



Original Article

Individual variation in predator behavior and demographics affects consumption of non-native prey

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Received 8 May 2014; revised 5 February 2015; accepted 9 February 2015; Advance Access publication 31 March 2015.

Non-native species can serve as a prey resource for native predators. Yet because there is often no shared evolutionary history between the predator and prey, individuals within a predator population may vary greatly in their willingness to consume a recently introduced, yet profitable prey. Here, we measured individual variation in diet, behavior, and demographic traits of the native predatory mud crab, *Panopeus herbstii*, and evaluated how these traits influenced an individual's consumption of a recently introduced, non-native crab, *Petrolisthes armatus*, using both simultaneous and no-choice assays. These same individual predatory mud crabs were also assayed to quantify their antipredator reaction and exploratory behavior. Results indicated significant variation in the diets of individual predators with 45% specializing on native mussels, 14% specializing on non-native *Petrolisthes*, and the remainder eating multiple prey species. When given a choice of alternative prey, individual *Panopeus* predators that consumed a larger proportion of *Petrolisthes* were female, smaller, and more likely to flee in response to predators. When given no choice of alternative prey, *Petrolisthes* was consumed more frequently by *Panopeus* that were female and less exploratory. We suggest that individuals that more readily consume non-native *Petrolisthes* may be attempting to reduce competition with conspecifics that are larger, more aggressive, exploratory, and male. Our results suggest that at least initially following invasion, adoption of a non-native prey species into the diet of a native predator may not occur universally within the population. Such nonuniform predation pressure could contribute to the non-native prey's release from natural enemies.

Key words: diet breadth, dietary conservatism, enemy escape hypothesis, neophobia, non-native prey, optimal foraging theory.

INTRODUCTION

Introductions of non-native species often alter predator–prey interactions, which are important drivers of many ecological and evolutionary processes (Mooney and Cleland 2001; Freeman and Byers 2006; Salo et al. 2007; Sih et al. 2010). However, because of the emphasis placed on understanding the negative impacts of invasive species, most studies of non-native species introductions have focused almost exclusively on the predatory roles of invaders as opposed to their role as prey (Carlsson et al. 2009). As prey, non-native species can serve as a new food source for native predators. Yet, the prevalence and success of many non-native species suggests that not all native predators readily adopt non-native prey into their diets (Colautti et al. 2004).

Conventional wisdom suggests that species with a wide ecological niche are more likely to succeed in adapting to novel conditions than

species with a narrow niche (Mayr 1965; Ehrlich 1989). Indeed, this hypothesis has provided a useful framework for testing the relationship between traits that typically correlate with niche generalism (i.e., ecological flexibility, behavioral innovation, and diet breadth) and the ability of species to invade novel environments (Lefebvre et al. 1997; Reader and MacDonald 2003). Likewise, this same framework could be used to understand traits that contribute to a native species' ability to successfully adapt to novel changes in its environment, such as the arrival of a non-native prey. Regardless of whether the predator or prey is non-native, evidence in support of the relationship between niche generalism and response to novelty has been mixed (Veltman et al. 1996; McLain et al. 1999; Kolar and Lodge 2001; Overington et al. 2011). For example, species with a generalist dietary niche (i.e., dietary generalism = niche generalism) do not always succeed in novel environments (Overington et al. 2011).

One reason for the variability in success among species that are dietary generalists is that these species may differ in terms of how variable generalist diets are among individuals in the population

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(Bolnick et al. 2003). For example, although the incorporation of new prey species into the diet of native predators might be associated with differences in niche breadth at the species level, there is also increasing evidence for variation in diet breadth at the individual level (Bolnick et al. 2003; Tinker et al. 2008). Generalist populations of fish, amphibians, and marine mammals are often composed of collections of individual specialists (Ford et al. 1998; Saulitis et al. 2000; Tinker et al. 2008), whereby some individuals specialize on one prey type and others within the same population specialize on a different prey type. An individual's diet could influence the consumption of a new prey species, depending on various factors such as the similarity between the native and non-native prey, ease of transferring foraging skills across species, and relative profitability of alternative prey types (Estes et al. 2003). This prevalence of within-population individual variation in diet can have important implications for the spread of novel behaviors (use of a novel resource) through a population as well as the amount of biotic resistance from predation pressure experienced by non-native prey.

