LIFE HISTORY, EXPANSION PATTERN AND INVASIVE-SPECIFIC MORPHOLOGICAL VARIATION OF THE INVASIVE LIZARD ANOLIS SAGREI

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Abstract

For economic, public health, and conservation purposes, detailed study of patterns of invasion are important. An understanding of initial colonization, expansion and acclimation/adaptation to novel environments is essential when predicting invasion patterns and potential for local ecological effects. This article defines physiological and demographic characteristics of successful invasive species, notes the variability within invading populations with respect to phenotypic plasticity, adaptation, and acclimation, and discusses the significant ecological, economic, and public health implications. In particular, the invasion and expansion patterns of the brown anole lizard *Anolis sagrei* has been highlighted for study and subsequent discussion will include the natural and life history traits, fundamental and realized niches, genetic/phenotypic variation, and a recent study of reproductive output patterns of female brown anoles. By combining this collective review of pertinent literature and recent studies, projections of the potential future invaded range of *A. sagrei*, its limitations, as well as its ecological implications will be analyzed.

Expansion pattern, life history and invasive-specific morphological variation of the invasive lizard *Anolis sagrei* in the southeastern United States

In 1999 it was estimated that 50,000 foreign species had been introduced to the United States by natural or anthropogenic mechanisms (Pimentel et al. 2000). Individuals at Cornell University translated this to $138 billion per year in preventative measures, infrastructure damage and reparations, resulting solely from these invasive species. For economic, public health, and conservation purposes, detailed study of patterns of invasion are important. An understanding of initial colonization, expansion and acclimation/adaptation to novel environments is essential to predicting over what geographical range various invasive species will spread, and how quickly, as well as what ultimate effect the invasion will have on native species, local ecology and infrastructure.

This article aims to elucidate the general physiological and demographic nature of successful invasive species, to analyze differences within invading populations with particular emphasis on the variability attributable to phenotypic plasticity as well as adaptation and acclimation, and to discuss the significant ecological, economic, and public health implications. In addition, the invasion and expansion patterns of the brown anole lizard *Anolis sagrei* will be discussed in more detail; the natural and life history traits, fundamental and realized niches, and genetic/phenotypic variation within the introduced population will be explored and discussed in terms of the species' own success as an invasive lizard. Lastly, parallels will be drawn between these known traits and a recent study of reproductive output patterns of females in various size combinations of cohabitation. By combining this collective review of pertinent literature and recent studies, projections of the potential future invaded range of *A. sagrei*, its limitations, as well as its ecological implications will be analyzed.

Characteristics of a Successful Invader

Before discussing the specific variability within, interactions between, and patterns of invasive species, it is important to understand what defines a species as “invasive”, what types of environments are susceptible to invasion, and what physiological or behavioral characteristics allow a species to become a successful invader. A particular species invasion is considered successful when the individuals have been able to colonize the initial area, establish a population with stable or increasing subsequent generation sizes, and spread by expanding the realized niche outward from the initial site of invasion to surrounding previously uninvaded areas (Sakai et al. 2001). These stages of invasion are facilitated through acclimation of the individual or adaptation of the population to the novel environment (Kolbe et al. 2014).

For most species, introduction to a novel environment would not lead to proliferation and introduced individuals would be unable to survive and reproduce for a number of reasons (Williamson 1996, Williamson and Fitter 1996). Invaders encounter new organisms with which they have never cohabitated including morphologically and behaviorally dissimilar predators and prey. Without the proper experience recognizing potential predators or toxic prey, new species may encounter high rates of mortality due to predation and ineffectual food resource utilization. Proficiency might also be lacking in an individual’s ability to defend itself from these new predators and to detect, pursue, catch, handle and consume novel prey species. These are issues that define the gap between the abiotic conditions in which an organism can survive (fundamental niche) and the combination of biotic and abiotic factors the organism is actually found living in (realized niche). The fundamental niche of an organism or population depends heavily on the climate in which they can survive. In certain temperatures, humidity levels, rainfall gradients and frequencies of disturbance events, certain organisms cannot compete with more locally adapted individuals and will not proliferate.

The environment being invaded plays a large role in determining the success of an invader. The tropics and subtropics are characterized by climatic conditions that broadly facilitate species biodiversity and abundance in their moderation. In warmer temperate conditions, metabolism reaches a higher efficiency due to increased enzymatic activity and there is an abundance of vegetation due to high photosynthetic rates. In a quintessential "bottom-up" trophic cascade, increase in the biomass of primary producers upregulates primary consumers, meta-predators and top-predators. Due to the increased temperatures and rainfall, biodiversity tends to increase as one moves closer to the equator. Environments with frequent disturbance events and habitat fragmentation are associated with increased invasion susceptibility (Elton 1958, Orians 1986a, Orians 1986b, Fox and Fox 1986, Hobbs and Huenneke 1992) although it is the intermediate disturbance theory which is said to account for increased biodiversity.

