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Behavioral variation post-invasion: resemblance in some, but not all, behavioral patterns among invasive and native praying mantids

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Abstract

Animal invasions can be devastating for native species. Behavioral variation is known to influence animal invasions, yet comparatively less is known about how behavioral variation influences invasive-native species interactions. Here we examined how the mean and variance surrounding several behavioral traits in two sympatric species of praying mantis differ and how these behavioral types translate to actual prey capture success using the introduced European mantis, *Mantis religiosa*, and the native bordered mantis, *Stagmomantis limbata*. We assayed time spent in the open (risk proneness), response towards a novel prey, and voracity within a population of *M. religiosa* and *S. limbata*. We found that the native and invasive mantids displayed no differences in their average behavioral tendencies. The native exhibited significant levels of repeatability in voracity while the invasive did not. The lack of repeatability in the invasive appears to be driven by lower levels of among-individual variation in voracity. This may have evolutionary consequences for native *S. limbata* if it results in strong selection in native levels of mean and among-individual variation. Significant levels of among-individual differences were found in other behaviors (response to a novel prey and risk proneness) across species, suggesting less selection on invasive behavioral variation in these traits. Risk proneness and response towards a novel prey also formed a behavioral syndrome across species, yet neither behavior was correlated with voracity in either species. Our results illustrate the need to examine the ecological effects of behavioral variation of both invasive and native species to determine how that might impact invasive-native interactions.

Keywords

Behavioural syndrome; Behavioural type; Invasion; Personality; Praying mantis

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Data Accessibility

All data from this project will be uploaded to Dryad upon final acceptance of the manuscript with the following statement: "Analyses reported in this article can be reproduced using the data provided by Jones and DiRienzo (2017)."

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The presence of invasive species can have detrimental effects on the fitness of native species (Ricciardi 2004; Clavero et al. 2005). Through means of resource exploitation, direct competition, and predation (e.g., Simberloff 1981; Diamond 1986; Petren and Case 1996; Kupferberg 1997; Bergstrom and Mensinger 2009), invasive species are often able to outperform their native competitors. Within the field of invasion ecology, there has been considerable focus on what life history and population level characteristics allow a species to pass through the multiple stages of invasion (e.g., Baker 1965; Crawley et al. 1986; Whittier and Limpus 1996; Sakai et al. 2001). In an effort to understand the mechanisms behind invasive and native species interactions, studies have examined their physiological (Lockwood and Somero 2011), anatomical (Callaway and Ridenour 2004), and behavioral differences (Holway and Suarez 1999). Behavioral comparisons have largely shown that invasive species on average exhibit greater aggression towards heterospecifics across contexts (e.g., Baker 1965; Dick et al. 1995; Petren and Case 1996; Gamradt et al. 1997). For example, in native and introduced amphipods, *Gammarus duebene celticus* and *G. pulex*, respectively, asymmetry in intra-guild predation favors *G. pulex*, and is a result of increased invasive aggression towards native amphipods (Dick et al. 1995).

Animal ‘personalities’ refer to consistent behavioral differences among individuals (Sih et al. 2004). Stemming from a greater appreciation for the impact animal personalities have on communities (Weis and Sol 2016), increasingly more studies have devoted attention to investigating the role of behavioral variation in invasion ecology. Much of this work has focused in behaviorally-mediated dispersal. Specifically, research has shown that individuals possessing certain behavioral types (e.g. more asocial and aggressive) are more likely to successfully invade new habitats, and that multiple behavioral traits may be correlated, forming a behavioral syndrome (Duckworth and Badyaev 2007; Cote and Clobert et al. 2010; Cote, Fogarty, and Brodin et al. 2010; Cote, Fogarty, and Weinersmith et al. 2010; Fogarty et al. 2011; Hirsch et al. 2016). Interactions between invasive species and the local fauna may also potentially alter the amount of variation expressed in invasive species. Entering a new habitat often consists of encountering and adapting to novelties (e.g. novel prey, novel predators); individuals with certain behavioral types should fare better than others when invading (Chapple et al. 2011). Given that invasive and native species have the potential to strongly interact, and that the results of behavioral type interactions across species are known to determine the outcome of various ecological processes (Pruitt et al. 2011; DiRienzo et al. 2013; Sweeney et al. 2013), it is likely that behavioral types are instrumental in the interaction between native and invasive species.

