Behavioral Types of Predator and Prey Jointly Determine Prey Survival: Potential Implications for the Maintenance of Within-Species Behavioral Variation

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Abstract: Recent studies in animal behavior have emphasized the ecological importance of individual variation in behavioral types (e.g., boldness, activity). Such studies have emphasized how variation in one species affects its interaction with other species. But few (if any) studies simultaneously examine variation in multiple interacting species, despite the potential for coevolutionary responses to work to either maintain or eliminate variation in interacting populations. Here, we investigate how individual differences in behavioral types of both predators (ocher sea stars, Pisaster ochraceus) and prey (black turban snails, Chlorostoma funebralis) interact to mediate predation rates. We assessed activity level, degree of predator avoidance behavior, and maximum shell diameter of individual C. funebralis and activity levels of individual P. ochraceus. We then placed 46 individually marked C. funebralis into outdoor mesocosms with a single P. ochraceus and allowed them to interact for 14 days. Overall, predator avoidance behavior and maximum shell diameter were positively associated with survival for C. funebralis. However, the effects of these traits depended on the predator’s behavioral type: greater predator avoidance behavior was favored with active P. ochraceus, and low predator avoidance behavior was favored with inactive P. ochraceus. We argue that, even in two-species interactions, trait variation in heterospecifics could be an important factor maintaining trait variation within populations.

Keywords: behavioral type, behavioral syndrome, frequency-dependent selection, personality, predator-prey interactions.

Introduction
Identifying the mechanisms maintaining trait diversity within populations is a perennial goal in ecology and evolutionary biology. Within behavioral ecology, a surge of recent literature has focused on consistent individual differences in behavior (e.g., in boldness or aggressiveness), over time or across contexts, that are commonly referred to as behavioral syndromes, temperament, and/or personality (see reviews in Dall et al. 2004; Sih et al. 2004; Bell 2007; Sih and Bell 2008). Here we refer to consistent behavioral variants as behavioral types (BTs) and correlations in behavior across trait types (e.g., activity, aggression) as behavioral syndromes. Although a large number of recent studies have quantified BTs and examined their proximate correlates (e.g., neuroendocrine correlates) or effects on components of fitness (e.g., effects of boldness on survival), to date, few studies have demonstrated how individual variation in BTs of multiple species influences interspecific interactions (but see Webster et al. 2009). Instead, evolutionary ecology studies typically consider intraspecific variation in only a single focal species and regard individuals of the other species as functionally identical to one another (e.g., Yoshida et al. 2003; Hairston et al. 2005; Meyer et al. 2006; Bell and Sih 2007; but see Smith and Blumstein 2010). However, we argue that within-species variation in two or more interacting species could be a general mechanism maintaining trait diversity within populations because variation in one interactor could maintain variation in another and vice versa via frequency-dependent selection (Roughgarden 1976; Tellier and Brown 2009).

In particular, we focus on predator-prey interactions. A large number of studies test how BTs influence predator-prey interactions (Sih et al. 2003; Biro et al. 2004, 2006; Bell and Sih 2007; Dingemanse et al. 2007; Carter et al. 2010; Smith and Blumstein 2010). For instance, in some prey species, bold BTs commonly enjoy higher growth rates but suffer greater susceptibility to predation (Biro et al. 2004; Pruitt and Krauel 2010; but see Réale and Festa-Bianchet 2003; Smith and Blumstein 2010). This trend stems from bold individuals’ tendency to exploit high-risk foraging opportunities, whereas other individuals forgo
these opportunities in favor of safety. In predators, variation in aggressiveness is known to influence the kinds of prey attacked (Riechert 1991; Maupin and Riechert 2001; Costantini et al. 2005), the tactics used to detect and subdue prey (Coleman and Wilson 1998; Wilson 1998; Pruitt et al. 2008), and the amount of food consumed during foraging bouts (Pruitt 2010; Pruitt and Krauel 2010; Smith and Blumstein 2010). However, to date, no study has simultaneously evaluated the effects of BTs in both predators and prey to test their overall impacts on the outcome of the interaction. Interestingly, this deficit persists despite recent data indicating that the performance effects of BTs likely depend on the individual traits of heterospecific interactants (Smith and Blumstein 2010).

