Behavioral Hypervolumes of Predator Groups and Predator-Predator Interactions Shape Prey Survival Rates and Selection on Prey Behavior

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ABSTRACT: Predator-prey interactions often vary on the basis of the traits of the individual predators and prey involved. Here we examine whether the multidimensional behavioral diversity of predator groups shapes prey mortality rates and selection on prey behavior. We ran individual sea stars (*Pisaster ochraceus*) through three behavioral assays to characterize individuals' behavioral phenotype along three axes. We then created groups that varied in the volume of behavioral space that they occupied. We further manipulated the ability of predators to interact with one another physically via the addition of barriers. Prey snails (*Chlorostome funebralis*) were also run through an assay to evaluate their predator avoidance behavior before their use in mesocosm experiments. We then subjected pools of prey to predator groups and recorded the number of prey consumed and their behavioral phenotypes. We found that predator-predator interactions changed survival selection on prey traits: when predators were prevented from interacting, more fearful snails had higher survival rates, whereas prey fearfulness had no effect on survival when predators were free to interact. We also found that groups of predators that occupied a larger volume in behavioral trait space consumed 35% more prey snails than homogeneous predator groups. Finally, we found that behavioral hypervolumes were better predictors of prey survival rates than single behavioral traits or other multivariate statistics (i.e., principal component analysis). Taken together, predator-predator interactions and multidimensional behavioral diversity determine prey survival rates and selection on prey traits in this system.

Keywords: behavioral hypervolume, behavioral syndrome, keystone species, marine ecology, personality, temperament.

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Introduction

Documenting and predicting the interactions of predators and prey is a staple of ecological research. Predators impose some of the most powerful selective forces on prey traits (Sih et al. 1985), they alter the way prey behave (e.g., space use; Lima and Dill 1990; Creel et al. 2008), and they reduce prey numbers and consumptive impacts (Bolker et al. 2003). These processes in turn have cascading influences to lower trophic levels, further altering carbon sequestration (Schmitz 2008, 2009), plant biodiversity (Schmitz 2008), and heterogeneity in the landscape (Creel et al. 2005). Trait-based ecology posits that a thorough understanding of organisms' traits can enhance the predictability of ecological outcomes (Violle et al. 2007; Villeger et al. 2008). For instance, there is evidence that interspecific variation in predator foraging mode can change the relative impacts of consumptive versus fear effects that predators have on prey (Preisser et al. 2007; Belgrad and Griffen 2016). In this study, we examine the degree to which individual variation in the behavior of predators and prey jointly mediate the outcome of their interaction. In particular, we focus on temporally consistent individual differences in behavior.

Many studies have now examined the ecological effects of consistent individual differences in behavior, also known as animal personality (Sih et al. 2012; Wolf and Weissing 2012). Such variation is intriguing from an ecological standpoint because of its potential to change the outcome of a variety of processes, including population dynamics (Pruitt 2013), range expansion/recession (Cote et al. 2011; Fogarty et al. 2011), trophic cascades (Griffen et al. 2012; Toscano and Griffen 2014), community assembly (Pruitt and Modlmeier 2015; Royaute and Pruitt 2015), and even extinction risk. To date, these studies have tended to focus on single

trait-outcome relationships. However, no biological trait—influential as it may be—operates in a vacuum. We thus explore here whether a more comprehensive understanding of behavior across multiple situations could further inform our understanding of the interactions between groups of predators and their prey. We term the multidimensional space occupied by an individual, population, or community a "behavioral hypervolume," akin to the niche hypervolume of general ecology (Van Valen 1965; Whittaker et al. 1973; Roughgarden 1974). The behavioral hypervolume represents an index of the variability among individuals in a multidimensional space formed by the traits analyzed, where groups made of more similar individuals in that multidimensional space show smaller hypervolumes. If individual variation in behavior maps to niche variation, then one might predict that populations of consumers that occupy a larger behavioral hypervolume (i.e., behavioral niche) may compete with each other less and deplete more resources overall (Villeger et al. 2008). This is because individual hypervolumes within these behaviorally diverse groups will tend not to overlap with one another.

More broadly, deploying a behavioral hypervolume approach may help to promote synergies between animal personality research and a variety of other aspects of trait-based ecology, adding to the campaign of characterizing links between functional diversity (whether intraspecific or interspecific) and system outcomes (e.g., species diversity vs. ecosystem function; Tilman 1999; Stachowicz et al. 2002; Hughes and Stachowicz 2004). Like other aspects of trait-based ecology (Blonder et al. 2014; Barros et al. 2016), we predict that the multidimensional behavioral diversity exhibited by individuals, groups, or even communities could be important metrics for predicting higher-order ecological phenomena.

To evaluate these ideas, we examined interactions between predatory sea stars (*Pisaster ochraceus*) and black turban snails (*Chlorostoma funebralis*). Groups of *P. ochraceus* are regularly observed foraging in tight clusters in the field (Robles et al. 1995), and interference competition and intraguild predation are common in sea stars (Menge and Menge 1974; McClintock et al. 2008). We reason that such predator-predator interactions are important because of their potential to negate the top-down effects of behavioral hypervolumes of predators on prey. We demonstrated in a previous study that individual *P. ochraceus* exhibit stable differences in their behavioral phenotypes and that these individual differences are linked with the selection regimes that sea stars impose on prey traits: active *P. ochraceus* primarily capture snails with less pronounced predator avoidance behavior, and sedentary *P. ochraceus* primarily capture snails with more pronounced predator avoidance behavior (Pruitt et al. 2012). This result generated the prediction that more behaviorally diverse populations of *P. ochraceus* could be more lethal to populations of

prey. However, it is still unknown how the behavioral composition or diversity of a population of sea stars affects their interactions with prey populations. This step is important because *P. ochraceus* forage in aggregations in situ; thus, a population-level perspective adds an additional layer of complexity and realism to this experimental system. Although *C. funebralis* are not a preferred prey item for *P. ochraceus*, it is estimated that as many as 25% of *C. funebralis* perish as a consequence of predation by *P. ochraceus* at some sites (Paine 1969). We are thus examining an asymmetrical species interaction where *P. ochraceus* is a major source of mortality and selection for *C. funebralis*, even though the snails are not the major source of food for the predator.

Our experiments here ask the following: (1) Does the behavioral hypervolume occupied by a group of predators predict the number or behavioral phenotypes of the prey consumed? (2) Are the behavioral hypervolumes occupied by groups of predators better predictors of prey consumption than simpler extrema metrics (e.g., trait ranges) or dimension-reducing multivariate approaches? (3) Do the effects of behavioral hypervolumes change depending on whether we allow predators to move about freely and physically interact? Specifically, we predict that negative predator-predator interactions—for example, in the form of interference competition—will decrease the number of prey killed and negate predator-driven selection on prey. Evaluating such questions and predictions has the potential to foster stronger connections between behavioral and community ecology, allowing intellectual and methodological exchanges that could advance both fields.

Methods

Collection and Laboratory Maintenance

Predatory sea stars (*Pisaster ochraceus*, $n = 28$) and black turban snails (*Chlorostoma funebralis*, $n = 680$) were collected from middle and lower intertidal habitats at Rincon Point, Santa Barbara County, California, in winter 2016. Animals were transported within 24 h of collection to a marine facility at the University of California (Santa Barbara). Groups of 20 randomly selected *C. funebralis* were housed together in 590-mL plastic deli containers with plastic grates along the sides and tops of the containers. This allowed seawater to flow through the holding containers. *Pisaster ochraceus* were all housed together in a large (1,000 L) circular holding tank and were provided mussels (*Mytilus californicus*) ad lib. as a food source. Sea stars were individually identified using natural variation in body size and color (e.g., red, orange, purple). Individual snails were identified using a unique series of colored dots painted atop their shells using high gloss nail polish.