Despite knowledge regarding what individuals drive invasions, comparatively less work has examined how behavioral variation within invasive and native species impacts their interaction post-invasion, both directly and for shared resources. Rapid displacement of native species can be attributed to an inability to adapt to the presence of invasive species, such as when higher levels of aggression within invasive species drives antagonistic interactions or competitive exclusion of the native (Dick et al. 1995; Gamradt et al. 1997; Holway and Suarez 1999; Snyder and Evans 2006; Duckworth and Badyaev 2007; Duckworth 2008, 2010; Hudina and Hock 2014). However, it is necessary to know what happens when both species are able to interact post-invasion, over longer periods of time.

One of the few examples examining these interactions studied the role of behavioral types on foraging interactions between invasive goldfish and native palmate newts (Winandy and Denoël 2015). Researchers found that fish varied in their aggression towards newts, with aggressive individuals more likely to exclude newts from foraging. Interestingly, newts differed in their willingness to forage in the presence of goldfish.

Differences in not only the average behavior of a population but also the behavioral variation within invasive and native populations have the potential to influence whether or not natives will persist. Furthermore, given that invasive and native species often compete for resources, it is important to understand how behavioral variation in both populations influences competition for shared resources. For example, if invaders have low variance and high voracity they will put stronger pressure on shared resources, thereby lowering the fitness for many natives that are unable to compete with invaders. Thus, in order to understand how mean behavior and behavioral variation within both invasive and native species translate to actual ecological effects, it is necessary to compare their behaviors and determine how these differences may impact relevant ecological processes.

The European praying mantis, *Mantis religiosa*, is an introduced species that evidently became established in the Sacramento Valley sometime between 1994 and 2004 (Maxwell personal comm; earliest record seen at the UC Davis Bohart Entomological Museum). First introduced in the United States in the late 1800s, it has been repeatedly introduced both deliberately and inadvertently (Gurney 1960; Vickery and Keyan 1983), and thus humans have facilitated its range expansion to encompass almost all of the continental United States as well as the southern regions of Canada (Cannings 2007). *Mantis religiosa*'s range expansion into California has placed it in contact with the native bordered praying mantis, *Stagmomantis limbata*. Both species have similar life histories and trophic interactions, acting as seasonal generalist arthropod predators (Roberts 1937; Rathet and Hurd 1983). In Davis, CA, *S. limbata* persists with both *M. religiosa* and the previously introduced species, *Iris oratoria* (Maxwell and Eitan 1998). While the overall impact of these introductions on *S. limbata* is unknown all three species continue to persist despite apparent direct and indirect competition (Jones and Gilbert unpublished data). This provides an ideal opportunity to study behavioral variation in invasive and native species post-invasion. Though it is not known how behavioral types affect intra- and interspecific competition in mantids, the presence and structure of behavioral types may play a role in the interactions between the native and invasive mantis species because they are threatened by the same predators and compete for similar prey and habitat resources.

In this study, we investigated how mean behavior and variation differs in native (*S. limbata*) and invasive (*M. religiosa*) species of mantids, whether correlations exist between traits, and how these differences have a direct ecological effect in terms of prey capture. We addressed these questions by testing both species in three different assays: (1) risk proneness (time spent in the open), (2) response to a novel prey, and (3) voracity (i.e., number of prey captured). These behaviors are relevant for the life history of both species and for addressing aspects of the invasion process. For example, invasive species typically encounter novel food sources in the invaded range (Sih et al. 2010), which necessitates individuals having a greater propensity to attack novel prey items and outperform native competitors in acquiring

resources (Rehage and Sih 2004; Martin and Fitzgerald 2005; Rehage et al. 2005; Pintor et al. 2008; Pintor and Sih 2009; Blackburn et al. 2009; Weis 2010; Wright et al. 2010). However, there is evidence that within invasive species, mean level behavioral types shift at the later stages of invasion (Duckworth and Badyaev 2007; Lee 2002; Colautti and Lau 2015), suggesting that “invasive traits” (such as response to novelty) may decline post-invasion. Therefore investigating behavioral variation within invasive and native species post-invasion yields insight into the patterns associated with population-level changes in behavioral variation that may influence coexistence.

