Short Note

Individual differences in boldness positively correlate with heart rate in orb-weaving spiders of genus *Larinioides*

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Consistent individual differences in behavior that occur across time, situation, or ecological context have received a surge of attention in recent years (Sih et al., 2004, Sih et al., 2012). These “behavioral syndromes” are of ecological significance because of their potential to generate performance trade-offs across contexts (Johnson and Sih, 2005), and because they may provide a general mechanisms for maintaining trait variation within populations (Riechert and Hedrick, 1993). In addition, these consistent individual differences can have enormous influences on higher-order ecological phenomena, ranging from individual fitness (Biro et al., 2004, Biro et al., 2006), to species interactions (Pruitt and Ferrari, 2011, McGhee et al., in press), to invasion success (Fogarty et al., 2011), or extinction risk (Pruitt, 2013). Thus, research aimed at exploring the underlying morphological and/or physiological correlates of these differences is of general significant for ecology and evolutionary biology alike. Mechanisms hypothesized to underlie consistent individual differences in behavior include, correlated selection, physical linkage, pleiotropy, neurocirculatory hormones, body state, and individual differences in metabolic rate (McElreath and Strimling, 2006, Bell and Sih, 2007, Biro and Stamps, 2010).

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One mechanism that may underlie consistent individual differences in behavior is individuals’ metabolic rate (Biro and Stamps, 2010). For instance, a more active metabolic rate may require behavioral traits that can keep up with and fuel higher energy expenditures. This means that behaviors linked to exploration, aggressiveness, and boldness should correlate positively with energy metabolism. This relationship of cause and effect, where higher metabolic rates drive the need for more aggressive/bold behavior is termed the Performance Model. In contrast, the Allocation Model argues that behaviors linked to exploration, aggressiveness, and boldness should correlate negatively with metabolic rate. In this model, an organism allocates much of its energy to maintaining a high resting metabolic rate and is thus limited in expending its energy to behaviors associated with activity, and vice versa. This is because any energy allocated to one need (metabolic rate or personality) cannot be spent on the other. Thus, these models predict opposing correlations between individuals’ metabolic rate and their aggressiveness, boldness, exploration, and/or activity level. A third less-frequently considered alternative is that activity-levels and/or aggressiveness are the driver of metabolic rate, since individuals with higher activity levels will tend to have higher metabolic rates, since they spend more of their time being active. This alternative again predicts a positive association between individuals’ metabolic rate and their aggressiveness, boldness, and/or activity level. One of the most common methods of estimating individuals metabolic rate is through the measurement of heart and/or respiration rate (McGhee et al., in press), which is the approach we take in this study.

Here we consider whether there is an association between boldness and heart rate in the spiders *Larinioides cornutus* and *L. patagiatus* (Araneae, Araneidae). Spiders have long served as a model for behavioral syndromes research. Behavioral syndromes have been noted in more than twenty species in ten families (Pruitt and Riechert, 2012, Pruitt et al., 2013), and generally involve an association between high exploratory behavior, activity level, aggressiveness, boldness, and low sociability (Riechert and Hedrick, 1993, Johnson and Sih, 2007, Pruitt et al., 2008, Kralj-Fiser and Schneider, 2012). Here we test whether spiders, like various species of vertebrate, exhibit a significant association between their behavioral tendencies (i.e., boldness) and their heart rate under standardized conditions. Specifically, we ask the following questions: (I) Do *Larinioides* exhibit consistent individual differences in boldness? (II) If yes, are consistent individual differences associated with body size or body condition? (III) Is boldness associate with individuals’ heart rate under standardized laboratory conditions?

1 Materals and Methods

1.1 Collection & laboratory maintenance

Adult *Larinioides cornutus* (*n* = 29) and *Larinioides patagiatus* (*n* = 9) were collected from around housing structures on the western side of Gibraltar Island in the Bass Island region of Lake Erie. We conducted our assays in an Ohio State University teaching laboratory space which lacked air conditioning between 1200–1600 hr each day (27.7–32°C). Our experiments took place during May 2013, when both adult males and females were present, and our assays occurred one day after a mayfly emergence. Thus, spiders received an *ad libitum* meal of mayflies immediately before collection. After 24 hours in captivity, the mass of each spider was measured on a digital balance to the nearest hundredth of a gram and their prosoma width was measured using digital calipers to the
nearest tenth of a millimeter. Spiders were housed individually in strawberry containers (15 cm × 15 cm × 13 cm) between behavioral assays.