Additionally, predator response to recently introduced, non-native prey might also be linked to within-population individual differences in personality (or alternatively behavioral syndromes, coping styles, or temperament) (Koolhaas et al. 1999; Gosling 2001; Sih et al. 2004; Reale et al. 2007). For example, individuals that are less exploratory might be more neophobic (Van Oers et al. 2005, but see Mettke-Hofmann et al. 2002; Herborn et al. 2010) and, thus, may be expected to be slower to adopt a new prey species into its diet. In contrast, an individual that is more exploratory might be less neophobic (i.e., neophilic) and, thus, faster to consume a novel food item. Yet an individual's initial response to novelty (i.e., neophobia) or willingness to explore might not necessarily be indicative of its propensity to incorporate a newly introduced prey species in the longer term (Marples and Brakefield 1995; Marples and Kelly 1999; Liebl and Martin 2014). Rather some individuals that overcome an initially fearful or neophobic response may still exhibit long-term avoidance of novel food, commonly referred to as dietary conservatism (Marples et al. 1998). The prevalence of dietary conservatism within a predator population has been shown to control the initial spread of prey phenotypes (e.g., prey color morphs within a population) within a population (Thomas et al. 2003, 2010; Marples and Mappes 2011) but could be equally as applicable to the spread of a novel, introduced species in a community. Therefore, individual variation in personality traits related to novelty could explain why a profitable introduced species may or may not be consumed by a native predator and ultimately elucidate how some non-native species escape their natural enemies.

A final factor that may influence dietary generalism in predators is demographic traits, such as body size and sex, which are also often found to influence diet (MacNulty et al. 2009; Hierlihy et al. 2013). For example, males and females often differ in dietary requirements (e.g., increased energy requirements for reproduction in females), which can lead to selection of different prey items (Williams and McBrayer 2011; Hierlihy et al. 2013). Body size often imposes fundamental and sometimes opposing constraints on predatory behaviors (e.g., larger fish have bigger gape sizes and bite force but slower burst acceleration to pursue prey; Nilsson and Bronmark 2000), which can influence the dietary niche of individuals (MacNulty et al. 2009). The most dramatic examples of body size affecting diet are exemplified by ontogenetic niche shifts such as those seen in freshwater fish (Osenberg et al. 1992). By affecting predator diet choice, intraspecific variation in behavior and morphology of native predators likely has important implications for

understanding how non-native species escape their natural enemies following introduction and, more broadly, for understanding optimal foraging and the evolution of diet breadth.

The recent invasion of the non-native, filter-feeding green porcelain crab, *Petrolisthes armatus*, in the South Atlantic Bight provides a potential prey item for the common mudcrab predator, *Panopeus herbstii*. *Petrolisthes* is a tropical crab that is historically reported from the coast of Brazil and the Pacific coast of Central America (Oliveira and Masunari 1995) and was first discovered near Cape Canaveral, FL (USA), around 1994 and has since spread north. By 2004, *Petrolisthes* was found to be fairly abundant in oyster reefs along the Georgia and South Carolina coasts (Hollebone and Hay 2007a, 2007b). Its expansion further northward is likely limited by cooler temperatures (Canning-Clode et al. 2011). In mesocosm trials, *Petrolisthes* was opportunistically consumed by some native fish and crab species, including *Panopeus* (Hollebone and Hay 2008), a relatively abundant native predator within oyster reefs occupied by *Petrolisthes* (Hollebone and Hay 2007a), and a known generalist predator, consuming oysters, mussels, and crabs (Dame and Vernberg 1982; Grabowski and Powers 2004). Although *Panopeus* has been shown to consume *Petrolisthes* (Hollebone and Hay 2007a), the rapid spread and continued high abundance of *Petrolisthes* along the Georgia coast 10 years following the initial invasion suggests that it might not experience high predation pressure by mud crabs. To evaluate the factors underlying the adoption of a recently introduced, abundant prey item into a predator's diet, we use the invasion of *Petrolisthes* to ask 1) Do individual *Panopeus* predators differ in their overall diet breadth? 2) Do individual *Panopeus* predators differ in their willingness to consume a recently introduced, non-native prey species? 3) Do differences in behavior (antipredator response and exploratory behavior) and demographic traits (size and sex) explain variation among individuals in the consumption of a recently introduced, non-native prey?

METHODS

Overview of experiments

To examine within-population individual variation in diet, behavior, and morphology, we tested 30 individual *Panopeus* predators across 4 experiments in August 2010 at the Skidaway Institute of Oceanography, Savannah, Georgia. These same individuals were tracked and tested repeatedly within and across experiments in order to quantify the repeatability and consistency of diet and behavior of these predators. Non-native *Petrolisthes* had been present at this site for approximately 6 years, and therefore, *Panopeus* predators were not naive to *Petrolisthes* as prey prior to the experiment. First, individual *Panopeus* were assayed in 2 behavioral experiments to quantify each individual's aggressiveness and exploratory behavior. Then these same 30 individual *Panopeus* predators were used in 2 prey choice experiments to evaluate whether individual *Panopeus* differ in their diet and consumption of non-native *Petrolisthes*. In the first prey choice experiment, we quantified the proportion of *Petrolisthes* consumed when each predator was given a choice among *Petrolisthes* and alternative native prey (simultaneous choice). In the second prey choice experiment, we quantified the consumption of *Petrolisthes* when predators were given no choice of alternative prey. To quantify individual differences in morphology, we recorded the size and sex of each individual used in the behavioral and prey choice assays.

