Current Zoology, 2017, 63(6), 633–638
doi: 10.1093/cz/zow116
Advance Access Publication Date: 16 January 2017
Article

Article

Smaller and bolder prey snails have higher survival in staged encounters with the sea star *Pisaster giganteus*

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Received on 26 October 2016; accepted on 7 December 2016

Abstract

Temporally consistent individual differences in behavior, also known as animal personality, can have large impacts on individual fitness. Here, we explore the degree to which individual differences in anti-predator response (or boldness) influence survival rates in groups of snails *Chlorostoma funebralis* when they encounter a predatory sea star *Pisaster giganteus*. The snail *C. funebralis* shows consistent individual variation in predator response where some fearful snails actively flee bodies of water occupied by predators whereas bolder snails consistently do not. We show here that bold snails are significantly more likely to survive encounters with a predatory sea star and, somewhat counterintuitively, fearful snails actually suffer higher mortality rates. We also found that smaller snails and those occurring at higher experimental densities experienced higher per capita survival rates. Positive effects of prey boldness on survival are not uncommonly reported in the animal personality literature; however, such results are inconsistent with classic animal personality theory borrowed from the optimal foraging literature. The findings herein add to the growing body of evidence that consistent individual differences in behavior can impact predator–prey interactions and that boldness is potentially under positive predator-driven selection in some systems.

Key words: behavioral syndrome, behavioral type, predation risk, personality, survival selection, temperament.

Over the past 12 years behavioral ecology has seen an increasingly large number of papers devoted to the topic of animal personality (Dall et al. 2004; Sih et al. 2004). Animal personality is defined as temporally consistent individual differences in behavior. For example, some individual animals may be bolder, more aggressive or more active than their shy, docile, or inactive counterparts (Carere and van Oers 2004; Johnson and Sih 2005). Thousands of papers have now documented such behavioral differences in a large number of animal species as well as several non-animals (e.g. microbes) (Sih et al. 2012; Wolf and Weissing 2012; Jandt et al. 2014). From a behavioral perspective, such individual differences are intriguing because they could imply an upper limit to the amount of behavioral plasticity that an individual can exhibit (Johnson and Sih 2005; Duckworth 2006) and because they provide an opportunity to explore the proximate mechanisms determining such differences (Biro and Stamps 2010; Bengston and Jandt 2014). From an ecological and evolutionary standpoint, such individual differences are intriguing, in part, because they are often associated with individual fitness (Smith and Blumstein 2008).

The fitness impacts of animal personality are perhaps most thoroughly studied in the context of predator–prey interactions. Many dozens of studies have shown that predator personality types can shape the foraging strategies that they deploy (Hedrick and Riechert 1989), the kinds of prey that they intercept and consume (Riechert 1991; Royaute and Pruitt 2015; Nakayama and Rapp 2016), and the degree of interaction between competing predators (Keiser and Pruitt 2013). For prey, personality can dictate the kind of anti-predator strategy deployed by individuals (Riechert and Hedrick 1990; Pruitt and Troupe 2010), the longevity or intensity of their response (Bell and Sih 2007; Johnson and Sih 2007), and an individual's probably of succumbing to predation (Reale and Festa-Bianchet 2003; Smith and Blumstein 2010). Despite considerable attention devoted to this topic, however, we maintain only a weak understanding of why associations between personality and survival differ markedly across systems. For instance, prey activity level or boldness are negatively associated with survival in some systems (Riechert and Hedrick 1990; Storfer and Sih 1998) but positively associated with survival in others (Reale and Festa-Bianchet 2003; Magnhagen and Staffan 2005; Blake and Gabor 2014). The potential explanations for such differences among systems are numerous: investigations have been conducted using predators with contrasting sensory systems and foraging modes (Belgrad and Griffen 2016), on prey species with wildly different ecologies (Riechert and Hedrick 1990; Biro et al. 2004), and in the laboratory and in the field (Biro et al. 2004; Pruitt et al. 2012). Determining the relative contributions of these factors represents a major challenge for the field. There is therefore a need for more studies to examine personality–performance associations in contrasting systems, because only with more information can the field begin to identify general patterns that hold across test systems.