We propose that BT by BT interactions are of general interest because they could maintain trait variation within populations through context-dependent performance trade-offs, where the fitness effects of different BTs in one species depend on the frequency of BTs in another interacting species. Frequency-dependent selection has been broadly appreciated for its role in the maintenance of genetic diversity (e.g., Carius et al. 2001; Kassen 2002; Roulin 2004), as well as species diversity (e.g., Chesson 2000). Here, we examine the possibility that joint frequency dependence might contribute to maintenance of variation in both predator and prey levels. In essence, we suggest that intraspecific variation in predator BTs represents a dynamic form of environmental heterogeneity for prey that can help to explain the maintenance of functional variation (e.g., in behavioral types). Specifically, if the prey BT that results in highest fitness depends on the predator’s BT, then variation in predator BT can help maintain variation in prey BTs. By parallel logic, variation in BTs in prey can help maintain variation in predator BTs. In essence, even in two-species interactions, diversity in one trophic level may help maintain it in another, and vice versa.

We use the black turban snail, Chlorostoma funebralis (formerly Tegula funebralis, Turbinidae, Vetigastropoda) and its predator P. ochraceus (Asteriidae, Forcipulatida) as models for our investigation. Chlorostoma funebralis is an abundant herbivore in the rocky intertidal from Vancouver Island to Baja California (occasionally exceeding 400 individuals/m²; Morris et al. 1980). Chlorostoma funebralis is preyed on by sea otters (Enhydra lutris), red rock crabs (Cancer antennarius), predatory snails, and, most prominently, the ocher sea star (P. ochraceus; Paine 1969; Morris et al. 1980). Chlorostoma funebralis readily responds to predators by climbing up rock walls out of the water or, if on a slope, releasing its grip from the rock surface and rolling downhill (Doering and Phillips 1983; Fawcett 1984). Though not a preferred prey item of P. ochraceus, it is estimated that P. ochraceus consumes 25%–28% of adult C. funebralis each year where the two species co-occur (Paine 1969). Thus, predation by P. ochraceus can be a major selective force for mature C. funebralis.

We ask the following questions. (1) Do C. funebralis and P. ochraceus exhibit consistent individual differences in behavior? (2) For C. funebralis, what BTs are associated with survival in staged mesocosm predation trials? (3) Are the survival consequences of various BTs in C. funebralis affected by the BTs of their predators (P. ochraceus)? (4) Are BTs in P. ochraceus associated with foraging success?

**Methods**

**Collection and Laboratory Maintenance**

Chlorostoma funebralis (N = 2,638) were haphazardly collected from mid-intertidal pools near Bodega Bay, California, from August to October 2010. Snails were transported to the laboratory and housed in a recirculating seawater system for the duration of their behavioral assays (<2 weeks). The salinity of the system ranged from 32 to 35 ppt, temperatures ranged from 17.1°C to 18.5°C, and the system was maintained on a 12L : 12D photoperiod. Snails were individually marked by painting their shells with a unique series of colored dots using high-gloss, metallic-colored nail polish. We measured snails’ maximum shell diameter before conducting our behavioral assays.

We opportunistically collected 62 size-matched (±12% average arm length) Pisaster ochraceus from the mid-intertidal pools near Bodega Bay from September to October 2010. Pisaster ochraceus were housed individually in outdoor flow-through seawater systems (1-m diameter, 0.5 m deep, 400 L) and provided an ad lib. diet of California mussels (Mytilus californianus).

**Snail Behavioral Type**

Before exposure to predators, the BT of individual C. funebralis was characterized by measuring activity level in the absence of predators and snail response to predator threat (termed their “predator avoidance response”). To determine activity level, we placed each snail (mean = 17.46 mm, SD = 3.12) in a 490-mL cylindrical container (width radius = 7 cm) in a table of recirculating seawater and allowed it to acclimate for 1 h. To allow us to plot the position of the snails at regular time intervals, containers were protracted every 45° with lines extending up the walls of the enclosures. After the acclimation period, the position of the snail was plotted every 15 min for 2 h. Snail activity level was estimated by summing their distance traveled over the 2-h period, assuming linear movement between positions. To assess repeatability of our activity-level measurement, 120 individuals were retested 1 week after their initial assay. During the week between
measurements, snails were housed individually in similar 490-mL containers in a table of recirculating seawater (17.1°–18.5°C). Snails used to estimate repeatability were excluded from subsequent assays.