We conducted the behavioral assays and simultaneous choice assays within 19-L rectangular, plastic tubs containers (Sterilite) filled with 6.6-L of seawater and aerated to maintain oxygen levels.

The no-choice assay was conducted in a 1.9-L, 33-cm diameter, round plastic tank filled 15-cm deep with seawater. During the course of all 4 experiments, we housed individual *Panopeus* within their experimental tank and we completely changed the seawater each day within each tub.

Experimental animals

We collected *Panopeus*, *Petrolisthes*, and 3 native prey species by hand from oyster reefs and dock pilings in the Wilmington River, Savannah, GA. Native prey used in the experiment included native ribbed mussels, *Geukensia demissa*, native clams *Mercenaria mercenaria*, native juvenile *Panopeus* mud crabs (crabs can be cannibalized by larger conspecifics), and non-native *Petrolisthes*. Species were held separately within flowing, seawater tables for 3 days before being used in experiments. A subsample of each prey species ($n = 10$ individuals) was measured using standard measurements for each prey type. Size ranges for each prey species included mussels (18–26 mm length), clams (15–19 mm length), juvenile mudcrabs (13–20 mm carapace width), and *Petrolisthes* (6–9 mm carapace width). Although juvenile mudcrabs had a larger carapace width than *Petrolisthes*, total body size was generally comparable. Furthermore, juvenile mudcrabs were well within the size range that the larger focal *Panopeus* predators could consume.

To account for the influence of size and gender of *Panopeus* predators, prior to the experiments, we recorded the carapace length (mm) and sex of each *Panopeus* (*Panopeus* is not sexually dimorphic in size). Additionally, we marked each individual with a unique number using paint pens. We used *Panopeus* from a single year-class, with individuals ranging in size from 27.05 to 40.02 mm. One experimental *Panopeus* did not consume any prey, nor did it display any behavior during the entire experimental period and was eliminated from the data set. Thus, the final sample size of individuals tested in this study was $n = 29$. We fed focal *Panopeus* individuals *G. demissa*, *M. mercenaria*, and juvenile *Panopeus*, ad libitum and then deprived them of food for 12-h prior to the experiment to standardize hunger.

Individual variation in behavior

Exploratory behavior

Tests of exploratory behavior are frequently conducted in the context of exploration of a novel environment (Dingemans et al. 2002, 2012; Mainwaring and Hartley 2013). Here, introduction of each *Panopeus* into its experimental tank prior to any other experiment being performed represented the exposure to a novel environment. Thus, on introduction, we continually measured its activity (i.e., movement) for 20 min. We defined movement as moving at least one whole body length during the 5-s observation period. Observation periods were spaced every 60 s. The proportion of time spent moving in a novel environment was estimated and used to represent an individual's exploratory behavior.

Antipredatory response

Crabs respond to a direct threat of a predator by either fleeing (walking away) or fighting (raising their claws) (Wasson and Lyon 2005). This fight or flee response has been frequently used as an indicator of an individual's antipredator response (Pintor et al. 2008; Morishita et al. 2009; de Barros et al. 2010; Huffard et al. 2010). Here, we threatened the crabs by approaching the front of the crab with a 10-inch piece of 1/4-inch-diameter PVC pipe starting from approximately 15 cm in front of the crab and then

slowly moving the PVC pipe toward the crab until it was approximately 0.5 cm in front of the crab. We recorded the response of the crab as either 1) claw raise, 2) move away, or 3) no response. The threat approach was repeated 3 times within a single assay (5 min total). To estimate the repeatability of an individual's antipredator response, we repeated the entire assay on each of the 2 following days. We used the proportion of times an individual raised a claw or fled to represent variation in an individual's antipredator response.

It is often important to formally test whether individuals not only differed in behavior but also consistently exhibited different behavioral types (i.e., some individuals consistently exhibit a flee response, whereas others consistently exhibit a fight response). Therefore, to ensure that antipredator response was a good trait to characterize individual differences in behavior, we estimated the repeatability of this behavior over the 3 testing days. Repeatability measures the extent to which individual differences in behavior (i.e., antipredator response) are consistent over time, for example, an individual that would exhibit a fight response consistently does so on each testing day (Lessells and Boag 1987; Bell et al. 2009). Formally, repeatability is equal to $r = s_A^2 / (s^2 + s_A^2)$, where s_A^2 is the variance among individuals and s^2 is the variance within individuals over time. We used a one-way Anova with individual *Panopeus* as a fixed effect to estimate the repeatability of aggressiveness (Lessells and Boag 1987). Standard errors were estimated as in Becker (1984).

