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An Experimental Study of Juvenile Competition and Habitat Niche Partitioning Between a Native Lizard (*Anolis carolinensis*) and an Introduced Congener (*Anolis sagrei*) in the Southeastern United States

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To the Graduate Council:

I am submitting herewith a dissertation written by Justin W. Walguarnery entitled "An Experimental Study of Juvenile Competition and Habitat Niche Partitioning Between a Native Lizard (*Anolis carolinensis*) and an Introduced Congener (*Anolis sagrei*) in the Southeastern United States." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Arthur C. Echternacht, Major Professor

We have read this dissertation and recommend its acceptance:

Hamparsum Bozdogan, Gordon M. Burghardt, Susan E. Riechert, Daniel Simberloff

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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(*Anolis sagrei*) in the Southeastern United States**

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Justin W. Walguarnery

August 2008

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ABSTRACT

Since its introduction to Florida, the brown anole, *Anolis sagrei*, has steadily expanded its range into that of its native congener in the southeastern United States, the green anole, *A. carolinensis*. *Anolis sagrei* achieves very high densities both in its native and invaded range and appears to impose population declines and shifts in the realized habitat niche of *A. carolinensis*. In order to investigate whether these effects arise prior to the adult age class in which they have previously been described, I studied the behavior of juvenile anoles at the individual, dyadic, and neighborhood levels. Contrary to some characterizations of adult microhabitat selection, distribution models of individual movement on laboratory thermal gradients indicate that juvenile *A. carolinensis* are likely to occupy warmer sites than *A. sagrei*, but with broad overlap in the full range of temperatures selected by these species. Staged dyadic encounters between socially naïve juveniles of these species, however, suggest that intrinsic individual characteristics influencing dominance and behavioral exclusion in the youngest juvenile anoles favor *A. carolinensis* over *A. sagrei*. To confirm these observations and explore their consequences under conditions representative of natural juvenile assemblages, I compared the behavior and habitat use of *A. carolinensis* juveniles in single-species field enclosures with *A. carolinensis* and *A. sagrei* juveniles in two-species enclosures and described changes in the partitioning of space over the first weeks of life. Within the first week, thermal microhabitat partitioning was apparent and juvenile *A. carolinensis* in the presence of *A. sagrei* juveniles exhibited an upward shift in mean perch height similar to that seen in reproductive males following experimental

imposition of sympatry in adults of these species. Despite the shift in structural habitat use of *A. carolinensis* juveniles in the presence of *A. sagrei*, there was no observed consequence of syntopy on growth rate or survival. This study suggests no immediate role of juvenile interactions on numerical declines in *A. carolinensis* in sympatry with *A. sagrei*, but does indicate that a more ontogenetically comprehensive approach is warranted in the characterization of niche differences and habitat partitioning.

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Chapter 1

Introduction

BACKGROUND AND RATIONALE

Community composition is influenced by a myriad of both abiotic and biotic factors. Invasions by non-native species may disrupt the balance of these factors and can pose a threat to indigenous species, but in doing so they provide a unique opportunity to investigate the effects of competition on the ecological niche and population dynamics. The importance and even the widespread existence of interspecific competition in natural communities have at times been issues of intense controversy (Conner and Simberloff 1979; Schoener 1983; Roughgarden 1983; Connell 1983; Schoener 1985; Hastings 1987). This is, at least in part, due to the inherent difficulty in studying what is often an ephemeral process easily observable only when resources become uncommonly scarce or in interactions from which competitive exclusion or resource partitioning have yet to develop (Wiens 1977; Rosenzweig 1981). If exclusion of one competing species by another should occur, it is, as C. S. Elton (1958) noted, "...a demographic event of whose interior causes we may be and usually are almost ignorant." After the fact, an understanding of these causes may be as irretrievable as the species or populations lost in the process. It is thus critical, having recognized it as an apparent factor contributing to an ongoing invasion, that competition be experimentally investigated so as to clarify its mechanisms and magnitude.

The invasion of the southeastern United States by the brown anole (*Anolis sagrei*; Sauria: Polychrotidae) into the range of its native congener, the green anole (*A. carolinensis*), has been well documented (Godley et al. 1981; Campbell 1996), and accumulated evidence suggests that competition between these species may be

contributing to declines in green anole prevalence (Campbell 2000). Since the establishment of *A. sagrei* in south Florida in the 1940's (Lee 1985), numerous anecdotal accounts have suggested significant reductions in populations of green anoles following contact with expanding populations of the invader. This impression has been strengthened by experiments quantifying habitat shifts and by those based on analyses of population manipulation effects relative to controls (Campbell 2000) as described and recommended by Connell (1983). Through the experimental introduction of *A. sagrei* onto islands occupied by *A. carolinensis* it is known that populations of the former consistently displace the native anole and can do so in a time span not exceeding a few years (Campbell 2000). As *A. sagrei*, following this trend, has increased its numbers within the U.S. to the point where it is now the most abundant lizard in peninsular Florida (Wilson & Porras 1983), and in some locales achieves densities of over one individual per square meter (Schoener & Schoener 1980), there should be little contention that this invasion represents a significant ecological phenomenon. While shifts in habitat use by adult *A. carolinensis* in response to *A. sagrei* have been reported in conjunction with this process, it is not clear whether this aspect of the interaction is directly responsible for the observed population declines (Campbell 2000). Studies have also suggested that declines may be due to lack of recruitment in *A. carolinensis* populations in years immediately subsequent to local introduction of *A. sagrei* (Gerber 2000).

The research described in this dissertation involves investigation of competition between green anoles and brown anoles as juveniles, specifically in the first weeks of life, and explicitly addresses mechanisms by which this competition may arise. In this dissertation I take the general approach of comparing the behavior of *A. carolinensis*

juveniles among conspecifics only, with that of *A. carolinensis* and *A. sagrei* juveniles together. This approach provides experimental representation of the initial biogeographic scenarios in the *A. sagrei* invasion of the southeastern United States. Furthermore, I consider the contribution of microhabitat and environmental characteristics to growth and survival of *A. carolinensis* juveniles. Coupling results from experiments at the individual, dyadic, and neighborhood levels in a comprehensive analysis, I test the overall hypothesis that sympatry with *A. sagrei* juveniles imposes shifts in microhabitat use by *A. carolinensis* juveniles and that these shifts have apparent fitness consequences that could be linked to observed population-level effects of *A. sagrei*. Finally, I compare patterns of microhabitat use and interspecific interaction in juvenile *A. carolinensis* and *A. sagrei* to those previously described for adults of these species in order to provide insight into the role of ontogeny in a biological invasion and in the assembly of ecological communities. Observed differences between age classes in the character and intensity of interspecific interactions indicate an ontogenetically dynamic response to an invasive congener and suggest that the importance of competition could differ by age class.

Competition

Competition has been defined as “the demand, typically at the same time, of more than one organism for the same resources of the environment in excess of immediate supply” (Crombie 1947). Birch (1957) amended this simple definition so as to include situations in which, given an adequate supply of resource, one or both organisms, in the

process of seeking that resource, nevertheless incur harm due to the actions of the other. Such detrimental interactions may arise if two animals choose to fight directly for possession of a single resource item, what has been termed “contest” by Nicholson (1954) and “interference” competition by Park (1954). In the most immediate realization of competitive effects on populations the participants in such interference competition may actually kill or mortally wound each other (Palomares & Caro 1999). More often competition exerts an influence on populations less directly, although still through increased levels of mortality, simply as a result of a reduction in the availability of the materials necessary to sustain life. Conversely, effects may be manifest in reduced reproduction or recruitment. In any case, it is alterations in the balance between birth and death rates that ultimately define a competitive interaction so that, as Rosenzweig (1981) stated “two species compete if and only if the sum of their equilibrium densities is less than the sum of their carrying capacities, at least partially because each depresses the other’s net per capita reproductive rate.”

As Tilman (1987) has pointed out, however, those studies that examine only the population (numerical) response of a species to changes in the abundance of a potential competitor (Connell’s type 1 experiment; 1983) cannot discern direct from indirect effects and fail to adequately describe all interspecific interactions. Mechanistic studies, those that measure a specific process by which competition may occur and also involve examination of relevant physiological, morphological, or behavioral aspects, may be more useful in developing predictive models of community interactions. Furthermore, mechanistic studies preclude the necessity of inferring process from pattern and thus avoid the inherent difficulties in that approach (Hastings 1987).

Taking a mechanistic approach requires quantification of some aspect of species interactions linking proposed competition with fitness or population effects. Conley (1976) stated that “a variable is required that can be measured and that integrates limitations caused by absolute abundance or behaviorally induced shortages of apparently abundant resources,” and suggested contention for space as such a variable. As all space will not be of equal value to an animal and can be expected to vary in food availability, shelter, and predator pressure, contention for specific locations, in addition to occupation of a certain size area, can be expected. Thus, an investigation of competition centered on habitat utilization potentially spans multiple levels of competition intensity and incorporates mechanistic elements without disregarding more overarching effects.

Many studies have shown competition based on habitat variables to have an important influence on the viability of interacting species. In what has become a classic among competition studies since its publication in 1961, Connell provided strong evidence not only that competition was occurring between the barnacles *Chthamalus stellatus* and *Balanus balanoides*, but also that its existence was mediated through the limited resource of suitable habitat. This study provided a cogent description of a system in which distributions of the two species are dictated by varying degrees of competitive ability across a microhabitat gradient. Earlier work by Park (1948) had produced similar results in laboratory experiments on *Tribolium* spp., showing that the outcome of a competitive interaction between two similar species of flour beetle was largely dependent on small differences in conditions of the habitat. However, it was also determined that the results of single species rearings under a range of environmental conditions were often an inadequate basis for predictions concerning the results of mixed species rearings.

Hence, the emphasis of investigations into the distributions and habitat utilization of multiple species necessarily remains on interactions between the species and is most reliably described through empirical study rather than deduction (Park 1954). Empirical evidence for habitat related competition between lizard species is particularly strong, and it has been suggested that competition is often influential in determining habitat use in these animals (Smith & Ballinger 2001).

Ecology of Anolis carolinensis and A. sagrei

Lizards of the genus *Anolis* occur throughout a wide geographic area spanning from the southeastern United States, through Mexico, Central America, and the West Indies, and into much of South America. Anoles are small to medium-sized, predominantly insectivorous, lizards. The over 300 species comprising this taxon, while all of a recognizable and largely conserved general habitus, exhibit a wide variety of fine morphological and behavioral features fitting them to a range of habitats including forest canopy, low shrub and herbaceous vegetation, scrub, grassy areas, rock outcrops, wetlands and even human impacted areas of garden, plantation, or full urban development (Williams 1983; Schwartz & Henderson 1991). Some of the larger of the Caribbean islands and continental areas support complex anole communities with sympatric species occupying complementary niches characterized by differing thermal and structural microhabitat preferences.

Within the Polychrotidae, only *Anolis carolinensis* is native to the United States, having colonized the mainland, presumably from Cuba during the Pliocene (Glor et al.

2005). Williams (1969) has described this species as an arboreal trunk-crown “ecomorph” based on habitat utilization in the West Indies, although in U.S. habitat free of invading congeners *A. carolinensis* also occupies regions lower in the vegetation and on the ground. In Florida, mesophytic hammock serves as the optimal habitat, although very high densities are also achieved in well-vegetated residential areas, sugar cane fields and citrus groves (Wilson & Porras 1983). The range of *A. carolinensis* extends from eastern Tennessee and North Carolina south throughout all of Florida, and west through the Gulf Coast region, southern Arkansas, southeastern Oklahoma, and into central Texas. The northern range limitations of this species appear to be imposed by annual low temperatures, whereas constraints on western range expansion are likely based on limited levels of precipitation (Gordon 1956). Adult males of this species attain snout-vent lengths of 7.5 cm while females are limited to lengths under 6 cm (Gordon 1956; Conant & Collins 1998).

Anolis sagrei is similar in size to *A. carolinensis*, with a somewhat lower maximum adult male snout-vent length of 6.4 cm but a potentially greater overall body mass (Conant & Collins 1998). Gross patterns of habitat utilization overlap with those of *A. carolinensis* in the middle and lower height regions of forested habitat (trunk-ground). While both species proliferate in edge habitats, *A. sagrei* is also apparently well suited to the entirely open, highly insolated and drier areas increasingly common with intensified urban development. Wherever it occurs, it tends to become extremely abundant so that, according to Williams (1969) “If any anole were to be singled out as a ‘dominant species’, *A. sagrei* would be that species.” *Anolis sagrei* and *A. carolinensis* share distinction as supreme colonizers among anoles. Originating on Cuba, *A. sagrei* occurs

elsewhere in the West Indies, including the Bahamas. Both Cuba and the Bahamas were sources for colonization of mainland North America by the species (Kolbe et al. 2004).