Personality assays were conducted in the order presented here. Trials were run January–March 2016. Sea stars were run through each of the following assays once each before their staged predator-prey interaction trials. For sea stars, two of the behavioral metrics below (activity level [$r = 0.71$] and latency to right [$r = 0.45$]) were previously shown to be highly repeatable over the course of a few days or weeks (Pruitt et al. 2012). The repeatability of the third metric (aggressiveness) was unknown at the start of this experiment. Thus, after being run through multiple predator-prey interaction trials, we reassessed the aggressiveness of each sea star five times each (one measurement per day per sea star) and used these posttrial assessments to estimate a repeatability for this new metric. For all three behavioral metrics, we further evaluated the long-term consistency of each trait by remeasuring each trait twice for each sea star in September 2016, more than 2 months after the rest of our studies had been conducted. We then tested for an association between a sea star's average behavioral measures (activity level, latency to right, aggressiveness) in spring 2016 versus the average of its responses in September of that same year.

Sea Star: Activity Level

To assess sea star activity level, we placed each individual in a flow-through seawater table (1.5 m × 0.75 m) with a 10 × 10-cm grid placed along the bottom. We allowed the sea stars 10 min to acclimate, which was long enough for all of the individuals to initiate movement, and then we recorded the number of lines crossed by the center of the body of the sea star over the next 30 min. After this time, the sea star was removed from the container, and lingering tube feet were scraped off the bottom of the grid. We chose to estimate sea star activity level because predator foraging mode (active foraging vs. sit-and-wait) is defined in terms of activity patterns (Huey and Pianka 1981; Scharf et al. 2006) and because activity level is tightly associated with the kinds of prey consumed by individual *P. ochraceus* (Pruitt et al. 2012). Sea star activity level is unrelated to their body size (generalized linear model [GLM]: $F_{1, 17} = 0.68$, $P = .42$).

Sea Star: Latency to Right

We used sea star's latency to right themselves as an estimate of their coordination, flexibility, and willingness to traverse the sides of our mesocosms or other irregularly surfaced environments (e.g., tide pools). Snails use the sides of mesocosms as a refuge from predation, and observations during another set of experiments with *P. ochraceus* indicated that some sea stars freely move up the sides of enclosures whereas others do not. Some sea stars will even orient several of their arms and their mouth upward toward groups of snails clustered together out of the water, exhibiting much flexibility. We therefore predicted that sea star flexibility and coordination might be an important determinant of their hunting performance in our experiments. Each sea star was placed in an open field (1.5 m × 0.75 m) flow-through seawater table upside down. We then recorded the latency for the sea star to right itself. The sea star was deemed righted when the ventral side of all five arms and the central portion of its body were in direct contact with the bottom of the enclosure. Sea stars vary widely in their latency to right themselves, and this metric is unrelated to their body size (GLM: $F_{1, 17} = 0.0009$, $P = .97$).

Sea Star: Aggressiveness

Each focal sea star was placed in a flow-through seawater table containing a rival sea star in possession of a mussel. Stimulus sea stars were housed in a Plexiglas cage immediately beneath the pipe that fed water into the seawater table, and the focal sea star was placed approximately 50 cm downstream of the stimulus sea star. *Pisaster* are attracted to chemical cues of foraging conspecifics, which presumably provide social information about food availability, leading to intense predator aggregations at some sites and predator absence at others. Sea stars can also steal prey from each other, fight (arm fencing), and even cannibalize each other (Menge and Menge 1974; McClintock et al. 2008). Thus, approaching a rival conspecific is not entirely without risk. We recorded the latency for the focal sea star to approach a foraging stimulus star and the minimum distance achieved over the course of 20 min. A focal sea star was deemed to have approached the stimulus star if the center of its body closed within 10 cm of the stimulus star's holding container. This distance corresponded to the focal sea star being in physical contact with the holding container in nearly 100% of trials. There were eight stimulus sea stars that were not used for any other purpose. The identity of the stimulus star was recorded for each trial, and we endeavored to use stimulus stars of similar body size (±15% of each other's arm length). The arm lengths of our focal sea stars ranged from 15 to 32 cm. Stimulus sea star identity was not significantly associated with a focal star's minimum approach distance ($F_{6, 72.88} = 0.37$, $P = .87$), which is the behavioral metric that we will focus on here. Sea star's minimum approach distance is related to their body size (GLM: $F_{1, 17} = 7.82$, $P = .01$), where larger sea stars move closer to foraging rivals. We reason that approaching rivals may be less risky for larger individuals.

When assessing repeatability of sea star aggressiveness (minimum approach distance) at the end of our studies, care was taken to alternate the identity of the stimulus star across consecutive measures. We conducted one aggressive

test per day for five consecutive days in May 2016 to assess short-term repeatability in sea star aggressiveness. To evaluate long-term consistency in sea star aggressiveness, we conducted another two aggression assays 2 months later in September 2016 and tested for an association between sea stars' average response in May 2016 and their average response 2 months later.

To further verify that *P. ochraceus* are attracted to foraging conspecifics more so than nonforaging conspecifics or mussels alone, we conducted a post hoc experiment in September 2016 comparing the minimum approach distance of 10 *P. ochraceus* to a mussel in a holding chamber, a nonforaging conspecific in a holding chamber, or a foraging conspecific in a holding chamber. The order of presentation and the identity of the nonfocal sea star were randomly determined for each trial. Each sea star was presented with all three treatments in the same day, again in a randomized order (app. A; apps. A, B are available online).

Snail: Predator Avoidance Behavior

Whole groups of 20 individually marked snails were placed along the edge at the bottom of a circular rope cooler (radius = 38 cm) containing 4 cm of fresh seawater. After 2 min of acclimation, a sea star was placed centrally within the container. *Chlorostome funebralis* respond to *Pisaster* chemical cues by crawling out of the water (Markowitz 1980; Doering and Phillips 1983). We performed scan samples every 2 min for the next 20 min and recorded whether each snail breached the water surface and the height each snail moved above the water surface, to the nearest centimeter. We deemed individuals that emerged farther out of the water to be more fearful or responsive to predators than other individuals. We focused on snails' predator avoidance behavior here because this metric was an informative predictor of prey survival rates in a prior study on predator-prey interactions in this system, and individual differences in this behavior are highly repeatable in northern populations near Bodega Bay ($r = 0.66$; Pruitt et al. 2012). However, to confirm that this antipredator measure was repeatable in our source population, we collected a pool of 30 *C. funebralis* and tested their predator avoidance behavior once each week for five consecutive weeks. The snails used to evaluate repeatability were not used for any other purpose.

Social context is known to have an impact on the expression of personality in many animals (Magnhagen and Bunnefeld 2009; Farine et al. 2015b). Yet we chose to examine snail predator avoidance behavior in groups (1) because this is the social context in which snails sense and respond to sea stars in nature (*C. funebralis* cluster in groups in the wild; Paine 1969) and (2) because we wanted to test snails under the same social conditions in which they would inter-

act with predators during their staged trials (i.e., in groups of 20 individuals).