Individual variation in diet

Simultaneous prey choice assay

To quantify individual differences in general diet and the proportion of *Petrolisthes* consumed by *Panopeus*, we quantified the number and identity of prey species consumed when *Panopeus* were given a choice of alternative prey. At the start of the experiment, we added 3 individuals of each of the 4 prey types to each focal *Panopeus*'s experimental tank (12 prey items total). Prey were randomly distributed throughout the entire tank. Once prey were added, the experiment began. We recorded the number and type of prey consumed every 60 min over a 6-h period of time ($n = 6$ observations total). At each hour observation, we replaced any prey that was eaten with a new, live prey to minimize the effect of prey choice being a consequence of decreased density or encounter rate with preferred prey. Between observations, the room was darkened to minimize disturbance and encourage foraging. At the end of the 6-h observation period, we removed any remaining prey and performed a complete water change. We then repeated the entire experiment on the same individuals on each of the subsequent 2 days. Repeating the experiment allowed us to estimate the repeatability (as described above) or consistency in the proportion of *Petrolisthes* consumed by *Panopeus* when given a choice among alternative prey. We used the total proportion of *Petrolisthes* consumed over the 3 testing days as a measure of *Petrolisthes* consumption by *Panopeus* when given a choice of alternative native prey.

To quantify and characterize individual differences in the diet of *Panopeus* predators, we used the proportional similarity index (PS_i) adapted to individual-level analyses to measure the amount of overlap in diet between an individual and the sampled population (Schoener 1968; Bolnick et al. 2002). More explicit details for the index can be found in Schoener (1969), Feinsinger et al. (1981), and Bolnick et al. (2002). Briefly, let N be a matrix of diet data, where element n_{ij} represents the number of diet items in individual i 's diet that fall into category j . This raw data matrix was then transformed

into a proportion matrix P with the variable p_{ij} describing the proportion of the j -th resource category in individual i 's diet, and q_j describes the proportion of the j -th resource category in the population's observed diet and are equal to:

$$p_{ij} = \frac{n_{ij}}{\sum_j n_{ij}}, \quad q_j = \frac{\sum_i n_{ij}}{\sum_i \sum_j n_{ij}}$$

The diet overlap between an individual i and the population is equal to:

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j| = \sum_j \min(p_{ij}, q_j)$$

PS_{*i*} values range from 0 to 1, where values near 1 indicate that an individual eats the same proportion of prey types as the population as a whole (i.e., conforms to the mean diet of the population), whereas values near 0 indicate that an individual does not conform to the diet of the population as a whole. Thus, we used an individual *Panopeus* predator's PS_{*i*} score to characterize the degree to which the individual exhibited a diet that was different from the population on average. Furthermore, for individuals that exclusively eat a single prey type (i.e., specialize), j , PS_{*i*} takes on the value of q_j . For individuals within the sampled population that specialized on 1 prey item, we quantified the percentage of those individual that specialized on each of the 4 prey types. We used the mean PS_{*i*} value across all individuals tested to describe the population-level incidence of diet specialization.

No-choice prey assay

We used a no-choice assay to quantify the consumption of *Petrolisthes* by *Panopeus* when predators were given no choice of alternative native prey. The no-choice assay was conducted 1 day after the completion of the simultaneous choice assay. Many details of the experimental setup were similar to those used in the simultaneous choice assay, but briefly, 3 *Petrolisthes* individuals were added into the experimental tank with the marked, focal *Panopeus*. Once *Petrolisthes* were added, the experiment began and the number of *Petrolisthes* consumed was recorded every 15 min over a 6-h time period ($n = 24$ observations per individual). Any *Petrolisthes* that were consumed were replaced. At the end of the 6-h observation period, we removed any remaining prey and performed a complete water change. The entire experiment was then repeated a second day in order to estimate the repeatability of an individual's consumption of *Petrolisthes*. We summed the total number of *Petrolisthes* consumed by an individual *Panopeus* over the 2 testing days. However, data were not normally distributed, so we analyzed consumption of *Petrolisthes* by *Panopeus* as a bivariate data set with individuals scored as either having consumed or not consumed *Petrolisthes*.

Data analysis for prey choice experiments

To examine whether the diet of individual *Panopeus* was consistent over the 3 testing days for the simultaneous choice assay (e.g., individuals that ate a larger proportion of *Petrolisthes* did so across the 3 testing days) and 2 testing days for the no-choice assay, we estimated repeatability of diet. Similar to estimates of repeatability in aggressiveness, we used a one-way Anova with individual *Panopeus* as a fixed effect to estimate the repeatability of the proportion of *Petrolisthes* consumed both in the choice and no-choice assays

(Lessells and Boag 1987). We also accounted for potential changes in diet over time as *Panopeus* learned to eat different items by including experiment day as a fixed effect in the models. Specifically, this allowed us to evaluate whether exposure to *Petrolisthes* on day 1 of the trial influenced the consumption of *Petrolisthes* on days 2 and 3 for the simultaneous choice assay and day 2 of the no-choice assay. Standard errors were estimated as in Becker (1984).

