ecologists begun to explore the underlying causes of intraspecific niche variation in natural populations [7].

Much of the literature on the causes of IS has aimed to understand why different populations vary in their degrees of intraspecific niche variation [7]. Optimal foraging theory and recent empirical evidence indicate that the magnitude of niche variation within populations is context-dependent. Thus, ecological gradients across the landscape, such as ecological opportunity and competition, can shape variation in IS across populations in space and time [2,8,9]. However, beyond the ecological context in which populations reside (i.e. extrinsic factors), the expression of individual niche variation also depends on intrinsic, individual-level factors (i.e. traits). Elucidating links between intraspecific trait variation and niche variation thus remains an under-evaluated piece to deciphering how individual diversity in niches emerges and is maintained.

Variation in three main trait categories have long been raised as possible drivers of individual niche diversity: behaviour, morphology and habitat use [1,7,10]. For instance, mounting evidence suggests that bold versus shy [11], small-sized versus large-sized [12] and pelagic versus littoral individuals [13] can differ substantially in their trophic niche over time, resulting in niche

divergence within populations. However, precious few studies have gathered the data needed to simultaneously evaluate the importance of contrasting trait categories in determining trophic niches in the wild. Here we studied solitary individuals of two sympatric species of theridiid spiders *Anelosimus studiosus* and *Theridion murarium*, which each exhibit substantial intraspecific variation in behaviour (aggressiveness, boldness), morphology (body size), extended phenotype (web volume) and microhabitat selection (host tree). Each of these traits has the potential to affect the prey community consumed by individual predators. We took advantage of this intraspecific variation to determine the importance of behaviour, morphology and microhabitat use in shaping intraspecific trophic niches.

## 2. Material and methods

### (a) Study system

Solitary nesting *A. studiosus* ( $n = 37$ ) and *T. murarium* ( $n = 32$ ) were identified on the tips of branching overhanging the Clinch River at Melton Hill Dam, Tennessee (35°89'N, 84°30'W) in May 2014. Both species are small-bodied (cephalothorax widths less than 5 mm) cobweb weaving spiders throughout much of the eastern United States. These species are ecologically similar enough for them to occasionally form mixed-species groups where individuals will compete and sometimes cooperate to subdue and share prey [14–16]. For our purposes, we selected isolated webs that contained only a single adult female of either species per host tree (at least 3 m between consecutive colonies). We haphazardly selected webs where the contents could be readily observed from the water surface by observers in kayaks or directly from the shore.

### (b) Data collection

We measured individuals' latency to attack a simulated prey in the web (aggressiveness), body size (cephalothorax width), web volume (cm<sup>3</sup>) and identified their host tree species. Latency to attack prey was determined by placing a 1 cm × 1 cm piece of computer paper in the web of the focal spider and vibrating it with a handheld vibrator (GoVibe, Doc Johnson). The vibrator had a 10 cm long metal rod that extended from its tip that was used to contact the paper, generating a fluttering motion. We recorded the time elapsed between the initiation of the fluttering until the moment the spider contacted the paper. Spider boldness (latency to resume movement) was assessed approximately 1 h after the latency to attack trials and before morphological measurements were taken. In brief, two rapid jets of air from an infant nose-cleaning bulb were applied to the spider in its web, which resulted in spiders retreating from the jets of air and then remaining motionless. We then recorded each spider's latency to resume movement and move one body length in its web. Latency to attack and latency to resume movement following an aversive stimulus are common metrics of aggressiveness and boldness, respectively, in web-building spiders (e.g. [17–19]).

Cephalothorax width was recorded by removing the spider from its web and measuring its cephalothorax width using handheld digital calipers. Each spider was then marked with a drop of acrylic paint atop its cephalothorax to verify its identity. Web volumes were determined by estimating the shape/s that composed each irregular web (e.g. cube + cone) and measuring the necessary exterior dimensions to compute an estimate of its volume. Each spider's latency to attack, latency to resume movement and web volume were re-estimated four weeks later, immediately

before a second assessment of the spider's trophic niche. Cephalothorax width was not recorded a second time because this measure remains fixed once a spider reaches maturity because the cephalothorax is sclerotized and inextensible [20].