Anole Reproduction and Juvenile Biology

The breeding season of *Anolis carolinensis* is defined by the activities of copulation and egg deposition. Gordon (1956) described this period as extending from the beginning of April through the end of August. This estimation was based on the earliest and latest observations of eggs at two New Orleans field sites in addition to an assumption of a six-week incubation time (observed for eggs in the laboratory). First copulation was estimated from laboratory determination of an approximately eighteen-day separation of egg fertilization and egg deposition. Corroborating this estimate are earliest field observations of copulation occurring in late March in Louisiana (Hamlett 1952) and as early as 1 April in Tennessee (Minesky 1999). Copulation is not observed in the field after August (Hamlett 1952; Gordon 1956; Jenssen et al. 1998). Gordon (1956) reported an unhatched egg in the field as late in the year as October, which also places the last egg laying in late August. In the laboratory no eggs were laid after August (Gordon 1956).

A widely cited value for potential reproductive output is that of one egg every 13-14 days reported by Hamlett (1952). Depending on the length of the breeding season, which varies with geographic locality (Crews 1980), this oviposition interval results in a maximum production of nine (Gordon 1956) or ten eggs (King 1966) during a breeding season. Hamlett's determination of a 13-14 day oviposition interval, however, was based

solely on laboratory observations and may be a low estimation of reproductive potential (Andrews 1985). Oviposition is influenced by environmental and social factors (Licht 1973; Andrews 1985) both of which may be sub-optimal under typical laboratory conditions (Andrews 1985). Under more natural laboratory environments and female densities, likely to better represent field conditions, mean oviposition intervals have been as low as 8.6 days (Andrews 1985), representing a potential seasonal output of 15 eggs.

Nest construction and egg deposition comprise the entirety of maternal behavior in *Anolis* (Gordon 1956; Stamps 1978; Propper et al. 1991). Nest construction by *A. carolinensis* generally consists of using the snout and forelimbs to dig a hole in soil or humus. The single egg is deposited in this hole and the nest is covered over with soil by alternating digging motions of the forelimbs. The snout is also employed in pushing and tamping down the soil. The total time spent in the deposition of an egg and related activities, as observed in the laboratory, ranges from 11 to 26 min (Propper et al. 1991).

Prior to oviposition a female may abandon a partially excavated nest, and it has been proposed that this behavior is indicative of an ability to determine whether or not a particular site is acceptable for embryonic development (Propper et al. 1991). Gordon (1956) reported egg deposition in association with increased environmental moisture, but egg retention during dry conditions in laboratory terraria. Stamps (1976) has demonstrated similar behavior in *Anolis aeneus*, with females exhibiting nest construction but failure to oviposit during brief droughts in the field. Females will retain eggs until moist habitat is encountered. However, eggs will not be retained indefinitely and females kept in enclosures lacking moisture will eventually deposit eggs in sites unsuitable for development (Gordon 1956). Laboratory observations of ovipositing

females conducted by Propper et al. (1991) also indicate a preference for relatively warmer sites for nest construction, and Gordon (1956) reported a preference in laboratory enclosures for Spanish moss over loam. In the field *A. carolinensis* eggs have been found in wood piles or holes in trees (Crews 1980) and in rotting logs (King 1966), at the bases of plants, between the stems of palms (Gordon 1956), in rock crevices (Rand 1967), and even in abandoned crab burrows (King 1966). At some sites where a canopy produces shade and limits the growth of underbrush it is not uncommon to find eggs completely exposed (Gordon 1956).

Eggs in the field incubate for approximately six to eight weeks prior to hatching (Crews 1980), although under laboratory conditions of room temperature and continuous high humidity an incubation time of 30 days is more common (Gordon 1956; Crews 1980). Studies of hatching in the field are scant, but the process has been described in detail for captive anoles (Gordon 1956; Greenberg & Hake 1990). Water loss by the egg, indicated by beads of water visible on the shell, occurs from a half hour (Greenberg & Hake 1990) to a day or more (Gordon 1956) prior to hatching. Greenberg & Hake (1990) report apparent neonatal movement and slitting of the egg occurring almost simultaneously with the first appearance of moisture on the surface of the eggs.

Subsequent to the emergence of the lizard's head from the egg, there is a pause of several minutes during which scanning behavior, consisting of head movement (Gordon 1956; Greenberg & Hake 1990) and tongue flicking (Gordon 1956) occurs. Sudden movement apparently detected by the emerging hatchling causes withdrawal into the shell (Gordon 1956). This surveillance behavior and apparent alertness are consistent with behavioral acts discussed by Burghardt (1977) for other neonatal reptiles in association with predator

evasion and environmental assessment. *Anolis carolinensis* hatched from lab incubated eggs emerge with snout-vent lengths of 22-25 mm, whereas those from field hatched eggs may be somewhat smaller at 19-25 mm (Hamlett 1952; Gordon 1956; King 1966; Gerber 2000).

Research concerning juvenile *Anolis* suggests that much of the behavioral repertoire of adults is present from hatching or develops shortly afterward. Head bobbing displays have been observed as early as 30 min after emergence from the egg (Greenberg & Hake 1990). In addition to head bobbing, more complex challenge displays integrating pushups, dewlap extension, and sagittal expansion are performed by hatchlings and have been observed both in the laboratory (Greenberg & Hake 1990) and in the field (Lovern 2000). Greenberg & Hake (1990) report tail-lashing behavior occurring even prior to head bobbing. Several newly hatched *A. carolinensis* were observed to tail-lash upon encountering a conspecific. Juveniles retreating from such encounters exhibited a change to dark brown coloration with an eyespot (Greenberg & Hake 1990) characteristic of adult response to defeat in a territorial challenge (Greenberg 1977). Juveniles will display both towards other juveniles and towards adults (Lovern 2000).

Studies describing the use of space by juvenile anoles and the potential influences of territoriality have been far less common than those involving adult lizards. A conspicuous exception to this trend is the work of Stamps (1978; Stamps & Krishnan 1994a, 1994b) on juvenile *Anolis aeneus*. This research has shown juvenile anoles to be as aggressive as their adult counterparts and to maintain territories in a manner similar to that of adults (Stamps 1978). Home ranges in these juvenile lizards vary according to available vegetation and size of the anole, with larger anoles most commonly occupying

territories centered on patches of vegetation (Stamps 1978). Smaller juveniles occupied areas between patches of vegetation (Stamps 1978). Territory diameters for juvenile *Anolis aeneus* are approximately 80-100 cm (Stamps & Krishnan 1994b). Home ranges of juvenile *Anolis carolinensis* have been reported by King (1966) and Lovern (2000). From field observations over a 12-week period King determined an average horizontal movement of 2.13 ± 0.86 m. Lovern reported mean home range volumes for male and female juvenile *A. carolinensis* as $13.7 \pm 5.2 \text{ m}^3$ and $3.4 \pm 0.9 \text{ m}^3$ respectively. These ranges and overlap between them result in mean nearest neighbor distances of 0.8 ± 0.1 m for male juveniles and 1.1 ± 0.3 m for female juveniles, with another juvenile as the nearest neighbor in 70% of the observations (Lovern 2000). The ranges of both male and female juveniles appear fairly stable over time periods of at least several weeks (Lovern 2000).

Juveniles use a limited portion of the total habitat available and exhibit a restricted distribution relative to that of adult anoles (Lovern 2000). In general, juvenile *A. carolinensis* occupy lower regions of vegetation and are more often found on or near the ground (King 1966; Greenberg & Hake 1990; Jenssen et al. 1998). King (1966) found the majority of *A. carolinensis* within 30 cm of the ground to be juveniles. Jenssen et al. (1998) have described a positive linear correlation of both perch height and perch diameter with body size, so that typically hatchlings are found among grasses or low annuals, small juveniles most often perch in low shrubs, and larger juveniles perch predominantly in taller shrubs. It is uncommon to observe a juvenile perched above 2 m, and Lovern (2000) reports such sightings as comprising only 3% of total observations. Juveniles are more likely to perch on herbaceous vegetation with overall lower heights

rather than on the lower regions of woody vegetation and trees, and are also more likely than adults to use leaves as perches (Gordon 1956; Jenssen et al. 1998).

The specific life history of *Anolis sagrei* in the United States is less thoroughly known than that of *Anolis carolinensis*, though it is generally similar. Field research by Lee et al. (1989) in southern Florida indicates that the two species largely overlap in reproductive seasons. As in *A. carolinensis*, the period of annual reproduction for *A. sagrei* is highly correlated with seasonal increases in precipitation (Lee et al. 1989). However, the period during which females can be found with oviductal eggs in Florida extends from March to October (Lee et al. 1989), so that the portion of each year during which eggs are laid potentially exceeds that for *A. carolinensis* by several months. Egg deposition in *A. sagrei* occurs in the same manner as for *A. carolinensis*, although eggs may more commonly be left in drier, more exposed areas of sand and leaf litter (Crews 1980).

The hatchlings of *A. sagrei*, although potentially smaller, may also have a greater resistance to desiccation than those of *A. carolinensis* (Gerber 2000) and therefore possess a competitive advantage in more open habitat. Whereas juveniles of both species commonly co-occur in areas of complex microhabitat, *A. sagrei* juveniles tend towards greater abundance in areas of lower vegetational complexity and are more terrestrial than those of *A. carolinensis* (Gerber 2000). Furthermore, when restricted to habitats of very low structural complexity, *A. carolinensis* juveniles experience decreased survival whereas no such trend is observed for juveniles of *A. sagrei* (Gerber 2000). This difference in habitat tolerance suggests that *A. carolinensis* may be especially susceptible

to detrimental effects of interspecific competition in areas altered by anthropogenic disturbance.

Project Rationale and Outline

The juvenile age class of *Anolis* lizards could be especially susceptible to effects of interspecific competition. Trophic relationships within the community to be studied are such that neonates obtain food from a resource pool much reduced relative to that of adults. Although adult anoles can consume larger prey than can juveniles, prey size categories of adults and juveniles are not exclusive, so that the entire population may feed in part on the prey to which juveniles are necessarily limited (Vitt 2000). In addition, the nutritional requirements and the demands of growth in reptiles are generally more pronounced in juveniles than they are for adults (Morofka 2000). Juveniles are also more vulnerable to predation and to physiological stresses imposed by environmental conditions (Vitt 2000); therefore constraints on habitat utilization imposed by competitors in this age class could be especially detrimental. While sexual size dimorphism exists within adults of both *A. carolinensis* and *A. sagrei* and may serve in decreasing overall levels of competition within that age class (Roughgarden 1995), no such dimorphism exists between juveniles, which necessarily pass through overlapping sizes as they grow to maturity. These facts lead to an expectation of increased competition among juveniles, effects of which may be observable in habitat shifts, growth rate reductions and increased mortality (Gerber 2000).

The research I have proposed, while centered on a question of interspecific competition and invasions, is relevant and important to the field of reptile neonatology and to conservation as well. As a result of the 3rd World Congress of Herpetology in Prague, Czech Republic in 1997, several priorities for research on early age classes were identified (Morofka et al. 2000). Among those that my research addresses are the need for information on the early post-paritive movement of juveniles, assessments of the relative contribution of this age class to population dynamics, and identification of factors influencing neonatal growth and survival. Data obtained in these areas may be critical in allowing for a better understanding of the ecological role of interspecific interactions in the juvenile age class and a more ontogenetically comprehensive approach to reptile conservation and community ecology.

The research described in this dissertation covers individual, dyadic, and neighborhood levels of investigation. Chapter 2 describes a laboratory investigation of physical and behavioral aspects of thermal biology in juvenile anoles. Environmental temperature is an important gradient along which habitat partitioning can occur in ectotherms. However, the simplest approaches to the characterization of site selection along a gradient are inadequate for accurate description of some patterns of resource use. In this chapter I first describe a quantification of heating and cooling rates in *A. carolinensis* and the pattern by which they vary according to body size in juveniles and adults. Secondly, I fit parametric, single-component and mixture models to the distributions of environmental temperatures selected by *A. carolinensis* and *A. sagrei* on laboratory thermal gradients and describe the advantages of this approach over that based only on central tendency and symmetric variance statistics. In Chapter 3 I examine the

response of *A. carolinensis* juveniles in their first week in their first encounter with another juvenile anole. I compare interactions with *A. sagrei* juveniles to interactions with conspecific juveniles and develop a predictive model of dominance in these initial agonistic interactions. In Chapter 4 I describe observations of *A. carolinensis* in neighborhood assemblages of juvenile anoles in experimental field enclosures containing either conspecifics only or a group of equal density split between *A. carolinensis* and *A. sagrei*. Based on these observations I test for species differences in patterns of microhabitat use in three dimensions and describe the magnitude and ontogeny of *A. carolinensis* niche shifts in the presence of *A. sagrei*. Finally, I relate initial microhabitat use of the youngest anoles to growth rates over the first three weeks and compare niche partitioning between juvenile *A. carolinensis* and *A. sagrei* to that previously described for adults of these species. Although I employ typical frequentist statistical tests in some of these analyses, throughout this dissertation I rely heavily on information-theoretic approaches to model development including the use of Akaike's information criterion (Burnham & Anderson 2002) and Bozdogan's inverse Fisher information formulation of ICOMP (Bozdogan 1987; 1988; 1990; 2000; 2004).