Snail predator avoidance behavior was measured as the distance snails crawled out of the water in response to sea star presence (Markowitz 1980; Doering and Phillips 1983). Distance above the waterline represents a natural trade-off between safety from marine predators and risk of desiccation; our model predator, *P. ochraceus*, does not willingly emerge from the water to forage but can be observed above the waterline during low tides (Morris et al. 1980). Thus, the farther out of the water a snail is, the less likely it is to be encountered by a sea star as the tide rises in the field. Circular arenas (45-cm diameter, 43 cm tall) filled with 15 L of seawater were marked every 3 cm up the side of the enclosure, which allowed us to estimate the distance out of the water traveled by each snail during counts with and without predators. Sets of these markings were placed every 45° around the arena. Observations were taken outdoors, at ambient air temperatures (20°–22°C) during daylight hours (1100–1600 hours). Before the start of the trial, the arena was filled with seawater to the 6-cm mark.

Groups of 12 individually marked, unsexed snails were placed in a ring (10-cm radius) within the enclosure and allowed 30 s to acclimate before a single *P. ochraceus* was placed centrally into the arena. We assayed snails in small groups because *C. funebralis* naturally occurs in clusters around suitable microhabitat in the field. Thus, although this species is known to respond to conspecific alarm cues and this doubtlessly affects their behavior (Jacobsen and Stabell 2004; Magnhagen and Bunnefeld 2009), our assay conditions mirror the social context snails experience both under natural conditions and in our subsequent mesocosm predation trials (i.e., conspecifics present). We recorded the height each snail traveled out of the water every 5 min for 30 min. Snails that failed to breach the water surface were given a score of zero. As a control, all individuals were run through a second trial without a predator. Chronological sequence of assays with predators present or absent was alternated among cohorts, and we failed to detect an association between trial sequence and individuals’ flight response (*P > .20*). These two measurements were separated by no more than 2 days. Our estimate of each individual’s predator avoidance response was the difference between the maximum height obtained during the predator-present and no-predator control treatments. To assess repeatability of our predator avoidance measure, a cohort of 101 individuals was retested with a predator 1 week after their initial assays. Snails used to estimate repeatability were excluded from our predation trials.

Sea Star Behavioral Type

Sea star activity level was assessed by measuring distance traveled for individual sea stars (arm length: mean = 15.18 cm, SD = 1.44) in standardized solitary enclosures (54 cm × 34 cm × 29 cm). Sea stars were allowed 3 days to acclimate before being provided an ad lib. diet of *M. californianus* for 3 days. Sea stars were allotted 3 days of acclimation time because preliminary observations indicated that sea stars expressed a heightened activity level and reduced tendency to accept food when first transported to laboratory. We assessed sea star activity level twice: 1 and 14 days after their ad lib. meal. Sea star activity levels were assessed during daylight hours (1100–1600 hours; from September to October 2010) by placing their enclosures on grids with 2 cm × 2 cm demarcations and plotting the position of the sea star every 15 min for 3 h. We estimated activity level as the distance traveled by each sea star assuming linear movement among plotted positions. Although for the remainder of our article we will refer to our two measures (i.e., 1 and 14 days) as “time since an ad lib. meal,” this period represents both time without food and time acclimating in a novel environment. These measurements were repeated for a group of 17 sea stars to assess repeatability. Sea stars used to obtain repeatability estimates were excluded from other assays.

To further characterize sea star BT, we estimated the ability of individual *P. ochraceus* to orchestrate movements across irregular landscapes (e.g., up the sides of enclosures or around rock faces) by measuring sea stars’ latency to right themselves once overturned. We adopted this measure because sea stars must orchestrate the movement of multiple arms, engage their tube feet, and exhibit considerable flexibility in order to overturn their bodies, providing an integrated measure of many activities. Additionally, this behavior is commonly assessed in interspecific comparisons (e.g., Ohshima 1940; Pollis and Gonor 1975). Sea stars were placed upside down in the center of a circular flow-through seawater system (1-m diameter, 0.5 m deep, 400 L). Using a stopwatch, we timed sea stars’ latency to right themselves. Individuals were deemed “righted” when tube feet from all five arms were in contact with the substrate and their ventral side faced downward. To assess the repeatability of *P. ochraceus*’s latency to right, 15 sea stars were assayed three times on consecutive days. Sea stars used to obtain repeatability were excluded from other behavioral assays.