Successful invaders show patterns of shared morphological characteristics, physiology, and behavior that all have been shown to facilitate invasion and expansion of their respective populations. As expressed in the brown anole, a generalized diet and habitat use aid a species in their ability to quickly adjust to a novel environment. The brown anole has a highly variable diet (eating prey proportionally larger than most anoline species of the same size) and tends to be able to utilize a wide range of perch diameters at variable heights displaying less arboreal and less specific preference for perch height than closely related organisms.

Organisms with a capacity for altering their morphology over short periods of time through phenotypic plasticity and acclimation are more likely to reduce the limitations that encumber many non-native species (Kolbe et. al. 2013) potentially allowing them to expand beyond the boundaries of their fundamental niche and, more generally, become a more productive and abundant species in the new area. Lopez-Darias et al. (2012) demonstrated that *A. sagrei* would exhibit a phenotypically plastic behavioral modification when exposed to a predator (*Leicephalus carinatus):* when the larger lizard predator was present in the study environment, *A. sagrei* shifted from lower level branch use to a higher spatial niche despite the favorability of the ground climatic conditions. In less than a month, the brown anole had adjusted its spatial use to better facilitate its survival upon introduction to a new predator (Lopez-Darias et al. 2012).

Short generation times and unique behavioral characteristics all contribute to this invasive success in *A. sagrei*. Ultimately, species that invade successfully can utilize a new environment that may offer them more abundant resources and fewer competitors, predators or parasites, all population-limiting factors in a typical niche. (Elton 1958, Orians 1986a, Orians 1986b, Crawley 1987, Pimm 1991, Pimm et al. 1991, Vermeij 1996, Williamson 1996, Williamson and Fitter 1996, Mack et al. 2000).

Patterns of introduction and expansion of *A sagrei* in the US and surrounding countries/territories

The brown anole is considered an “exceptional invader” in the context of its rapid movement from islands in the Caribbean to the United States and is “among the best” at invading and colonizing new islands (Williams 1969, Losos et al. 1993). According to Campbell (1996), of the eight distinct anole species in Florida (Meshaka et al. 1997), *A. sagrei* is expanding most rapidly over the largest geographical area and can easily reach densities of 1 lizard/meter^2 in certain locations (Schoener and Schoener 1983, Losos and Spiller 1999). Using studies from the past five decades in which population numbers and phenotypic diversity was quantified through historical census data and molecular genetic analysis (Kolbe et al. 2004), it is possible to elucidate the approximate invasion times of successive and simultaneous introductions, expansions and general origin locations of *A. sagrei* parent populations (Bell 1953, Godley et al. 1981, Campbell and Hammontree 1995, Campbell 1996, Kolbe et al. 2007a, Kolbe et al. 2007b).

The native range of the brown anole consists of Cuba, the Bahamas, western and central Jamaica, Little Cayman I and surrounding islands, and potentially the Atlantic coast of Mexico (Williams 1969) although it has been suggested that the Mexican populations, showing a high degree of measurable morphologic difference from the Caribbean populations, could have just as easily been the result of a very old colonization event (Lee 1992). This anole species was first found in the Florida keys in the 1800s (Williams 1969) but subsequent spread to the Florida mainland was not confirmed until the 1950s (Lee 1985). One of these 1950s Florida mainland populations (now localized to Miami) was determined to have originated from a population in western Cuba (Kolbe et al. 2014) but is only one of multiple simultaneous or slightly temporally staggered introductions to different areas of the Florida mainland. An Orlando population arose from multiple populations in western, central and eastern Cuba approximately two decades later in the 1970s. A third population (localized in Tifton, Georgia) was analyzed for morphological and genetic similarities and its invasion timeline was estimated to have occurred in the 1990s potentially from nearby Valdosta, Georgia whose population was derived of western and central Cuban sources (Kolbe et al. 2014). These small, disjointed populations in Georgia occur primarily near and along interstate highways (Campbell 1996) suggesting a truck route method of dispersal. In 2003, the invasive range of *A. sagrei* extended from 24.5° N to 33° N spanning much of the latitudinal gradient of mainland Florida, parts of Georgia, Hawaii and Taiwan.