Staged Predator-Prey Trials

The same groups of 20 snails were placed in a flow-through seawater table (1.5 m × 0.75 m × 40 cm) along the edges of the arena. Standpipes were cut and placed to create a water depth of 20 cm. After 5 min of acclimation, four randomly selected sea stars were introduced to the arena. We placed one sea star in each of the corners of the arena, and care was taken not to place the sea stars directly atop any of the snails. A Plexiglas sheet was then placed atop the seawater table to prevent animals from escaping, and sea stars and snails were left to interact for the next 7 days.

Predators were either allowed to or prevented from interacting with one another. In our noninteracting predator treatment, Plexiglas dividers physically separated all four sea stars. Arches (7 cm wide, 6 cm high) were cut in both the bottom and top of the dividers, which allowed snails to move between cells containing individual predators but trapped each predator into a specific quarter of the arena. In our interacting predator treatment, Plexiglas dividers were placed within the arena, but this time very large arches were cut into the bottom of the dividers (25 cm wide, 10 cm high), which allowed both predators and prey to move freely about the environment. Our ability to successfully manipulate predator-predator interactions using these dividers was evident by the fact that no predators were observed in direct physical contact during daily checks in our noninteracting predator treatment. In contrast, at least two predators per enclosure were in direct physical contact with each other during each daily check in our predator interacting treatment. Frequently, all four predators were clustered together in just one corner. We conducted 10 replicates of each predator-predator interaction treatment; however, one replicate was removed from our analysis because two of the sea stars spawned in the arena. The average behavioral hypervolumes of our predator interacting and noninteracting treatment groups did not differ significantly (t-test [$t = -2.04$, $P = .06$] or Wilcoxon signed-rank [$W = 23$, $P = .08$]).

At the end of each 7-day trial, we recollected all of the remaining snails, recorded their identity, removed the sea stars and standpipes, and scrubbed the enclosure. The next trial was initiated within 48 h. A wasting disease has recently decimated the sea star populations of the western United States (Bates et al. 2009; Hewson et al. 2014). Thus, to conduct a sizeable number of replicates in a responsible manner, it was necessary to use individual sea stars in more than one trial. However, each combination of four sea stars was unique for each trial. Also, for animal welfare purposes, care was taken to provide each sea star with at

least 7 days of rest between trials. Sea stars were provided with mussels ad lib. during these resting periods.

Statistical Methods

To estimate the behavioral hypervolume occupied by each group of four sea stars, we calculated the volume of the minimum convex polyhedron in behavioral space using each sea star's activity level (the average of five measures), latency to right (single measure), and the minimum distance of approach toward a rival sea star (single measure). To allow for comparison among behaviors, each measure was first scaled by subtracting the mean of the behavioral measure and dividing by the standard deviation (i.e., z-transformed). In the behavioral hypervolume analysis, each predator becomes a single point in a three-dimensional behavioral space, and we calculated the volume of the convex polyhedron captured between the four sea stars comprising each replicate. To illustrate the three-dimensional behavioral hypervolume of sea stars in our experiment, we present in figure 1 the behavioral hypervolumes of a few sample replicates and all sea stars together. The behavioral hypervolumes of all replicates are provided in appendix B. Volumes were computed in MATLAB using the convhulln function.

One must consider that using hypervolumes as a multivariate metric of trait diversity is not without drawbacks. Hypervolumes and other extrema statistics have been used in a variety of other subfields of ecology, and their pros and cons are consequently quite well documented (Blonder et al. 2014; Barros et al. 2016). First, when comparing hypervolumes across groups, the number of dimensions used will shape hypervolume estimates and thus should be held constant to ensure comparability. Second, all units will need to be standardized, centered, and scaled, and axes should generally not be highly correlated. Third, particular care must be taken when selecting which traits to add to a hypervolume analysis, because a lack of variability in some traits or the addition of superfluous traits will weaken the analysis. Fourth, like all extrema statistics, estimates of a behavioral hypervolume are sensitive to sampling effort and sampling bias. Although population estimates of extrema statistics do eventually converge on stable values, they do so more slowly and less reliably than some other approaches. However, in spite of all of these concerns, hypervolume statistics are still commonly used by a variety of fields of ecology and are well suited for many multivariate questions, such as those regularly posed by animal personality research.

We assessed the predictive value of the behavioral hypervolume occupied by predators against a variety of univariate extrema and principal component statistics using the Akaike information criterion (AIC). This procedure helped eliminate issues of multicolinearity and sim-

plified the process of comparing rival metrics. Models were compared using AIC and Akaike weights; lower AICs and higher Akaike weights convey superior (more informative) models (Akaike 1987; Burnham and Anderson 2002). An identical series of models were constructed for each of two response variables: (1) the proportion of prey that survived the duration of the experiment and (2) the selection gradient imposed on snails' predator behavior within each replicate.

Selection gradients were estimated using logistic regression analysis, with individual survival as the response variable and individuals' predator avoidance behavior as the predictor variable (for a detailed methodology, see Janzen and Stern 1998; Calsbeek and Irschick 2007). Individuals' predator avoidance behavior scores were transformed to mean 0 and unit variance for selection analysis. A separate selection gradient was estimated for each replicate (group of 20 snails).

To examine the effect of predator behavior and physical interactions on prey survival and selection gradient, we compared the following models: (1) predator interaction treatment ($\pm$ predator interactions), behavioral hypervolume occupied by the predators, and their interaction term; (2) interaction treatment, range of activity levels exhibited by predators, and their interaction term; (3) interaction treatment, range of latencies to right, and their interaction term; (4) interaction treatment, range of minimum approach distances, and their interaction term; (5) interaction treatment, range of principal component (PC) 1 scores, and their interaction term; (6) interaction treatment, range of PC2 scores, and their interaction term; (7) interaction treatment, the product of the ranges of PC1 and PC2, and the interaction term between this product and treatment; (8) interaction treatment only; (9) a behavioral hypervolume only; and (10) an intercept-only null model. Models were deemed to be superior if their AIC score was 2 or more points lower than rival models. Effect sizes are provided as least squares means and 95% confidence intervals (CIs) and unstandardized regression (β) coefficients with 95% CIs. Effect sizes and CIs were estimated using maximum likelihood. Full information on our principal components analysis is provided in table 1. The above analyses were run in JMP 12.0. Repeatabilities of sea stars' minimum approach distance to rivals and snail's predator avoidance responses were estimated using the intraclass correlation coefficient (ICC) package in R.