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Chapter 2

Thermal Dynamics and Multimodal Microhabitat Selection in Juvenile Anoles

ABSTRACT

Microhabitat selection is critical to thermoregulation in ectotherms, particularly in small-bodied organisms for which low thermal inertia imposes rapid acquisition of thermal equilibrium with the environment. However, typical approaches to the characterization of site selection along a gradient are inadequate for accurate description of some patterns and can lead to oversight of important features of the fundamental niche. I measured thermal time constants for hatchling lizards *Anolis carolinensis* and compared thermal microhabitat selection of this species with that of an invasive congener, *A. sagrei*, based on a universally applicable approach using information theoretic selection of parametric, single-component and mixture models of the resource utilization function. In keeping with the exceptionally low mass of these hatchlings, heating and cooling rates were extremely high and more similar to those of some insects than to those of other terrestrial vertebrates. Furthermore, the relationship between thermal time constant and mass in hatchlings differed significantly from that in adults. Unimodal, single-component probability density functions failed to fit the observed distributions of selected temperatures on a laboratory thermal gradient. Both species exhibited a bimodal pattern of site occupancy along the gradient. Contrary to unimodal characterizations of adult microhabitat selection, these distributions indicate that hatchling *A. carolinensis* are likely to occupy warmer sites than *A. sagrei*. Overall, these results demonstrate the importance of examining the fundamental niche and potential interspecific niche overlap across age classes and suggest that evaluations of differences in resource use are best made via comparison of continuous, potentially multimodal, distribution models.

INTRODUCTION

Resource use by a population is often characterized through reference to single continuous resource descriptors, such as environmental temperature or prey size, that serve as axes of the fundamental multidimensional niche (Schoener 1974; Magnuson et al. 1979). The total population niche width for any one dimension is commonly reported as the mean and variance of a sample tested along the relevant gradient, and these metrics alone are provided as a quantification of the assumed resource utilization function (Huey & Webster 1976; Hertz & Huey 1981). Although central tendency and breadth of the niche are described, this approach fails to adequately quantify relative resource use intensity within the region demarcated by those metrics (Fig. 2.1), and provides only a minimal description of the full pattern of resource utilization. Additionally, representation of a distribution by a mean can be problematic and misleading in cases for which there is substantial skew or other deviations from normality, and under such conditions comparisons via standard frequentist statistical tests can produce invalid conclusions (Hertz et al. 1993). Histograms are often provided to indicate the shape of the resource utilization functions, but these are rarely analyzed. The importance of the shape of resource utilization distributions was recognized early in the development of models describing species packing along single niche dimensions (MacArthur & Levins 1967). Roughgarden (1974) discussed, in particular, the substantial effects of kurtosis and the shape of distributions at the tails on community invasibility. Certain deviations from normality are well recognized in resource use distributions (DeWitt & Friedman 1979) and have been recorded through the measurement of skew (Schoener & Gorman

1968) or quantile endpoints (Goodman & Walguarnery 2007). Nevertheless, fully descriptive investigation of the form of resource use distributions remains uncommon, and multimodality is rarely considered.

In ectotherms, temperature is a principal quantity linking whole animal biological functioning and the environment, and has, therefore, been a preeminent concern of ecology. Heat exchange with the environment governs behavioral, physiological and chemical processes connected to feeding (Beaupre et al. 1993; Ayers & Shine 1997; Belliure et al. 1996), growth (Avery 1984), development (Bull 1980; Georges et al. 2005), performance (Bennett 1990; Angilletta et al. 2002) and, ultimately, survival and reproduction (Dawson 1975; Spotila & Standora 1985). In some cases environmental temperature appears to be a primary direct determinant of animal movement, habitat selection and territory establishment (Kearney 2002; Kearney et al. 2003; Downes & Bauwens 2004). As a universal characteristic of potential habitat and an influence on fitness, environmental temperature serves as a natural axis defining the fundamental multidimensional niche (Hutchinson 1957; Magnuson et al. 1979).

The *Anolis* lizards have been heavily studied in regard to ecological differentiation and multidimensional niche partitioning. This work has resulted in a classic conceptualization of species recurrently evolving toward occupancy of a distinct set of niches (Losos et al. 2003), each associated with a specific ecomorph, or suite of morphological and ecological characteristics (Williams 1983). Sympatric *Anolis* appear to predominantly partition resources along only three axes: prey size, structural habitat, and thermal environment (Schoener 1974). Most studies of niche partitioning among anoles, and particularly those regarding thermal habitat, have focused exclusively on

adults. However, body size has major effects on heat flux with the environment (Stevenson 1985) and could therefore substantially influence selection of microhabitat across age-classes.

In this study I combined examination of heat flux in hatchling anoles with parametric and functional form description of selected temperature distributions to allow for a comprehensive comparison of fundamental thermal niche differentiation between two widespread *Anolis* species. I hypothesized that the combination of lower thermal inertia, greater sensitivity to the effects of temperature extremes, and a potentially lower thermoregulatory competence in hatchlings of these species results in more complex distributions of selected thermal microhabitat. I considered well known probability density functions and fit these models to observed distributions of environmental temperatures selected by hatchlings. I extended this goal by fitting mixture models composed of two component distributions in order to examine the performance of potentially multimodal distribution models. To discriminate between these models, I first employed typical goodness of fit statistics for model adequacy but then selected the best fitting model for each species according to an information theoretic approach. I demonstrate the use and advantages of information theoretic criteria in selecting among variants of a universally applicable multinomial model for the description of species resource use along a gradient.

METHODS

Study Species

Since its introduction to the southeastern United States in the 1940's (Lee 1985), the Cuban brown anole, *Anolis sagrei*, has steadily expanded its range into that of its native congener, the green anole, *A. carolinensis* (Campbell 1996), presenting an excellent opportunity for direct investigation (as opposed to retrospective inference) of the processes that shape anole communities. The similarly sized, common, and abundant *A. carolinensis* and *A. sagrei* are characterized as occupying substantially overlapping structural habitat niches. Therefore, the degree to which these formerly allopatric congeners differ in the full fundamental niche has become a question critical to an understanding of their ongoing interaction. Tested on laboratory thermal gradients, adult *A. carolinensis* select body temperatures between 28 and 36 °C with a mean near 31 °C (Licht 1968; Brown & Griffin 2005). Field body temperatures for this species can average somewhat higher and overlap with those recorded for *A. sagrei* (Lister 1976). However, adult *A. sagrei* occupy the most open, insolated habitats, are observed to maintain body temperatures higher than those of sympatric congeners, and show mean selected temperatures as high as 33 °C (Lister 1976).

Collection and Maintenance of Hatchlings

Adult reproductive female *Anolis carolinensis* and *A. sagrei* were collected in Jacksonville, Duval County, Florida in June 2005. In July 2005, additional adult female *A. carolinensis* were collected by a commercial supplier (Candy's Quality Reptiles) from a single population in LaPlace, Saint John the Baptist County, Louisiana. Adult anoles were housed individually at the University of Tennessee, Knoxville in screen-topped 3.8 L glass enclosures containing wooden dowels for perching, large leaves for cover, and a calcium carbonate sand substrate (Zoo Med Vita-Sand) of approximately 3 cm depth. Light was provided in all enclosures by UVB full spectrum (Reptisun 5.0) and cool white 40-W fluorescent bulbs on a 14:10 hour light:dark cycle. Temperature in the enclosures ranged from 22 °C during the night to 27-31 °C during the day. Anoles were misted with water at least twice daily and fed vitamin-dusted crickets *ad libitum*. Each adult anole was housed in the laboratory for 4-10 weeks. Every two days, the substrate of each enclosure was thoroughly searched for eggs. Eggs visible on the surface between searches were immediately removed from the enclosure for incubation. All eggs were incubated at 30 °C in sealed 250 mL, opaque, plastic containers in a mixture of 20 g vermiculite and 20 mL water.

Prior to testing, hatchlings were housed individually in screen-topped 10.6 L glass enclosures containing wooden dowels for perching and sphagnum moss for cover. Housing enclosures for hatchlings received UVB full spectrum and cool white fluorescent illumination on a 12:12 hour light:dark cycle. Temperatures in enclosures followed a diurnal cycle, with daily highs of 32-34 °C in light and 28-30 °C in shade and

nightly lows of 23-25 °C. Hatchling enclosures were misted with water several times daily, and hatchlings were provided with an *ad libitum* supply of flightless fruit flies and pinhead crickets. No food was available to hatchlings in the 24 hours prior to measurement of selected thermal microhabitat.

Measurement of Hatchling Thermal Dynamics

Heating and cooling curves following step transfer of hatchling *A. carolinensis* between differing thermal environments were inspected in order to determine the specific temporal relationship between core body and environmental temperatures and to inform subsequent examination of environmental temperature selection. Both a cooling and a heating curve were recorded for each of 17 anoles (age range = 1-24 days; mass range = 0.247-0.741 g) obtained in the laboratory from Louisiana females. Because of the prohibitive difficulty in accurately and humanely measuring core body temperature in live lizards of the size examined in this study, cooling and heating were measured for animals freshly euthanized by isoflurane inhalation. Each anole was equilibrated to an initial core body temperature of approximately 28 °C and then transferred to a substrate in a temperature gradient chamber of either 18 °C or 38 °C (for details of thermal gradient chamber construction and temperature regulation see Goodman & Walguarnery 2007). A cloacally inserted thermocouple probe and single-channel digital microprocessor thermometer (Omega HH23, OMEGA Engineering, Inc, Stamford, CT) provided a measurement of core body temperature recorded every 10 s until an apparent point of equilibrium.

Thermal time constants were determined from the heating and cooling curves following step changes in environmental temperature. A thermal time constant is the time over which a body progresses through $(1-1/e) \approx 63\%$ of the difference between its starting temperature and its equilibrium temperature under the conditions into which the body has been transferred. The thermal time constant is invariant with size of the temperature step and is therefore more useful for comparative purposes than are other metrics of the rate of temperature change. I determined thermal time constants and calculated equilibrium body temperatures simultaneously according to the iterative curve-straightening approach described by Bakken (1976b; Claussen & Art 1981). Differences between calculated equilibrium temperatures and equilibrium temperatures observed at the end of the heating/cooling curve experiments are assumed to give an indication of variability in environmental conditions over the course of the experiment. Time constants obtained from heating and cooling curves were compared and regressed against body mass in order to determine the relationship between body size and the rate at which equilibrium is attained. This relationship was then compared to a regression of previously published data for adult *A. carolinensis* (Claussen & Art 1981) with an asymptotic Chow test for equality of regression coefficients (Goldfeld & Quandt 1978). All analyses were conducted in the statistical computing environment, R (R Development Core Team 2005).

Thermal Microhabitat Selection

Four thermal gradient chambers were used to test anole selection of thermal microhabitat (for details of thermal gradient chamber construction and temperature regulation see Goodman & Walguarnery 2007). These chambers allowed anoles free, undisturbed movement over a 100 cm linear thermal gradient (18 to 46 °C) and permitted simultaneous observation of anole position and substrate temperature. For each temperature preference trial, a single anole (age range: 8-13 days) was placed haphazardly within one randomly selected temperature gradient chamber between 10:30 and 11:00 h local time and allowed to acclimate for one half hour. Following the acclimation period, an observation was made of the anole's position (designated by the point of the body centered between the fore- and hindlimbs) along the gradient and the temperature at that point at every half hour for four hours. During trials, the temperature gradient chamber was uniformly and diffusely illuminated by 40W overhead fluorescent lamps, and ambient laboratory temperature was maintained between 25.5 and 26.5 °C. Twenty-five *A. carolinensis* hatchlings (13 male, 12 female; mean \pm SE mass = 0.260 ± 0.029 g) and 19 *A. sagrei* hatchlings (9 male, 11 female; mean \pm SE mass = 0.175 ± 0.021 g) were each tested once for thermal microhabitat preference. To guard against an influence of any potential maternal effects, no more than one hatchling from each mother was included in this study.

Information-Theoretic Selection of Representative Thermal Microhabitat Models

As a first analysis of the thermal microhabitat selection data, the median selected temperatures of the two species were determined and tested for significant departure from equality by a Mann-Whitney U test. This non-parametric statistic requires minimal assumptions concerning the respective distributions of the samples, and serves here as a representative hypothesis-testing approach to the characterization of potential differences between two species in habitat use along a gradient. Selected temperatures were regressed on individual mass to test for a linear relationship with body size. Subsequently, data were converted to frequencies of occurrence within disjoint classes (bins; each of 2 ° C width) along the utilized portion of the temperature gradient, histograms of these data were produced, and resource use overlap (Pianka 1973) was computed as an additional common means of comparing species differences with respect to a gradient.