Life History Traits and Niche Utilization by *A. sagrei*

The brown anole lizard is a cosmopolitan species of many sunny habitat types including human-dominated areas and homes. They are an inherently territorial species, usually defending an area of approximately 400 square feet per individual or mating pair. During territorial encounters, the defender typically displays dark coloration and behavioral head-bobbing and, in males, dewlap extension to warn off invaders. *A. sagrei* utilizes a wide range of perch diameters and is known for perching at lower heights than many other species and is active later in the day than related anolines. Relative to their more arboreal cousins, the brown anole has a larger home range area. The males typically have larger ranges dependent upon body size (increased size intimates increased territory size) and females do not display this same allometric pattern (Schwartz and Henderson 1991).

The brown anole's variability of habitat use has been shown to diminish intraspecific competition as competing members of the same species have a wider range of potential habitat use. Population density has been shown to be positively correlated with incidence of parasitism; reduction of *A. sagrei* density by the cosmopolitan nature of microhabitat selection might aid in reducing the relative incidence. The brown anole is parasitized by a diverse range of species and studied incidences of infection include various trematodes, nematodes and Acanthocephali (Schwartz and Henderson 1991). They have also been shown to have carried a species of helminth to Hawaii (Norval et al. 2011).

A. sagrei tend to consume proportionally larger prey than similarly sized species and consequently spend a longer period of time undertaking meal consumption. One of the behaviors that makes the species well adapted for over-water invasion is the brown anole's ability to float on the water for an extended period of time. When experimentally placed on a small fragment of island, more than 1/3 leaped into the water and were able to remain buoyant for 1 hour. 30% were still floating after 24 hours. This unique ability to breach characteristically impervious geographical barriers provides another possible mechanism for expansion of *A. sagrei* to neighboring islands (Schwartz and Henderson 1991).

In recent study conducted at Oklahoma State University, we sought to analyze potential relationships between the size of female cohabitating brown anoles and proportion of energy each female allotted toward reproduction (Grammer et al. 2015). Twenty-two female brown anole lizards of the same age were bred, marked and characterized as a "big" or "little." They were separated into either mismatched pairs (one big and one little), size-matched pairs (two of the same size) or isolated controls. We aimed to determine whether the relative size of the cohabitating females would alter how the energy budget of each individual was utilized. Operating under the assumption that each organism possesses a limited amount of energy which must be utilized to drive all functions of the body (i.e. reproduction, body maintenance, body growth and pursuit of prey), we sought to determine whether, through daily interaction with lizards of the same size or a different size, reproductive energy expenditure would differ.

In order to determine how much energy each lizard allotted toward reproduction, eggs were counted and the mass and snout-vent length measurements were taken from hatchlings. A limitation to this study was that due to the nesting nature of reproductively active female brown anoles, the maternity of each single-egg clutch was not able to be determined and, instead, we focused on the relative variances in egg mass or hatchling mass to make inferences about the biological principles at work. One of the observations supported the “Rival Hypothesis” in that mismatched pairs produced more eggs than size-matched pairs. This hypothesis postulated that the uncertain dominance hierarchy of two same-sized lizards cohabitating would encourage more of the energy budget of each lizard to be allotted toward body maintenance and growth while leaving less for reproduction.

A separate measurement of hatchling mass supported the contradictory “Bully Hypothesis”. The variance in hatchling mass of the mismatched lizards was significantly higher than that of the offspring of the size-matched lizards. This result suggested that less energy would be expended for reproduction and more for body size growth/maintenance by the smaller lizard in each mismatched pair due to aggression or exclusion by the larger. This measurement is limited as described above in our inability to determine the maternal origin of each of the clutches. While these hypotheses contradict one another, the determination of statistical significance related to the relative body size of cohabitating lizards suggests that there is a relationship with reproductive energy expenditure although the specifically correlated variable or variables have yet to be determined (Grammer et al. 2015).

Morphological variation within invader populations

Depending on the characteristics of differing novel environments upon colonization events by the same founding populations, they may diverge and can develop substantial differences from one another through the process of “character release” (Campbell and Echternacht 2003). Relatively constant factors characterizing a population (such as average male body size and average body condition) are often constrained by limiting factors like resource availability, population density or predator density (Campbell and Echternacht 2003). When two subsets of the same founding population are differentially “released” from one or more of these restrictions unilaterally, a character (such as average body size) may be released from the limitation and remain free to increase well past that of the typical individual. Character release is often seen when an island population moves on to invade and inhabit a mainland due to the general release from the island’s limited food supply (Campbell and Echternacht 2003). Andrews (1979) notes that the release of body size can be “explained by abundant dietary resources” when shifting from island to mainland inhabitation. The pattern is seen when average male and female body sizes of Floridian and Mexican brown anoles are compared to their island-inhabiting counterparts. *A. sagrei* body size is comparable between the two mainland populations but both are significantly larger than any island population (Andrews 1979).