Results

Whether or not predators were allowed to interact with one another had the greatest impact on the selection gradient on prey avoidance behavior. When comparing models for predicting selection gradients on prey traits, the model including predator interaction treatment and no other predictor variables
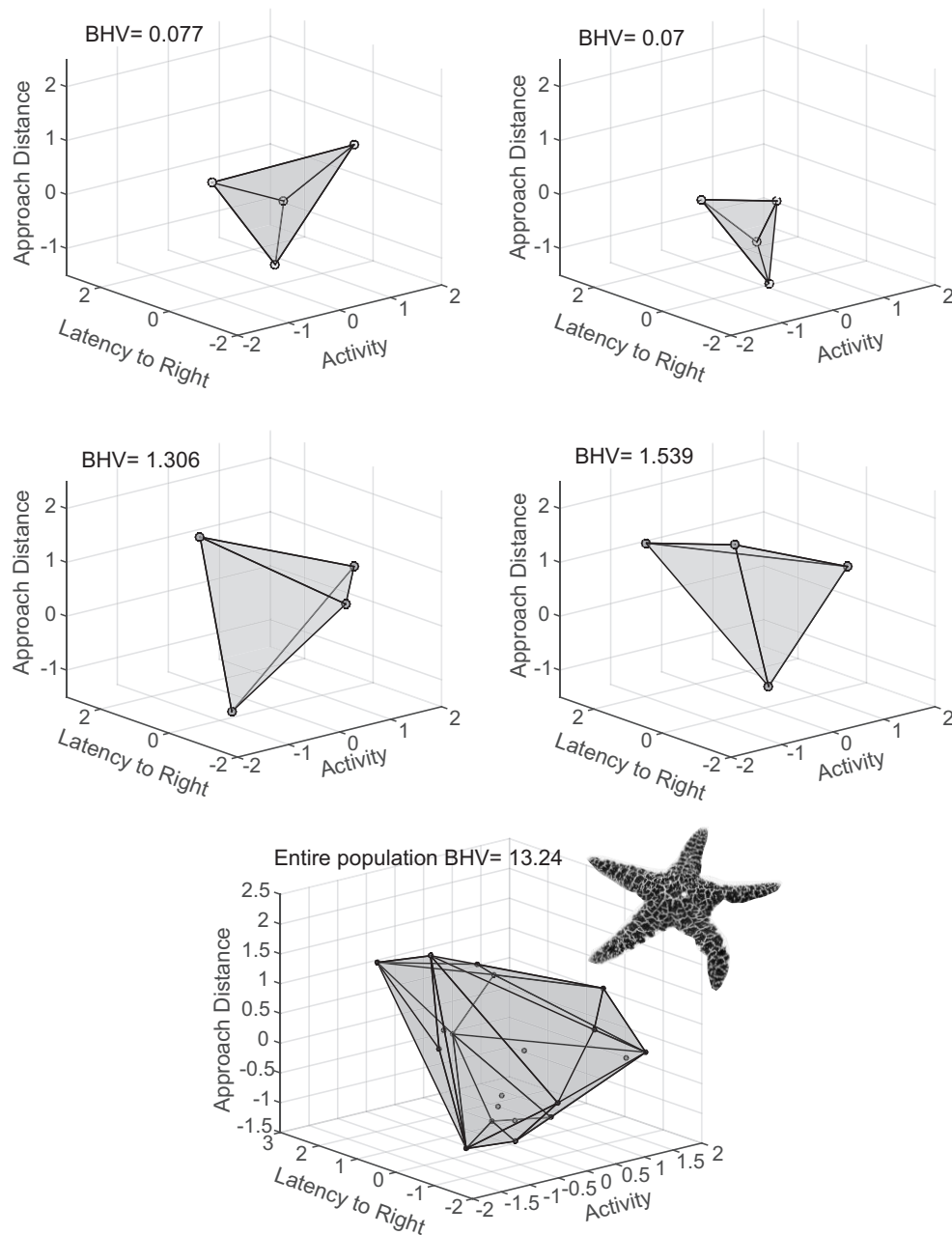
Figure 1: Graphical depiction of the behavioral hypervolume (BHV) occupied by *Pisaster ochraceus* trial groups with a low BHV (*top*) and a high BHV (*middle*) and BHV of all sea stars used in the experiment (*bottom*). The three behavioral axes depicted are activity level in an open field, latency to right when overturned, and minimum distance each sea star approached a rival sea star. Values were *z*-transformed. Each circle represents a single sea star, which was run once through each behavioral assay.

exhibited an Akaike weight nearly twice that of any rival model (table 2; fig. 2; corrected AIC [AICc] $= -11.43$, $\omega = 0.31$). Preventing predators from interacting with each other physically resulted in a stronger selection gradient on predator avoidance behavior, where more reactive (flight-prone or fearful) snails enjoyed higher survivorship (predators inter-

acting least squares mean $= 0.20$, 95% CI $= 0.10$–0.30). In contrast, we did not detect a significant selection gradient on predator avoidance behavior when predators were allowed to interact with one another physically (predators noninteracting least squares mean $= 0.015$, 95% CI $= -0.09$ to 0.12). Daily visual checks consistently revealed very high

Table 1: Principal component (PC) analysis of the predators' behavioral traits

			Loadings		
PC	Eigenvalue	Variance explained (%)	Activity level	Latency to right	Minimum distance to approach
PC1	1.33	44.31	−.56	.62	.8
PC2	.98	32.56	.74	.66	.01
PC3	.69	23.13	.38	−.44	.6

Note: Factors included in the analysis were sea star activity level, latency to right, and minimum distance with which they approached a rival sea star.

levels of predator aggregation when predators were allowed to interact freely, potentially suggesting a role of physical interactions, interference competition, or conspecific attraction (e.g., in response to cues of successfully foraging conspecifics) in these outcomes.

When predator groups occupied larger behavioral hypervolumes, prey were less likely to survive. The single best model predicting the proportion of prey that survived the duration of the experiment included the behavioral hypervolume occupied by the group of predators and no other terms (AICc = −23.03, ω = 0.95). The Akaike weight of this model was more than 20 times greater than the next best model (table 2). In this model, groups of predators that occupied a larger region in behavioral space killed a larger proportion of prey snails (β = −0.30, 95% CI = −0.33 to −0.07; fig. 3).

Because variation in individual fitness provides the underlying opportunity for selection on prey traits, we further conducted a post hoc exploratory analysis to test for an association between prey survival rates (predictor variable) and the selection gradients that predators imposed on prey traits (response variable). We also included predator interaction treatment and its interaction term with prey survival rate as predictor variables in our model. All three terms were significant (predator interaction treatment: $F_{1,15}$ = 6.56, P = .02; prey survival rates: $F_{1,15}$ = 6.50, P = .02; predator interaction treatment × prey survival rates: $F_{1,15}$ = 19.77, P = .0005). Lower prey survival rates were associated with greater positive selection on predator avoidance behavior in prey; however, this held only for situations where predators were prevented from interacting with one another freely. The relationship between prey survival rates and selection on prey traits was flat when predators were free to move about and interact (fig. 4).

Sea stars' minimum approach distance toward foraging rival sea stars was found to be highly repeatable across five consecutive days (ICC = 0.45, 95% CI = 0.24–0.68). Behavioral consistency within this context is further verified by a strong positive correlation between sea star's average responses in May versus September 2016 (r = 0.62, df =

19, P = .004; app. A). Activity level (r = 0.65, df = 19, P = .002) and sea star's latency to right (r = 0.67, df = 19, P = .001) were similarly consistent across several months (app. A). Likewise, snail predator avoidance behavior was consistent over the course of 5 weeks (ICC = 0.49, 95% CI = 0.32–0.66). Finally, as indicated by various natural history observations on this species, we found that sea star's minimum approach distance toward foraging conspecifics was 50%–75% lower than their approach distances toward prey mussels alone or nonforaging conspecifics ($F_{2,27}$ = 9.88, P < .0001; app. A).