All further analyses were conducted under the framework of a general multinomial distribution model. This framework confers universal applicability of the procedures below to data collected in either continuous or ordinal form. The joint probability density function of a multinomial distribution with k classes is:

$$P(f_1, f_2, \dots, f_k) = (n! / f_1! f_2! \dots f_k!) p_1^{f_1} p_2^{f_2} \dots p_k^{f_k},$$

where n is the sample size (number of observations), f_k is the frequency observed in bin k ,

and p_k is the parameter specifying the probability of occurrence in bin k ($\sum_{i=1}^k f_i = n$;

$\sum_{i=1}^k p_i = 1$). The multinomial log-likelihood for the parameter vector \mathbf{p} is:

$$l(\mathbf{p}) = \sum_{i=1}^k f_i \ln(p_i).$$

Any single candidate distribution (e.g. normal, Poisson) can be assessed in the multinomial framework by obtaining maximum likelihood estimates for the parameters of the distribution, given the data, and then using the cumulative density function for that fitted distribution to give estimated class probabilities. Maximum likelihood estimation of distribution parameters for grouped (frequency) data is performed in the manner typical for ungrouped data, equating the first derivative (slope) of the log-likelihood function with respect to each parameter to zero and then solving for the respective parameter. Log-likelihood functions for grouped data are merely formulated in terms of frequencies of class midpoints (k values each repeated a number of times specified by their respective frequencies) rather than in terms of a sample of n potentially unique values. In the case of mixture distributions comprised of m components, the log-likelihood is extended to:

$$l(\mathbf{p}, \boldsymbol{\pi}) = \sum_{i=1}^k f_i \ln\left(\sum_{j=1}^m \pi_j p_i\right),$$

where π_j is the proportion of the sample from component distribution j (i.e. the weighting of component j relative to the overall mixture). Explicit estimates for the π 's are not attainable via analytic solutions to the zero equated derivatives of the log likelihood, and, therefore, the π 's must be determined through the use of iterative, numerical methods.

I fit five single component candidate models and four mixture distribution candidate models to the data for each species. Among the single distributions considered, normal, lognormal, Poisson, and Weibull (two-parameter) comprise a set of models capable of representing data exhibiting symmetry, positive skew or negative skew. The uniform distribution was included to represent the null hypothesis of a lack of selection along the temperature gradient or the case in which selection was governed solely by an upper and lower temperature limit. To restrict the total number of candidate models to a parsimonious set, I considered only mixtures comprised of two components of the same functional form. Therefore, the candidate mixture distributions were of two normal components, two lognormal components, two Poisson components, and two Weibull components. I estimated parameters for normal, lognormal, Poisson and uniform distributions through analytical means and estimated parameters for Weibull distributions numerically according to the Newton-Raphson method. Mixtures were fit using the *Rmix* (Du 2002) package for *R*. This package estimates proportions and component parameters through a combination of Newton-Raphson and expectation-maximization (EM) algorithm (Dempster et al. 1977) methods.

Candidate model fit was first assessed by chi-square goodness of fit tests to give an indication of absolute fit. Models were subsequently distinguished with reference to Akaike's Information Criterion (AIC) scores (Akaike 1973) for assessing relative fit.

Information-theoretic criteria compare candidate models based on a relationship between the expected estimated Kullback-Leibler distance (Kullback & Leibler 1951), which describes the information lost through the use of a particular approximating model of reality, and the maximum log-likelihood function for parameter estimation. Maximum likelihoods alone are biased criteria in that they provide an exaggerated estimate of model fit. Parameterization to maximize the likelihood is with respect to the specific data in a particular sample (rather than the actual unknown generating distribution). Additional parameters permit a closer fit to that specific data and, therefore, a greater bias above what would be the fit to the true, underlying distribution. Akaike showed that, asymptotically, the bias is corrected by a factor equal to the number of estimable parameters, k , in the parameter vector, Θ . The typical formulation of AIC is:

$$\text{AIC} = -2(l(\Theta)) + 2k.$$

In using this criterion, the candidate model yielding the lowest AIC score is selected as that which provides the best balance between fit and parsimony. Samples that are small, particularly relative to the number of estimated parameters, are known to lead to additionally biased likelihood estimates, and models fit to these samples are more judiciously compared with respect to a small-sample consistent, second-order bias adjusted criteria, AIC_c (Hurvich & Tsai 1989):

$$\text{AIC}_c = -2(l(\Theta)) + 2k(n / (n - k - 1)).$$

In the current study, the normalized likelihoods of the complete candidate models were also compared in the form of Akaike weights (Burnham & Anderson 2002) or evidence ratios, based on the difference in AIC_c scores, Δ_i between each model and that having the lowest AIC score of the R candidate models:

$$\text{weight}_i = (e^{(-0.5\Delta_i)}) / \left(\sum_{r=1}^R e^{(-0.5\Delta_r)} \right).$$

These weights, ranging from 0 to 1, indicate the relative evidence that a particular model is the best of the available candidates.

In the case of mixture models providing the best fit to the overall species temperature selection data, I then calculated the fit of that mixture and each of its components to the data sets for each individual of the species according to log-likelihoods in order to parse the relative contributions of intra- and inter-individual variation in generating the observed distributions.

RESULTS

Thermal time constants calculated for hatchling anoles were inversely proportional to mass and ranged from approximately 27 to 109 s. Mean difference between the observed and calculated equilibrium temperatures was -0.03 ± 0.04 °C. Regressions of log time constant on log mass (Fig. 2.2) were not significantly different for heating and cooling curves ($P = 0.694$). Mean absolute difference between time constants calculated from heating and cooling curves (assumed proportional to the

measurement error) was 7.5 s. Comparison of the log-log regression of heating time constants on mass for hatchlings to the same regression for adults, published by Claussen & Art (1981), showed a highly significant difference by asymptotic Chow test ($P < 0.001$). The exponent for the allometric heating equation for hatchlings was 0.768, whereas that for adults was 0.263. Respective R^2 values for these regressions were 0.72 and 0.42.

The median selected temperatures of the two species were significantly different ($n = 382$, $P < 0.001$) at 31.1 and 27.4 °C for *A. carolinensis* and *A. sagrei*, respectively. For sampling based on individual medians, the species medians were of a marginally non-significant difference ($n = 44$, $P = 0.068$) at 31.1 for *A. carolinensis* and 28.4 °C for *A. sagrei*. For neither species was the regression of individual median selected temperature on body mass significant (*A. carolinensis* $P = 0.412$, *A. sagrei* $P = 0.702$). Resource use overlap along the temperature gradient was 0.860.

All single distribution models for *A. carolinensis* and for *A. sagrei* showed a significant lack of fit to the temperature selection data (Tables 2.1 & 2.2; all tables and figures appear in the Appendices.) Fit to the *A. carolinensis* data, the normal, lognormal, and Weibull mixture models provided adequate fit according to goodness of fit statistics (Table 2.1). Fit to the *A. sagrei* data, these mixtures were also the only ones to provide adequate fit (Table 2.2).

The ranking of models based on AIC_c did not differ from the ranking based on AIC (Tables 2.1 & 2.2). According to AIC_c , the temperature selection data for *A. carolinensis* was best fit by a Weibull mixture (Fig. 2.3). Akaike weights indicate appreciable evidence for the Weibull mixture (weight = 0.4320), lognormal mixture

(weight = 0.3347), and normal mixture (weight = 0.2420) models. The temperature selection data for *A. sagrei* was best fit by a normal mixture (Fig. 2.3). Akaike weights for models fit to *A. sagrei* data indicate substantial evidence in favor of only two models, the normal mixture (weight = 0.6060) and the lognormal mixture (weight = 0.3711).

Of individual *A. carolinensis* data sets, 44% were best fit by the mixture model selected for that species, whereas 56% were best fit by the upper component of that mixture. No individual *A. carolinensis* distribution of selected temperatures was best fit by the lower component alone. For *A. sagrei*, approximately 42% of individual distributions were best fit by the mixture model selected for that species, whereas 21% were best fit exclusively by the lower component and 37% were best fit by the upper component of the model.

DISCUSSION

According to heating and cooling curve experiments, hatchling anoles can change core body temperature according to time constants of less than 30 s. To my knowledge, these lizards are the smallest for which rates of heat flux have been examined in the laboratory. As heat flux is typically examined in adult lizards, the body mass of many subjects is two to four orders of magnitude greater than that of the animals in this study. Study of thermal biology in other vertebrate ectotherms of comparable size is also extremely limited, but sub-adult African reed frogs (*Hyperolius viridiflavus*) of masses as low as 0.35 g have been shown to have thermal time constants of 29 ± 9 s in moving air (Kobelt & Linsenmair 1995). Ectotherms of body masses equivalent to those of

hatchling anoles are actually more prevalent among insects. However, dragonflies with body masses within this range change temperature in air according to time constants ≥ 60 s (May 1976), and hoverflies of 0.15-0.20 g exhibit thermal time constants ≥ 85 s (Bressin & Willmer 2000). These disparities in time constants highlight the underlying complexity of biophysical interactions affecting heat flux.

Although heat capacitance is a constant property of an animal, both the overall conductance and the operative environmental temperature are properties arising from the interaction of the animal and a specific environment. Convective heat exchange is affected by wind speed, and conduction is affected by the composition and surface of the substrate (Bakken 1976a). Even controlling for operative environmental temperature, the mode by which heat is transmitted affects the rate at which it is transmitted. Relative to the exclusively radiative and convective heating in typical heliothermy, thigmothermy has been shown to lead to higher rates of heating in small lizards, presumably due to the combined effects of direct conduction through the substrate and radiative heating from the warmed air of the boundary layer in contact with the substrate (Bakken 1989; Belliure & Carrascal 2002). The typical body proportions and postures of terrestrial vertebrate ectotherms, including reptiles and amphibians, place a large portion of the body surface in contact with the substrate and, therefore, in a role of conductive heat transfer. Indeed, during the temperature selection experiments anoles rested with the entire venter in contact with the substrate except when moving between positions on the thermal gradient. The resultant close connection between core body temperature and substrate temperature, as well as the extremely rapid observed convergence of these temperatures on the experimental gradients, both validates the use of selected substrate temperature as

a proxy for selected body temperature in hatchling lizards, and demonstrates the potentially exceptional importance of microhabitat selection to these animals.

Consistent relationships between time constants and the body mass of ectotherms have been observed from regressions in previous studies. The simplest effective models explaining these relationships consider relative rates of heat transfer at the surface and within the body as well as the scaling of various dimensions with mass. For small animals in air, these models simplify to a proportional relationship dependent on a length measurement (the thickness of the layer separating the surface of the animal and its isothermal core), and therefore time constants are expected to scale approximately as $\text{mass}^{1/3}$ (Grigg et al. 1979). For animals in water, heat exchange at the surface is much greater than for animals in air, surface temperature approximates ambient temperature, and thermal time constants scale according to the allometric relationship between surface area and mass. Based on measurements for several species across greater than three orders of magnitude in body mass, Grigg et al. (1979) observed an actual exponent of 0.69 relating surface area to mass in lizards. Log-log regression of heating time constants on body mass for our data on hatchling anoles yielded an exponent of approximately 0.77. This regression is much closer to that predicted for heating in water than for heating in air and is significantly different from that describing the relationship in adult anoles. I take this result as an indication of the predominance of substrate conduction rather than heat transfer to air in the observed overall heat flux in these very small lizards and a clear indication of the importance of examining thermal interactions across both differing environmental conditions and age classes.

Differences between species were apparent from comparison of *Anolis* hatchling selected temperatures on a laboratory gradient. The difference in median selected temperature of *A. carolinensis* and *A. sagrei* was statistically significant and, surprisingly, in the opposite direction of that in adults of these species. At over 3.5 °C, this substantial difference in medians appears likely of biological significance as well. However, the resource overlap of 0.860 along the temperature gradient suggests that separation in thermal resources is far from complete. Furthermore, no single, unimodal distribution, normal or other, provided an adequate fit to the distribution of selected temperatures for either species. This result suggests that single metrics of central tendency could be of limited use in describing the overall patterns of thermoregulation and resource use in hatchling anoles.

Based on significance tests alone, multiple mixture models provided adequate fit to the selected temperature distributions for both species. Ranking according to AIC scores confirmed the superiority of the mixture models, but also further distinguished among them to show a normal mixture as the best fit to the observations for *A. sagrei*. Although there was some minimal evidence in favor of a mixture of normal distributions to model temperature selection in *A. carolinensis*, there was much greater evidence in favor of a Weibull mixture, substantially supporting the conclusion that resource use by these species differs in functional form.