METHODS

Experimental design

We used field caught individuals of both species of mantid, invasive *M. religiosa* ($n = 50$) and native *S. limbata* ($n = 27$). Mantids were captured in August of 2016 in Davis, CA and Winters, CA ($38^{\circ} 31' 24.798''$ N $121^{\circ} 47' 2.2272''$ W and $38^{\circ} 37' 17.796''$ N $121^{\circ} 59' 21.8724''$, respectively) where they are sympatric. Specimens were kept in individual 16oz deli containers (top diameter 12cm; bottom diameter 10cm; height 8cm) and were held in the laboratory at UC Davis in 12:12h light:dark cycle at 24°C . While there are no studies on predatory behavioral changes across ontogeny, changes in anti-predator behaviors have been shown to cease as mantids near adulthood (Liske et al. 1999; Watanabe and Yano 2010), therefore only adults (27; 14 male and 13 female *M. religiosa* and 11; 6 male and 5 female *S. limbata*) and juveniles (23; 10 male and 13 female *M. religiosa* and 16; 8 male and 8 female *S. limbata*) at or above the penultimate instar were captured. However, only mature specimens were assayed, so any captured juveniles were first reared to maturity before undergoing trials. All specimens were fed *ad libitum* *Gryllodes sigillatus* crickets for one to two months before experimentation. Prior to starting trials, specimens were given five large (0.3–0.5 g) crickets in order for the mantids to become fully satiated. Individuals who consumed all five crickets in a 24 h period were given an additional 3 crickets. Individuals were deemed ‘sated’ and massed when crickets remained after 24h. Specimens were then food restricted until their mass reached $75 \pm 2\%$ of their mass at satiation to control for hunger motivation. This was done to thoroughly control for effects of hunger motivation, as state has been shown to influence behavior (Luttbeg and Sih 2010). Individuals reached this stage after approximately two weeks at which time we calculated their optimal prey size following the methods of Holling (1964). This equation uses the geometry of the femur and tibia of the foreleg to calculate the optimal size to elicit a strike from a mantis. Once food restricted, we conducted assays in the order of time to reach a perch, response to a novel prey, and voracity towards a common prey item. The three assays were conducted on the same day separated by 15 minutes. Within fifteen minutes all mantids resumed normal activity, remaining motionless on a perch. The assay order was chosen as this was believed to minimize effects from the previous assay. For example, variation in prey items consumed could influence measurements of response to a novel prey item if response to a novel prey is influenced by hunger motivation. Trials were conducted in the lab between 12:00–16:00. Individuals were assayed twice, separated by 15 days. All individuals were again satiated and food restricted before the second round of behavioral assays.

Risk Proneness

We placed individuals in an open arena and provided a structure for them to navigate towards to assess if individuals varied in their time spent in the open (i.e., on the ground). Remaining on the ground can be dangerous for these species as anecdotal evidence suggests they are more conspicuous to visual predators (e.g., reptiles and birds) on the substrate than when on perches. Indeed, although both species can be found low to the ground, they are almost always found in vegetation (personal obs; Jones and Gilbert *in prep*), suggesting that remaining in the open is a potentially risky behavior. Individuals were placed in a vial (50 mL) which was placed on the edge of a plastic circle (12 cm diameter) under the sand in the center of a sand-filled arena (27 × 52 cm). We placed plastic plants (18 cm in height) on opposite ends of the arena, which pilot studies revealed were preferential perches for mantids in the absence of alternatives. The vial was placed so that when individuals emerge from the vial, they would be exposed on the circle. Individuals crawled out of the vial upon being placed in the arena at which time we recorded the time it took to make their first movement (TTM; i.e., orienting their head, grooming, or crawling), exit the circle (TTLC), and reach either perch (TTP). Individuals were given 20 min to reach a perch before cessation of the trial. Individuals were deemed to have reached a perch once all six legs were on the perch. In only 11 out of 142 trials did an individual fail to reach a perch, these trials were scored as NA. In all trials individuals left the circle.