Mesocosm Predation Trials

To test whether sea star and snail BT affected the outcome of predator-prey interactions, we staged encounters between snails and sea stars whose BT was characterized in
of the above assays. Randomly selected, individually marked snails (37–46 individuals) were placed within each of 18 rectangular mesocosms (54 cm × 34 cm × 29 cm) and allowed 15 min to acclimate before a randomly selected *P. ochraceus* was placed in the enclosure. Post hoc analyses confirmed there was no significant association between BTs of *P. ochraceus* and the mean (*P* > .70) or variance (*P* > .25) of BTs in their randomly selected pools of prey. *Pisaster ochraceus* were starved 5 days before the start of our mesocosm experiments. Lids to the mesocosms were then sealed and left undisturbed for 14 days. At the end of this period, we recorded the number of snails consumed and noted their IDs. A snail was considered “consumed” if all that remained of it was its empty shell (i.e., no soft tissue). Mesocosm experiments were run outside under ambient lighting conditions from late September to November 2010. Mesocosms were connected to an outdoor flow-through seawater system at Bodega Bay Marine Laboratory. A hole was drilled in the top of each mesocosm, which allowed a steady flow of cool (16.1°–17.5°C) seawater to cascade into the enclosures. Eight holes (1.5-cm diameter) were drilled 15 cm above the base of the mesocosm on all sides, which allowed water to fill the bottom of the chamber and flow out all sides. This design permitted snails an approximately 14-cm refuge above the waterline to escape predation. Within a few days, diatoms were observed growing on the surface of our mesocosms, and grazing by snails near refuges was common.

To obtain repeated estimates of the selective foraging effects of individual *P. ochraceus*, we replicated this experiment three times with each sea star (*N* = 18). To avoid confounding effects of mesocosms’ placement, the positions of sea stars were randomized among temporal replicates. Mesocosms were scrubbed clean between replicates and rinsed thoroughly with seawater.

**Statistical Methods**

We used ANOVA and partitioning of variances to estimate repeatability (after Boake 1989) and nonparametric Spearman’s correlations to test for associations among behavioral traits (i.e., behavioral syndromes) in both the snails and sea stars. To assess the traits associated with survival in *C. funebralis*, we calculated selection gradients 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 predator avoidance response (cm), maximum shell diameter, and a correlated selection term (i.e., their interaction term) for each mesocosm independently. We used logistic regression for our significance tests (after Janzen and Stern 1998) and multiple linear regression to estimate selection gradients (after Calsbeek and Irshick 2007). We did not include nonlinear selection terms in our models owing to limited degrees of freedom, but visual inspection of the data indicated no nonlinearity. From our selection analyses we obtained a selection gradient estimate for each *P. ochraceus* based on the average of their three repeated mesocosm predation trials.

To estimate the effects of predator BT and body size on sea star foraging effects, we used multiple regression with two response variables: (1) the percentage of snails captured and (2) the average selection gradients imposed. We included the following predictor variables in our models: sea star activity level (1 day since an ad lib. meal), sea star activity level (14 days since an ad lib. meal), sea star’s latency to right, and average arm length. Because of the limited number of sea stars in our selection experiments (*N* = 18), we lacked the degrees of freedom to include interaction terms in our models. All of our statistics were run using JMP 8.0.

**Results**

**Behavioral Types of Snails and Sea Stars**

We found considerable variability in behaviors among individuals of both snails and sea stars (fig. 1), and an individual’s behavior was generally consistent across repeated trials. We detected a significant difference in the maximum height obtained by snails in the presence and absence of a predator (Wilcoxon sign rank *Z* = 31.58, df = 2,146, *P* < .0001; fig. 2A), and predator avoidance responses were consistent across trials with the same individual (*F*1,110 = 4.75, *P* = .002, *r* = 0.66; fig. 2B). However, we failed to detect a significant repeatability for our estimate of snail activity level (*F*1,119 = 1.27, *P* = .09, *r* = 0.13), and thus, we exclude these measures from our selection analyses. In contrast, we detected significant repeatability of sea star activity level both 1 day (*F*16,33 = 10.04, *P* < .001, *r* = 0.71) and 14 days (*F*16,33 = 5.61, *P* < .001, *r* = 0.59) after an ad lib. meal, and sea star activity levels were correlated across repeated measures (table 1). Sea stars’ latency to right themselves was also repeatable (*F*14,44 = 6.89, *P* < .001, *r* = 0.45). None of our measures of sea star BTs were associated with body size (i.e., their average arm length; activity level 1 day: *r* = −0.13, df = 18, *P* = .62; activity level 14 days: *r* = −0.01, df = 18, *P* = .97; latency to right: *r* = 0.05, df = 18, *P* = .85), and we detected only a weak positive association between snails’ maximum shell diameter and their predator avoidance response (*r* = 0.07, df = 1,823, *P* = .003).
Effects of BT on Outcome of Predator-Prey Interactions