Here, we examine the degree to which snail anti-predator behavior impacts survival with a predatory sea star *Pisaster giganteus*. Black turban snails *Chlorostoma funebralis* are long-lived invertebrate herbivores that inhabit mid and lower intertidal rocky shore habitats throughout California (Morris et al. 1980). In previous work, we demonstrated that individual *C. funebralis* exhibit temporally consistent individual differences in their anti-predator behavior (Pruitt et al. 2012). Some individuals respond to predators by climbing uphill and out of the water in an effort to avoid the predator (Feder 1963; Markowitz 1980; Doering and Phillips 1983), whereas other individual snails are consistently unresponsive (Pruitt et al. 2012). This anti-predator behavior is similar to that observed in other snails (Yee and Murray 2004). Here, we test whether these individual differences in anti-predator response are associated with snail survival in staged laboratory interactions with the predator *P. giganteus*. In particular we test the hypothesis that less evasive snails will be more likely to succumb to predation. We also evaluate the degree to which snail body size contributes to survival in staged encounters. In this case, because sea stars are primarily chemosensory and tactile predators (Morris et al. 1980; Fawcett 1984), we reason that larger snails will be susceptible to predation.

Materials and Methods

Collection and laboratory maintenance

Chlorostoma funebralis ($N = 703$) were collected opportunistically by hand from the rocky intertidal region of Rincon Beach (34° 23.000 N; 119° 50.503 W) from May to August 2016. Three *Pisaster giganteus* were collected by hand on scuba from the Goleta Sewer Pipe (34° 24.162 N; 119° 49.532 W) from May to June 2016. Two additional *P. giganteus* were borrowed from the UCSB Marine Teaching Laboratory for use in this experiment, bringing the total number of *P. giganteus* used to 5.

All *C. funebralis* individuals were kept in 1.3 m × 0.75 m × 0.13 m flow-through water tables until they were sorted into cohorts of 50 snails. These tables are lined with naturally occurring microalgae and diatoms that provide natural forage for the snails. After being sorted, individual cohorts were housed in 18.93 L containers, within 1.3 m × 0.75 m × 0.30 m water tables that were free of other snails and predator cues. The cohort housing containers each had 24 holes of 7.5 mm diameter to allow water to flow through the top of the enclosure and cascade out the sides. *Pisaster giganteus* individuals were housed in an identical manner in a separate series of tables until predation trials began. Throughout the experiment, all animals were exposed to open air conditions and natural day–night cycles. All seawater used in this experiment was filtered and pumped directly in from the ocean, so that the snails and sea stars were exposed to the normal variation in water temperature (9–11°C) and salinity. This experiment was carried at the UCSB Marine Laboratory from June to September 2016.

Assessment of snail behavioral types

To determine the behavioral types of *C. funebralis* individuals, snails were first grouped into cohorts of 50 individuals. Snails within each cohort were labeled by applying unique series of colored dots to their shell using high-gloss colored nail polish. All individuals were measured from the edge of the operculum to the widest point across the shell.

To test the individual snail behavioral types in response to the presence of a predator, we took half of each cohort and placed them in a 68.13 L open topped container. The container used was graduated with markings every 2 cm leading up the walls to allow us to track the snail position relative to the water surface. We then filled the containers with seawater up to a standard demarcation, providing enough water to allow the snails and sea star to be submerged. Half cohorts (25 snails) of *C. funebralis* were positioned along the side of the arena such that each snail was ~5 cm from the wall of the container. One *P. giganteus* individual was then placed in the container such that it sat in the middle of all of the snails. This allowed all snails to begin 3–5 cm away from an arm of the sea star. After the *P. giganteus* had been placed, the snails were monitored, and the height of each snail above the water surface was recorded every 2 min for 30 min. After 30 min the snails were removed and placed in fresh seawater. Each cohort of snails was tested 5 separate times to confirm repeatability of individuals' predator avoidance responses in the presence of *P. giganteus*. Seawater was changed between each trial and the testing enclosure was scrubbed clean to ensure uniformity in seawater conditions. Between periods of evaluating snail behavioral types, cohorts of snails were kept in 18.93 L enclosures within a recirculating seawater table.