Response to a Novel Prey

Following the perch seeking assay, we assessed variation in praying mantis' response to novel prey items. Individual mantids were placed on a plastic plant (18 cm in height) and allowed to acclimate for 15 min. A plastic circular wall encompassed the base of the plastic with 15 cm between the wall and the base of the plastic (Fig 1). After individuals had settled for 15 min (indicated by lack of movement and being positioned upside down), we introduced a hermit crab, *Coenobita spp.*, that was 85% of the individual's optimal prey size to the base of the plant. The circular wall ensured that the crab would always be equidistant to the plant. Hermit crabs were used because there is a low probability that mantids would encounter a crab in the wild and despite being too bulky to be captured by mantids, their movement resembles that of normal prey and should therefore elicit predatory responses (see Prete et al. 1990 and Prete and McLean 1996 for mantis responses to movement patterns). Praying mantids perform predatory strikes towards potential prey that consists of the raptorial arms facing forward when lunging towards the item. This differs from 'deimatic' anti-predator strikes that consist of flashing wings and curling the abdomen along with striking with raptorial arms outwards presumably as to not grab the perceived threat (Maldonado 1970). We did not observe any anti-predator behavior in response to crabs and all strikes were predatory strikes. The behaviors of individuals and the movement pattern of the crabs therefore suggest that hermit crabs are perceived as a potential prey item by mantids.

Praying mantids visually orient towards prey by moving their prothorax towards an item of interest (Cleal and Prete 1996). Preliminary trials to validate accuracy of relying on animal head movement consisted of placing two clear containers at either side of a mantis. One container contained a live cricket; the other contained a dead cricket. We counted the

number of times individuals oriented towards the moving vs. dead cricket. Analysis revealed that individuals oriented towards a moving item more than towards a stationary item (Chi-squared test: *M. religiosa*: $\chi^2 = 45.00$, $df = 1$, $p < 0.05$; *S. limbata*: $\chi^2 = 36$, $df = 1$, $p < 0.05$). Therefore, we used an individual's orientation as an indicator that it has seen a moving item.

We recorded the latency to approach the crab once they oriented towards it (LTS). Approaching was determined by the mantis moving two legs towards the crab while retaining orientation towards the crab. We also recorded latency for an individual to strike at the crab (LTS), ending the trial after an individual struck the crab or after 10 minutes passed. In only 25 trials did mantids not strike at the crab and only six did they not approach the crab (although they oriented towards the crab).

Voracity

The final assay tested if individuals varied in the number of prey captured during an open arena assay. Individuals were placed on the floor of a sand-covered arena (27×26 cm) consisting of clippings of shrubs and grasses to simulate the natural habitat of mantids. Fifteen *G. sigillatus* crickets that were 60% of the individual's optimal prey size were placed in the arena and given 5 min to settle, at which time a mantis was introduced into the arena and recorded for 15 minutes. Crickets of this prey size ranged from approximately 0.50 to 1.93 cm in length depending upon the individual mantis and were used to reduce the likelihood that mantids would be sated after consuming one or two prey items. This also allowed mantids to catch and consume multiple crickets both sequentially and simultaneously. We waited until individuals struck at a cricket before starting the timer because mantids differed in the time it took to settle and exhibit predatory behavior. All individuals struck at prey items within five minutes of being placed in the arena. We recorded how many crickets were captured by mantids in the 15 minute time interval. After the assay, individuals were removed from the arena and massed before being placed in their home container. In all trials individuals captured and consumed more than one cricket.

Statistical analysis

We assessed species differences in the three behavioral assays (perch seeking, response to novel prey, voracity) using generalized linear mixed models. Our response variable for the perch-seeking assay included the latency to first movement, time to leave the circle, and the time to reach the perch. We added 1 to latency to move measures and all latency measures were natural log transformed to achieve normality. Response to novel prey measures were not log transformed and included the latency to approach the novel prey and the latency to strike at the novel prey. The voracity trials included a single response of the number of prey eaten. All models included the main effects species, sex, and mass. Because analysis was carried out across species, mass was centered to a mean of zero and standard deviation of 1 by subtracting the total average mass from each observation and dividing by the total standard deviation. Individual ID was included as a random effect in all models. Count data (number of prey eaten) was modeled with a Poisson distribution and all latency measures (latency to move, time to leave circle, time to reach the perch, and time to approach and strike at the novel prey) were modeled using a Gaussian distribution.

