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Use of locomotor performance capacities reflects the risk level associated with specific cue types in two cursorial spider species

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Abstract. Understanding when and how animals use their performance capacities can yield insights into the selection pressures driving high performance. Using two species of cursorial spiders, *Schizocosa ocreata* (Hentz 1844) and *Rabidosa rabida* (Walckenaer 1837) (Araneae: Lycosidae), we investigated the escape speeds exhibited by individuals of various body sizes in response to three aversive stimuli (jets of air, seismic cue, prodding) to determine how individuals use their performance capacity in response to different stimuli. We found that large individuals of both species exhibited their highest observed escape speeds in response to jets of air, whereas smaller individuals exhibited their fastest observed escape performances in response to prodding. We hypothesized that differences in escape behavior may reflect differences in risk associated with each cue type: fast moving jets of air may announce the arrival of an avian predator, and large individuals may be at greater risk of avian predation owing to their more conspicuous body size; whereas smaller individuals may be more susceptible to arthropod predators, which attack from the level of the spider, similar to a prod. We then performed an unreplicated mark-recapture, avian-exclosure experiment for both species, where we tracked individuals' persistence for 30 d. Consistent with our predictions, we found that larger individuals enjoyed greater persistence in our avian exclosure treatment, but their advantage was lost when avian predators were allowed to enter. Our results suggest that these spiders express their highest performances in only their most dire situations.

Keywords: Behavioral compensation, foraging mode, locomotion, Lycosidae

Variation in performance capacities has been linked with fitness components in a variety of species. For instance, higher running speed may be associated with greater survivorship (Calsbeek & Irschick 2007; Pruitt 2010), stronger bite forces may help individuals establish dominance (Lailvaux et al. 2004; Perry et al. 2004) and greater endurance may help animals obtain prospective mates (Stoltz & Andrade 2010; Stoltz et al. 2009). Although everyday tasks require that animals use their performance capacity somewhat regularly, identifying the specific selection pressures driving maximum performance can be difficult. This difficulty stems, in part, from the fact that the same actions are used across many tasks: capturing prey, avoiding predators, maintaining territories and displaying courtship (Irschick & Garland 2001). Thus, any number of context-specific selection pressures could drive the evolution of animals' maximum performance. One way to gain insights into the selective pressures driving maximum performance is to understand when and how animals use their performance capacity. The hypothesis underlying this notion is that individuals are expected to approximate maximum performance capacity in situations most important for their survival or reproductive success and express sub-maximal performance in other, less dire situations (Irschick 2000a,b; Irschick & Garland 2001; Husak & Fox 2006; Pruitt & Husak 2010). Here we define individuals' "maximum" or "highest" performance as the peak performance individuals exhibited across all observed contexts (after Husak & Fox 2006), although we acknowledge that even these values may fall short of absolute potential.

A small number of studies have shown that individuals tend to express their highest performance in the ecological contexts most pertinent to their success. For example, within a population of collared lizards (*Crotaphytus collaris*), females exhibit their highest observed running speeds when escaping predators. Males, however, reserve their highest speeds for territorial encounters. Neither sex uses high speeds when attempting to capture prey (Husak & Fox 2006). Males and females experience differing selective pressures in this system, as evidenced by differences in how the sexes use their performance capacities. Males are territorial and risk suffering a potentially high cost to their fitness if they do not rapidly respond to intruding rivals (Husak et al. 2006; Husak et al. 2008), whereas females are non-territorial and have little selective pressure to respond intensely to rival females. Thus, strength of selection on locomotor importance may differ considerably across demographic groups within a single population.

Similarly, in the funnel-web spider *Agelenopsis aperta* Gertsch 1934, individuals show population-level divergence in how they use their maximum running speeds (Pruitt & Husak 2010). This species occupies a habitat mosaic of arid and riparian zones; arid zones are characterized by few foraging territories, low prey availability, and few predators, whereas riparian habitats are lush environments with many suitable foraging territories, high prey availability and many predators (Riechert & Hedrick 1990; Riechert 1993; Riechert et al. 2001). Consistent with our understanding of this species' ecology, offspring from parents collected in arid habitats exhibited their highest observed running speeds during territorial encounters, but responded slowly to simulated predator threats. In contrast, offspring from parents collected from riparian sites expressed their highest observed speeds in response to simulated predator threats, but were slower to attack rivals (Pruitt & Husak 2010). Here again, data suggest animals scale the use of their performance capacities to the significance of the task or challenge at hand.