Snail predator avoidance behavior was assessed as a function of how far an individual would climb out of the water and up the wall of the container in response to the presence of a predator *P. giganteus*. The 2 cm mark denotes the waterline in these trials and climbing above this point could present a desiccation risk to *C. funebralis* in natural conditions. Due to the trade-off between marine predation within the water and desiccation outside of the water, it would be expected that snails should remain in the water unless prompted to leave by a predation threat. Two prior studies conducted by our laboratory have confirmed that individual snails breach the water more frequently, more quickly, and breach farther out of the water in response to the chemical cues of sea star predators, including *Pisaster*.

Mesocosm predation trials

In order to evaluate the relationship between snail behavioral type and their survival with a predator, we staged encounters between stars and snails in 18.93 L circular enclosures with individual seawater supplies. The enclosures had eight 7.5 mm holes drilled around the enclosure at a height of 15 cm, which kept the water level at that height throughout the experiment. *Pisaster giganteus* is a sub-tidal predator that rarely breaches the water surface; therefore, breaching above the water surface provides a viable refuge for fearful snails. The enclosures had a total height of 36 cm, allowing a 21 cm region above the water in which snails could escape predators.

We ran two types of encounters using a similar design: single-density trials and double-density trials. Single-density trials involved splitting a cohort of snails into equal halves and placing each of them in 2 separate enclosures such that each enclosure had 25 snails. Assignment of snails to enclosures was randomly determined. To each enclosure, 1 *P. giganteus* was then added, and a lid with a thick mesh grate was sealed atop the enclosure. Lids were created using a plastic mesh to allow natural light and air to enter the enclosure and prevent snails from escaping. Double-density trials involved an identical procedure, save that each cohort (all 50 snails) was placed in a single enclosure instead of being split into 2. One sea star was again placed in the double-density enclosures, simulating an environment in which the predator density was the same but prey density was doubled. Six cohorts of 50 snails were tried using the single-density treatment, and 8 using the double-density treatment. The sea stars were each given individual identifications so that sea star identity could be tracked for each trial (for use as a random effect in our statistical models). This was necessary to account for the possibility that individual sea stars could vary in their foraging mode, hunting efficiency, motivation to feed, and so on. While for statistical power it would be ideal to use a separate sea stars for each replicate, this was not possible because a wasting disease decimated the sea star populations of southern and central California several years ago (Hewson et al. 2014), and the *Pisaster* populations are only beginning to show very slight signs of recovery.

These predation trials were allowed to progress undisturbed for 14 days, with the trial beginning and ending mid-day. After 14 days, we removed the *P. giganteus* from each of the enclosures and recorded which snails had been consumed during this time. Snails were deemed to be consumed if all of their soft tissues had been digested and all that remained was their empty shell. Snails that were actively being consumed by a sea star upon the cessation of the trial were also deemed consumed. The mesocosm enclosures were washed thoroughly with seawater and scrubbed clean in between predation trials.

Statistical methods

We used a GLMM with a binomial error distribution and log–link function to evaluate selection on prey traits. We included the individuals' average maximum height out of the water obtained across their 5 anti-predator assays (height above water), max shell diameter (shell diameter), and prey density treatment (density treatment: 25 or 50 snails) as predictor variables in our model. We used snail survival as our binary response variable and individual *P. giganteus* identity and replicate ID as random effects in our model. We tested for an association between shell diameter and anti-predator behavior (height above water) using a Pearson's correlation. We further explored the degree to which other metrics of anti-predator behavior (time out of water, peak height ever obtained) were inter-correlated with one another using Pearson's correlations. We did not include interactions terms in our statistical models here because of limited number of replicate trials and the need to reuse *P. giganteus* in multiple trials. All statistical analyses were run through JMP 12.0.