We also examined all continuous predictor variables for evidence of multicollinearity using Spearman's rank correlations. No significant correlations between predictor variables were found (exploratory behavior vs. size: $r = 0.07$, $P = 0.71$; exploratory behavior vs. antipredator response: $r = 0.34$, $P = 0.07$; antipredator response vs. size: $r = 0.05$, $P = 0.81$).

To evaluate how variation in exploratory behavior, antipredator response, sex, and size of *Panopeus* explained the proportion of *Petrolisthes* in an individual's diet when given a choice among prey (i.e., simultaneous choice assay), we ran a series of general linear models. Residuals were visually examined to check assumptions of normality. These models included an empty, null model and then all possible single, 2-, 3-, and 4-factor models. The most parsimonious model was identified according to Akaike's information criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002; Symonds and Moussalli 2011). ΔAIC_c scores and Akaike weights (w_i) were used to compare the different models and assess the relative strengths of each of the candidate models (Burnham and Anderson 2002; Symonds and Moussalli 2011). Akaike weights close to 1 indicated greater confidence in the selection of the best model. We also used the model weights to estimate the relative importance of the 4 predictor variables (i.e., RVI scores). Specifically, we summed the Akaike weights for each model in which a variable appeared. These summed weights were then used to rank the 4 predictors in terms of their importance in explaining the proportion of *Petrolisthes* in the diet of *Panopeus* predators.

Next, to evaluate factors that influence whether an individual *Panopeus* consumed *Petrolisthes* when given no choice among prey (i.e., no-choice assay), we ran a series of logistic regressions exploring the roles of exploratory behavior, antipredator response, sex, and size of *Panopeus*. We also included the average proportion of *Petrolisthes* consumed in the simultaneous choice assay in the model to account for any influence of prior exposure and consumption of *Petrolisthes* in the simultaneous choice assay, which was run before the no-choice assay. These models included an empty, null model and then all possible single, 2-, 3-, 4-, and 5-factor models. As in the general linear models above, the most parsimonious model was identified according to AIC_c. All statistical analyses were run in JMP, Version 10. Finally, we ran a series of general linear models and logistic regressions using conventional hypothesis testing. Overall, results were very similar to those reported using Akaike's criterion.

RESULTS

Individual variation in behavior (exploratory and antipredator response)

Individuals within the sampled population varied considerably in exploratory behavior with individuals actively exploring a novel environment on average 27.6%, \pm SD 18.4% of the 20-min observation period, and ranging from 0% to 55%. Individuals also varied considerably in aggressiveness. Individuals exhibited a claw raise

antipredator response on average 14.1% of the time, \pm SD 23.1%, and responses ranged from 0% to 92%. Repeatability of antipredator response was equal to $r = 0.33$, \pm SE 0.10. Repeatability of this behavior was slightly lower relative to the average repeatability of behaviors found in other studies (average $r = 0.37$, Bell et al. 2009). Exploratory behavior and antipredator response were not significantly correlated (Pearson's correlation coefficient, $r = 0.34$, $P = 0.07$), but there was a trend toward a positive relationship. Additionally, there was no effect of sex and size of predators on exploration (sex: $P = 0.42$, size: $P = 0.90$) or antipredator response (sex: $P = 0.38$, size: $P = 0.80$).

Individual variation in the diet of native *Panopeus*

Simultaneous choice feeding trials

The sampled *Panopeus* population as a whole consumed 82% mussels, 16% *Petrolisthes*, 1% clams, and 1% juvenile mudcrabs. Individual PS_i scores ranged from 0.16 to 0.98, with the average PS_i score being equal to 0.75. Individuals with a PS_i score near 1 exhibit a diet that conforms with the population as a whole (e.g., 82% mussels, 16% *Petrolisthes*, etc.), whereas individuals with a PS_i score approaching 0 exhibited a diet that did not conform (i.e., ate something other than predominantly mussels). Note that although individuals that conformed to the population diet consumed all 4 prey types, they largely specialized on mussels. Individuals within the sample population varied considerably in diet, with 37.9% conforming to the diet exhibited by the population as a whole, 44.8% eating exclusively mussels, 13.8% eating exclusively *Petrolisthes*, and 3.4% eating a relatively equal proportion of mussels and *Petrolisthes*.

Individuals within the sampled population varied considerably in the proportion of *Petrolisthes* consumed by an individual *Panopeus* when given a choice of alternative native prey: mean percent of *Petrolisthes* in the diet = 22.4%, \pm SD 34.9%, range = 0–100% (Anova, individual *Panopeus*: $F_{29,89} = 5.22$, $P < 0.0001$). There was no significant effect of experiment day, suggesting that individuals did not increase or decrease their consumption of *Petrolisthes* from day 1 through 3 of the experiment (Anova, experiment day: $F_{2,89} = 1.4$, $P = 0.17$). Repeatability of the proportion of *Petrolisthes* consumed over the 3 testing days was equal to $r = 0.48$, \pm SE 0.11. Individuals also varied considerably in the total number of *Petrolisthes* consumed when given a choice of alternative native prey: mean number of *Petrolisthes* in the diet = 0.46, \pm SD 0.98, range 0–7.