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A primary insight gleaned from the studies detailed above is that different populations or demographic groups within them experience divergent selection pressures, and these pressures are echoed in how animals use their performance capacities. However, the possibility that individuals may differ in their responsiveness to different cue types within a context (e.g., predator avoidance) has been largely overlooked. Here we explore this topic using two species of temperate wolf spider, *Schizocosa ocreata* (Hentz 1844) and *Rabidosa rabida* (Walckenaer 1837 (Araneae, Lycosidae). Specifically, we test whether individual variation in body size is associated with how individuals respond to different cue types. For example, large individuals might exhibit slow running speeds in response to cues resembling arthropod predators, but high-speed responses towards cues resembling avian/vertebrate predators. We then test whether performance matches risk of predation in the field using an unreplicated mark-recapture, predator exclusion experiment. Documenting associations between performance use and body size has important general implications for understanding how animals of different body states (e.g., age, viability, reproductive status) use their performance capacities.

METHODS

Collection and laboratory maintenance.—Wolf spiders (family Lycosidae) are cursorial, non-web building spiders that traverse leaf litter and low-lying vegetation in search of prey. We collected spiders for use in our aversive stimuli trials in March–April (*Schizocosa*) and July–August (*Rabidosa*) of 2010. *Schizocosa ocreata* (n = 46) were collected amid fallen leaf litter from a deciduous forest habitat (35°47′56″N, 84°14′01″W), and *Rabidosa rabida* (n = 28) were collected among mixed herbs and grasses from an early successional meadow habitat (36°00′49″N, 84°02′32″W) in East Tennessee. We selected our two test species because they occur commonly at our test sites and because of their divergent ecologies: they occupy different habitats, exhibit divergent phenologies, and differ distinctly in body size (see Results section). Spiders were collected at night using a spotlight. They were spotted, chased into pill vials, and transported to a laboratory at the University of Tennessee, Knoxville. They were housed individually in 490-ml opaque deli cups, provided a maintenance diet of two three-week old crickets once weekly, and maintained under ambient lighting conditions. A moist paper towel was provided as a water source. Upon reaching maturity (≈1–3 weeks), individuals were selected for use in our aversive stimuli trials, and all aversive stimuli trials were completed within two weeks of individuals' final molts. Only mature females were used in our aversive stimuli trials and mark-recapture experiments.

Individuals' body measurements were collected one day after their first routine feeding as mature individuals. Each individual was weighed to the nearest 0. 1 mg, (Mettler-Toledo XP205) and its cephalothorax length and abdomen length and width were measured to the nearest millimeter using Leica digital imaging software and a stereomicroscope (Leica M80).

Aversive stimuli trials occurred three days after a routine feeding, and 24 h elapsed between trials. We used a standardized feeding-level for our trials because previous data indicate recent meal size (via the resulting increase in body mass) can negatively impact spiders' escape performance (Pruitt 2010), and we limit our investigation to recently matured females. Sex and reproductive status have significant impacts on spiders' escape performance (Pruitt and Troupe 2010). To avoid potential confounding of trial order, the sequence of the trials was alternated among individuals. Thus, each individual was tested three times, once with each stimulus.

Aversive stimuli.—Aversive stimuli trials were run at 2000–2200 at low light conditions (30–50 lux) to mimic the nocturnal/crepuscular nature of most wolf spiders (*Schizocosa*: Cady 1983; general wolf spider ecology: Foelix 1996; but see Uetz et al. 1999). Spiders were placed on a 30-cm track in a clear plastic collection vial and allowed 30 sec to acclimate before the vial was lifted. Spiders were then given another 30 sec of acclimation before an aversive stimulus was applied. Tracks were lined with graphing paper with 0.5 cm demarcations. Tracks were 6 cm wide and the walls extended 8 cm up on all sides. We video-recorded spiders' escape responses using an infrared Bullet Security Camera (Sony CSP-LR560IR) and noted individuals' flight speed (cm/s) over 15 cm of track. Data from trials where spiders paused or turned were removed from our analyses, as is standard in the animal performance literature. In such instances (n = 6), spiders were given 15 min to recover before the trial was repeated.