A summary of our selection analyses for each mesocosm is provided in table 2. From observing table 2, we see both positive and negative selection gradients on snails’ predator avoidance behavior and maximum shell diameter in different mesocosms. To test whether variation in selection gradients is associated with sea star attributes, we averaged the gradients across the three replicates for each sea star and used these averages in our subsequent analyses.

Before testing for associations between sea star phenotypes and their effects on prey populations, we first tested whether the percentage of snails consumed and selection gradients imposed by each sea star were repeatable among replicates. We detected significant repeatabilities for both the percent of prey consumed ($F_{1,36} = 3.99, P < .001, r = 0.67, 5\%–85\%$ mortality, mean = 41\%) and the selection gradients imposed (predator avoidance response: $F_{1,36} = 7.51, P < .0001, r = 0.71$; maximum shell diameter: $F_{1,36} = 3.23, P = .002, r = 0.65$) by individual sea stars.

We next tested whether sea star attributes were asso-
associated with either the average percent of prey consumed or the selection gradients they impose on their prey. Our full models predicting the percentage of prey items killed \((F_{1,17} = 0.89, P = .50, r^2 = 0.22)\) and the selection gradient imposed on maximum shell diameter \((F_{1,17} = 0.82, P = .54, r^2 = 0.20)\) were nonsignificant. In contrast, our full model predicting selection gradients on snails’ predator avoidance response was significant \((F_{1,17} = 5.46, P = .008, r^2 = 0.51)\). Using Akaike Information Criterion (AIC) model selection criterion (Akaike 1987), the best model predicting selection on predator avoidance response included sea star activity level after 14 days without food and no other terms (fig. 3A; appendix); active sea stars tended to capture prey with low predator avoidance responses, whereas inactive sea stars tended to capture snails exhibiting high predator avoidance responses. In a side-by-side comparison against the null model, the model containing activity level after 14 days and no additional terms boasted an Akaike weight closely resembling one \((W_i = 0.99)\). In a side-by-side comparison against the second most informative model, the model containing activity level after 14 days and no additional terms possessed an Akaike weight three times that of the alternative model \((W_i = 0.78)\).

Finally, we tested whether the percent of prey consumed by sea stars was associated with the selection gradients they impose on their prey (table 3). We detected a significant positive association between the average percent of prey consumed by individual \(P. ochraceus\) and the selection gradient they impose on maximum shell diameter (table 3; fig. 3B); however, this trend was differentially influenced by one highly voracious sea star, and, when removed, the trend was nonsignificant \((r = 0.42, df = 17, P = .09)\). We detected no significant association between selection imposed on predator avoidance behavior and the percent of prey consumed by individual sea stars (table 3).

**Discussion**

Identifying the mechanisms maintaining trait variation within populations is a core goal in ecology and evolutionary biology; one commonly proposed variance-sustaining mechanism is context-dependent trait performance, where the performance of a trait depends on the environment in which it is expressed. Here, we document a pattern in which the performance of BTs in one species is dependent on the BTs of heterospecific interactors. Specifically, we provide evidence that (1) the BTs associated model predicting selection on predator avoidance response included sea star activity level after 14 days without food and no other terms (fig. 3A; appendix); active sea stars tended to capture prey with low predator avoidance responses, whereas inactive sea stars tended to capture snails exhibiting high predator avoidance responses. In a side-by-side comparison against the null model, the model containing activity level after 14 days and no additional terms boasted an Akaike weight closely resembling one \((W_i = 0.99)\). In a side-by-side comparison against the second most informative model, the model containing activity level after 14 days and no additional terms possessed an Akaike weight three times that of the alternative model \((W_i = 0.78)\).