AIC_c model comparison indicated that a 2-variable model containing sex and size was the best model predicting the proportion of *Petrolisthes* in the diet of *Panopeus* predators (Table 1). Specifically, *Panopeus* that were female and smaller in size had a greater proportion of *Petrolisthes* in their diet in comparison to males (Figure 1). There was also evidence that sex in combination with antipredator response and sex alone predicted the proportion of *Petrolisthes* consumed. Specifically, individuals that fled in response to a predator and that were smaller in size had a higher proportion of *Petrolisthes* in their diet. Sex, however, was a predictor in all top models and its relative importance in predicting the proportion of *Petrolisthes* in the diet was more than 2 times higher ($RVI_{sex} = 0.98$) than size ($RVI_{size} = 0.43$) and 3 times higher than antipredator response ($RVI_{agg} = 0.25$).

No-choice feeding trials

Thirty-four percent of the *Panopeus* individuals tested consumed *Petrolisthes* when given no alternative choice of prey. Individuals within the sampled population varied considerably in the total

Table 1

Best-ranked general linear models (models whose ΔAIC_c scores were ≤ 5) examining the effect of demographic and behavior predictor variables on the proportion of *Petrolisthes* consumed by *Panopeus* predators during the simultaneous choice assay

Model	k	AIC _c	ΔAIC_c	w_i
1 SX + SZ	2	17.226	0	0.316
2 SX	1	17.511	0.285	0.274
3 SX + AGG	2	18.438	1.212	0.172
4 SX + SZ + EXP	3	20.082	2.856	0.076
5 SX + EXP	2	20.183	2.957	0.072
6 SX + EXP + AGG	3	21.253	4.027	0.042
7 SX + SZ + EXP + AGG	4	21.867	4.6409	0.031

SX, sex; SZ, size; EXP, exploratory behavior; AGG, aggressive behavior.

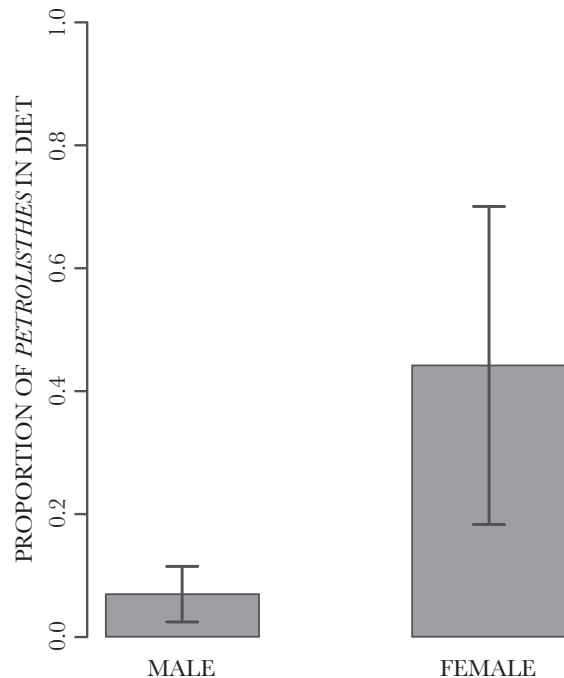


Figure 1

On average, female *Panopeus herbstii* predators consumed a significantly greater proportion of *Petrolisthes armatus* than males (means, \pm CI) in the simultaneous choice assay.

number of *Petrolisthes* consumed when given no choice of alternative native prey, average number of *Petrolisthes* consumed per individual = 0.72, \pm SD 1.22, range = 0–4 (Anova, individual *Panopeus*: $F_{29,57} = 20.90$, $P < 0.0014$). There was no significant effect of experiment day, suggesting that individuals did not increase or decrease their consumption of *Petrolisthes* from day 1 to day 2 of the experiment (Anova, experiment day: $F_{1,57} = 0.02$, $P = 0.79$). Repeatability of the total number of *Petrolisthes* consumed over the 2 testing days was equal to $r = 0.54$, \pm SE 0.13. Eighty-six percent of individuals that did not consume *Petrolisthes* during the simultaneous choice assay also did not consume them during the no-choice assay, further showing that individuals exhibit consistent individual differences in the consumption of *Petrolisthes* and that exposure to *Petrolisthes* in the previous simultaneous choice assay did not influence their consumption tendencies in the no-choice assay. Results of the AIC_c model comparison indicated that a single-variable model containing exploratory behavior was the best model predicting

whether *Panopeus* predators would consume *Petrolisthes* when given no choice of alternative prey (Table 2). Specifically, individuals that were less exploratory (i.e., spent less time actively moving) ate more *Petrolisthes*. There was also evidence that exploratory behavior in combination with sex explained the consumption of *Petrolisthes* by *Panopeus* predators. Specifically, individuals that were females more frequently consumed *Petrolisthes* when given no choice of alternative prey. Exploratory behavior, however, was a predictor in the most top models and its relative importance in predicting the consumption of *Petrolisthes* was approximately 2 times higher ($RVI_{exp} = 0.78$) than sex ($RVI_{sex} = 0.42$).