Our three aversive stimuli were a prod, a puff of air, and a seismic cue. For our prod test, we touched the rear end of the spider with a thin (3 mm wide) paintbrush. This prod was designed to mimic the tactic cue of an approaching predatory spider or insect. For our 'puff' test, we used a camera lens cleaning bulb to apply rapid jets of air on the dorsal, posterior portion of the spiders from 5 cm distance: two fast, consecutive puffs were applied. Puffs of air have been used to simulate the approach of an avian predator in a number of investigations on spiders (Riechert & Hedrick 1990; Riechert 1993; Riechert et al. 2001; Pruitt et al. 2008; Jones et al. 2011a,b). This cue is relevant because most spiders lack acute vision and instead detect the approach of avian predators using minute vibratory-sensing setae, the trichobothria (Foelix 1996). We applied a seismic cue by dropping a 1.2 kg biology textbook from 1m off the ground, 30 cm away from the spider. This seismic cue was modeled to resemble the distant approach of a large vertebrate (e.g., a deer, coyote or a human collecting spiders). After we recorded their reaction, spiders were returned to their individual cups.

Selection on body size.—To assess whether individuals of different body sizes were more or less susceptible to avian predation, we estimated selection on body size in field exclosures from March–July 2008 (March for *S. ocreata* and July for *R. rabida*). We established four 3 m × 3 m exclosures: two to assess selection on body size for *R. rabida* at a meadow site (Riechert Farm: 36°00′49″N, 84°02′32″W) and two to assess selection on *S. ocreata* at a deciduous forest site (House Mountain: 35°47′56″N, 84°14′01″W). Thus, our predator present/absent treatment was unreplicated within each species, but two parallel studies were conducted with two different species.

Exclosures were lined with aluminum flashing around the perimeter; flashing extended 40 cm above the ground and 15 cm below. To prevent immigration and emigration across the aluminum border, herbaceous plants were trimmed back