To determine if perch-seeking or response to novel prey predicted voracity, we utilized an information theoretic approach to discern which variable best predicted the number of prey eaten. The model set included only models with a single main effect. Thus, we had eight models containing a fixed effect of either species, sex, weight, time to move (TTM), time to leave circle (TTLC), time to reach the perch (TTP), latency to approach (LTA), and strike (LTS). All aforementioned models included a random effect of individual ID. We also included a null model which included only individual ID. Given the modest sample size, we used Aikaike Information Criterion with small sample size correction (AICc) for model comparison. Models within two AIC were deemed to have equivalent fits (Burnham and Anderson 2003; Richards 2005). We also calculated AIC weights, which describe the probability of the model being the best fit relative to the other models in the set.

We calculated correlations different measures and behavioral traits (i.e., behavioral syndromes) using Pearson's correlations. We calculated the adjusted repeatabilities across and within species of all behavioral measures using the R package 'rptR' (Stoffel et al 2017). Within species repeatabilities were calculated using the same model structure used to assess mean differences, minus the main effect of species and fit to the appropriate subset of data (e.g. just *M. religiosa* or *S. limbata*). We calculated 95% confidence intervals via parametric bootstrapping procedures (number of simulations = 1000) and p-values via permutation tests (number of permutations = 1000).

RESULTS

Descriptive statistics for males and females for each species are presented in the Supporting Information (Table S1). Although many of the response variables for perch-seeking and novel prey assays were correlated, we did not conduct a PCA as the results were universally negative regarding species effects. As there was no risk of a false positive biasing our interpretation we chose to keep the behavioral variables in their individual form as to ease interpretation.

Only latency to move and time to leave circle measurements were significantly influenced by any of the included parameters (Table 1). Males took longer to move and leave the circle while larger individuals also took longer to move. Due to the potential for species and sex or size to interact, we conducted a posthoc analysis by fitting species interaction models where either sex or mass predicted one of the response variables. We fit a model between species and mass predicting time to move, TTM, and species and sex predicting TTM and TTLC and found that species differed in the effects of sex and mass on these behaviors (reported in supporting information Table S2). Specifically, larger *S. limbata* were predicted to have longer TTM values and female *S. limbata* were predicted to have longer TTM and TTLC values. Time to reach perch appeared to also be marginally influenced by sex (Table 1), whereby males took longer to reach the perch.

Latency to approach and strike a novel prey and voracity were not significantly influenced by any of the included parameters (Table 2). Species did not have any influence on measured behaviors. The model with individual weight was identified by Aikaike Information Criterion as the top model for predicting voracity (AICc to next model = 2.2, $\omega_i = 0.726$). Larger

individuals consumed more prey ($\beta = 0.220 \pm 0.063$, $p < 0.001$; Fig. 2; Table S3). There were no species differences in average voracity despite invasive *M. religiosa* being larger than *S. limbata* (two-sample $t_{140} = 2.38$, $p = 0.019$). Sex was determined to not be a confounding variable despite sexual dimorphism in both species as neither sex alone, additive with weight, nor an interactive term between sex and weight improved predictive power over the model containing only weight, suggesting that mass, not sex, drives this relationship (Table S4).

Our measures of response to novel prey and perch-seeking were negatively correlated. Overall, within both species, rapidly seeking perches, as indicated by the shorter latencies to become active, leave the circle, and reach the perch, was negatively correlated with latency to approach and strike a novel prey item (Tables 3 and 4). Yet, none of these variables were correlated with the number of prey consumed during the voracity assay, and species showed generally the same levels of trait correlations.

Significant repeatability values were found within species for most measured behaviors (Table 5). We only found non-significant repeatability values for the time to leave circle in *S. limbata* and voracity in *M. religiosa*. In both cases the reduced repeatability was driven by lower levels of among-individual variation (*S. limbata* vs. *M. religiosa* time to leave circle $AIvar = 0.147$ vs. 0.798 ; *S. limbata* vs. *M. religiosa* voracity $AIvar = 0.245$ vs. 0.069) (Table 5).