In a study conducted in Campbell and Echternacht (2003) simulated invasions of two populations from the same source (Pahokee) in two different habitats characterized by presence of or lack of dense vegetation showed significantly different body sizes and rates of population growth. Authors concluded that the dense vegetation and soil fertility was a more conducive habitat for arthropod proliferation and that the differences in prey abundance between the two islands fully explained the sustained release of body size for Population 2 (P2-vegetated island), and the initial but not sustainable body size release of Population 1 (P1-less vegetated island).

Variability in population growth rate can also occur due to an invader population’s differential habitat selection. In this same study, the population on the less vegetated island experienced a more rapid initial growth rate while P2 showed a much more gradual increase (Campbell and Echternacht 2003). This effect was attributed to the fact that P1 was released from its native predators to an environment that fostered very few, allowing for a release in population growth rate. The much more predator-rich island invaded by P2 received no such release.

Introduction of new species, human facilitated and otherwise, into a novel environment has demonstrated a number of effects on local ecology. The main impacts cited range from ecological in the reduction of native species populations or biodiversity of an area, to economical in the destruction/infestation of previously unaffected areas and subsequent need for infrastructure repair. Because of these innate character differences between initially genetically and morphologically identical populations, it becomes apparent that many additional factors must be considered when trying to make ecological predictions of the future dynamics of an introduced species and the interactions between or impacts on native biota.

Intrinsic Genetic and Phenotypic Variation and Subsequent Facilitation of Species Expansion

A population subset that colonizes an area with limited gene flow does not carry with it the full allelic diversity of the source population. In these instances, the new colony has experienced the Founder effect and the genetic diversity of the newly established population is some fraction of the source population’s. How, then, is genetic variability introduced to an invading population?

Frequently, multiple invasions of the same species into the same area will occur over some span of time (Dlugosch and Parker 2008). If the two (or more) invading populations originate from different sources along the species’ expansive natural range, genetic diversity may be introduced by the local adaptations of the sources. Kolbe et al. (2014) determined that physiological variation between individuals of the same species may occur in a pattern specific to the latitudinal gradient of each population's inhabitation. They chose to analyze the brown anole because of the species' broad invasive range and ample ecological, molecular and physiological information available. These invasions may occur simultaneously, sequentially or over a long period of time and theoretically each subsequent introduction increases the invading population's allelic diversity.

Secondary invasion of the same source population introduces genetic diversity as well, but if these events are separated on a large temporal scale, there is a greater likelihood local selective pressures will incur allopatric genotypic change. With a greater difference between the alleles contained in the colonizing population and those of the source population (a difference exacerbated over many generations), a second reintroduction from the same source many years after the first is likely to incorporate more genetic diversity than two rapid, sequential introductions.

Not all variation within a population is attributable to local adaptation, however, and the roles of phenotypic plasticity and acclimation in facilitating the expansion of an invader's fundamental niche have undergone careful study (Kolbe et al. 2010, Urban et al. 2007, Kearney et al. 2008). We have discussed how good invaders often possess the capacity to rapidly adjust to a novel environment, but there is still a limit to the range of climatic conditions a particular species is prepared to rapidly adjust to. The fundamental niche is still defined at some extent and the initial generation of invaders will be slowed or stopped at such a barrier. Kolbe et. al. (2010) suggests that as a population acclimates to slightly more extreme conditions along the boundary of the fundamental niche, survival rates increase and the increased population density puts pressure on the population in terms of food and spatial resources. A study of Australian Cane toads shows a pattern of increased thermal maximum tolerances in toads which had acclimated to slightly more physiologically stressful environmental temperature extremes (Urban et al. 2007, Kearney et al. 2008) prompting an expansion of the Australian Cane toad population's fundamental niche. Genetic diversity incurred by local adaptation, multiple introductions, and physiological tolerance allowed by acclimation capacity and phenotypic plasticity have demonstrated a powerful potential for allowing species to utilize the edges of their fundamental niche and, potentially, expand that niche over a relatively short period of time.

Species occupying a specific ecological niche often experience dispersal limitations. These limitations manifest in the form of barriers to expanding species including mountain ranges, oceans, or simply inclement, inhospitable stretches of land/water that discourage or prevent further expansion. Despite this natural restriction of niche occupation, some individuals may breach the barrier due to increased competition for resources in the initial utilized habitat space. In the case of European starlings in the US between 1918 and 2003, for example, some individuals travelled a significantly greater distance from the bulk of the population and colonization of those novel areas by the invasive bird followed. Humans also facilitate this barrier-crossing. One of the most highly publicized examples of costly invasion of non-native species is that of the brown tree snake (*Boiga irregularis*) and its explosive expansion in Guam due to human activity after World War II.