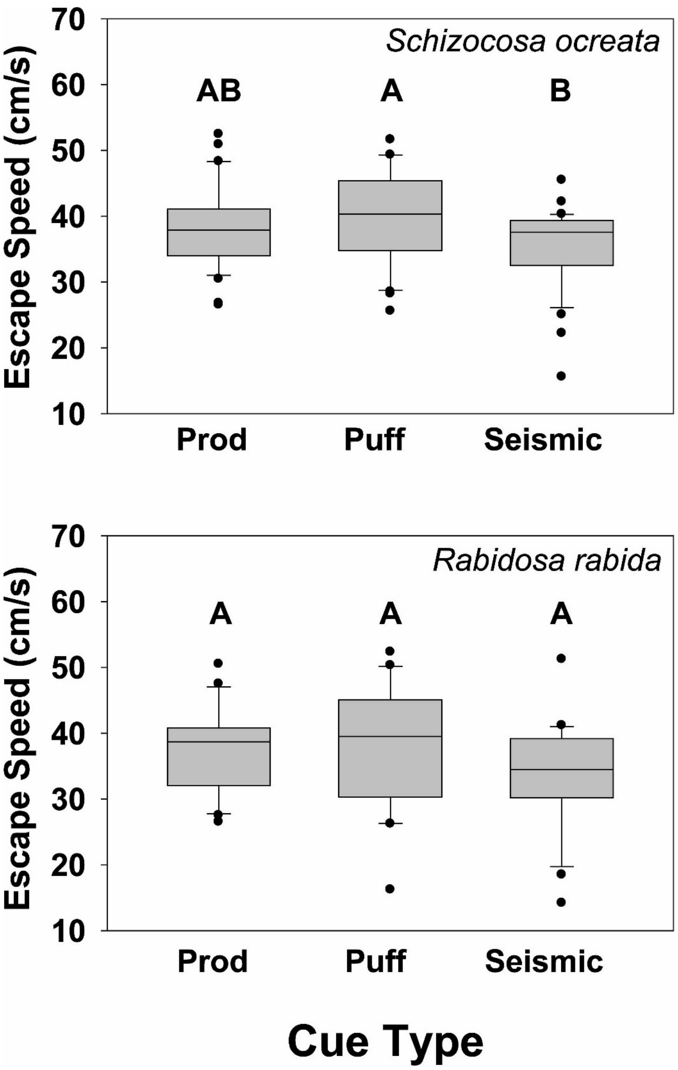

Figure 1.—Box plot depicting the raw (cm/s) escape speeds exhibited by both test species (*Schizocosa ocreata*, *Rabidosa rabida*) in response to our three aversive stimuli. Vertical shaded bars represent interquartile range and vertical lines represent the 90th and 10th percentiles. Within BT compositions, bars not sharing letter flagging are significantly different at $\alpha = 0.05$ using post-hoc Tukey tests.

Table 1.—Summary of our general linear models predicting relative speed in response to three aversive stimuli. Relative speed was obtained by dividing the flight speed (cm/s) obtained by an individual in response to each stimulus by the mean flight speed exhibited across all three stimuli; *df* indicates degrees of freedom.

Schizocosa ocreata			
Source	*df*	*F*	*P*
Combined Model, $R^2 = 0.36$	5	3.866	0.03
Intercept	1	58.791	<0.001
Body Size	1	0.45	0.87
Stimulus type	2	10.227	<0.001
Body Size*Stimulus Type	2	7.2	<0.001
Error *df*	91		

Rabidosa rabida			
Source	*df*	*F*	*P*
Combined Model, $R^2 = 0.34$	5	7.289	<0.001
Intercept	1	40.826	<0.001
Body Size	1	0.03	0.99
Stimulus type	2	13.006	<0.001
Body Size*Stimulus Type	2	13.455	<0.001
Error *df*	57		

on either side of the flashing using pruning shears, and both sides of the flashing were topped with a 7-cm-wide strip of Tanglefoot tree pest barrier. For each pair of exclosures, one was left with an open top (avian predators present) and the second was topped with a grid of two perpendicular series of monofilament fishing lines placed every 4 cm in either direction. Fishing lines were anchored into a wooden frame, which we fastened atop the aluminum flashing, thus generating a monofilament 'table top' that effectively excluded birds (Hubbs & Boonstra 1997; Krebs et al. 1995). Although we did not directly observe avian predation in this study, birds are known to be important predators for at least one of our test species (*Schizocosa ocreata*: Lohrey 2007; Lohrey et al. 2009) and are thought to be major predators of spiders in general (Foelix 1996; reviewed in Riechert & Hedrick 1990; Gunnarsson 2007). Although our exclosure design likely excluded other vertebrate predators (e.g., bats, raccoons) and not just birds, we will refer to our exclosures as 'avian exclosures' throughout this paper.

Before initiating an experiment, we systematically sampled each exclosure by sifting through leaf litter and removing all *S. ocreata* and *R. rabida* therein. Non-focal arthropods (spiders or otherwise) were replaced within our exclosures before the start of our marked-recapture experiment. We removed 41 and 26 *S. ocreata* from our exclosures at House Mountain, and 12 and 5 *R. rabida* at the Riechert Farm. A pool of mature female conspecifics was collected from adjacent habitats, measured using digital calipers, individually marked, and placed within our exclosures. Individuals' assignment to treatment (avian predators present/absent) was determined randomly using statistical software. We placed 35 *S. ocreata* in each plot at House Mountain and 20 *R. rabida* in each plot at the Riechert Farm. Spider densities were a compromise between 1) our desire to replicate natural densities of both test species at our test sites, and 2), our desire to maximize the statistical power of our experiment. Each test spider was assigned a unique letter/number combination, and a corresponding tag was adhered to its prosoma using non-toxic liquid adhesive (Testors). Care was taken to use a minimal amount of adhesive, since excessive adhesive may reduce spider mobility. Exclosures were left undisturbed for 30 d.

After the 30-d selection period, we resampled each plot and collected all individuals therein. Plots were sampled for four days by sifting through leaf litter and turning over each individual leaf. Individuals that were not recovered during our four-day search period were assumed to be dead. Importantly, all of the spiders recovered from within our plots were marked, thus indicating a low probability of emigration or immigration across our exclosure barriers.