As parameterized, both Weibull components comprising the model for *A. carolinensis* temperature selection exhibit a negative skew and a short upper tail. The shape of these Weibull components is such that, although both the overall median for the *A. carolinensis* model and that of its upper component are higher than those for the *A.*

sagrei model, the upper tail of the *A. sagrei* distribution extends beyond that of the *A. carolinensis* distribution. These disparities in shapes and limits of the distributions can be interpreted as indicating both a greater sensitivity to a higher maximum temperature in *A. carolinensis* and a higher density of selected temperatures immediately below this maximum, and collectively suggest greater precision in *A. carolinensis* thermoregulation. This interpretation is further supported by the more even proportional split between the two components comprising the *A. sagrei* distribution. Since the differences between species in the component medians are less than the species differences in overall medians (and are in opposite directions for comparisons at the lower and upper components), it is clear that the species differences in central tendency arise primarily from the relative contributions of the lower versus upper components.

What is the significance and implication of multiple components in the gradient use distributions? Although unimodality is almost universally assumed in body temperature distributions for active vertebrate ectotherms, some observed distributions clearly suggest multimodality (e.g. Lillywhite et al. 1973; Schoener & Gorman 1968). In cases where habitat structure dictates discrete thermal environments, multimodality could appear in body temperature distributions merely through full or partial thermoconformity. This effect would be especially apparent for animals with low thermal inertia in discontinuous thermal landscapes. Due to the extremely rapid equilibration with environmental temperature of hatchling anoles on our laboratory gradients, essentially all movements entailed some change in body temperature. Given a certain overall level of movement on a linear gradient, bimodality could arise at the individual level through thermoregulatory shuttling across a preferred region or through corrective step

movements of the animal towards the center of the gradient when encountering temperatures outside the voluntary thermal minimum and maximum. Alternatively, multimodality could arise from inter-individual variation in a population for which physiological or behavioral polymorphism or age and size classes lead to differences in gradient use. In the case of hatchling anoles, our data do not suggest that bimodality in the overall gradient use distributions is due primarily to consistent adherence of individual behavior to that suggested by the mixture models. Only a large minority of individual data sets for both species were best fit by the respective mixture model rather than by one of the components. The shape of the overall species gradient use distributions is seen, therefore, to emerge from a combination of both intra- and inter-individual variation in temperature selection. If, indeed, bimodality in resource use is characteristic of sub-adults but not adults of these species, then the relative timing of the ontogenetic shift in each species could significantly impact the cumulative pressure of interspecific competition for thermal resources. Certainly, this aspect of thermoregulation should be examined in the context of both age-specific interspecific aggression and multidimensional microhabitat selection in order to determine how these thermal resource utilization distributions of apparently broad overlap but differing functional form translate to realized niches under sympatry in nature.

As demonstrated by this study, characterization of resource use along a gradient by continuous parametric distribution models confers several advantages. Most importantly, determination of adequate distributional models allows for distinctions to be made between potentially highly disparate distributions that, by the most commonly used statistics, could appear quite similar. The most widely employed distributional models

are fully specified by only two fitted parameters and can therefore describe a resource use distribution with greater economy than can even a very coarse histogram. Modern computational resources allow both simple (single component) and more complex mixture distributions to be fit efficiently by maximum likelihood and numerical methods. Use of these continuous distributional models facilitates comparisons between data sets. Distributions can be fit without partitioning a gradient into arbitrary discrete categories. Conversely, for artificially or naturally discretized gradients, continuous distribution models can be fit based on expected and observed values of the multinomial distribution. Coupled with the use of information theoretic model selection criteria, this approach also better extracts biological “signal” from the inherent “noise” or random error present in any sample from nature and thereby provides greater insight into underlying generative processes and true population patterns.

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Appendix: Chapter 2

Table 2.1. Model fitting results for *Anolis carolinensis* distribution of selected temperatures on a laboratory thermal gradient. The χ^2 values in bold face type indicate significant model goodness of fit. Proportions, descriptive statistics and parameters are listed for each component of the best fitting model.

Distribution	AIC	AICc	AIC weights	χ^2	χ^2 critical
Normal	1044.3121	1046.0791	0.0000	57.6	16.9
Lognormal	1074.7138	1076.4808	0.0000	85.9	16.9
Poisson	1056.9037	1058.4110	0.0000	58.3	18.3
Weibull	1023.7045	1025.4715	0.0003	36.5	16.9
Uniform	1081.0739	1082.8409	0.0000	324.7	16.9
2-Normal	1009.1820	1011.8618	0.2420	7.6	12.6
2-Lognormal	1008.5328	1011.2126	0.3347	6.9	12.6
2-Poisson	1066.0217	1068.0705	0.0000	53.5	15.5
2-Weibull	1008.0647	1010.7445	0.4320	9.0	12.6

2-Weibull mixture is the best model

proportion	mean	SD	median	mode	scale parameter	shape parameter
0.0940	20.03	1.76	20.26	20.67	20.7972	13.9172
0.9061	31.07	3.95	31.49	32.35	32.7415	9.4319

Table 2.2. Model fitting results for *Anolis sagrei* distribution of selected temperatures on a laboratory thermal gradient. The χ^2 values in bold face type indicate significant model goodness of fit. Proportions, descriptive statistics and parameters are listed for each component of the best fitting model.

Distribution	AIC	AICc	AIC weights	χ^2	χ^2 critical
Normal	819.7116	822.2048	0.0528	25.3	16.9
Lognormal	818.7549	821.2480	0.0853	25.0	16.9
Poisson	819.6512	821.7736	0.4178	32.1	18.3
Weibull	823.7096	826.2027	0.0072	19.7	16.9
Uniform	821.1701	823.6633	0.0255	30.4	16.9
2-Normal	804.3897	808.1939	0.2485	4.7	12.6
2-Lognormal	805.3705	809.1747	0.1522	5.0	12.6
2-Poisson	821.8215	824.7181	0.0024	15.7	15.5
2-Weibull	811.1760	814.9802	0.0084	8.2	12.6

2-Normal mixture is the best model

proportion	mean	SD	median	mode
0.2837	20.91	2.33	20.91	20.91
0.7163	30.29	4.62	30.29	30.29

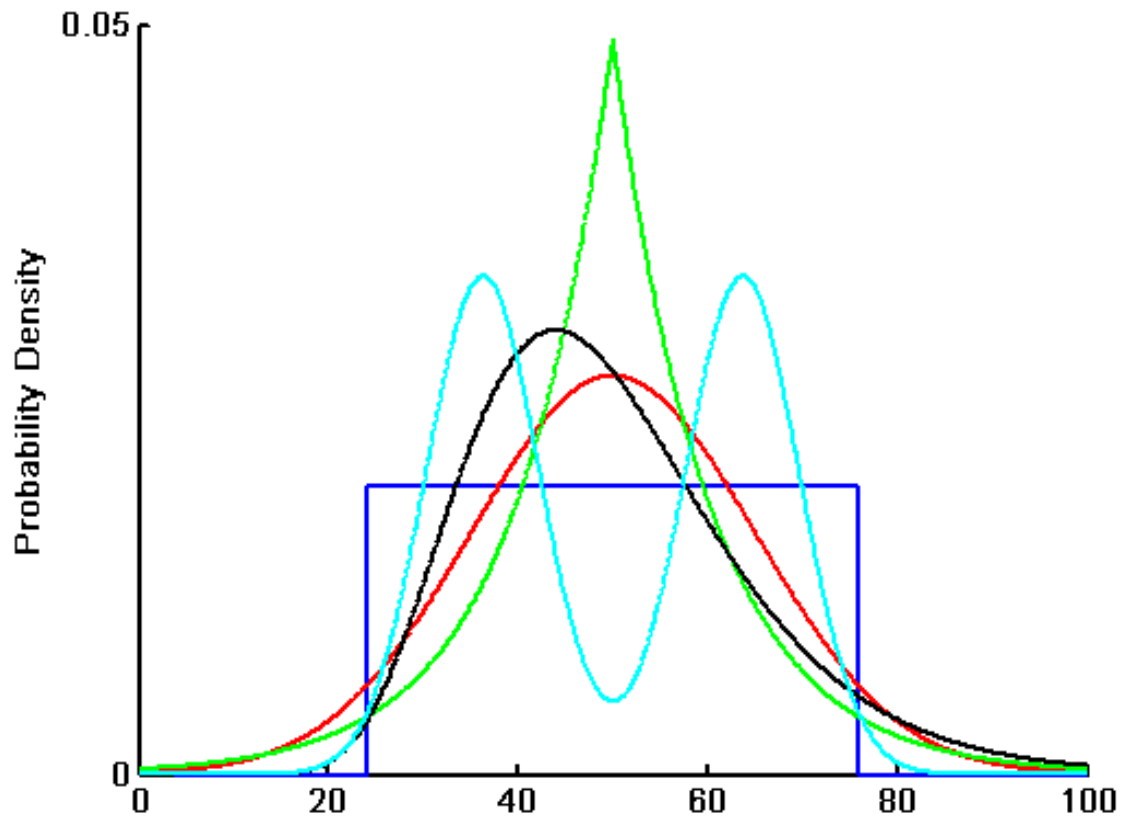


Figure 2.1. Example distributions for populations with mean = 50 and variance = 225. Despite obvious differences in density across the gradient, these distributions would be indistinguishable by the most typical parametric statistical tests.

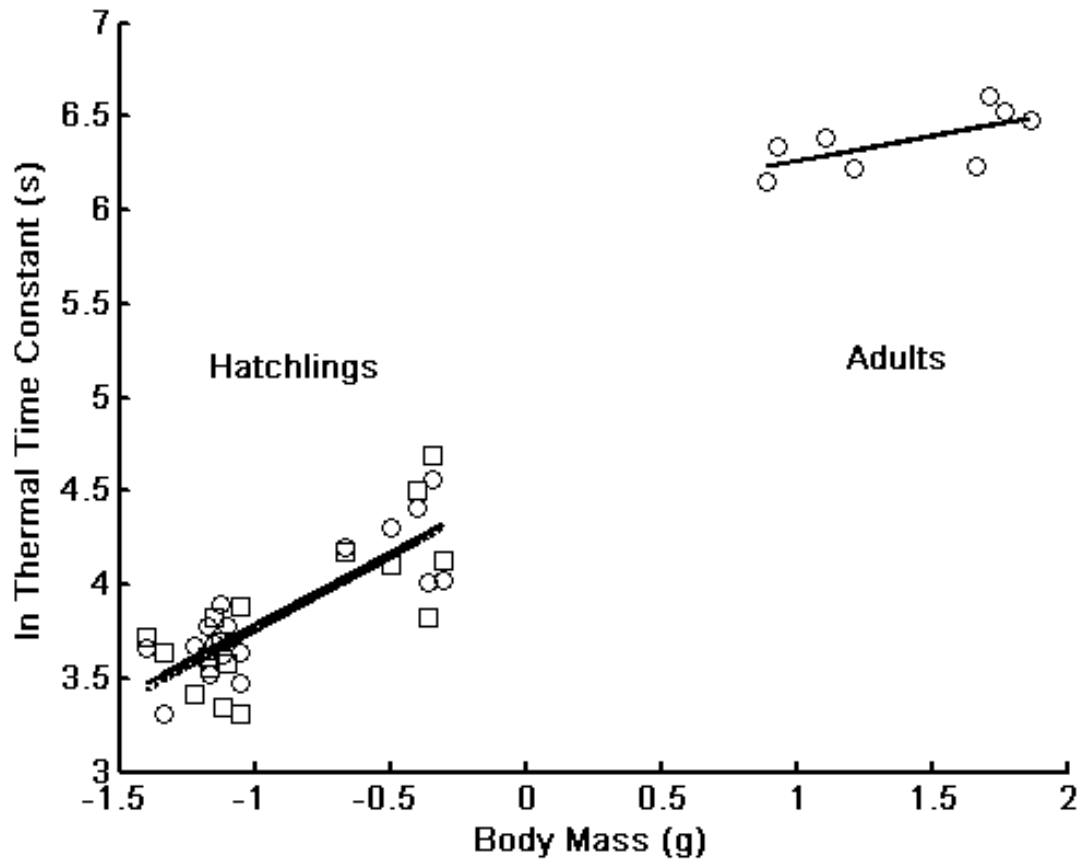


Figure 2.2. Relationships between thermal time constant and body mass for hatchling and adult *Anolis carolinensis*. Observations for heating curves are shown as circles with fitted regressions as solid lines. Observations for cooling are shown as squares with the fitted regression as a dashed line. Adult heating data is from Claussen & Art (1981).