Spiders' trophic niches were estimated by performing round-the-clock observations of the prey captured in their webs. Prior to observations, all the old prey remains within each web were gently removed with forceps. Observations were then performed every four hours for 24 h. Red light filters were used for nocturnal observations to minimize the risk of artificially attracting insects; many insects are less attracted to longer wavelengths of light [21,22]. At each time point, we noted if the spider had captured any prey in its web and the taxonomic order of the prey item captured. We performed two such trophic niche assessments, with four weeks between consecutive observations.

We quantified three different aspects of the trophic niche of individual spiders (total number of prey captures = 460). As a measure of each spider's overall prey capture success, we counted the number of prey captured by each spider during each 24 h observation period. To summarize the main axes of variation in diet composition across individuals, we used a non-Metric Multi-dimensional Scaling (nMDS). Finally, we calculated a measure of individual-level niche breadth using an adaptation of Schoener's proportional similarity index (PS<sub>i</sub>) [23]. We averaged of PS<sub>i</sub> values for all conspecific individuals to obtain the population-wide measure of individual specialization (IS index), which varies from near 0 (maximum individual specialization) to 1 (no specialization) [23].

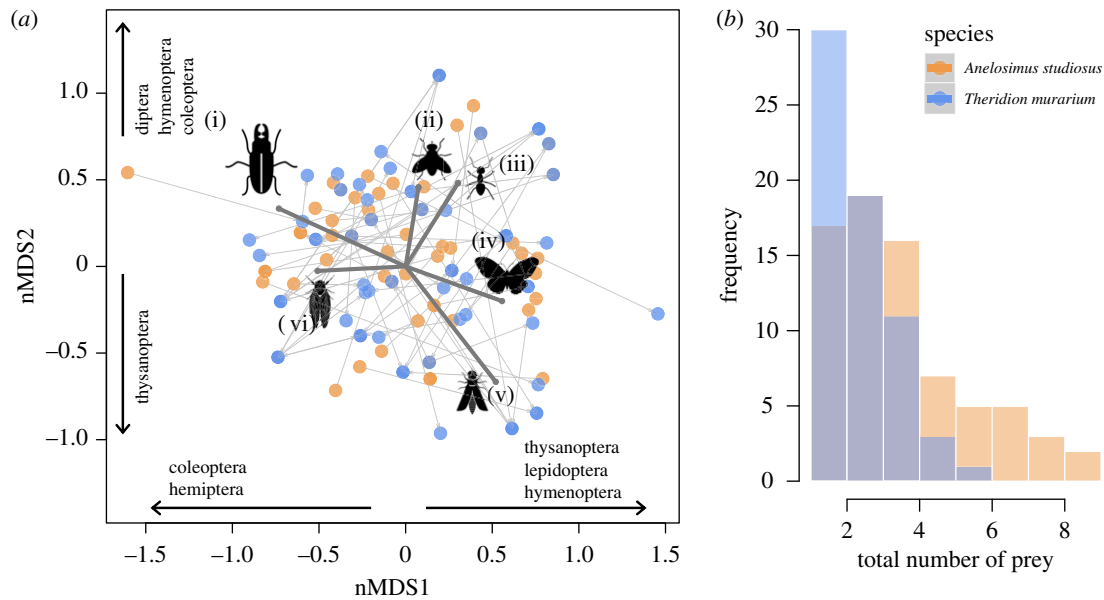
To quantify temporal diet variation within-individual (i.e. diet plasticity over four weeks), we calculated for each individual the Bray–Curtis dissimilarity between diet composition observed in each time step. Therefore, this metric quantifies how consistent individuals were in their trophic niche through time (e.g. within-individual variation).