Statistical analyses.—To test for differences in escape speed (cm/s) in response to our three aversive stimuli, we used one-way ANOVAs with post-hoc Tukey tests. To assess the relationship between body size and performance, we used

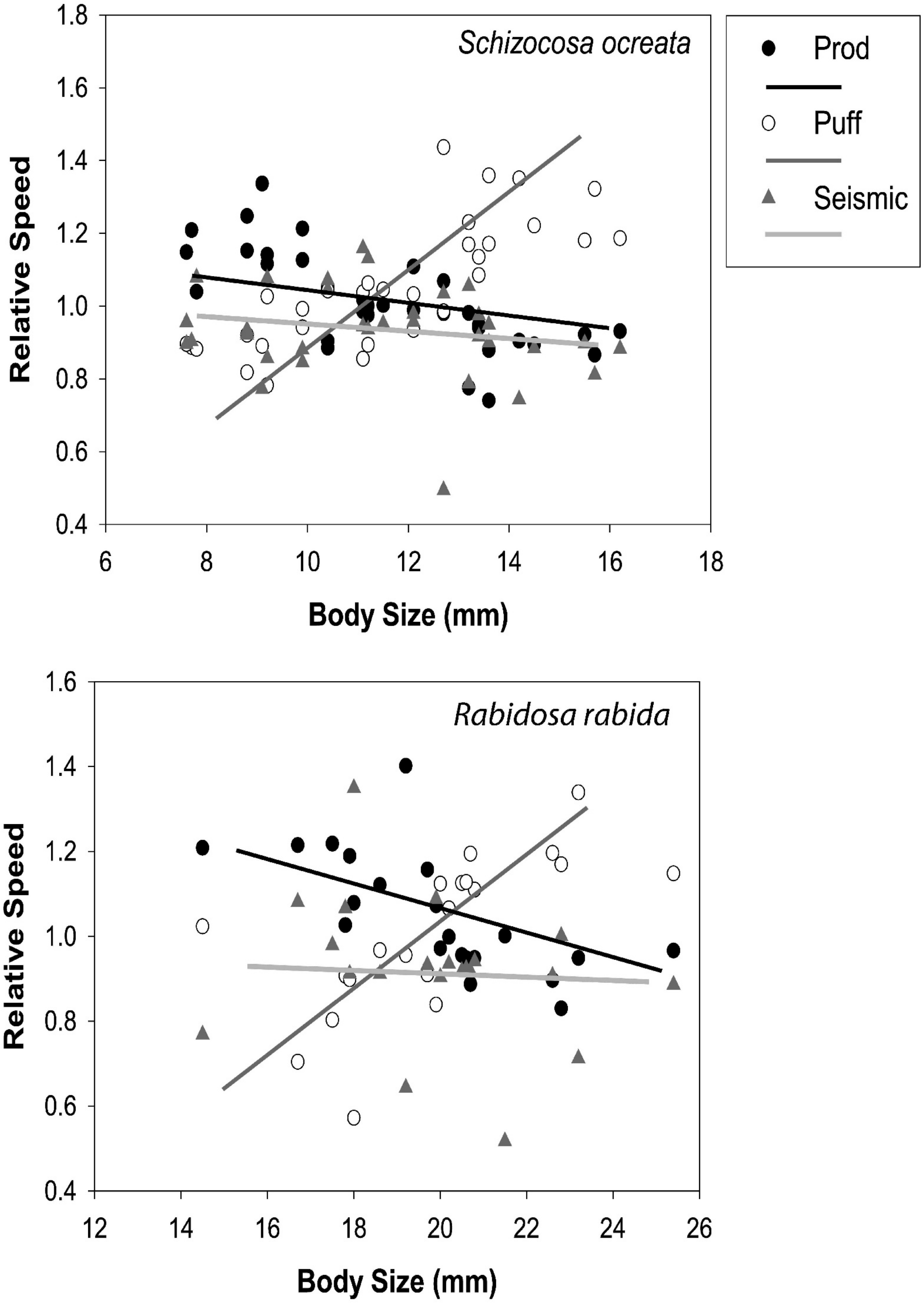

Figure 2.—Relationship between individuals' body size (abdomen + cephalothorax length) and relative speed exhibited (speed displayed with a given stimulus/average speed displayed across stimuli) in response to various stimuli for *Schizocosa ocreata* (top) and *Rabidosa rabida* (bottom).

repeated measure ANOVAs and analyzed each species independently. We included stimulus type, body size (cephalothorax length + abdomen length) and their interaction term in our models, and used 'relative speed' as our response variable. Relative speed was calculated by dividing the flight speed (cm/s) obtained by an individual in response to each stimulus by the mean flight speed exhibited across all three stimuli.