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**Table 1:** Spearman’s correlation coefficients and \(P\) values for repeated measures of sea star activity levels

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<th>M2D1</th>
<th>M1D14</th>
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<tr>
<td>M1D14</td>
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<td>(P)</td>
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Note: Measurements were taken 1 and 14 days after an ad lib. feeding bout. \(M = \) measurement, \(D = \) day (e.g., M1D1 = measurement 1 at day 1).
with survival in *Chlorostoma funebris* vary depending on the BTs of its predator, *Pisaster ochraceus*; snails exhibiting greater predator avoidance responses experience higher survivorship with active sea stars than with inactive sea stars (fig. 3A). (2) Although the survival consequences of snails' maximum shell diameter also differed among individual sea stars (table 2), we failed to detect an association between selection on maximum shell diameter and any sea star attributes. Finally, (3) we provide evidence that the *Pisaster-Chlorostoma* system meets the necessary preconditions for multispecies frequency-dependent selection, where the fitness consequences of BTs in one species depend on the frequency of BTs in another. We discuss each of these points in more detail below.

As in many other systems, we found evidence for behavioral types in *C. funebris* and *P. ochraceus*. *Chlorostoma funebris* exhibited repeatable differences in their tendency to flee from *P. ochraceus*, and *P. ochraceus* exhibited consistent individual differences in activity level across repeated measures separated by more than 30 days (table 2). More interestingly, individual differences in behavior in *C. funebris* were associated with survival in staged encounters with *P. ochraceus*, and, if predator avoidance behavior is heritable, differential survivorship could lead to evolution in snails' antipredator response. Although at present we lack data on the heritability of antipredator behavior in *C. funebris*, two lines of evidence suggest among-individual differences in response to predators have some genetic basis. First, we detected strongly repeatable individual differences in flight response, and in species with long generation times (e.g., *C. funebris* take >5 years to reach maturity; Paine 1969), repeatabilities are often used as rough proxies for narrow-sense heritability (i.e., because repeatability sets an upper limit to heritability; Boake 1994). Second, previous data comparing flight responses among populations of *C. funebris* revealed that populations with more predators exhibit greater predator avoidance responses (Fawcett 1984), and these behavioral differences are maintained following reciprocal transplants. Fawcett (1984) argues that population differences in predator avoidance behavior are likely the result of local adaptation, because in field selection experiments, greater predator avoidance responses were associated with higher survivorship in localities with more predators. However, several studies have documented tremendous within-population variation in predator avoidance behavior (Markowitz 1980; Doering and Phillips 1983; Fawcett 1984), and little is known about how this variation is maintained.

Although *C. funebris* BT affected its survival, the BTs favored differed among individual sea stars. When paired with active *P. ochraceus*, *C. funebris* expressing greater predator avoidance responses enjoyed higher survivorship;
Figure 3: A, Positive relationship between sea star activity levels after 14 days without food and the selection gradients they impose on predator avoidance behavior in their prey (*Chlorostoma funebralis*; *F* = 23.42, *P* < .001, *r*² = 0.41). B, Positive relationship between the average percent of prey consumed by individual sea stars averaged across three replicates and the selection gradient they impose on maximum shell diameter in their prey (*C. funebralis*). Positive values indicate greater predator avoidance responses or larger *C. funebralis* experienced higher survivorship. Negative values indicate unresponsive or smaller individuals experienced higher survivorship.

however, predator avoidance behavior was disfavored in encounters with inactive *P. ochraceus*. Instead, unresponsive individuals were more likely to survive encounters with inactive *P. ochraceus* (fig. 3A). Although the mechanism behind this trend is unresolved, the data resemble those from classic literature on foraging mode (Huey and Pianka 1981; Scharf et al. 2006): active-foraging species tend to capture sedentary prey and sit-and-wait predators tend to capture active prey. Similarly, active *P. ochraceus* are perhaps more likely to make contact with unresponsive *C. funebralis*, while inactive *P. ochraceus*, which appear to adopt a sit-and-wait foraging strategy, tend to capture prey with greater predator avoidance responses, perhaps because fleeing snails are more likely to make contact with the inactive predator. Interestingly, we failed to detect an association between sea star foraging success (i.e., total number of prey killed) and the selection gradients *P. ochraceus* imposed on snails’ predator avoidance response, and this suggests that foraging strategy does not influence the number of prey consumed by individual *P. ochraceus*. In other words, whether *P. ochraceus* are active or inactive, they are able to capture a similar number of snails, provided there is a diversity of prey phenotypes present. This finding is important because if any BT consistently experienced higher foraging rates, we would expect rapid selection and fixation of that variant within the population.