### (c) Statistical analyses

We contrasted six categories of statistical models: (i) null model, (ii) morphological (spider size and web volume as fixed effect), (iii) behavioural (latency to attack and latency to respond), (iv) microhabitat use (host tree species), (v) combined models (including two of the previous three types of models) and (vi) full model (electronic supplementary material, table S1). After visual inspection, we also compared models including quadratic terms for behaviour and morphological traits. All these mixed models were constructed in the package *lme4* [24] and included species identity as a fixed factor (interacting with the others) and individual identity as a random factor. We compared candidate models using the difference in the Akaike information criterion (AIC<sub>c</sub>) relative to the most parsimonious model (lowest score). To model within-individual variation, we used a similar approach, but we constructed generalized linear models with Bray–Curtis dissimilarity as response variable (electronic supplementary material, table S3). *P*-values from the most parsimonious models were obtained using Type-II Wald chi-square tests. We performed all data analyses in R 3.5.1.

## 3. Results

Individual spiders varied considerably in their behaviour and morphology within each species. While some individuals showed high attack speeds, others attacked prey slowly (latency to attack range, *T. murarium*: 13–273 s; *A. studiosus* 5–23 s). Cephalothorax width varied approximately 2- and 3-fold within *A. studiosus* and *T. murarium*, respectively, and extended phenotype (web volume) varied approximately 15-fold within each species. Webs occurred in six different



**Figure 1.** Non-metric multidimensional scaling (nMDS) summarizing variation in diet composition across individuals of two theridiid spiders *Anelosimus studiosus* and *Theridion murarium*. (a) Prey types: (i) Coleoptera, (ii) Diptera, (iii) Hymenoptera, (iv) Lepidoptera, (v) Thysanoptera and (vi) Hemiptera; (b) distribution of number of prey captured by these two species. (Online version in colour.)

**Table 1.** Most parsimonious candidate models ( $\Delta_i < 2$ ) to explain variation in trophic niche components between-individuals (total number of prey, prey composition and niche width) and within-individuals (prey composition variation) of two species of theridiid spiders. Predictors include three types of individual-level traits: behavioural (LA = latency to attack, LR = latency to resume movement), morphological (BS = body size, WV = web volume) and microhabitat (Tree = taxonomic identity of the host tree). All models include species identity interacting with the other predictors and individual identity as a random effect.