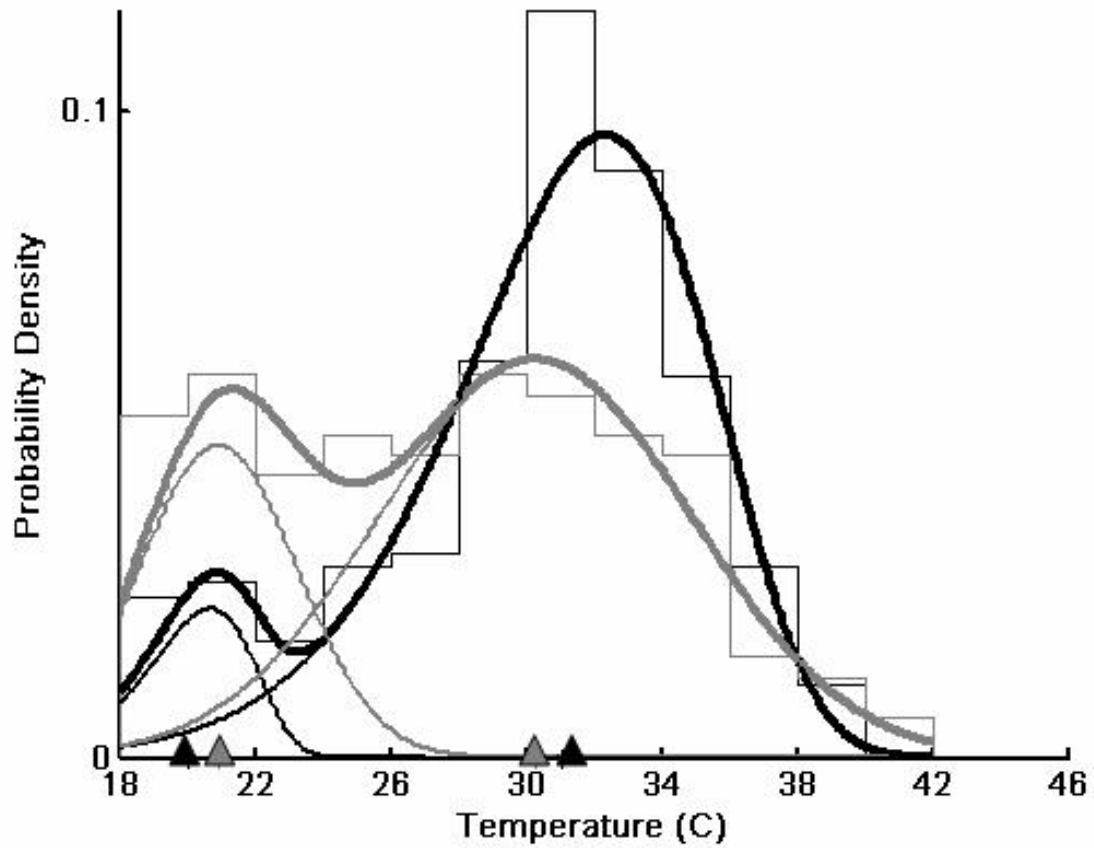


Figure 2.3. Histograms of observed selected temperatures for *Anolis carolinensis* and *A. sagrei*. Histograms, best fitting mixture model and components for *A. carolinensis* are shown as dark lines; component means are shown as dark triangles. Histograms, best fitting mixture model and components for *A. sagrei* are shown as light lines; component means are shown as light triangles.

Chapter 3

Dominance and Display Behavior of Juvenile Green Anoles *Anolis carolinensis* in First Encounters with an Invasive Congener

ABSTRACT

Behavioral responses of native species to ecologically similar nonindigenous species can influence the success and impact of biological invasions. The Caribbean lizard *Anolis sagrei* is an introduced species in the southeastern United States and may detrimentally affect the native, North American *A. carolinensis*. I staged first encounters between socially naïve juveniles of these species and compared the nature and outcome of the associated interactions to those in conspecific *A. carolinensis* encounters. Based on these encounters, I developed predictive models of the probability of a juvenile *A. carolinensis* subject obtaining social dominance in a first encounter with another juvenile. The estimated best predictive model suggests that the species of an encountered individual (conspecific or heterospecific) and whether the subject initiates interaction have the strongest effect on the probability of dominance. Neither species was significantly more likely to initiate interaction, but *A. carolinensis* that did initiate were substantially more likely to obtain dominance than those that did not. Heterospecific encounters were more likely to yield a dominant individual as *A. carolinensis* interactions with conspecifics were largely characterized by balanced agonism and lack of exclusion. *Anolis sagrei* juveniles were very rarely dominant over *A. carolinensis* juveniles and dominated only in encounters escalating to attacks that included biting. Contrary to the results of adult interaction studies, there was limited evidence supporting an influence of size-asymmetry on dominance. Dominant individuals moved more in the vicinity of a potential opponent and actually displayed less than those individuals that did not distinguish themselves as dominant. These results suggest that dominance and behavioral

exclusion in juvenile anoles are dependent on intrinsic individual characteristics and that direct interference in initial encounters among juveniles favors *A. carolinensis* over invasive *A. sagrei*.

INTRODUCTION

Agonistic interaction and the establishment of dominance relationships can have major effects on individual fitness and resource use (Lappin & Husak 2005; Fero et al. 2007; Schubert et al. 2007). When such interactions encompass heterospecifics, asymmetries in interspecific agonism can lead to the competitive displacement of one species by another from specific resources or whole habitats (Alatalo & Moreno 1987; Case et al. 1994; Griffis & Jaeger 1998, Langkilde & Shine 2004). Biological invasions, in providing unique opportunities for the study of interactions between ecologically similar species during the initial stages of contact, can provide important insight into the role of agonism in community assembly (Holway & Saurez 1999). In particular, discrimination of individual characteristics influencing the outcome of first encounters could elucidate how direct behavioral interaction contributes to the establishment of species coexistence or exclusion.

Several species of *Anolis* lizards have been introduced outside of their native ranges so that they now encounter congeners possessing recent ecological and evolutionary histories separate from their own (Losos et al. 1991). Overlap in the well-defined ecological niches of *Anolis* species in their allopatric native ranges (Williams 1969; Williams 1983), along with observational and experimental inference of competition in sympatry (Schoener 1975; Jenssen 1973; Roughgarden et al. 1984; Losos & Spiller 1999; Campbell 2000; Gerber 2000), suggest that native species would benefit from behaviorally excluding some congeneric invasives. Agonism, including stereotypical displays that potentially escalate to direct physical combat, is common in

anoles (Jenssen 1970; Echelle et al. 1971; Stamps & Barlow 1973; Ruibal & Philibosian 1974; Hover & Jenssen 1976; Greenberg 1977; Scott 1984). Although the stereotyped agonistic display sequences of these lizards can vary widely between species and can be of several, identifiable pattern types within species (Hover & Jenssen 1976; Jenssen & Rothblum 1977; Decourcy & Jenssen 1994), they are consistently comprised of a common set of display components and modifiers including headbobs, pushups, dewlap extension, sagittal expansion of the body, and expansion of the gular region (Jenssen 1977; Jenssen 1978). These displays are most conspicuous in the context of breeding territoriality among adult male anoles but have also been described in females (Evans 1938; Andrews & Summers 1996) and juveniles (Stamps 1978; Lovern & Jenssen 2001) in regard to resource defense.

Anolis carolinensis is the only anole native to North America north of Mexico (Conant & Collins 1998), but its range has become increasingly occupied by the widespread, invasive Caribbean anole *A. sagrei* since the introduction of that species to the southeastern United States in the 1940s (Lee 1985; Campbell 1996). Both species are medium-sized, largely arboreal, generalist insectivores with overlapping insolation and temperature preferences (Licht 1968; Corn 1971; Lister 1976), similar breeding phenology (Licht 1973; Lee et al. 1989) and territorial, polygynous social structures (Evans 1938; Schoener & Schoener 1980; Jenssen & Nunez 1998). Potential negative effects of *A. sagrei* on *A. carolinensis* include habitat niche contraction (reduction in the distribution of perch heights used within the vegetation) (Campbell 2000), predation (Gerber & Echternacht 2000), reduced reproductive output (Vincent 2002), and increased juvenile mortality (Gerber 2000). These species are similar in size and shape although *A.*

sagrei is somewhat stouter and more terrestrial (Licht & Gorman 1970), has a reddish-orange, rather than a typically pink, dewlap (Williams & Rand 1977; Macedonia et al. 2003), and a variably mottled, brown body coloration rather than the more uniformly, autonomically regulated brown or green coloration assumed by *A. carolinensis* (Conant & Collins 1998; Greenberg 1977). Therefore, aggressive interaction and interspecific territoriality between these species could arise either as an adaptive response to interspecific competition (Jenssen et al. 1984; Robinson & Terborgh 1995; Genner et al. 1999) or as a result of mistaken conspecific recognition (Murray 1981; Nishikawa 1987; Tynkkynen et al. 2006). In staged encounters between these species, *A. carolinensis* appears to distinguish between conspecific and heterospecific individuals and exhibits a lesser degree of aggression and display behavior towards *A. sagrei* (Tokarz & Beck 1987; Brown 1988), but these interactions have been examined only in reproductive adult males, and it is unknown how socially naïve, nonreproductive individuals would respond to a congeneric invader.

Juvenile anoles exhibit the same core display components as adults (Stamps 1978; Lovern & Jenssen 2003). In *A. carolinensis*, two of three distinct display types (A and B), defined by the cadence of the headbobbing component, develop during postnatal maturation (Lovern & Jenssen 2003). Most juvenile displays, however, are of a C type present in the repertoire from hatching and exhibited in identical form by males and females (Lovern & Jenssen 2001). In general, although juvenile display interactions appear to occur only in the context of aggression, they are less ritualized than the territorial interactions of adult males and are unlikely to include certain key signal modifiers associated with intense arousal such as the darkening of post-orbital dermal

eyespot (Lovern & Jenssen 2001). Furthermore, the C display, typical of juvenile interactions, has been suggested as the fundamental (phylogenetically antecedent) *A. carolinensis* display and, therefore, potentially more similar to displays of closely related, congeneric species (Lovern & Jenssen 2001; Lovern & Jenssen 2003).

For a juvenile *A. carolinensis* encountering another anole for the first time, what factors influence dominance as displayed through direct behavioral exclusion of individuals from specific locations? In this study I considered species, body size asymmetry, and initiation as factors in the development of predictive models of dominance in socially naïve *A. carolinensis* juveniles encountering conspecific and *A. sagrei* juveniles under controlled laboratory conditions. Previous research has shown that these factors strongly influence dominance in adult anoles (Tokarz 1985; Tokarz & Beck 1987; Brown 1988; Gerber 2000; Summers 2001; Korzan et al. 2006), and, therefore, if anole agonism is based on innate characteristics with consistent influences across ontogeny then each of these factors should also appear in a best predictive model of dominance in juvenile first encounters. Additionally, I tested the hypothesis that the probability of *A. carolinensis* dominance in interspecific encounters differs between individuals from a population in sympatry with *A. sagrei* and from a population outside the invaded range. Finally, I tested the hypotheses that *A. sagrei* and *A. carolinensis* juveniles in heterospecific encounters exhibit different behavior patterns than *A. carolinensis* juveniles in conspecific encounters, and that individuals concluding interactions as dominant behave differently in those interactions than those that do not distinguish themselves as dominant. This is the first study to examine interspecific interactions between juvenile anoles in their first social encounters. As individual social

and environmental histories have been shown to significantly alter aggression and display behavior in anoles (McMann 2000; Yang et al. 2001; Forster et al. 2005; Korzan et al. 2007), controlling for these factors could be critical in discerning innate, species-specific responses.

METHODS

Juvenile anoles were obtained from eggs laid in the laboratory by wild-caught females. Adult, reproductive, female *A. carolinensis* were collected in Evans, Columbia County, Georgia and Jacksonville, Duval County, Florida in June 2004. Adult, reproductive, female *A. sagrei* were collected in Jacksonville in the same month from the same site. Adult anoles were housed individually at the University of Tennessee, Knoxville in screen-topped 3.8 L glass enclosures containing wooden dowels for perching, large leaves for cover, and a calcium carbonate sand substrate (Zoo Med Vita-Sand) of approximately 3 cm depth. Light was provided in all enclosures by UVB full spectrum (Reptisun 5.0) and cool white 40-W fluorescent bulbs on a 14:10 hour light:dark cycle. Temperature in the enclosures ranged from 22 C during the night to 27-31 C during the day. Anoles were misted with water at least twice daily and fed vitamin-dusted crickets *ad libitum*. Each adult anole was housed in the laboratory for between four and ten weeks. Every two days the substrate of each enclosure was thoroughly searched for eggs. Eggs visible on the surface between searches were immediately removed from the enclosure for incubation. All eggs were incubated at 30 °C in sealed 250 mL, opaque, plastic containers in a mixture of 20 g vermiculite and 20 mL water.

