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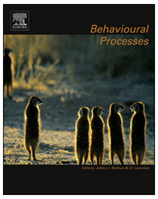

Behavioral variation post-invasion: Resemblance in some, but not all, behavioral patterns among invasive and native praying mantids

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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.

1. Introduction

The presence of invasive species can have detrimental effects on the fitness of native species (Ricciardi 2004; Clavero and a-Berthou, 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 et al., 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 et al., 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 et al., 2010a,b,c; 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.

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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 1800 s, it has been repeatedly introduced both deliberately and inadvertently (Gurney, 1950; Vickery and Kevan, 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, 2001; 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.

2. Methods

2.1. 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° 31′ 24.798″ N121° 47′ 2.2272″ W and 38° 37′ 17.796″ N121° 59′ 21.8724″, respectively) where they are sympatric. Specimens were kept in individual 16oz deli containers (top diameter 12 cm; bottom diameter 10 cm; height 8 cm) and were held in the laboratory at UC Davis in 12:12 h 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 24 h. Specimens were then food restricted until their mass reached 75 ± 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 min. 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.