Discussion

Although individual variation in behavior is known to have a variety of ecological effects, whether the combined behavioral diversity of populations impacts ecological outcomes remains unresolved. We argue that a multitrait perspective is an important next step because no phenotype (behavior or otherwise) ever operates in isolation. Here we examined the degree to which the multidimensional behavioral diversity of predator groups mediates their interaction with prey and whether these relationships change on the basis of whether predators are permitted to interact with one another physically. Multidimensional behavior diversity was estimated here as the behavioral hypervolume occupied by predator groups in behavioral space and via various principle component methods (ranges of PC1, PC2, and the product of these ranges). Consistent with a priori predictions, we found that more behaviorally diverse predator groups killed a larger number of prey (fig. 3). However, selection on prey traits appeared to be unrelated to the behavioral hypervolume occupied by predator groups. Instead, we found that selection on prey traits was primarily determined by predator-predator interactions. Snails with higher predator avoidance scores enjoyed superior survival when predators were prevented from interacting, but the advantage of predator avoidance behavior was lost when predators could interact with one another physically and freely move about the environment. This difference in treatments was most pronounced in the most lethal of the noninteracting predator replicates

Table 2: Comparison of our models predicting the predator-driven selection gradients on prey's predator avoidance behavior and the proportion of snails that were killed by sea stars over the course of the trial

Model	df	R^2	F	P	AICc	ΔAICc	Akaike weight
Selection gradient:							
Treatment	1, 17	.28	6.67	.019	−11.43	0	.314
Hypervolume	1, 17	.23	5.22	.035	−10.23	1.2	.172
Treatment, range of PC1 scores, treatment × range of PC1 scores	3, 15	.46	4.30	.02	−9.94	1.49	.149
Treatment, hypervolume, treatment × hypervolume	3, 15	.45	4.07	.026	−9.46	1.97	.117
Treatment, product range PC1 × PC2, treatment × product range PC1 × PC2	3, 15	.42	3.69	.04	−8.64	2.79	.078
Intercept	0, 18				−8.01	3.42	.057
Treatment, range of activity levels, treatment × range of activity levels	3, 15	.40	4.21	.047	−7.89	3.54	.054
Treatment, range latency to right, treatment × range latency to right	3, 15	.37	2.89	.069	−6.83	4.6	.032
Treatment, range of minimum approach distance, treatment × range of minimum approach distance	3, 15	.32	2.32	.12	−5.39	6.04	.015
Treatment, range of PC2 scores, treatment × range of PC2 scores	3, 15	.29	2.09	.14	−4.79	6.64	.011
Proportion of prey surviving:							
Hypervolume	1, 17	.55	20.74	.0003	−29.19	0	.945
Treatment, hypervolume, treatment × hypervolume	3, 15	.57	6.61	.0046	−23.03	6.16	.043
Treatment	1, 17	.22	4.31	.053	−18.37	10.82	.004
Treatment, range of PC1 scores, treatment × range of PC1 scores	3, 15	.42	3.75	.03	−17.66	11.53	.003
Intercept	0, 18				−16.89	12.3	.002
Treatment, range latency to right, treatment × range latency to right	3, 15	.38	3.09	.06	−16.18	13.01	.001
Treatment, range of minimum approach distance, treatment × range of minimum approach distance	3, 15	.29	2.09	.14	−13.68	15.51	.000
Treatment, range of activity levels, treatment × range of activity levels	3, 15	.31	2.13	.14	−12.77	16.42	.000
Treatment, product range PC1 × PC2, treatment × product range PC1 × PC2	3, 15	.43	3.69	.04	−8.64	20.55	.000
Treatment, range of PC2 scores, treatment × range of PC2 scores	3, 15	.29	2.09	.14	−4.79	24.4	.000

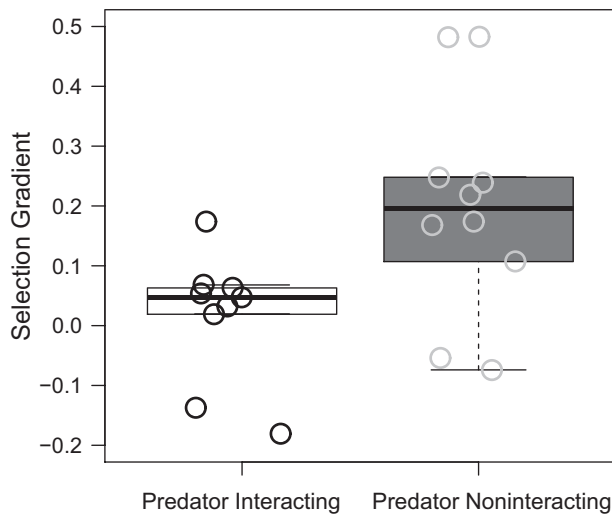Note: AICc, corrected Akaike information criterion; PC, principal component.

Figure 2: Selection coefficients on prey's predator avoidance behavior when predators were permitted to interact with one another freely (*left*) and when they were prevented from interacting with one another via physical barriers (*right*). Horizontal lines within boxes indicate the median, boxes indicate the lower and upper quartiles, and whiskers extend to the 1.5 interquartile range. Circles indicate individual observations.

(fig. 4). Taken together, it appears that behavioral hypervolumes and predator-predator interactions combine to mediate the effects of predators on their prey.

Predator-Predator Interactions and Selection on Prey Traits

Predator-predator interactions changed the selection gradients that predators imposed on prey traits. When predators were prevented from interacting with each other physically, we observed that more fearful prey with higher predator avoidance scores enjoyed superior survivorship. This is consistent with results seen in some systems (Riechert and Hedrick 1990; Storfer and Sih 1998; Biro et al. 2004) but not others (Reale and Festa-Bianchet 2003; Smith and Blumstein 2010). However, this relationship vanished when predators were permitted to interact with one another freely and no single snail phenotype enjoyed higher survivorship. This softening of selection—but not predator lethality (fig. 4)—could help to promote phenotypic diversity in prey populations. When sea stars were permitted to interact, we regularly observed tight aggregations of predators in corners of enclosures, often immediately beneath a cohort of snails that had fled above the water surface. It is perhaps possible that the barriers that prevented sea stars from interacting with one another physically also provided snails with additional refugia or other mechanisms of deploying

predator avoidance strategies (e.g., moving across a barrier when being pursued). However, we observed a nonsignificant trend of higher mortality rates in our predator noninteracting treatment, that is, when the barriers were present (fig. 3). It is further possible that interference competition among predators prevented predators from deploying their preferred foraging strategies, resulting in a more haphazard distribution of prey phenotypes among those snails that perished versus those that survived. Indeed, our observations of dense predator aggregations during virtually all of our daily checks suggest that interference competition (e.g., predators stealing prey and threatening each other) is a plausible explanation for these patterns.