DISCUSSION

Here we investigated how the mean and variation of several behavioral traits differ between two sympatric praying mantis species, the invasive *Mantis religiosa* and native *Stagmomantis limbata*. We found no mean behavioral differences between the invasive and native species of mantids. However for each species, we generally found moderate to high repeatability (Bell et al. 2009) in most measures of risk proneness and response towards a novel prey. Voracity was significantly repeatable in *S. limbata*, but not *M. religiosa*, while a single risk proneness measure (TTLC - time to leave the circle) was significantly repeatable in *M. religiosa*, but not *S. limbata*. In both cases the lack of repeatability was driven by low among-individual variation. Across both species we found a behavioral syndrome composed of propensity to attack a novel prey item and seek a perch. However, these behavioral traits were not correlated with voracity in either species. Thus, although the species did not differ in their mean behavior, for one trait they did vary in the presence or absence of consistent among-individual differences.

There were no average species differences in any measured behaviors, counter to our expectations. While there are numerous examples of invasive species differing from natives in traits associated with increased fitness (e.g., Rice and Pfennig 2008, Godoy et al 2011; but see Davidson et al 2011), these differences may not be detectable between coexisting native and invasive species post-establishment. In this system, native *S. limbata* continues to persist with the invasive *M. religiosa*. To our knowledge, the impact of the *M. religiosa* invasion on *S. limbata* has not been well-studied. The persistence of *S. limbata* and the lack of average species differences possibly suggest that *M. religiosa* may not have the traits necessary to

completely displace *S. limbata*. However there is insufficient evidence to suggest whether average behavioral similarities existed pre-establishment or if behaviors of both species converged post-establishment. Alternatively, lack of species differences could be driven by other factors being the driving force of *M. religiosa*'s successful establishment such as predator release whereby parasitoids of *S. limbata* do not limit the population of *M. religiosa* (Fagan and Folarin 2001; Fagan 2002), or asymmetrical inter- or intraspecific aggression (e.g., Holway et al. 1998; Suarez et al. 1999; Keane and Crawley 2002; Holway et al. 2002; Hudina et al. 2015). Similarly, if *M. religiosa* did not impose high selection on *S. limbata* upon initially invading, we may not see mean differences in native behavior (e.g., character displacement). Other factors, specifically sex (time to move and leave circle) and mass (time to move), better explained behavioral traits. Males took longer to move, leave the circle, and took marginally longer to reach the perch. Larger individuals also took longer to move. Sex differences in behavioral types have been reported across a variety of taxa and can result from life history tradeoffs associated with each sex (Johnsson et al. 2001; Øverli et al. 2006; Schuett et al. 2009; Hedrick and Kortet 2011). For example, differences in male-female nutritional requirements required for mate attraction may lead to females being more motivated to seek a perch in preparation to ambush prey (Barry 2013; Barry and Wilder 2013). Other studies have shown relationships between size or sex and risk proneness, such that larger individuals or males engage in riskier behaviors (Brown and Braithwaite 2004; Brown et al. 2007; Ingley et al. 2014). While this may be the case in our study, size was not associated with any other risk proneness behaviors across species. Yet, a final explanation for the successful invasion and coexistence may be due to species-specific effects of sex and mass. Indeed, a post-hoc analysis revealed that species interacted with both sex and mass for time to move measurements, and interacted with sex for time to leave circle measurements. Larger and female *S. limbata* took longer to move and female *S. limbata* took longer to leave the circle. This suggests that sex and size differences in behavior are more pronounced in native *S. limbata*, which, if such interactions translate to fitness differences could influence native persistence.

Regarding patterns of variation, we found that the native *S. limbata*, but not the invasive *M. religiosa*, population displayed significant repeatability in voracity, which was driven by higher among-individual variation. These results may be indicative of previous hypotheses that the invasion process selects for certain behavioral types (and therefore less behavioral variation) to become established (Phillips and Suarez 2012). If interspecific competition is strong, we may expect this lack of variance associated with invasive variance to select for shifting native mean or invasive variance. However *M. religiosa* has been established at the field sites sampled in this study for a number of generations (at least 14). We may expect greater levels of behavioral variation in the invasive species post-invasion, as a result of the invasive species undergoing changes post-establishment (for example, Lee 2002). This may partially explain why levels of repeatability in response to novel prey and risk proneness behaviors are similar across species. If selection on those traits among the invasive species is relaxed post-invasion, levels of behavioral variation may not differ between species. Further exploring of these hypotheses requires comparisons of behavioral variation between known source and invasive populations and invasive and native species populations that vary in how

long they've interacted with each other. Indeed similar results supporting this effect have been found within native and invasive hymenoptera (Monceau et al. 2015).