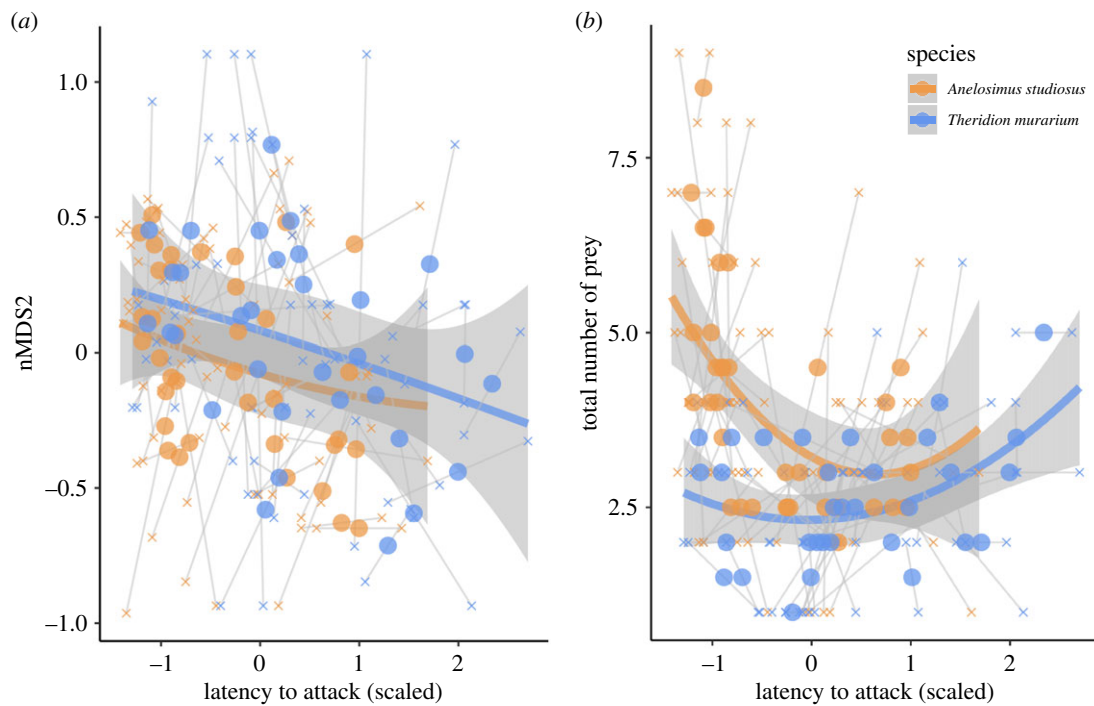
| trophic niche component          | most parsimonious model(s) | formulation                                       | AIC <sub>c</sub> | AIC <sub>c</sub> weight |
|----------------------------------|----------------------------|---|------------------|-------------------------|
| between-individual variation     |                            |   |                  |                         |
| total number of prey (NP)        | behaviour + morphology     | $NP \sim BS^2 + WV^2 + LA^2 + LR^2$               | 496.01           | 0.8                     |
| prey composition                 |                            |   |                  |                         |
| nMDS1                            | behaviour + morphology     | $nMDS1 \sim BS^2 + WV^2 + LA^2 + LR^2$            | 207.48           | 0.95                    |
| nMDS2                            | behaviour + morphology     | $nMDS2 \sim BS^2 + WV^2 + LA^2 + LR^2$            | 197.01           | 0.72                    |
| niche width ( $PS_i$ )           | morphological model        | $PS_i \sim BS^2 + WV^2$                           | -72.49           | 0.43                    |
|                                  | behavioural model          | $PS_i \sim LA^2 + LR^2$                           | -72.30           | 0.35                    |
|                                  | null model                 | $PS_i \sim 1$                                     | -70.85           | 0.18                    |
| within-individual variation      |                            |   |                  |                         |
| prey composition ( $\Delta PC$ ) | full model                 | $\Delta PC \sim BS^2 + WV^2 + LA^2 + LR^2 + Tree$ | -34.84           | 0.37                    |
|                                  | null model                 | $\Delta PC \sim 1$                                | -33.88           | 0.23                    |
|                                  | morphological model        | $\Delta PC \sim BS^2 + WV^2$                      | -33.15           | 0.16                    |

tree species: *Acer negundo*, *Juniperus virginiana*, *Ostrya virginiana*, *Prunus serotina*, *Rhus glabra* and *Tilia heterophylla*.

Although *A. studiosus* captured more prey overall, species presented similar and overlapped trophic niches in terms of prey composition (PC) (figure 1). Hemiptera was the most consumed prey item for both species, corresponding respectively to 39.47% and 37.2% of *A. studiosus* and *T. murarium* population diets. Two major axes of diet variation were summarized by the nMDS (two dimensions, stress = 0.16). The first axis (nMDS1) was positively associated with the consumption of Lepidoptera and Thysanoptera and negatively associated with Coleoptera and Hemiptera. In turn, positive scores in the second axis (nMDS2) represent more

contribution of Coleoptera, Hymenoptera and Diptera (figure 1). These species also presented similar degrees of individual niche specialization both in the first ( $IS_{A.studiosus} = 0.52$ ,  $IS_{T.murarium} = 0.5$ ) and second time steps ( $IS_{A.studiosus} = 0.58$ ,  $IS_{T.murarium} = 0.43$ ).

Between-individual variation in a total number of prey and PC was overall best explained by a combined model including morphological and behavioural traits (table 1; electronic supplementary material, table S1). Latency to attack was the major predictor of these dimensions of trophic variation (number of prey and nMDS2) (figure 2). Shorter latencies to attack resulted in higher numbers of prey overall and an increased relative consumption of Hymenoptera,



**Figure 2.** Effects of latency to attack on trophic niche composition (nMDS2, (a)) and total number of prey (b) in two species of theridiid spiders. Crosses represent observations at each time point (observations from the same individual spider are linked) and circles represent the average of these values for each individual.