Synthesis and Future Directions

A familiar idea in evolutionary ecology is that negative frequency dependence, a rare type advantage, can be important in maintaining variation within or among species (Chesson 2000; Sinervo and Calsbeek 2006). However, here we identify the preconditions for multispecies frequency-dependent selection in a predator-prey system, whereby the mechanism of frequency-dependent selection on BTs in each species depends on BTs of the other species, which are themselves under frequency-dependent selection. We propose this scenario can result in “joint frequency-dependent selection” in overall predator-prey interactions via the following feedback sequence: (1) if a system has mostly active predators that primarily eat unresponsive prey, this favors prey that actively avoid predators; (2) selection then favors more responsive prey, and the prey population gradually expresses greater predator avoidance behavior; (3) responsive, fearful prey populations then favor inactive predators that can catch more prey without absorbing the costs of high activity levels; however, (4) when inactive predators become more common, this favors unresponsive prey, which in turn favors active predators. It is important to note that although we outline this feedback in terms of intraspecific trait variants, the sequence could as easily be illustrated with suites of predator and prey species (Huey and Pianka 1981). Theoretically similar cycles have been outlined in models on gene-for-gene coevolution in host-parasite interactions (Frank 1992), in which multispecies frequency-dependent cycles can have either stabilizing or destabilizing effects depending on a multitude of factors (Tellier and Brown 2007, 2009).

In nature, the *Pisaster-Chlorostoma* system is probably usually too complex for a simple, two-species, joint frequency-dependent selection scenario to hold. Although *Chlorostoma funebralis* experiences intense predation by
Table 3: Spearman’s correlations between the average percent of prey consumed by individual sea stars and the selection gradients they impose on their prey

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<thead>
<tr>
<th>Selection on predator avoidance response</th>
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</tbody>
</table>

*Pisaster ochraceus, C. funebralis* constitutes a relatively minor portion of *P. ochraceus’s* diet (i.e., the interaction is highly asymmetrical; Paine 1969). However, our study successfully illustrates the potential for such feedbacks to occur, and many of the necessary preconditions identified here are met in other predator-prey systems (e.g., Smith and Blumstein 2010); thus, similar feedback mechanisms could be quite general. We propose the reason such mechanisms have not been characterized previously is that most evolutionary ecologists (behavioral or otherwise) tend to focus on traits in only a single species and regard heterospecifics as passive, nonevolving selective agents (Yoshida et al. 2003; Biro et al. 2004; Hairston et al. 2005; Meyer et al. 2006; Bell and Sih 2007; Smith and Blumstein 2010). Further work is required to determine the possible importance of our joint frequency-dependent selection hypothesis in other test systems that (1) exhibit a more symmetrical predator-prey interaction and (2) have shorter generation times.

Acknowledgments
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APPENDIX

Table A1: Summary of model statistics predicting selection gradients sea stars impose on snail predator avoidance behavior

<table>
<thead>
<tr>
<th>Model</th>
<th>No. parameters</th>
<th>$r^2$</th>
<th>AIC</th>
<th>$\Delta iAIC$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Activity level 14 days</td>
<td>1</td>
<td>.411</td>
<td>-14.108</td>
<td>0</td>
</tr>
<tr>
<td>Latency to right</td>
<td>1</td>
<td>.1085</td>
<td>-6.6489</td>
<td>7.4591</td>
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<tr>
<td>Arm length</td>
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<td>.102</td>
<td>-6.5173</td>
<td>7.5907</td>
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<tr>
<td>Activity 1 day</td>
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<td>.0025</td>
<td>-4.6259</td>
<td>9.4821</td>
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<td>2.017</td>
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<tr>
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<td>3.012</td>
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<td>-3.6158</td>
<td>10.4922</td>
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<td>Arm length, latency to right, activity 1 day, activity level 14 days</td>
<td>4</td>
<td>.5263</td>
<td>-6.1077</td>
<td>8.0003</td>
</tr>
</tbody>
</table>
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Editor: Mark A. McPeek

White-lipped snail or Helix albolabris. “That the sense of smell is enjoyed by the snail has long been known, since they will oftentimes
travel some distance in quest of food for which they have a particular fondness.” From “The Land Snails of New England,” by E. S. Morse