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Research Letters

Investigating movement behavior of invasive Burmese pythons on a shy–bold continuum using individual-based modeling

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ABSTRACT

Burmese pythons are established in the Everglades and are expanding their population in Florida to more urbanized and fragmented habitats. Understanding movement and dispersal behavior contributes to our knowledge of how landscape factors influence the persistence of pythons in Florida's habitat. Our goal was to examine personality-dependent dispersal in juvenile Burmese pythons by creating behavioral scenarios of risk-taking behavior on a shy–bold continuum using an individual-based model. We observed that a behaviorally plastic strategy best resembled empirically derived patterns of the Burmese python's expansion from the Everglades into the increasingly urbanized landscapes of Homestead and Miami, Florida. This result is consistent with the notion that animal personalities can be flexible in different situations and that animals must make decisions based on trade-offs while dispersing.

Introduction

Invasion biology has a long tradition of identifying traits that could explain between-species dissimilarities in species' abilities to succeed as invaders (Cote et al., 2010). However, examining the average behavioral response of a population as a whole masks the variation between individuals that likely drives invasion dynamics, particularly those characteristics that may only be advantageous in certain phases of the invasion. The process of an invasion is composed of several stages starting with initial introduction and spread and ending with integration into the ecological community (Vermeij, 1996). Researchers are increasingly focusing on different behaviors that help invaders transition from one stage to another while recognizing that these behaviors may not be as beneficial to the persistence of the invasive population in the next phase of invasion (Cote et al., 2010).

Personality-dependent dispersal, where personality types such as boldness, aggressiveness, and sociability are linked to the propensity to disperse, is particularly relevant in studying the spread of invasive populations (Duckworth and Badyaev, 2007; Sih et al., 2012). The net movement of the most dispersive individuals of a population determines its rate of expansion, even when long-distance dispersal events are rare (Neubert and Caswell, 2000; Bartón et al., 2012). Fraser et al. (2001) demonstrated that movement behavior is heterogeneous within a population, thus intraspecific differences in demography, behavior, or personality are important for describing dispersal kernels for an invading population. For example, western bluebirds (*Sialia mexicana*) on an expanding front across the western United States were more likely to be aggressive and to thus outcompete sister taxa; however, individuals behind the front in the established range were more likely to be less aggressive because aggressiveness was correlated with poor parental care in males (Duckworth and Badyaev, 2007). Invasive cane toads (*Chaunus* [*Bufo*] *marinus*) in Australia employed a range of sociality depending on their position along the colonization front (González-Bernal et al., 2014). Boldness has been linked to dispersal tendency in a variety of species (e.g., *Lepomis gibbosus*, Coleman and Wilson, 1998; *Parus major*, Dingemanse et al., 2003; *Vulpes velox*, Bremner-Harrison et al., 2004; *Neogobius melanostomus*, Myles-Gonzalez et al., 2015).

Boldness is the tendency of organisms to explore and move through unfamiliar space and novel situations (Wilson et al., 1993). Bold individuals tend to move greater distances and to be riskier in how they explore unfamiliar landscapes and in their antipredator response (Bartón et al., 2012). While bolder dispersers move greater distances, they also have higher probabilities of mortality (Azevedo and Young, 2006). For example, the boldest reintroduced swift foxes in Montana moved the farthest from their release sites but experienced lower survival compared to individuals who limited their movements (Bremner-Harrison et al., 2004). Clearly,

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behaviors that maximize an individual's dispersal distance may not be advantageous to individual survival (Bartón et al., 2012). This suggests that the expansion of a population is driven by within-individual variation in balancing risk and dispersal distance (Zollner and Lima, 2005), or that boldness varies between individuals with those on the expanding front bolder than the average individual in the core population and the rare, bold survivor driving the expansion (Fraser et al., 2001; Bartón et al., 2012).

Among the most significant biological invasions currently taking place in the eastern United States is the Burmese python in southern Florida. Pythons are well established in the Everglades, but they appear to be expanding their range northward into more urbanized and heterogeneous landscapes (Dorcas and Willson, 2011). While south Florida's habitat is ideal for the python (e.g., abundant prey, similar climate as native range), it is not without risks of mortality (e.g., predators, road networks, machinery).