A final hypothesis is that predator-predator interactions in the form of aggregations are responsible for the observed shifts in selection on prey traits. *Pisaster ochraceus* are known to aggregate in response to chemical cues of successfully foraging conspecifics (Paine 1969; Fawcett 1984; Robles et al. 1995), and aggregation was regularly observed during our experiments. This kind of predator-predator interaction effectively concentrates risk into predation hotspots and produces cold spots (predator-free zones) where
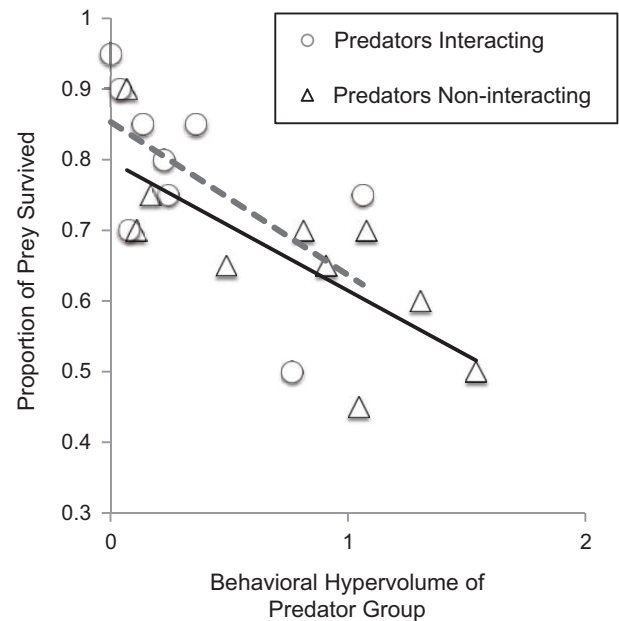

Figure 3: Relationship between the volume occupied by predator sea star groups in behavioral space and the proportion of prey snails that survived the trial period: predator interacting treatment (circles, dashed line) and predator noninteracting treatment (triangles, solid line). There were no significant differences between predator interaction treatments in the number of prey killed or the relationship between prey mortality and the behavioral hypervolume occupied by predator groups.
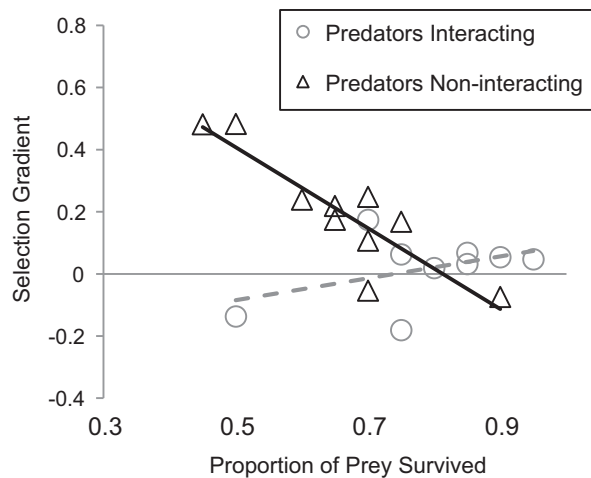
Figure 4: Relationship between the proportion of prey that survived the trial and selection on predator avoidance behavior: predator interacting treatment (circles, dashed line) and predator noninteracting treatment (triangles, solid line). When predators were prevented from interacting freely, more lethal sea star groups generated stronger positive selection on prey's antipredator behavior. No such relationship was detected when predators were permitted to move around freely in the environment (interaction treatment × proportion surviving: $F_{1, 15} = 19.77$, $P = .0005$).

prey of many phenotypes could escape. In a sense, predator-predator aggregations such as these can create a landscape of fear, but one driven by social interactions among predators and not landscape features per se (Laundre et al. 2001; Suraci et al. 2016). A further consideration is that the movement of predators becomes nonindependent under these conditions, resulting in predators moving together like one giant collective entity. This too could alter selection on prey traits. Social interactions such as these are a kind of predator-predator interaction—and an important one—that we had not considered a priori. Such aggregations are also quite common in a variety of other systems: flocks of birds gathering around successfully foraging conspecifics at experimental feeders (Aplin et al. 2015; Farine et al. 2015*a*), Komodo dragons cuing in on the volatile blood scent of recently bitten buffalo (Walpole 2001), bats recruiting to each other's feeding buzzes (Gillam 2007), and so on. Such tendencies to aggregate often override aspects of interference competition that would otherwise prevent grouping behavior. We therefore reason that our results could be generalizable to a variety of other group-hunting or group-foraging species.

Behavioral Hypervolumes and Prey Survival Rates

We further found that more behaviorally diverse predator groups were more lethal to their prey. In a prior study, we

found a relationship between the activity level of a sea star and the personality type of the snails it captures. Active sea stars tend to capture snails with less pronounced predator avoidance behavior, and sedentary sea stars tended to capture snails with more pronounced predator avoidance behavior (Pruitt et al. 2012). Similar associations between the behavioral tendencies of individual predators and the selection gradients they impose on prey behavior have since been identified in several other systems (DiRienzo et al. 2013; McGhee et al. 2013; Sweeney et al. 2013). We thus predicted here that more behaviorally diverse groups of sea stars would kill a larger number of prey because, for any one prey type, there is a greater chance that at least one of the predators present would exhibit a behavioral phenotype that is adept at killing snails of that type. Indeed, more behaviorally diverse predator groups tended to capture more snails, and this effect was nontrivial. Behaviorally homogenous predator groups often killed <15% of snails, whereas behaviorally diverse predator groups killed more than 50% of the snails, given equal amounts of time (fig. 3). At odds with our last study, predator activity level by itself was not a highly informative predictor of this relationship, and neither were any of the other single trait or multivariate trait models (table 2). Instead, our data suggest that multi-dimensional metrics that capture the irregular contours of the trait space occupied by predator groups are a more powerful predictor than measures of lower dimensionality. This result is intriguing because it suggests that single-variable approaches and dimension-reducing multivariate methods may be outperformed by hypervolume statistics in predicting some ecological outcomes.

The mechanisms underlying the increased lethality of behaviorally diverse groups of predators are admittedly uncertain. However, we feel that the most likely explanation is that variation in activity level, aggressiveness, and latency to right (coordination/flexibility) map to important differences in predator foraging mode and style. How activity level is predicted to impact foraging mode is perhaps the most intuitive, because activity level is the defining trait behind that classic categorizations of predators foraging modes: sit-and-wait versus active predators. Differences in predator aggressiveness—measured here as individuals' tendency to approach foraging rivals—are also likely to impact the lethality of predator groups. More aggressive individuals are intuitively more likely to join foraging conspecifics and subsequently move, hunt, and feed in physical contact with other sea stars. In contrast, less aggressive individuals are predicted to hunt primarily as solitary, fearful entities. Having both types of predators in the mesocosm may help to ensure that no one prey strategy can consistently evade all predator foraging types (singleton vs. aggregated predators). Finally, latency to right plausibly maps to sea star's willingness to explore the sides of their enclosures

or to maneuver near and around physical barriers. Here again, having individuals with various levels of coordination may help to create a heterogeneous landscape that prevents any one prey type from enjoying high survivorship. More detailed observations of individual sea stars with different behavioral tendencies and also groups of predators occupying various behavioral hypervolumes are needed to critically evaluate these predictions.

Behavioral Hypervolumes Revisited

Finally, our data indicate that behaviorally diverse groups or heterogeneous populations could outperform homogenous groups or populations. Prior studies on acorn ants (Modlmeier and Foitzik 2011; Modlmeier et al. 2012), social spiders (Pruitt and Riechert 2011; Pruitt et al. 2011), honeybees (Mattila and Seeley 2007; Burns and Dyer 2008), mosquito fish (Fogarty et al. 2011), and various mix-species bird flocks and ungulate herds (Morse 1970; Dolby and Grubb 1998) have found that phenotypically diverse groups enjoy superior performance. Such positive effects can stem from adaptive division of labor (Beshers and Fewell 2001), reduced competition among group mates (Bergmuller and Taborsky 2010), adaptive social niche construction (Saltz and Nuzhdin 2014), or other aspects of trait complementarity. In contrast to many other systems, *P. ochraceus* groups are not highly cooperative, yet there is still a positive effect of within-group variability on collective performance, even when the sea stars could not interact with one another physically (fig. 3). This result is similar to experimental work in agroecosystems, which has shown that behaviorally diverse groups of predators are better at suppressing pests (wolf spiders: Royaute and Pruitt 2015; parasitoid wasps: Finke and Snyder 2008). Thus, there is now a taxonomically diverse and growing body of literature that behaviorally diverse groups function better (or at least differently) than homogenous groups. We also note that this signature holds for a variety of systems, including loosely aggregative species, cooperative breeders, and eusocial societies in marine, freshwater, terrestrial, and agricultural systems as well as vertebrates and invertebrates. The novel element of our results here on *P. ochraceus* is that it is the multidimensional behavioral diversity of groups that appears to be most informative and important. This is in contrast to the prior studies mentioned above, where singular axes of trait variability (e.g., aggressiveness, sociability, decision-making rules, prey preferences) are informative on their own. We therefore urge other investigators to examine the effects of multidimensional behavioral diversity in other groups and even populations of nonsocial animals. Such investigations will help us further explore and document the generality of such relationships across the animal kingdom.