I staged three classes of dyadic encounters crossed by population, each with an *A. carolinensis* juvenile (age = 4-5 days) as the subject. The three classes differed in the stimulus individual of the dyad as follows: conspecific class – subject paired with a juvenile *A. carolinensis* (age = 4-5 days); heterospecific age class 1 – subject paired with an *A. sagrei* juvenile (age = 4-5 days); heterospecific age class 2 – subject paired with an *A. sagrei* in its third week after hatching (age = 21-26 days). By this arrangement the *A. carolinensis* were paired with stimulus individuals of varying size (Table 3.1). Total sample size was 101 dyads. Sample sizes for each class by population combination were partially dictated by hatching rates and the simultaneous availability of anoles of the ages specified for the dyad classes. These sample sizes were; FL conspecific = 15, GA conspecific = 16, FL heterospecific age class 1 = 15, GA heterospecific age class 1 = 24, FL heterospecific age class 2 = 15, GA heterospecific age class 2 = 16. Because *A. sagrei* hatch at a smaller size than *A. carolinensis* this distribution of samples by encounter classes produced a normal distribution of mass differences between subject and stimulus individuals (mean \pm SE = 0.037 ± 0.011 g; min. = -0.223 g; max. = 0.308 g). These absolute mass differences represent a range of proportional differences (subject mass / stimulus mass) from 0.493 to 3.444.

Test vivaria in which encounters were staged consisted of glass enclosures measuring 76 x 32 x 31 cm. A removable, opaque partition bisected these enclosures into compartments each measuring 38 x 32 x 31 cm. Individual compartments contained a substrate of white sand, a 4 cm diameter plastic water dish, approximately 100 cm³ of sphagnum moss, and a 10 cm length, 0.5 cm diameter wooden perch supported at its base and directed upwards and towards the partition at a 50° angle above horizontal. All

objects within compartments of a vivarium were positioned so as to form a mirror arrangement to that in the opposite compartment.

For conspecific and age class 1 encounters, individual anoles were placed in a test vivarium (with the partition in place) immediately after hatching, so that each *A. carolinensis* subject was paired with either another *A. carolinensis* or an *A. sagrei* in the opposite compartment. Assignment of individuals to either the left or right compartment of a vivarium was random. Small marks were applied to members of conspecific dyads using a Sharpie pen (Sanford) to aid in distinguishing individuals. *Anolis carolinensis* juveniles can be easily distinguished from *A. sagrei* juveniles, and, therefore, anoles used in heterospecific encounters were not marked. Anoles were given three days to acclimate to the test vivaria prior to initiation of experimental encounters.

Anoles to be used in age class 2 experiments were housed individually from hatching in glass enclosures measuring 22 x 22 x 22 cm. These enclosures contained the same set of objects included in the test vivaria. The walls of these enclosures were opaque and thereby precluded visual interaction between anoles. Three days prior to the start of an encounter, pairs of anoles were moved to the separate compartments of test vivaria to permit acclimation. Housing enclosures and test vivaria for hatchling subjects were maintained under the same lighting and temperature conditions as the housing enclosures for reproductive adults. Enclosures were misted with water several times daily, and anoles were provided with an *ad libitum* supply of flightless fruit flies and pinhead crickets. No food was available to hatchlings in the 24 hours prior to dyadic encounters.

Dyadic Encounter Procedures

Following the acclimation period, encounters were initiated by the removal of the partition separating the two compartments of the test vivaria. I recorded date, time of day, and initial and final positions of anoles for all encounters, each of which lasted for 40 min. The masses of subject and stimulus individuals were measured immediately following encounters. I recorded the following behaviors for both individuals throughout each encounter: headbob (HB), sagittal expansion (SE), gular expansion (GE), pushup (PU), approach (AP), approach within one body length or approximately 2 cm (BL), retreat (RT), flee (FL), and attack with biting (AT) (Table 3.2). In addition to recording the occurrence, frequency, and sequence of behaviors, I identified each *A. carolinensis* subject as dominant or not dominant (subordinate or unresolved) based on the outcome of the encounter using published criteria for anole agonism (Crews 1975; Cooper 1977; Talbot 1979; Ortiz & Jenssen 1982; Jenssen et al. 1984). Specifically, subordinate individuals were those that retreated and never approached, were the only member of a dyad to exhibit flight, to be displaced from their starting position, or to fail to reciprocate an attack. Dominant subjects were those that imposed subordinate status on the stimulus individual. All dyadic encounters were staged between 1100 and 1600 hrs and were conducted in a darkened room so as to limit observer effects on anole behavior.

Predictive Models of Dominance

I analyzed dominance of juvenile *A. carolinensis* in dyadic encounters as a dependent binary response (dominant/not dominant) in predictive logistic regression models (PROC LOGISTIC, logit link, SAS 9.1 2002). Individual predictors considered were (1) those implied by the class of encounter; including species of the stimulus individual (SPECIES), mass difference between subject and stimulus (SIZE), and population of the subject (POP); and (2) whether the subject initiated the interaction (INITIATE) by being the first to display or to approach within approximately one body length (~ 2 cm). In addition to a null model consisting only of an intercept term, twelve alternative a priori hypotheses were considered and compared according to an information complexity approach to model selection using the small-sample bias adjusted AIC score (AIC_c) of Hurvich & Tsai (1989) and model evidence ratios based on normalized Akaike weights (Burnham & Anderson 2002). These twelve models included those based on each of SPECIES, SIZE, and INITIATE as the sole predictor, one based on the main effects and interaction between SPECIES and POP as predictors, the three two-predictor, main effects models from the set of SPECIES, SIZE, and INITIATE, the three models obtained from adding interaction terms to these two-predictor models, a three main effects model based on SPECIES, SIZE, and INITIATE, and the model obtained by adding interaction terms to this three-predictor model.

Comparison of Behavioral Patterns

I used nonmetric multidimensional scaling (NMDS) to transform the multivariate behavioral frequency data of all individuals to a reduced set of synthetic variables representing the major patterns of behavioral variation. NMDS is an ordination method with objectives and applications similar to those of principal components analysis and canonical correspondence analysis but without the restrictive assumption of linear relationships among variables. NMDS seeks by iterative search to arrange samples in the space defined by a specified number of dimensions so as to maintain the same ranked distances between samples in this ordination space as in the higher-dimensional space defined by the full set of original variables. Departure from monotonicity in the relationship between sample distances in the original and ordination spaces is reflected in a normalized stress value (Mather, 1976) scaled to range from 0 (perfect representation of the original distances in the ordination space) to 1 (no representation of the original distances in the ordination space). Three NMDS axes were produced from a Bray-Curtis distance matrix (Bray & Curtis 1957) based on the frequency of HB, SE, GE, PU, AP, BL, RT, and FL using the PROC MDS routine in SAS 9.1 (2002). Specification of any fewer than three ordination axes led to unfavorably high stress values (> 0.15). In order to guard against identification of an ordination yielding a local, rather than global, minimum in stress, I ran the iterative NMDS construction routine from 75 random starting configurations (McCune & Grace 2002). To test the hypotheses that *A. sagrei* and *A. carolinensis* juveniles in heterospecific encounters behave differently than *A. carolinensis* juveniles in conspecific encounters, and that individuals concluding

interactions as dominant behave differently in those interactions than those that do not distinguish themselves as dominant, I compared the NMDS scores on each axis for these groups. Differences in NMDS scores were tested by nonparametric Kruskal-Wallis tests followed by multiple comparison Z-tests.

RESULTS

Predictive Models of Dominance

Overall, 32.7% (33/101) of encounters resulted in a clearly dominant individual (6.5% (2/31) of conspecific encounters; 44.3% (31/70) of heterospecific encounters). Judged by AIC_c, all single predictor (SPECIES, SIZE, INITIATE) models of *A. carolinensis* dominance were better than the null, intercept-only model. An interaction between SPECIES and POP was not indicated. Adding POP and the interaction between SPECIES and POP to the model based only on SPECIES increased AIC_c by 4.214, suggesting that *A. carolinensis* should not be distinguished by population in predicting dominance in heterospecific encounters.

The selected best predictive model of dominance in dyadic encounters was that which included the categorical variables SPECIES and INITIATE as the sole two predictors (Tables 3.3 and 3.4). This model yielded an R² of 0.28. The estimated odds ratio for an interspecific encounter versus a conspecific encounter was 17.751 and the odds ratio for initiating an interaction versus not initiating was 8.538. These odds ratios give the following predicted probabilities of dominance for a juvenile *A. carolinensis*;

0.0165 in a conspecific encounter in which it does not initiate an interaction, 0.1232 in a conspecific encounter in which it does initiate, 0.2261 in a heterospecific encounter in which it does not initiate, and 0.7139 in a heterospecific encounter in which it does initiate (Table 3.4). In heterospecific encounters, neither species was significantly more likely than the other to initiate interaction (Fisher's exact test; $p = 0.233$).

The Akaike weight of the selected best predictive model of dominance was 0.494. There was appreciable evidence (Akaike weight > 0.05) for only two other predictive candidate models. Compared to the selected model, the model comprised of the main effect predictors, SPECIES, INITIATE and SIZE was $0.273/0.494 = 0.553$ as likely to be the best predictive model among the set of candidates, and the model comprised of SPECIES, INITIATE, and their interaction was $0.228/0.494 = 0.462$ as likely.

Comparison of Behavioral Patterns

Overall, 76.2% (77/101) of dyadic encounters involved displays by one or both members of the dyad. Among conspecific encounters, 90.3% (28/31) involved displays and among heterospecific encounters 70.0% (49/70) involved displays. This difference between the proportion of conspecific and heterospecific encounters involving at least one display is significant by a Fisher's Exact test ($p = 0.041$). Considering only the *A. carolinensis* subjects, the difference between the proportions is again significant ($p < 0.001$) with 83.9% (26/31) of subjects having displayed in conspecific encounters and only 31.4% (22/70) of subjects having displayed in heterospecific encounters.

Significantly more of the *A. sagrei* in those heterospecific encounters displayed: 62.9% (44/70, $p < 0.001$).

Attacks involving biting were rare and occurred in only 5.9% (6/101) of all encounters. Of those individuals attacking, one was an *A. carolinensis* in a conspecific encounter, three were *A. carolinensis* in heterospecific encounters, and two were *A. sagrei*. Attacks were brief and did not involve grappling, although in one heterospecific encounter the *A. carolinensis* attacked twice. None of the attacks were reciprocated, and all attackers were dominant in their encounter.

The three NMDS axes explained most of the variance in the behavioral frequency data ($R^2 = 0.99$) and were obtained with a low stress value of 0.11. Instability of the ordination solution (standard deviation in stress over the last 10 iterations) was very low (0.0003). Pearson correlations of the behavioral frequencies and the NMDS axes (Table 3.5) suggest that two axes can easily be given clear, biologically meaningful interpretations. Axis 1 was substantially correlated with AP, BL, and RT, suggesting that this axis represents rate of movement in the vicinity of the encountered individual. Axis 2 was substantially correlated with HB, SE, GE, and PU, indicating that this axis represents overall rate of display. Axis 3 was not strongly correlated with any of the original behavioral variables. The variance represented by this axis is, therefore, not readily amenable to a clear, concise and unambiguous interpretation. Scores along this axis did not differ significantly among any of the tested groups.

As indicated by NMDS Axis 1 (Fig. 3.1), rate of movement in the vicinity of an encountered individual was significantly lower for *A. sagrei* than for *A. carolinensis* in both conspecific and heterospecific encounters (Kruskal-Wallis $\chi^2 = 43.4$, d.f. = 2, $p <$

0.001; *A. sagrei* – conspecific encounter *A. carolinensis* Z-score = 5.65, *A. sagrei* – heterospecific encounter *A. carolinensis* Z-score = 5.70, Bonferroni corrected critical Z-score at experimentwise α of 0.05 = 2.39). As measured by NMDS Axis 2 (Fig. 3.2), overall rate of display was significantly lower for *A. carolinensis* in interspecific encounters than for *A. sagrei* in those encounters or *A. carolinensis* in conspecific encounters (Kruskal-Wallis $\chi^2 = 26.3$, d.f. = 2, $p < 0.001$; heterospecific encounter *A. carolinensis* – *A. sagrei* Z-score = 4.35, heterospecific encounter *A. carolinensis* – conspecific encounter *A. carolinensis* Z-score = 4.47, Bonferroni corrected critical Z-score at experimentwise α of 0.05 = 2.39). Across species, individuals concluding interactions as dominant exhibited a higher rate of movement in the vicinity of the encountered individual (Kruskal-Wallis $\chi^2 = 15.9$, d.f. = 1, $p < 0.001$) and a lower overall display rate (Kruskal-Wallis $\chi^2 = 4.4$, d.f. = 1, $p = 0.035$) as measured, respectively, by NMDS Axes 1 and 2 (Fig. 3.3 & 3.4). Overall, there was a weak but significant correlation between display rates of individuals within dyads (Pearson correlation = 0.24, $p = 0.017$).