1.2 Boldness assay: latency to resume movement

To assess spiders’ boldness towards predator cues, we use a “puff test” following the protocol of Riechert and Hedrick (1993). Similar protocols have been utilized in numerous studies on web-building spiders (Kralj-Fiser and Schneider, 2012; Grinsted et al., 2013; Pruitt et al., 2013). Boldness assays occurred 6 h after weighing and measuring spiders and again 24 h after that. Trials are initiated by lifting off the lid to spiders’ containers and moving them to a novel open field environment. The open field environment was a 50 cm × 50 cm square plastic enclosure lined with computer paper, which was replaced between trials. Spiders were permitted 60 s acclimation time before the application of an aversive stimulus. We then “puffed” the spider’s anterior, dorsal side with two rapid jets of air using an infant ear-cleaning bulb. Spiders universally responded by huddling, with their legs drawn toward their cephalothorax. Boldness was estimated as the time taken for spiders to resume movement following this cue. Spiders with shorter latencies to resume movement are deemed more “bold”, whereas spiders with longer latencies are termed more “shy”. Trials ended when the spider initiated movements or after 10 minutes, whichever happened first. To obtain more intuitive values for “boldness”, individuals’ latencies to resume movement in seconds were subtracted from the maximum value of 600 seconds. Thus, a greater latency to resume movement corresponds with a smaller boldness value.

1.3 Heart rate

Spiders’ heart rates were measured 2 hours after spiders’ second boldness measure. Trials were initiated by removing individuals from their home containers and transferring them to a clear, plastic, circular enclosure (radius=4 cm), with their dorsal side up. This container was then placed beneath a dissecting microscope (Leica M80) and the spiders were given 60 s to acclimate. We then counted the number of heart beats that the spiders exhibited over a 15 second interval, waited 60 s longer, and measured their heart rate for another 15 seconds. In spiders, the heart runs along the dorsal anterior portion of the abdomen back posteriorly. Individual heart beats were evidenced by the acute expansion and retraction of the pigmented cells on the dorsal anterior portion of the abdomen (Carrel and Heathcote, 1976, Bromhall, 1987). The number of beats over 15 seconds was used to calculate the number of beats per minute, and the first and second measures (separated by 60 s) were compared in order to confirm that individuals had reached a relatively stable heart rate during our procedure. We assume that our protocols were stressful to the animal, and thus, we interpret our heart rate measure as having occurred during an acutely stressful event.

1.4 Statistical methods

To assess repeatability in heart rate and individual boldness we used nested ANOVAs to partition variances into the proportion of variation explained by within- versus between individual differences. Repeatability is defined herein as the proportion of total variation explained by between individual differences (Boake, 1989; Falconer and McKay, 1996). We tested the repeatabilities for each species independently. To test for an association between boldness and heart rate we performed species-wise linear mixed effect models, where individual intercept and slope were included and only the average metabolic rate was used to explain boldness.
2 Results

We detected significant repeatabilities of both boldness and heart rate in *L. cornutus* but not *L. patagiatus*. *L. cornutus* boldness ($F_{28,57}=2.64$, $r=0.77$, $P=0.006$) and heart rate ($F_{28,57}=5.23$, $r=0.84$, $P<0.0001$), *L. patagiatus* boldness ($F_{8,17}=1.31$, $r=0.53$, $P=0.35$) and heart rate ($F_{8,17}=2.70$, $r=0.71$, $P=0.08$). And, we detected no significant differences in individuals’ heart rates in our first versus second measurement ($T=0.08$, $df=56$, $P=0.77$). The two species also differed in their average boldness, where *L. cornutus* was 200% – 400% bolder than *L. patagiatus* ($F_{1,66.11}=1.31$, $r^2=0.62$, $P=0.009$).