The Impact of Invasive Species

While cosmopolitan species are not at a high risk for extinction from competition introduced by a non-native invader, endemic species are greatly threatened and have historically been eliminated by new species (Pimentel et al. 2000). This phasing out of natives is typically due to the greater success of some introduced species in competing for limited resources. This is especially detrimental to natives with a specific, non-generalized diet and a relatively small niche.

Historically, the intentional and (more often) unintentional introduction of non-native species to novel environments has led to encroachment on the resources and habitats of the native species. Reasons for introduction range from pest control to pet animals and from food production to landscape restoration (Pimentel et al. 2000). According to a report on the economic and environmental costs of invasive species, more than half of the occupants of the endangered species list are at risk primarily due to competition with or predation by a non-native species. Feral domestic cat populations, for example, initially introduced as companion animals, now pose a serious threat to native bird populations. The brown tree snake (*Boiga irregularis*) which became an invasive species to Guam after World War II has “dramatically reduced native bird, mammal, and lizard populations” reducing the 13 native bird species and 12 native lizard species to 3 and 3 respectively (Pimentel et al. 2000).

The brown anole has also been shown to have an effect on native U.S. species such as the green anole (*A. carolinensis)*. The relative numbers of green anoles throughout *A. sagrei*’s invaded range has been reduced, however experimentally re-created rapid adaptation of the native species to the invaders has demonstrated *A. carolinensis*’ capacity for altering its niche in response to the additional competition for resources. Specifically in terms of niche occupation, the lower-living brown anole has caused a shift in the perch height and toepad size of the native species (Stuart et al. 2014).

In addition to effects on local species, the brown tree snake had a significant impact on Guam’s infrastructure. It was estimated that due to property damage of utility poles and consequent frequent incidences of snake-induced power outages (approximately 86 per year), the economic effect of the brown tree snake on local businesses is estimated to be at least $1 million per year. This effect on infrastructure is not isolated to the brown tree snake invasion and can be translated to a number of other clades encompassing a vast number of species. Many species of zebra mussel have been introduced to the US from Europe and now are found in many freshwater habitats not only outcompeting native fauna for oxygen and other abiotic and biotic resources but clogging water intake pipes and filtration system, and causing billions of dollars in damages each year (Pimentel et al. 2000).

Due to the similarities between the invasive brown anole and native anolines of the United States, most local environments and infrastructure are already accustomed to the presence of similar species. Contrary to a location with no previous exposure to a particular organism’s dietary and habitat requirements as well as behavioral aspects, the introduction of another anoline species has not impacted the invaded areas with the same level of ecological and economic damage.

Lastly, a major concern of invaders is their potential for transmission of new diseases to local plants, animals and human inhabitants. In 1999 it was estimated that approximately 97 of the 1000 bird species of the United States were considered exotic. Of these, one of the most costly bird invaders is the common pigeon (*Columbia livia*). Nearly ubiquitous to cities of the world, the pigeon has costs associated with cleaning and repairing fouled buildings exceeding $1 billion per year, however they are also "vectors for more than 50 human and livestock diseases" (Pimentel et al. 2000). At this point in time, it is not thought that *A. sagrei* transmits diseases zoonotic to humans and it is unlikely that (if they did provide a vector for disease transmission) the green anole wouldn't also have been a suitable host due to their biological and spatial occupation similarities.

Cumulative studies of a particular invasive species like this are essential when considering the implications of introducing a new non-native species or of allowing one to proliferate to its fundamental capacity rather than employ the economic resources to curb its expansion. It is difficult, however, to ascertain reliable ecological predictions based on the study of the organisms in their native ranges due to the tendency for invading populations to expand in variability of body size, behavioral traits and niche utilization depending on changing pressures and releases of resources, predators and competing species. In the case of *A. sagrei*, while the species has reached the limits of its fundamental niche, we have shown the capacity of organisms of high invasive potential to acclimate to different abiotic conditions, adapt over time to these pressures, and potentially expand beyond current capacity. This further expansion would be dependent on a number of other ecological factors such as local competitive pressure increases and would be highly variable in occurrence and degree based on local ecology. Not a known cause for concern in terms of zoonotic disease transmission, extinction of indigenous populations or infrastructure damage, the brown anole is not an invasive species whose spread is inherently dangerous or requiring of immediate containment. They are, however, useful organisms for further study into general invasion patterns, population ecology and local acclimation and adaptation to ecological pressures in the southeastern United States.

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