To assess the effects of body size on survival in *S. ocreata* and *R. rabida*, we calculated selection gradients for each species independently by transforming trait values to mean zero and unit variance, and survival scores (1,0) were transformed into relative fitness (individuals' fitness/average fitness of their cohort). Selection gradients (i.e., the change in expected fitness per standard deviation of trait value) were calculated for each exclosure, independently using multiple

Table 2.—Summary of our combined models predicting spiders' persistence in our avian exclosure, mark-recapture experiments. The effects of body size on persistence differed significantly among treatments (predators present vs. absent).

Schizocosa ocreata			
Source	*df*	*F*	*P*
Combined Model	3	10.35	0.002
Intercept	1	0.11	0.74
Treatment	1	5.09	0.02
Body Size	1	0.19	0.66
Treatment*Body Size	1	6.55	0.01

Rabidosa rabida			
Source	*df*	*F*	*P*
Combined Model	3	11.51	<0.001
Intercept	1	0.51	0.64
Treatment	1	5.85	0.03
Body Size	1	0.43	0.45
Treatment*Body Size	1	6.36	0.01

linear regression (Lande & Arnold 1983; Calsbeek & Irschick 2007). To test whether selection gradients differed among exclosures (avian predators present vs. absent treatment) we used a combined multiple logistic regression model with treatment, body size, and the interaction term treatment × body size as predictor variables. For all analyses we used logistic regression for our significance tests (after Janzen & Stern 1998) and multiple linear regression to estimate selection gradients (after Calsbeek & Irschick 2007). We did not include non-linear selection terms in our models owing to limited degrees of freedom, but visual inspection of the data indicated no non-linearity.

RESULTS

We detected significant differences in the escape speeds exhibited in response to our three aversive stimuli for *S. ocreata* ($F_{2,93}$ = 4.21, *P* = 0.02), but not *R. rabida* ($F_{2,62}$ = 1.48, *P* = 0.16). In *S. ocreata*, individuals exhibited higher escape speeds in response to rapid jets of air (mean speed = 39.95 cm/s, SE = 1.31) than to seismic cues (mean speed = 35.23 cm/s, SE = 1.11), and their responses to prodding (mean speed = 38.36 cm/s, SE = 1.12) were intermediate and indistinguishable from responses to the other stimuli (Fig. 1).

Our combined models predicting individuals' relative escape speeds were significant for both *S. ocreata* ($F_{5,93}$ = 3.86, *P* = 0.03) and *R. rabida* ($F_{5,62}$ = 7.29, *P* <0.001). We detected significant effects of stimulus type and the interaction term stimulus type × body size for both species (Table 1). From examination of the interaction plot between body size and stimulus type (Fig. 2), we found a strong positive relationship between body size and individuals' relative escape speed in response to puffs of air. In contrast, we observed negative trends in the relationship between relative escape performance and body size with both the prod and seismic cues (Fig. 2). That is, larger individuals responded more slowly to prod and seismic cues, but responded faster after experiencing a puff of air.

Our combined models predicting persistence in our mark-recapture avian exclosure experiment were significant for both species: *S. ocreata* ($F_{3,67}$ = 10.35, *P* = 0.002) and *R. rabida* ($F_{3,37}$ = 11.51, *P* <0.001). We detected a significant effect of treatment (avian predators present vs. absent) and a significant interaction between individuals' body size and treatment for both species (summarized in Table 2). From examination of body size distribution of the "surviving" versus "dead" spiders in each treatment (Fig. 3), we found that surviving individuals tended to be larger in our predator exclusion treatments. However, this trend disappeared (*S. ocreata*) or was reversed (*R. rabida*) in our predator inclusion treatment.