Results

A combination of prey size, behavior, and density predicted prey survival. Larger snails (Figure 1) and snails with higher average breaches above water in response to predators (Figure 2) were less likely to survive staged encounters with *P. giganteus*. We also found that prey had higher per capita survival rates in the double density treatment (summarized in Table 1), potentially because of the relative long handling time for these predators. All 3 metrics of snail anti-predator behavior were highly correlated with each other. However, none of these metrics were significantly correlated with snail shell size (Table 2).

Discussion

Shell size and prey density

We found that smaller snails (Figure 1) and those in high-density treatments (Table 1) were more likely to survive encounters with predators. We propose 2 non-mutually exclusive hypotheses that could explain why larger snails were more susceptible to predation by *P. giganteus*. First, it is plausible that *P. giganteus* merely prefer larger snails. This seems conceptually plausible because larger snails likely provide more calories per unit handling time than smaller snails. However, inconsistent with this hypothesis, in all our observations of these predators, we never observed signs of a predator rejecting a prey item (i.e. seizing it and then letting it go). Second, we propose that larger snails could be easier to detect or handle for *P. giganteus*. *Pisaster giganteus* is very large relative to *C. funebralis*, and superficially, larger snails appear as though they could come into contact with predators' tube feet more easily.

The finding that *C. funebralis* enjoy higher survivorship in greater densities is somewhat easier to explain. *Pisaster giganteus* and *Pisaster ochraceus* each take 1–2 days to consume a single *C.*

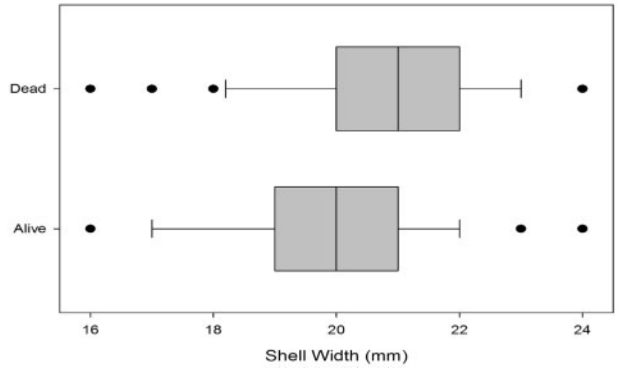

Figure 1. Box plots detailing the relationship between snail shell width and survival rates of *C. funebralis* in mesocosm trials. Dots represent putative outliers, lines represent 10th and 90th percentiles, gray boxes indicate the interquartile range, and the central line depicts the median.

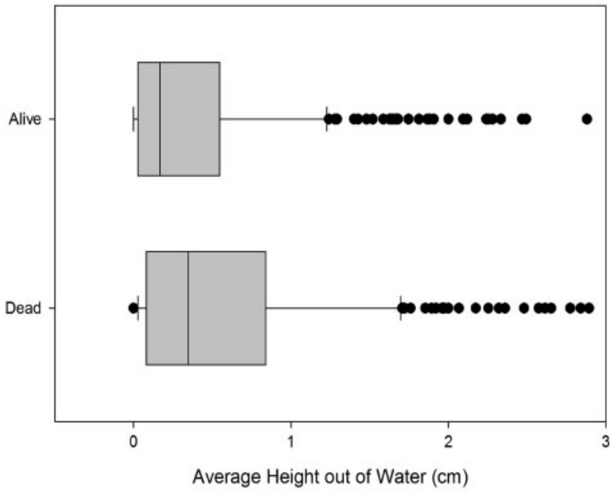

Figure 2. Box plots showing differences in average height reached above water by surviving versus dead *C. funebralis* in our mesocosm trials. Dots represent putative outliers, lines represent 10th and 90th percentiles, gray boxes indicate the interquartile range, and the central line depicts the median.