Literature Cited

Akaike, H. 1987. Factor-analysis and AIC. Psychometrika 52:317–332.

Aplin, L. M., J. A. Firth, D. R. Farine, B. Voelkl, R. A. Crates, A. Culina, C. J. Garroway, et al. 2015. Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. Animal Behaviour 108:117–127.

Barros, C., W. Thuiller, D. Georges, I. Boulangeat, and T. Munkemuller. 2016. *N*-dimensional hypervolumes to study stability of complex ecosystems. Ecology Letters 19:729–742.

Bates, A. E., B. J. Hilton, and C. D. G. Harley. 2009. Effects of temperature, season and locality on wasting disease in the keystone predatory sea star *Pisaster ochraceus*. Diseases of Aquatic Organisms 86:245–251.

Belgrad, B. A., and B. D. Griffen. 2016. Predator-prey interactions mediated by prey personality and predator hunting mode. Proceedings of the Royal Society B 283:20160408.

Bergmuller, R., and M. Taborsky. 2010. Animal personality due to social niche specialisation. Trends in Ecology and Evolution 25:504–511.

Beshers, S. N., and J. H. Fewell. 2001. Models of division of labor in social insects. Annual Review of Entomology 46:413–440.

Biro, P. A., M. V. Abrahams, J. R. Post, and E. A. Parkinson. 2004. Predators select against high growth rates and risk-taking behaviour in domestic trout populations. Proceedings of the Royal Society B 271:2233–2237.

Blonder, B., C. Lamanna, C. Violle, and B. J. Enquist. 2014. The *n*-dimensional hypervolume. Global Ecology and Biogeography 23:595–609.

Bolker, B., M. Holyoak, V. Krivan, L. Rowe, and O. Schmitz. 2003. Connecting theoretical and empirical studies of trait-mediated interactions. Ecology 84:1101–1114.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Burns, J. G., and A. G. Dyer. 2008. Diversity of speed-accuracy strategies benefits social insects. Current Biology 18:R953–R954.

Calsbeek, R., and D. J. Irschick. 2007. The quick and the dead: correlational selection on morphology, performance, and habitat use in island lizards. Evolution 61:2493–2503.

Cote, J., S. Fogarty, T. Brodin, K. Weinersmith, and A. Sih. 2011. Personality-dependent dispersal in the invasive mosquitofish: group composition matters. Proceedings of the Royal Society B 278:1670–1678.

Creel, S., J. A. Winnie, D. Christianson, and S. Liley. 2008. Time and space in general models of antipredator response: tests with wolves and elk. Animal Behaviour 76:1139–1146.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397.

DiRienzo, N., J. N. Pruitt, and A. V. Hedrick. 2013. The combined behavioural tendencies of predator and prey mediate the outcome of their interaction. Animal Behaviour 86:317–322.

Doering, P. H., and D. W. Phillips. 1983. Maintenance of the shore-level size gradient in the marine snail *Tegula funebralis* (A. Adams): importance of behavioral responses to light and sea star predators. Journal of Experimental Marine Biology and Ecology 67:159–173.

Dolby, A. S., and T. C. Grubb. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. Animal Behaviour 56:501–509.

Farine, D. R., J. A. Firth, L. M. Aplin, R. A. Crates, A. Culina, C. J. Garroway, C. A. Hinde, et al. 2015a. The role of social and ecological processes in structuring animal populations: a case study from automated tracking of wild birds. Royal Society Open Science 2: 150057.

Farine, D. R., P.-O. Montiglio, and O. Spiegel. 2015b. From individuals to groups and back: the evolutionary implications of group phenotypic composition. Trends in Ecology and Evolution 30:609–621.

Fawcett, M. H. 1984. Local and latitudinal variation in predation on an herbivorous marine snail. Ecology 65:1214–1230.

Finke, D. L., and W. E. Snyder. 2008. Niche partitioning increases resource exploitation by diverse communities. Science 321:1488–1490.

Fogarty, S., J. Cote, and A. Sih. 2011. Social personality polymorphism and the spread of invasive species: a model. American Naturalist 177:273–287.

Gillam, E. H. 2007. Eavesdropping by bats on the feeding buzzes of conspecifics. Canadian Journal of Zoology 85:795–801.

Griffen, B. D., B. J. Toscano, and J. Gatto. 2012. The role of individual behavior type in mediating indirect interactions. Ecology 93: 1935–1943.

Hewson, I., J. B. Button, B. M. Gudenkauf, B. Miner, A. L. Newton, J. K. Gaydos, J. Wynne, et al. 2014. Densovirus associated with sea-star wasting disease and mass mortality. Proceedings of the National Academy of Sciences of the USA 111:17278–17283.

Huey, R. B., and E. R. Pianka. 1981. Ecological consequences of foraging mode. Ecology 62:991–999.

Hughes, A. R., and J. J. Stachowicz. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proceedings of the National Academy of Sciences of the USA 101:8998–9002.

Janzen, F. J., and H. S. Stern. 1998. Logistic regression for empirical studies of multivariate selection. Evolution 52:1564–1571.

Laundre, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1401–1409.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Magnhagen, C., and N. Bunnefeld. 2009. Express your personality or go along with the group: what determines the behaviour of shoaling perch? Proceedings of the Royal Society B 276:3369–3375.

Markowitz, D. V. 1980. Predator influence on shore-level size gradients in *Tegula funebralis* (A. Adams). Journal of Experimental Marine Biology and Ecology 45:1–13.

Mattila, H. R., and T. D. Seeley. 2007. Genetic diversity in honey bee colonies enhances productivity and fitness. Science 317:362–364.

McClintock, J. B., R. A. Angus, C. Ho, C. D. Amsler, and B. J. Baker. 2008. A laboratory study of behavioral interactions of the Antarctic keystone sea star *Odontaster validus* with three sympatric predatory sea stars. Marine Biology 154:1077–1084.

McGhee, K. E., L. M. Pintor, and A. M. Bell. 2013. Reciprocal behavioral plasticity and behavioral types during predator-prey interactions. American Naturalist 182:704–717.

Menge, J. L., and B. A. Menge. 1974. Role of resource allocation, aggression and spatial heterogeneity in coexistence of two competing intertidal starfish. Ecological Monographs 44:189–209.

Modlmeier, A. P., and S. Foitzik. 2011. Productivity increases with variation in aggression among group members in *Temnothorax* ants. Behavioral Ecology 22:1026–1032.