DISCUSSION

Documenting how animals employ their performance capacities can help to elucidate the selective pressures driving performance. Specifically, data from a wide range of taxa suggest that animals express their highest speeds in the contexts/situations most vital in determining their direct fitness and survival (Domenici & Blake 1997; Husak & Fox 2006; Husak et al. 2008; Irschick & Garland 2001; Pruitt & Husak 2010). Our data here demonstrate that even within a single context (anti-predator behavior) animals may differ in their responsiveness. Specifically, we demonstrate that, in *R. rabida* and *S. ocreata*, larger individuals tend to exhibit higher running speeds in response to puffs of air, whereas smaller individuals of both species tended to exhibit greater burst speeds in response to mechanical stimuli (i.e., prodding). Concordantly, we found that in the absence of avian predators, larger individuals enjoy higher survivorship in the field. In contrast, when avian predators were not excluded, the advantage of large body size was lost or reversed. Our data add an additional point of note to standard investigations on animal performance and indicate experiments that use only a single cue type may overlook important condition- or trait-dependent variation in performance utilization.

Individuals of different body sizes tended to express their highest observed performances in response to different aversive stimuli, and we infer that this finding reflects differences in the selection pressures they experience. In both species, larger spiders were more likely to express their highest observed speeds in response to puffs of air. Given that birds are primarily visual predators, it is plausible that larger spiders are more likely to be spotted and attacked owing to greater conspicuousness, and thus large individuals express higher escape speeds in response to sudden jets of air. Certainly, behavioral data in at least one of our test species (*S. ocreata*) have demonstrated that individuals exhibit anti-predator behavior in response to bird songs (Lohrey et al. 2009), and a number of bird species have been observed feeding directly on *S. ocreata* (Lohrey 2007); thus, we argue that birds are likely some of the more important vertebrate predators of these spiders. In contrast, smaller spiders are perhaps less conspicuous to avian predators, but are no doubt more susceptible to attacks by other spiders and predaceous insects, which attack cursorially (i.e., similar to a prod). Hence, we argue that the greater responsiveness of smaller individuals to the prod stimulus may reflect a greater threat of arthropod predation.

Given that larger individuals tended to exhibit higher speeds in response to puffs of air, we predicted that larger individuals would suffer greater mortality as a result of avian predation.