Understanding resource distribution and habitat suitability as well as movement and behavior is important in predicting the python population's ability to persist in novel, fragmented habitats outside of the Everglades (Taylor et al., 1993; Knowlton and Graham, 2010). Dispersal and movement are recognized as key processes involved in measuring landscape connectivity for particular species (Taylor et al., 1993). However, little is known about the behavior and movement of dispersing juvenile pythons due to their evasiveness and their use of remote habitat. Because of the lack of information on Burmese python dispersal behavior, there is little direct evidence that Burmese pythons display personality types; however, the pervasiveness of behavioral syndromes in well-studied species suggests a high likelihood that Burmese pythons display consistent differences in behavior related to movement and exploration (Sih et al., 2004). Preliminary research on boldness in Burmese pythons indicates an effect of relatedness on risk-taking strategy in laboratory trials (Pittman, unpubl. data). Additionally, Pittman et al. (2014) found that pythons have sophisticated navigational abilities which could contribute to behavioral decisions during dispersal. Studying the behavioral components of how pythons move through Florida's landscape thus contributes to our understanding of their ability to spread into novel habitat. Additionally, knowledge of patterns of dispersal aids our ability to plan control methods that could manage the spread of Burmese pythons and other invasive species in the state.

Our objective was to use a spatially explicit individual-based model (IBM) to investigate boldness on the expanding front of the Burmese python population in southern Florida as the population expanded from the Everglades into human-dominated landscapes. IBMs can illustrate the interaction between individual behaviors and landscape configuration and characteristics, an interaction that drives animal movement behavior (Zollner and Lima, 1999). Our goal was to simulate individual behaviors on the edge of the population so we could observe the rare dispersal events that drive a population's expansion. We predicted that individuals on the front characterized as bold would move faster and farther than shy individuals, and that the rate of expansion of bold individuals would most closely resemble the rate observed in the field. We also predicted that the final range occupied by pythons as facilitated by bold dispersers would most closely resemble the observed range during this same time frame. We expected bolder individuals to experience higher rates of mortality and establish home ranges farther away from their release locations in comparison to shyer individuals.

Material and methods

Model overview

Our goal was to simulate risk-taking behavior in dispersing juvenile Burmese pythons on the leading edge of an expanding front. We created 6 behavioral scenarios on a shy–bold scale and modeled dispersal of 25 virtual pythons per scenario per dispersal season. Each scenario ran for a dispersal season of 6 months over a 10-year period from 2004 to 2013. The Early Detection & Distribution Mapping System (EDDMapS) database provided extensive python presence data recorded over 10 years (2004–2013) that we used to pattern-match (Grimm and Railsback, 2013) our model outputs (see Appendix A, Model study system and Main Text, Analysis). We only modeled individuals on the leading edge of the front; at the beginning of each dispersal season, we determined the new leading edge and selected a new random sample of 25 individuals. Thus, we were able to simulate python expansion across our study site while restricting our focus to virtual snakes on the leading edge of the population.

Modeling framework

We used the spatially explicit individual-based model Spatially Explicit Animal Response to Composition of Habitat (SEARCH). SEARCH simulates animal dispersal and home-range establishment on a virtual landscape with a high degree of behavioral complexity (Pauli et al., 2013). The program interfaces with ArcGIS (ESRI, Redlands, CA, USA) to build a virtual landscape, which is comprised of vector-based maps representing animal movement, foraging opportunities, risk of mortality, habitat suitability, and exclusive occupancy of resident animals (Pauli et al., 2013; Table 1). Each map contains specific field definitions based on different GIS classifications, and virtual animals individually alter their behavior or physiological state based on these parameters (Pauli et al., 2013). Dispersers can be introduced to the landscape via a point release map or may be "born" on the landscape through the reproduction of resident animals (Pauli et al., 2013). Each individual generates its own memory map. This represents the information it perceives from its environment and is used in making settlement decisions. Virtual animals respond to per timestep mortality and energetics and change behavioral states (e.g., searching vs. foraging, risky vs. safe) as they interact with the landscape (Pauli et al., 2013; Table 1). Parameters governing behavior, energetics, home-range requirements, and resident reproduction can be modified to include heterogeneity in animal response caused by sex, time, and behavioral state (Pauli et al., 2013; Blythe et al., 2011). Appendices are available in the supplementary online material. See Appendix A for a full description of the model study system, map inputs, and model parameterization and the word box for details on behavioral scenarios.

Model study area

We simulated dispersal and home range establishment of juvenile pythons on an agricultural and urban interface in southern Florida between the southeastern Everglades, Homestead, and south Miami (Fig. 1 and Table 1). Southern Florida is located in a subtropical climate characterized by a wet and a dry season. This section of the Everglades is comprised of freshwater sloughs, marl prairies, tropical hardwood hammocks, and pinelands. Agricultural lands and low-density urban development characterize Homestead, Florida, while urbanization intensity increases rapidly as Homestead connects to southern Miami and approaches the city center. These areas are anthropogenically connected via a dense road network and canal waterways. We chose this study area because it was comprised of land cover types from which we had empirical data on juvenile python movement (Table 1; Appendix A, Model study system). See Appendix B for a full description of why and how we chose this modeling extent.