DISCUSSION

Although *Panopeus* is thought to be a generalist predator, results of our prey choice assays suggest that there are within-population, individual differences in diet, with some individuals specializing or predominantly consuming mussels, others eating only the non-native *Petrolisthes*, and others consuming a mixed diet. There were consistent, repeatable differences in the proportion or general consumption of non-native *Petrolisthes* among individuals, with some individuals consistently consuming many *Petrolisthes* and other individuals consuming none. Similarly, there were consistent, individual differences in antipredator response (e.g., fight or flee). Model comparisons indicated that individual *Panopeus* that consumed a larger proportion of *Petrolisthes* when given a choice of alternative native prey were female and also tended to be smaller and would flee in response to a predator. However, sex was approximately 3 times as important at explaining the proportion of *Petrolisthes* consumed in comparison to size and antipredator response. When given no choice of alternative prey, model comparisons indicated that individuals that would readily consume *Petrolisthes* were those that were less exploratory and female. Exploratory behavior was twice as important at explaining variation in the consumption of *Petrolisthes* in contrast to predator sex. Thus, our results show that individual variation among *Panopeus* predators in behavior and morphology affects its rates of consumption of this recently introduced, non-native prey.

Table 2

Best-ranked logistic regression models (models whose ΔAIC_c scores were ≤ 5) examining the effect of demographic and behavior predictor variables on whether *Panopeus* predators consumed *Petrolisthes* when given no choice of alternative prey

Model	k	AIC_c	ΔAIC_c	w_i
1 EXP	1	40.932	0	0.275
2 SX + EXP	2	42.137	1.205	0.151
3 EXP + PP	2	43.460	2.528	0.078
4 EXP + AGG	2	43.584	2.652	0.073
5 SX	1	43.851	2.919	0.064
6 SX + SZ + EXP	3	44.800	3.868	0.040
7 SX + EXP + AGG	3	44.963	4.031	0.037
8 SX + EXP + PP	3	45.014	4.082	0.036
9 PP	1	45.689	4.757	0.256
10 AGG	1	46.086	4.989	0.227

The proportion of *Petrolisthes* consumed during the previous simultaneous choice experiment was also included as an predictor variable in the models. Relative variable of importance scores were as follows: $RVI_{exp} = 0.78$, $RVI_{sx} = 0.42$, $RVI_{pp} = 0.24$, $RVI_{agg} = 0.24$, and $RVI_{sz} = 0.16$. SX, sex; SZ, size; EXP, exploratory behavior; AGG, aggressive behavior; PP, proportion of *Petrolisthes* consumed in simultaneous choice assay.

These consistent, individual differences in the diet and the consumption of *Petrolisthes* prey more than 6 years postinvasion suggest a longer-term avoidance of *Petrolisthes*. In other words, we suggest that a proportion of this *Panopeus* predator population exhibits dietary conservatism. Even when given no alternative choice of food, some individual predators would consistently not consume *Petrolisthes* prey, despite *Petrolisthes* being fully edible and energetically as profitable per gram of tissue as mussels (Hostert 2014). This contributes to the growing body of work demonstrating variation in the expression of dietary conservatism within populations of birds (Marples and Brakefield 1995; Thomas et al. 2003, 2004; Kelly and Marples 2004), fish (Thomas et al. 2010; Richards et al. 2014), and now, invertebrates. The majority of these previous studies have looked at predators choosing among different color morphs of the same prey species and found that the prevalence of dietary conservatism in the predator population is often strong enough to drive a novel color morph in the prey population from initial rarity to fixation (i.e., abundance) within a population. Here, we suggest that the prevalence of dietary conservatism could be a mechanism driving a novel species (e.g., non-native *Petrolisthes*) from initial rarity to abundance within an invaded ecosystem and may contribute to the escape of many non-native species from their natural enemies following introduction.