Our species-wise linear mixed effect models detected a strong positive correlation between boldness and heart rate in *L. cornutus* ($F_{1,27}=14.73$, $r^2=0.56$, $P<0.001$, Figure 1). However, we failed to detect an association between boldness and heart rate in *L. patagiatus* ($F_{1,7}=1.31$, $r^2=0.20$, $P=0.28$, Fig. 1), perhaps owing to low sample sizes.

3 Discussion

In this study, the heart rates of individual *L. cornutus* of differing degrees of boldness were compared by measuring their heart rates during an acute, stressful event. First, we found that our estimates of individuals’ boldness were highly repeatable in *L. cornutus*, consistent with data collected on dozens of other species of spider (Pruitt and Riechert, 2012). Second, we found that our two species differed in their average boldness. Third, we found a strong, positive association between individuals’ boldness and their heart rates for *L. cornutus*. Thus, we reason that individual differences in key metabolic functions (e.g., metabolic rate, heart rate) may underlie individual differences in boldness in these species.

Inter-individual variation in boldness was found to be repeatable in *L. cornutus*. Consistent individual differences in boldness are widespread among many species of spiders, and the repeatability estimates of *L. cornutus* ($r=0.77$) are of a similar magnitude to those obtained from other species of web-building spiders (Bell et al., 2009, Pruitt and Riechert, 2012). This is a fortuitous result for the use of *L. cornutus* as a general model spider for the studies herein, because the strength of the signature of personality in this species is typical for these animals. However, we failed to detect a significant repeatability for *L. patagiatus*, presumably due to very low sample sizes ($n=9$). Though, even for this species, our estimate of repeatability was high as compared to most study systems ($r=0.53$).

Two commonly used models for explaining the connection between behavior and metabolic rate are the *Performance Model*, which predicts a positive correlation between metabolic rate and boldness, aggressiveness, and activity-level, and the *Allocations Model*, which predicts negative correlations (Careau et al., 2008; Biro and Stamps, 2010; Reale et al., 2010). Results from this experiment reveal a positive correlation between boldness and heart rate for *L. cornutus*, which is consistent with the Performance Model. This model argues that high metabolic rates actually require than animals exhibit greater boldness, aggressiveness, and activity-level in order to procure the resources required to sustain their metabolisms. This result is intriguing, because it may provide a mechanism for maintaining variation in personality and metabolic rates within populations, because of spatiotemporal variation in resource availability. Specifically, we argue that metabolic rates may be favorable under high resource conditions, because boldness, aggressiveness, and activity-level can be amply fueled and could even be advantageous for securing resources against rivals. However, spiders’ foraging ecology is characterized by boom-and-bust, feast-or-
famine resource dynamics, where most individuals suffer extended periods of starvation between foraging bouts (Foelix, 1996; Maupin and Riechert, 2001). Under these conditions, we reason excessively high metabolic rates may limit individuals’ ability to survive these intervening periods, and instead favor individuals with lower metabolic rates. Consistent with this interpretation, studies on the spider *A. aperta* have found that aggressive individuals are less selective in terms of the prey they accept, potentially reflecting the need to fuel a higher metabolic rates for these individuals (Riechert, 1991).

The argument that some phenotypes will be favored because of their low resource needs bears thematic resemblance to classic resource competition theory (i.e., R*) (Tilman, 1982). Importantly, the success of R* Theory as a general explanation for competitive dominance in community ecology has been marred by insufficient field tests. Thus, we caution that although the ideas outlined above have intuitive appeal, future studies that orthogonally manipulate resource availability, population density, and ratios of different personality types are badly needed to address whether these models hold true. As a growing number of studies document basic associations between metabolic traits and personality (like this one), the most important, illuminating studies will be those that directly and explicitly test these models’ predictions either in laboratory mesocosms or (preferably) *in situ*. For our study, we must recognize that all of our measurements were taken immediately following an intense feeding bout. It, thus, remains unclear whether the relationship between boldness and heart rate observed here would hold under severe food limitation. Although, the idea that the relationship between basic physiological measurements and animal personality will emerge/disappear as a consequence of system’s resource regimes is itself an exciting and little-explored hypothesis.

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Fig. 1 An interaction plot depicting the relationship between heart rate and boldness for *Larinioides cornutus* (fill dots, black line) and *L. patagiatus* (open dots, grey line)