Modlmeier, A. P., J. E. Liebmann, and S. Foitzik. 2012. Diverse societies are more productive: a lesson from ants. Proceedings of the Royal Society B 279:2142–2159.

Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. Ecological Monographs 40:119–168.

Paine, R. T. 1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. Ecology 50:950–961.

Preisser, E. L., J. L. Orrock, and O. J. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. Ecology 88:2744–2751.

Pruitt, J. N. 2013. A real-time eco-evolutionary dead-end strategy is mediated by the traits of lineage progenitors and interactions with colony invaders. Ecology Letters 16:879–886.

Pruitt, J. N., G. Iturralde, L. Aviles, and S. E. Riechert. 2011. Amazonian social spiders share similar within-colony behavioural variation and behavioural syndromes. Animal Behaviour 82:1449–1455.

Pruitt, J. N., and A. P. Modlmeier. 2015. Animal personality in a foundation species drives community divergence and collapse in the wild. Journal of Animal Ecology 84:1461–1468.

Pruitt, J. N., and S. E. Riechert. 2011. How within-group behavioral variation and task efficiency enhance fitness in a social group. Proceedings of the Royal Society B 278:1209–1215.

Pruitt, J. N., J. J. Stachowicz, and A. Sih. 2012. Behavioral types of predator and prey jointly determine prey survival: potential implications for the maintenance of within-species behavioral variation. American Naturalist 179:217–227.

Reale, D., and M. Festa-Bianchet. 2003. Predator-induced natural selection on temperament in bighorn ewes. Animal Behaviour 65: 463–470.

Riechert, S. E., and A. V. Hedrick. 1990. Levels of predation and genetically based antipredator behavior in the spider, *Agelenopsis aperta*. Animal Behaviour 40:679–687.

Robles, C., R. Sherwoodstephens, and M. Alvarado. 1995. Responses of a key intertidal predator to varying recruitment of its prey. Ecology 76:565–579.

Roughgarden, J. 1974. Niche width: biogeographic patterns among *Anolis* lizard populations. American Naturalist 108:429–442.

Royaute, R., and J. N. Pruitt. 2015. Varying predator personalities generates contrasting prey communities in an agroecosystem. Ecology 96:2902–2911.

Saltz, J. B., and S. V. Nuzhdin. 2014. Genetic variation in niche construction: implications for development and evolutionary genetics. Trends in Ecology and Evolution 29:8–14.

Scharf, I., E. Nulman, O. Ovadia, and A. Bouskila. 2006. Efficiency evaluation of two competing foraging modes under different conditions. American Naturalist 168:350–357.

Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. Science 319:952–954.

———. 2009. Effects of predator functional diversity on grassland ecosystem function. Ecology 90:2339–2345.

Sih, A., J. Cote, M. Evans, S. Fogarty, and J. N. Pruitt. 2012. Ecological implications of behavioral syndromes. Ecology Letters 15:278–289.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics 16:269–311.

Smith, B. R., and D. T. Blumstein. 2010. Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*). Behavioral Ecology 21:919–926.

Stachowicz, J. J., H. Fried, R. W. Osman, and R. B. Whitlatch. 2002. Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. Ecology 83:2575–2590.

Storfer, A., and A. Sih. 1998. Gene flow and ineffective antipredator behavior in a stream-breeding salamander. Evolution 52:558–565.

Suraci, J. P., M. Clinchy, L. M. Dill, D. Roberts, and L. Y. Zanette. 2016. Fear of large carnivores causes a trophic cascade. Nature Communications 7:10698.

Sweeney, K., R. D. H. Gadd, Z. L. Hess, D. R. McDermott, L. MacDonald, P. Cotter, F. Armagost, et al. 2013. Assessing the effects of rearing environment, natural selection, and developmental stage on the emergence of a behavioral syndrome. Ethology 119:436–447.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455–1474.

Toscano, B. J., and B. D. Griffen. 2014. Trait-mediated functional responses: predator behavioural type mediates prey consumption. Journal of Animal Ecology 83:1469–1477.

Van Valen, L. 1965. Morphological variation and width of ecological niche. American Naturalist 99:377–390.

Villeger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301.

Violle, C., M. L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.

Walpole, M. J. 2001. Feeding dragons in Komodo National Park: a tourism tool with conservation complications. Animal Conservation 4:67–73.

Whittaker, R. H., S. A. Levine, and R. B. Root. 1973. Niche, habitat, and ecotope. American Naturalist 107:321–228.

Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology and evolution. Trends in Ecology and Evolution 27:452–461.

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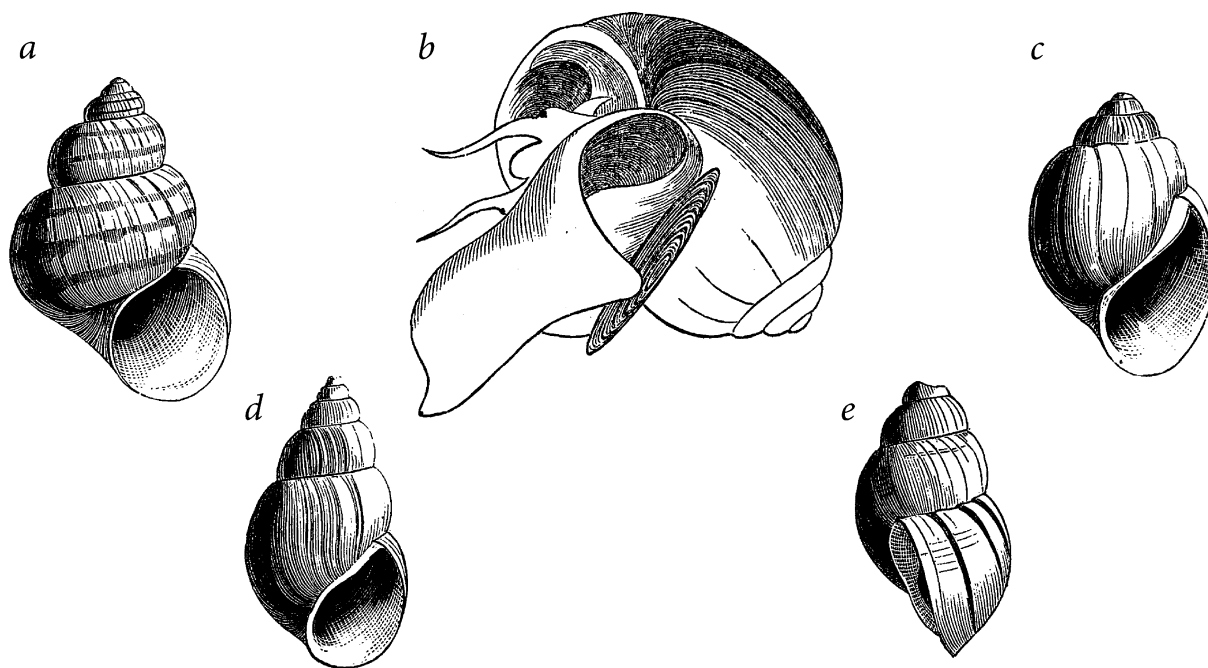
a, Vivipara contectoides W. G. Binney; *b* and *c, Melantho ponderosa* Say; *d, Melantho coarctata* Lea; *e, Melantho decisa* Say. From "Our Common Fresh-Water Shells" by E. S. Morse (*The American Naturalist*, 1869, 3:530–535).