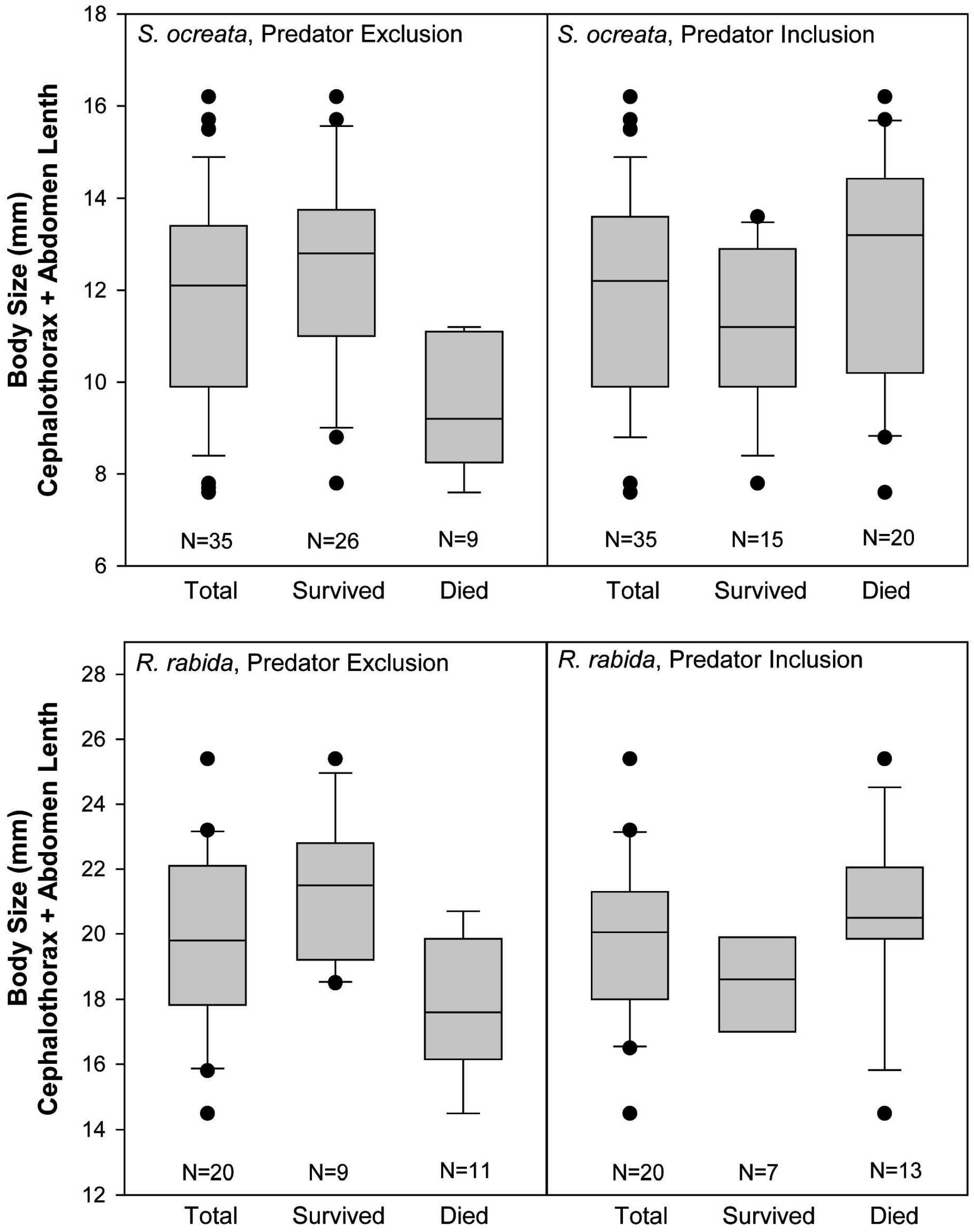

Figure 3.—Relationship between individuals' body length and survivorship in an avian predator exclusion experiment for the wolf spiders *Schizocosa ocreata* (top) and *Rabidosa rabida* (bottom). Larger body sizes were associated with higher survivorship in the absence of large vertebrate predators, and this advantage was lost with large vertebrate predators were present. Vertical shaded bars represent interquartile range and vertical lines represent the 90th and 10th percentiles.

Concordantly, we found that larger individuals of both species exhibited greater persistence in our avian exclusion treatments. However, this advantage was diminished or reversed in our avian inclusion treatment (Fig. 3). Thus, our results are consistent with the interpretation that avian predation is a major selective force on large spiders, and is one plausible driver of escape speed in these animals. These findings are at odds with the results of Wise and Chen (1999), whose data suggested that avian predators were not influential in *Schizocosa* population dynamics. In contrast, the data herein and those of Lohrey and collaborators (Lohrey 2007; Lohrey et al. 2009) do document significant effects/responses of *Schizicosa* to the threat of avian predation. Our parallel prediction that smaller individuals are more likely to fall victim to predation by other arthropods remains untested. However, it seems plausible that heterospecific arthropods and/or cannibalism by larger conspecifics could impose selection on small individuals. Consistent with this hypothesis, smaller individuals in our predator exclusion treatment were generally less likely to survive our 30-day selection period, perhaps as a result of size-dependent cannibalism or predation by other arthropods. Data from congeners of *S. ocreata* provide some evidence that invertebrate predators impose significant effects on individual survival (e.g., Punzo 1997).

However, we caution that all of these results must be interpreted as tentative, since our predator exclosure treatments were not replicated within each species.

Finally, our results bring to light an important methodological concern for the animal performance literature. Specifically, the vast majority of studies on animal performance assess individuals' behavior in only a single ecological context (typically an escape response) and use only a single aversive stimulus such as chasing the animal with a broom/brush (e.g., Prenter et al. 2012; Prenter et al. 2010; Pruitt 2010). A potential criticism of these studies is that they could limit our understanding of animal performance by assessing performance under a narrow range of conditions and thus lead to erroneous conclusions.

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