We found a behavioral syndrome composed of a negative correlation between propensity to attack a novel prey item and seek a perch. While it is unclear how such a correlation arose, remaining prone and not seeking a perch is clearly a potential risky behavior for mantids as they are generally more conspicuous to predators when on the substrate. On the other hand, individuals more likely to remain prone are also more likely to attack a novel prey item, which could be beneficial if the novel prey item is appropriate. This correlation between risk proneness and attacking novel prey could be maintained if there are tradeoffs associated between individuals with increased risk of mortality yet increased foraging opportunities due to responsiveness to novel items, and reflects similar "boldness-aggression" syndromes found across taxa (e.g., Sih et al. 2004; Kortet and Hedrick 2007; Bell and Sih 2007; Moretz et al. 2007). However, neither risk-proneness nor response to novel prey was correlated with voracity. This contrasts with typical findings of positive correlations between similar behaviors (e.g., Pintor et al. 2008; Royauté et al. 2014; Biro et al. 2014). An absence of correlation between voracity and any other measured trait in this system suggests that it is either a separate behavioral trait and not linked response towards novel prey or risk-proneness, or that that these behaviors are poor indicators of actual feeding success. Collectively, these results highlight the need for researchers to understand the role, if any, of behavioral variation in co-occurring invasive and native species. Determining the role shifting levels of behavioral variation have on native species' ability to resist displacement and reciprocally, the influence of behavioral variation on the degree of invasive species-imposed selection could prove insightful for native species management.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

- Mean and variance of behaviors are thought to drive species invasions.
- We assessed levels of behavioral variation in native and invasive praying mantids
- Individual variation in most traits did not differ
- Invasive mantids showed low levels of variation in voracity
- This suggests stronger selection for voracity in this invasion system

Figure 1.

Experimental design of response to novel prey. Individual mantids (represented by the asterisk) were placed on a plastic tree (represented by the black pole). Around the base of the tree was a barrier. One fiddler crab was placed on the bottom of the substrate and was free to move around the perimeter of the plastic tree.

Figure 2.

The number of crickets eaten in a 15 minute interval was best predicted by individual weight (centered) as determined by AIC model comparison (AIC_c to next model = 2.2, $\omega_j = 0.726$). The fit line represents the positive relationship between weight ($\beta = 0.220 \pm 0.063$, $p < 0.001$) and voracity. A total of 142 trials were conducted on 77 individuals.

Table 1

General linear mixed model outputs predicting time to move, leave circle, and reach perch. Mantis weight was centered to a mean of zero and standard deviation of one before fitting. Female and *M. religiosa* were the reference binary variables. A total of 142 observations were made for 77 individuals.

	Time to move				Time to leave circle				Time to reach perch			
Random effects	Estimate				Estimate				Estimate			
ID	1.078				0.714				0.635			
Residual	0.939				0.889				1.258			
Fixed Effects	β	SE	t	p	β	SE	t	p	β	SE	t	p
Intercept	2.851	0.444	6.419	<0.001	3.860	0.385	10.024	<0.001	4.732	0.403	11.741	<0.001
Species <i>S.L.</i>	0.522	0.334	1.562	0.118	0.094	0.290	0.323	0.746	0.122	0.304	0.400	0.689
Sex Male	1.604	0.735	2.183	0.029	1.419	0.637	2.227	0.026	1.300	0.667	1.950	0.051
Weight	0.772	0.375	2.056	0.040	0.553	0.326	1.698	0.090	0.596	0.341	1.747	0.081
Marginal R2	0.054				0.056				0.035			
Conditional R2	0.560				0.476				0.359			

General linear mixed model outputs predicting the latency to approach and strike a novel prey item and number of prey eaten. Mantis weight was centered to a mean of zero and standard deviation of one before fitting. Female and *M. religiosa* were the reference binary variables. A total of 142 observations were made for 77 individuals.