Optimal foraging theory provides additional insights into why some, but not all, individual *Panopeus* predators exhibit a longer-term avoidance of non-native *Petrolisthes*. Changes in the encounter rates with prey following invasion, along with differences in handling time among alternative prey, might make a non-native prey less profitable for certain individuals. For example, variation in learning and memory can generate differences in foraging efficiency and handling time (Hughes et al. 1992; Estes et al. 2003). These differences have been shown to contribute to individual variation in feeding rates on particular prey species and prey preferences within and across populations (Edwards and Huebner 1977; Dunkin and Hughes 1984; Hughes and Dunkin 1984). If individual *Panopeus* predators are foraging optimally, then individuals with longer handling times of *Petrolisthes* might avoid them for a longer period of time in favor of more profitable native prey species.

Individuals that did not exhibit dietary conservatism and would consume *Petrolisthes* were small females that would consistently flee in response to a predatory threat. Of these 3 influential traits (size, sex, and antipredator response), sex was the most important variable predicting the proportion of *Petrolisthes* consumed. Differences in diet between males and females are often common, particularly during the breeding season (Shine 1991; Williams and McBrayer 2011). Reproduction is energetically expensive for females, which could suggest that specializing on *Petrolisthes* is related to nutritional benefits. Alternatively, claw morphology in crabs strongly influences prey choice (Smith and Palmer 1994; Seed and Hughes 1995) and could generate differences in diet between males and females, who tend to have weaker claws (Buck et al. 2003). For example, species that typically consume rapidly moving prey (e.g., *Petrolisthes*) generally have fast, but weaker claws, whereas those that specialize on slower or sedentary, more heavily armored prey (e.g., *Guekensia* mussels) have slower, but stronger claws (Seed and Hughes 1995). These species-level differences in diet and claw morphology can also apply within a species and contribute to differences in the proportion of fast-moving, mobile *Petrolisthes* consumed relative to sedentary native prey.

Although predator size and antipredator response had lower relative importance in the top models explaining the proportion of

Petrolisthes consumed by individual *Panopeus* predators, their contributing influence, along with sex, suggests that consumption of novel prey might be related to social dominance. Specifically, smaller size and a flee response are traits typically associated with individuals that are subordinate in a population (Hazlett 1981; Sneddon et al. 1997). Therefore, individual *Panopeus* predators that were female, smaller in size, and fled in response to predators might specialize or consume a greater proportion of *Petrolisthes* because they are poor competitors for native prey. These subordinate individuals might choose to consume *Petrolisthes* in order to reduce the cost of competition over familiar, preferred prey. Taken together, this suggests that *Petrolisthes* may be the less profitable prey item and that subordinate individuals might consume a greater proportion of the non-native prey to avoid competition with more dominant *Panopeus* individuals.

When given no choice, individuals that were female and that had less exploratory personalities would actively consume *Petrolisthes*. Individuals that are less exploratory are often also less aggressive (Koolhaas et al. 1999), which could further suggest that consumption of *Petrolisthes* may be associated with social dominance. However, greater consumption of *Petrolisthes* by less exploratory females may also be associated with predatory tactics. For example, individuals with less exploratory personalities have been often shown to exhibit sit-and-wait predatory tactics in contrast to more exploratory individuals who display more active search tactics (Wilson and McLaughlin 2007; Kobler et al. 2009). Sit-and-wait or ambush predators tend to consume different prey (Shine and Sun 2003; Hagman et al. 2008; Staudinger and Juanes 2010), which are often more mobile (e.g., mobile crabs vs. sedentary mussels) than the prey types consumed by active predators (Elliott 2005). Therefore, differences in consumption of *Petrolisthes* may be associated with individual variation in predatory tactics of *Panopeus*.

Variation in the consumption of novel, non-native prey among individuals within a native predator population may have important implications for the invasion success and control of *Petrolisthes*. *Panopeus* is a widespread, relatively abundant predator in oyster reef communities. However, if only a proportion of individuals in the population are consuming *Petrolisthes*, the population as a whole might not exert strong enough predation pressure to deter an invasion or control a non-native prey's abundance following establishment. Over time, population-wide predation rates might change as individuals gain experience and learn to consume non-native prey. However, if variation in predation rates of *Petrolisthes* is due to its lower quality or profitability relative to native prey, then control of *Petrolisthes* abundance might only arise if predators experience significant reductions in native prey and increase consumption of the more abundant *Petrolisthes*. In the meantime, if predation on novel, non-native prey is largely a function of static individual differences in behavior of a predator population, then lower overall predation levels on the non-native prey could be an important mechanism that contributes to the prey's release from natural enemies following introduction into a new ecosystem.

FUNDING

Funding was from the University of Georgia Office of VP for Research and The Ohio State University's Ohio Agriculture Research and Development Center.

We would like to acknowledge C. Yeager for assistance with collecting organisms for the experiments and J. Carlton for assistance with species identification. We would also like to thank Dr L. Simmons, Dr J. Mappes,

and 2 anonymous reviewers for their helpful and constructive comments on the manuscript. We dedicate this article to J. Carlton, who continues to inspire and advance a deeper understanding of invasion ecology.

Handling editor: Johanna Mappes

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