Diptera and Coleoptera. Niche width ( $PS_i$ ) was similarly predicted by morphological and behavioural models, and within-individual variation by the full model (electronic supplementary material, table S2), although the null model is also parsimonious in these cases. The identity of the tree species in which spiders built their webs was an important driver of within-individual diet variation (electronic supplementary material, table S3).

#### 4. Discussion

The data herein convey that intraspecific trophic variation in these spiders is mainly driven by a combination of behaviour and microhabitat use. In particular, individual variation in latency to attack had a sizable effect on between-individual trophic niche variation, emphasizing that individuals' behavioural tendencies are a central force causing the emergence and maintenance of niche variation. Yet, temporal variation in trophic niche within individuals was most strongly associated with the psychical environment (i.e. host tree identity) in which the web was placed. Together, these results indicate that multiple individual-level traits act simultaneously to shape variation in trophic niche both within and between individuals.

Latency to attack prey was the most prominent determinant of between-individual differences in trophic niche (figure 2). Latency to attack prey is arguably the most common metric used to assess aggressiveness in spiders. More aggressive individuals are often more likely to attack prey, mates and fellow conspecifics and exhibit riskier behaviour during territorial disputes [25–27]. Prior studies have shown that more aggressive spiders tend to capture more prey, in part, because their fast attack speeds result in fewer prey escaping the web [28,29]. Aggressiveness can further increase individuals' willingness to attack dangerous prey,

like stinging insects, or large prey that might be confused with predators. Consistent with these hypotheses, we found that more aggressive spiders were more likely to have Hymenoptera, Diptera and Coleoptera in their diets. Our observations included instances of spiders consuming hard-to-subdue and presumably dangerous bugs from these Orders. For example, Coleoptera contained the largest insects observed ensnared in the webs of either species. It stands to reason that only aggressive individuals are willing to attempt subduing such prey, and/or that only an aggressive prey capture sequence can prevent these prey from escaping. More details on the prey capture sequence are needed to differentiate between such interpretations. Because lots of animals differ in their behavioural tendencies in temporally consistent manners [10,30], these results imply that variation in aggressiveness could be a contributor to intraspecific niche variation in a variety of species.

Specific microhabitats, in our case tree species, are likely to attract different subsets of prey. This, in turn, is likely to shape the prey community available to resident spiders and how that prey community changes through time. For example, we found that spiders with webs on Boxelder maple (*A. negundo*) exhibited low temporal dissimilarity in their diets, suggesting that a similar community of prey can be found on this species throughout the early summer. By contrast, we found that webs constructed on White Basswood (*T. heterophylla*) exhibited a high level of temporal dissimilarity in trophic niche, conveying that the prey community that resides on this host tree varies more dynamically through time. Such associations convey that the microhabitat choices made by individual spiders will determine the prey resources that are available to them, and how those resources change through time. Settlement decisions are likely to be particularly impactful for sit-and-wait predators or relatively sessile organisms [31,32], like web-building spiders.



Our findings add a novel level of complexity to our understanding of trophic niche variation in natural populations by uncovering how multiple individual-level traits together drive resource use. In particular, our results suggest that behavioural traits play a critical role in determining individuals' trophic niche, emphasizing the need to understand not only the extrinsic causes of intraspecific trophic diversity (i.e. ecological context) [7] but also its intrinsic, individual-level drivers. An important next step is to clarify whether and how extrinsic (e.g. competition, prey diversity) and intrinsic factors interact with each other to shape niche variation across populations and individuals. We predict that

interactions between these factors are likely to be pervasive, and there will be much for ecologists to explore together.

**Data accessibility.** Data are archived in the Dryad Digital Repository [33].

**Authors' contributions.** R.C.-P. and J.P. conceived the ideas and wrote the manuscript; J.P. collected and R.C.-P. analysed the data. Both authors approved the final version of the manuscript.

**Competing interests.** We have no competing interests.

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