Table 1. Effect tests and parameter estimates for our GLMM predicting prey survival

A) Parameter estimates

Term	Estimate	SE	Chi-square	Prob > ChiSq
Intercept [0]	−6.06	0.88	47.59	<0.0001*
Density [25]	0.21	0.08	6.78	0.0092*
Snail width (mm)	0.27	0.04	40.78	<0.0001*
Average height (cm)	0.35	0.11	9.62	0.0019*

B) Effect likelihood ratio tests

Source	Nparm	Df	LR Chi-square	Prob > ChiSq
Density	1	1	6.84	0.0089*
Snail width (mm)	1	1	47.01	<0.0001*
Average height (cm)	1	1	10.98	0.0009*

Table 2. Correlations between various metrics of snail anti-predator behavior and snails' shell size

	Snail width (mm)	Peak height (cm)	Average height (cm)	Average time out
Snail width (mm)	1			
Peak height (cm)	0.0953	1		
Average height (cm)	0.0734	**0.7764**	1	
Average time out	0.0974	**0.5909**	**0.8279**	1

Note: Bolded values are significantly correlated at $P < 0.001$.

funebralis. These long handling times are predicted to generate rapid predator saturation, and therefore, enhance the per capita survival rates of snails in denser groups. This pattern may further help to explain why *C. funebralis* aggregate in very large numbers in the field (Paine 1969, Morris et al. 1980, Fawcett 1984): aggregations may help to overwhelm the handling time of sea stars (*Pisaster*), even when sea stars occur in large numbers, and this could provide snails with survival benefits via dilution of risk (Bednekoff and Lima 1998, Beauchamp 2008). Such effects are potentially important for this system because > 20% of *C. funebralis* succumb to predation by sea stars each year (Paine 1969).

Boldness and survival

Much of the early theory on animal personality was borrowed from optimal foraging theory and predicted that bold prey should enjoy a foraging benefit as a result of being willing to forage under risky conditions (Sih 1980; Biro et al. 2004). Yet, this riskiness is also predicted to incur a significant cost in terms of increased predation risk. Several dozen studies have now examined this hypothesis in a variety of test systems. In aggregate, the literature has recovered only mixed support for these predictions. Some studies have found that boldness confers foraging success and enhanced predation risk (Riechert and Bishop 1990; Biro et al. 2004; Biro et al. 2006); however, another set of studies have shown that bold individuals actually enjoy superior survivorship (Reale and Festa-Bianchet 2003; Smith and Blumstein 2010; Blake and Gabor 2014). This has led to the development of more complex models predicting that bold individuals may also be in better condition, therefore offsetting their increased risk of predation with superior energy stores and physical performance (e.g. faster burst speeds, more effect physical defenses, etc.) (Luttbeg and Sih 2010). Such models also predict positive feedback loops between boldness, foraging success, and reduced predation risk that should increase individual differences over development (Sih et al. 2015). However, many studies have shown that individual differences in boldness are heritable (Dochtermann et al. 2015). If this is the case, then joint positive effects of boldness on both foraging success and survival should quickly erode away genetic variability in this trait (unless boldness negatively impacts individual performance in some other way). This raises the yet unexplored prediction that, in systems where boldness is positively related to survival and foraging success, individual variation in boldness should be primarily determined by individual body condition or experience. In contrast, in systems where boldness mediates a tradeoff between foraging success and predation risk, differences in boldness are more likely to be genetically determined.