Table 2

	Latency to approach				Latency to strike				Number of prey eaten				
Random effects	Estimate				Estimate				Estimate				
ID	27887				31057				0.125				
Residual	11288				0.9382								
Fixed Effects	β	SE	t	p	β	SE	t	p	β	SE	z	p	
Intercept	373.973	65.049	5.749	<0.001	490.077	67.016	7.313	<0.001	1.077	0.196	5.512	<0.001	
Species <i>S.L.</i>	-10.707	48.832	-0.219	0.826	-14.257	50.309	-0.283	0.777	0.071	0.147	0.481	0.630	
Sex Male	-161.216	107.483	-1.500	0.133	210.085	100.697	-1.898	0.058	1.057	0.320	0.178	0.859	
Weight	-70.858	54.886	-1.291	0.197	-80.694	56.507	-1.429	0.152	0.253	0.163	1.551	0.121	
Marginal R2	0.027					0.049					0.106		
Conditional R2	0.720					0.779					0.385		

Table 3

Pearson correlations and associated p-values (in parentheses) between the various behavioral measures across *S. limbata*. TTM, TTLC, and TTP refer to time to move, time to leave circle, and time to reach perch, respectively. LTA and LTS refer to the time to approach and strike the novel prey, respectively.

	TTM	TTLC	TTP	LTA	LTS	Voracity
TTM		0.773 (0.000)	0.572 (0.000)	-0.523 (0.000)	-0.609 (0.000)	0.08 (0.552)
TTLC			0.699 (0.000)	-0.5429 (0.000)	-0.706 (0.000)	-0.038 (0.793)
TTP				-0.395 (0.004)	-0.5325 (0.000)	0.027 (0.857)
LTA					0.845 (0.000)	0.032 (0.826)
LTS						-0.005 (0.976)

Table 4

Pearson correlations and associated p-values (in parentheses) between the various behavioral measures across *M. religiosa*. TTM, TTLC, and TTP refer to time to move, time to leave circle, and time to reach perch, respectively. LTA and LTS refer to the time to approach and strike the novel prey, respectively.

	TTM	TTLC	TTP	LTA	LTS	Voracity
TTM		0.763 (0.000)	0.383 (0.000)	-0.473 (0.000)	-0.596 (0.000)	0.172 (0.100)
TTLC			0.519 (0.000)	-0.623 (0.000)	-0.697 (0.000)	0.045 (0.665)
TTP				-0.232 (0.025)	-0.331 (0.001)	-0.141 (0.177)
LTA					0.891 (0.000)	0.022 (0.838)
LTS						-0.071 (0.500)

Table 5

Table of repeatabilities across treatment groups (All) and within species (*M. religiosa* and *S. limbata*). Confidence intervals were estimated via parametric bootstrapping, and repeatability p-values were estimated by permutation tests. TTM, TTLC, and TTP refer to time to move, time to leave circle, and time to reach perch, respectively. LTA and LTS refer to the time to approach and strike the novel prey, respectively.

Behavior	Group	Repeat	95% CI	P	Alvar	95% CI	RESvar	95% CI
LTM	MR	0.510	0.300 – 0.702	0.002	1.186	0.503 – 2.086	1.139	0.697 – 1.595
	SL	0.495	0.147 – 0.777	0.020	0.555	0.130 – 1.195	0.565	0.293 – 0.889
TTLC	MR	0.461	0.204 – 0.676	0.002	0.798	0.316 – 1.502	0.934	0.582 – 1.334
	SL	0.160	0.000 – 0.577	0.306	0.147	0.000 – 0.597	0.774	0.385 – 1.165
TTP	MR	0.281	0.000 – 0.565	0.048	0.630	0.000 – 1.429	1.609	0.983 – 2.285
	SL	0.403	0.048 – 0.728	0.047	0.380	0.015 – 0.921	0.563	0.265 – 0.906
LTA	MR	0.697	0.535 – 0.828	0.001	27892	16324 – 43473	12149	7676 – 17068
	SL	0.657	0.386 – 0.857	0.002	18575	7123 – 35683	9695	4757 – 15429
LTS	MR	0.779	0.637 – 0.879	0.001	32249	19257 – 49746	9126	5470 – 12951
	SL	0.660	0.394 – 0.858	0.001	19173	7556 – 37690	9859	4542 – 15283
Voracity	MR	0.212	0.000 – 0.331	0.082	0.069	0.000 – 0.137	-	-
	SL	0.483	0.000 – 0.624	0.011	0.245	0.000 – 0.434	-	-