In the study presented here, we provide evidence that boldness positively impacts snails' survival with predators. These results are therefore not consistent with early theory from animal personality literature. It has yet to be determined whether boldness also confers a foraging advantage in this system. However, if such an association does occur, this raises the question of what could be maintaining the diversity of behavioral tendencies seen in many *C. funebralis* populations (Markowitz 1980; Doering and Phillips 1983, Pruitt et al. 2012). We propose that individual differences are potentially driven by variation in snails' experience, or that other factors apart from predation may favor fearful phenotypes.

Predator foraging mode is an underappreciated factor that could help to reconcile system-specific relationships between prey boldness and predation risk (Griffen et al. 2012; Toscano and Griffen 2014; Belgrad and Griffen 2016). In a prior study we showed that the survival effects of boldness in *C. funebralis* depended on the foraging mode of the predator: sedentary sea stars *Pisaster ochraceus* tended to capture fearful snails and active sea stars tended to capture bolder snails (Pruitt et al. 2012). Individual differences in *C. funebralis* were also found to be highly repeatable (ICC = 0.66 Pruitt et al. 2012, ICC = 0.49, Pruitt et al. 2016). If these data hold for *C. funbralis*' interactions with other predators, then one would predict that *P. giganteus* would be inactive than *P. ochraceus* (because less predators tend to capture fearful prey, consistent with the pattern observed here). Concordant with this prediction, we found in a post hoc follow-up comparison that *P. giganteus* exhibits average activity levels 40% lower than *P. ochraceus* in open field assays (Pruitt et al. 2016). These results suggest that variation in predator activity level, and therefore foraging mode, is potentially a determinant of how boldness influences predation risk across systems. Data from several other systems support this conclusion. Studies conducted with stickleback and pike (McGhee et al. 2013), domestic crickets and jumping spiders (Sweeney et al. 2013), field crickets and black widows (DiRienzo et al. 2013), mud crabs and fish predators (Belgrad and Griffen 2016), and even among networks of spider predators (Keiser and Pruitt 2013) have independently demonstrated that the outcome of predator–prey interactions depend on the behavioral tendencies of the specific individuals involved, and thus no one behavioral type in predators or prey consistently enjoys superior performance. In all cases, individual differences in boldness and activity level jointly interact to determine prey survival. We therefore urge the development of predator–prey models for the animal personality literature that attempt to account for differences in locomotor patterns both within and across species (Scharf et al. 2006; Scharf et al. 2008). The data necessary to critically evaluate such models are likely already available for many systems.

In conclusions, in order to understand the evolutionary maintenance of animal personality, it is first necessary to understand how individual differences in behavior shape success in contrasting contexts and situations. Predator–prey interactions are particularly amenable to exploring the performance consequences of animal personality because the negative impacts of ill-suited personality types can be revealed rapidly. In this study, we evaluated the degree to which individual differences in anti-predator behavior (often termed "boldness" or "fearfulness") impacted prey survival in staged interactions with a chemosensory predator, *P. giganteus*. We found that snails with more pronounced anti-predator responses were less likely to survive encounters with predators and that larger snails were more susceptible to predation as well. These data add to the growing body of literature documenting the impacts of personality on species interactions, and suggest that individuals' personality types could play an important role in determining individuals' performance in different environments.

Aknowledgments

We are indebted to the California Coastal Commission for issuing research and collection permits (SCP-13458). We would also like to thank Christoph Pierre for collecting the animals for these studies and assisting in their laboratory maintenance. Funds for this work were generously provided by the University of California, Santa Barbara as start-up to J.N.P., NSF grant awards to J.N.P. (No. 1352705 and No. 1455895), and an NIH grant awarded to J.N.P. (No. 20161380). This project was designed and executed as a part of an undergraduate honors thesis project by W.C.F. and G.T.C.

Funding

Funds for this work were generously provided by the University of California, Santa Barbara as start-up to J.N.P., NSF grant awards to J.N.P. (No. 1352705 and No. 1455895), and an NIH grant awarded to J.N.P. (No. 20161380).

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