DISCUSSION

The most probable best predictive model for *A. carolinensis* dominance in first encounters between juvenile anoles indicates that dominance is influenced by initiation of an interaction and by the species of the anole encountered, but not by body size asymmetry. Juvenile *A. carolinensis* encountering a conspecific were highly likely to exhibit social behavior, and over 90% of conspecific encounters involved display

interaction. However, the predicted probability of dominance in a conspecific encounter, even for the *A. carolinensis* initiating an interaction, is only approximately 12%. Most conspecific encounters were therefore characterized by balanced agonism and apparent coexistence. In contrast, most *A. carolinensis* juveniles encountering an *A. sagrei* juvenile did not initiate an interaction and fewer than a third performed any display behaviors. In such cases, *A. carolinensis* juveniles nevertheless have a higher predicted probability of dominance than they do in any conspecific encounter, and in cases where an *A. carolinensis* does initiate an interaction with an *A. sagrei* its probability of dominance exceeds 70%.

In first encounters between juvenile anoles, *A. carolinensis* clearly has an agonistic advantage over invading *A. sagrei*. In almost all heterospecific encounters there was either no clearly dominant individual or the *A. carolinensis* juvenile dominated the *A. sagrei* juvenile. Therefore, it appears highly unlikely that juvenile *A. carolinensis* would be displaced by juvenile *A. sagrei*, at least following a single interaction in which both individuals could perceive themselves as a resident encountering another anole at the border of an area with which it is familiar.

In what ways do behavioral patterns differ among individuals in conspecific and heterospecific *A. carolinensis* encounters, and how might such differences explain disparities in the symmetry of agonism? Ordination of behavior frequencies indicated that much of the variance in behavior was along an axis representing overall display frequency and an axis representing movement in the vicinity of the encountered anole. Based on comparisons of group medians for these representative synthetic variables, I first found that *A. carolinensis* in heterospecific encounters not only display less than in

conspecific encounters, but that they display less than *A. sagrei* in those heterospecific encounters as well. Furthermore, because, the display rates of *A. sagrei* in the heterospecific encounters did not differ from the display rates of *A. carolinensis* in conspecific encounters, the reduced response of *A. carolinensis* in heterospecific encounters cannot be attributed to the weak overall correlation between individual display rates within dyads. Secondly, *A. sagrei* move less in the vicinity of an encountered *A. carolinensis* than *A. carolinensis* move in the vicinity of either conspecifics or *A. sagrei*. Together, these patterns suggest that an asymmetry between species in behavior is coupled with the observed interspecific asymmetry in dominance. *Anolis sagrei* displays towards *A. carolinensis* while maintaining a distance, whereas *A. carolinensis* shows little recognition or response to *A. sagrei* at all. The only two *A. sagrei* juveniles that were dominant were those that attacked and bit the *A. carolinensis* juveniles. In no heterospecific encounter, including those in which the *A. sagrei* was twice as large, was an *A. carolinensis* displaced as a response to approach and display alone.

Although *A. carolinensis* in the United States has been isolated from other anoles for four million years or more (Buth et al. 1980; Glor et al. 2005), *A. sagrei* occurs in sympatry and shares a recent coevolutionary history in the Caribbean with several other anoles including those comprising a “*carolinensis* complex” from which the North American *A. carolinensis* is descended (Williams 1969; Buth et al. 1980). *A. sagrei* and the Caribbean *A. carolinensis* equivalents partition structural habitat in all age classes (Schoener 1968) apparently in response to direct competition (Schoener 1975). Relative to other anoles, *A. sagrei* has very broad geographic and habitat distributions, exists at

higher densities, and individuals maintain more exclusive territories (Schoener & Schoener 1980). A predisposition towards exclusive partitioning of space through avoidance or display interactions with both conspecific and heterospecific anoles might therefore be an adaptive trait acquired by *A. sagrei* in its native range. Paradoxically, this history of interspecific interaction could thereby initially put *A. sagrei* juveniles at an apparent disadvantage in single agonistic interactions with socially naïve North American *A. carolinensis* juveniles for which there has been no selection for response to conventional displays (Hurd 2004) and threat of aggression from congeners in this age class.

Interspecific dominance relationships between juveniles of *A. carolinensis* and invasive *A. sagrei* differ qualitatively from previously reported relationships between adults of these species. Resident versus intruder encounters established in the laboratory by Tokarz & Beck (1987) between adult male *A. sagrei* and adult male *A. carolinensis* from an allopatric population produced interactions in which most individuals displayed, there was relative parity in agonism, little aggressive escalation, and no reported trend in interspecific dominance. Brown (1988) used adult males collected from a single location, and a resident versus resident scenario similar to that of the present study, and found higher levels of interspecific aggression than those reported by Tokarz & Beck and a tendency for *A. carolinensis* to escalate more than *A. sagrei*, but still no trend toward interspecific displacement. It is not clear whether the differences between the results of these two studies of adults might be attributable to differences in their respective experimental designs, differences in the interspecific social history of the individuals examined, or evolved behavioral differences between populations. In the present study

there was no indication of population differences in *A. carolinensis* response to heterospecifics.

Whether due to a proactive aggressive predisposition (Barlow et al. 1986; Korzan et al. 2006) or a decision based on opponent assessment (Jackson 1991), initiation of an agonistic interaction is strongly predictive of dominance in juvenile *A. carolinensis*. Contrary to the observed effect of species on juvenile *A. carolinensis* dominance, the effect of agonistic initiation is entirely concordant with the results of adult interaction studies. Among adult male *A. carolinensis* dyads, the individual that first displays almost always achieves dominant status (Korzan et al. 2006). In the present study, dominant juveniles moved more in the vicinity of an encountered juvenile and were more likely to initiate display interaction, but actually exhibited a lesser overall display rate, further suggesting that it is the initial display rather than the cumulative display behavior that is most closely linked to dominance.

It remains to be determined how the disparate patterns of juvenile and adult interspecific agonism are linked by ontogeny and whether subsequent interactions would modify the outcome of first encounters. Since juvenile *A. carolinensis* appear to largely share a behavioral repertoire with adults, and, like adults, distinguish between conspecific and heterospecific individuals, these apparent differences in outcome of interspecific encounters could be governed by factors other than those explicitly examined in this study. In particular, changes in previous social experience, perceived resource value, and relative costs of behaviors could all influence ontogenetic differences in interspecific agonism. Consequently, it would be useful to examine the effect and persistence of

species identity and initiation of agonism on juvenile dominance in more complex social and environmental scenarios.

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Appendix: Chapter 3

Table 3.1. Mean body mass and snout-vent length (SVL) of juvenile anoles paired in the three classes of dyadic encounters.

Anole Category	Mass (g) mean \pm S.E.	SVL (mm) mean \pm S.E.
Subject: <i>A. carolinensis</i> (4-5 days)	0.287 \pm 0.012	23.0 \pm 2.6
Stimulus: <i>A. carolinensis</i> (4-5 days)	0.295 \pm 0.012	23.3 \pm 2.6
Subject: <i>A. carolinensis</i> (4-5 days)	0.291 \pm 0.011	23.2 \pm 2.6
Stimulus: <i>A. sagrei</i> (4-5 days)	0.154 \pm 0.003	18.0 \pm 1.0
Subject: <i>A. carolinensis</i> (4-5 days)	0.277 \pm 0.011	23.0 \pm 2.6
Stimulus: <i>A. sagrei</i> (21-26 days)	0.321 \pm 0.009	21.7 \pm 1.8

Table 3.2. Description of agonistic behaviors recorded for each individual in staged encounters between juvenile anoles

Behavior	Description
Headbob (HB)	rapid series of vertical oscillations of the head
Sagittal expansion (SE)	increase in the sagittal profile of the body through lateral compression
Gular expansion (GE)	increase in the apparent size of the throat through extension of the hyoid apparatus
Pushup (PU)	raising and lowering of the forebody by flexion and extension of the forelimbs
Approach (AP)	movement that decreases the distance from an encountered anole
Approach within one body length (BL)	movement to within approximately 2 cm of an encountered anole
Retreat (RT)	movement that increases the distance from an encountered anole
Flee (FL)	rapid, abrupt, uninterrupted movement that increases the distance from an encountered anole by several body lengths
Attack (AT)	rapid approach resulting in physical contact and biting of an encountered anole

Table 3.3. Information complexity assessment results for candidate predictive models of juvenile *A. carolinensis* dominance. The predictors included in each k parameter candidate model are listed and followed by the AIC_c score for that model, the difference between the AIC_c scores for that model and the best model, and the Akaike weight in favor of that model.

Model	k	AIC_c	AIC_cΔ	AIC_c weight
1. Intercept only	1	126.598	28.784	0.000
2. SPECIES	2	113.927	16.113	0.000
3. SIZE	2	120.870	23.056	0.000
4. INITIATE	2	115.003	17.189	0.000
5. SPECIES x POP	4	118.141	20.327	0.000
6. SPECIES, INITIATE	3	97.814	0.000	0.494
7. SPECIES x INITIATE	4	99.358	1.544	0.228
8. SIZE, INITIATE	2	112.651	14.837	0.000
9. SIZE x INITIATE	3	114.727	16.913	0.000
10. SPECIES, SIZE	2	112.533	14.719	0.000
11. SPECIES x SIZE	3	114.236	16.422	0.000
12. SPECIES, SIZE, INITIATE	3	99.002	1.188	0.273
13. SPECIES x SIZE x INITIATE	7	107.129	9.315	0.000

Table 3.4. Parameter estimates and odds ratios for the best predictive model of juvenile *A. carolinensis* dominance.

Parameter	D.F.	Estimate	S.E.	Odds Ratio
Intercept	1	-4.1066	0.8783	
SPECIES (heterospecific)	1	2.8764	0.8308	17.751
INITIATE (subject initiates)	1	2.1445	0.5413	8.538

Table 3.5. Pearson correlations between behaviors and each of the three axes produced in a nonmetric multidimensional scaling ordination.

Behavior	Axis 1	Axis 2	Axis 3
HB	0.1683	-0.4656	-0.0832
SE	-0.0010	-0.6331	-0.1204
GE	0.0796	-0.5957	-0.1554
PU	0.1495	-0.5379	-0.0944
AP	0.8404	0.2145	0.0812
BL	0.3983	-0.0253	-0.0909
RT	0.7808	0.2353	0.1669
FL	-0.2047	0.0185	0.0148

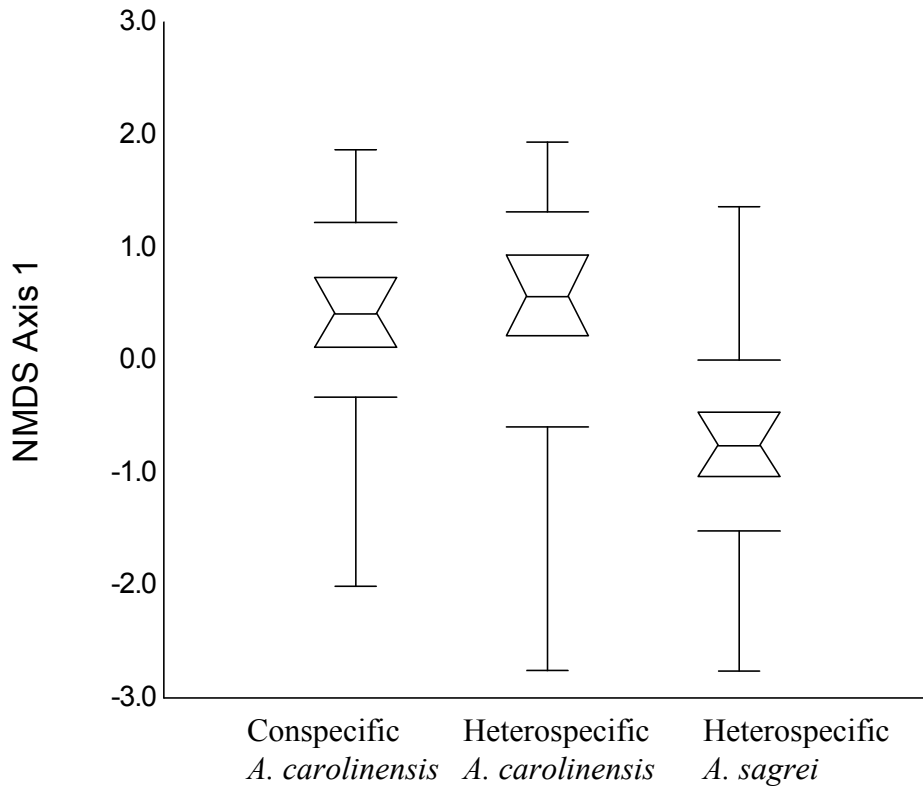


Figure 3.1. Comparison of NMDS ordination Axis 1 scores (correlated with movement in the vicinity of an encountered anole) among juvenile anoles. Non-overlap of notched boxes indicates significant difference in median by nonparametric Bonferroni-corrected multiple comparison Z-test. Inner and outer fences encompass 50th and 75th qauntiles, respectively.

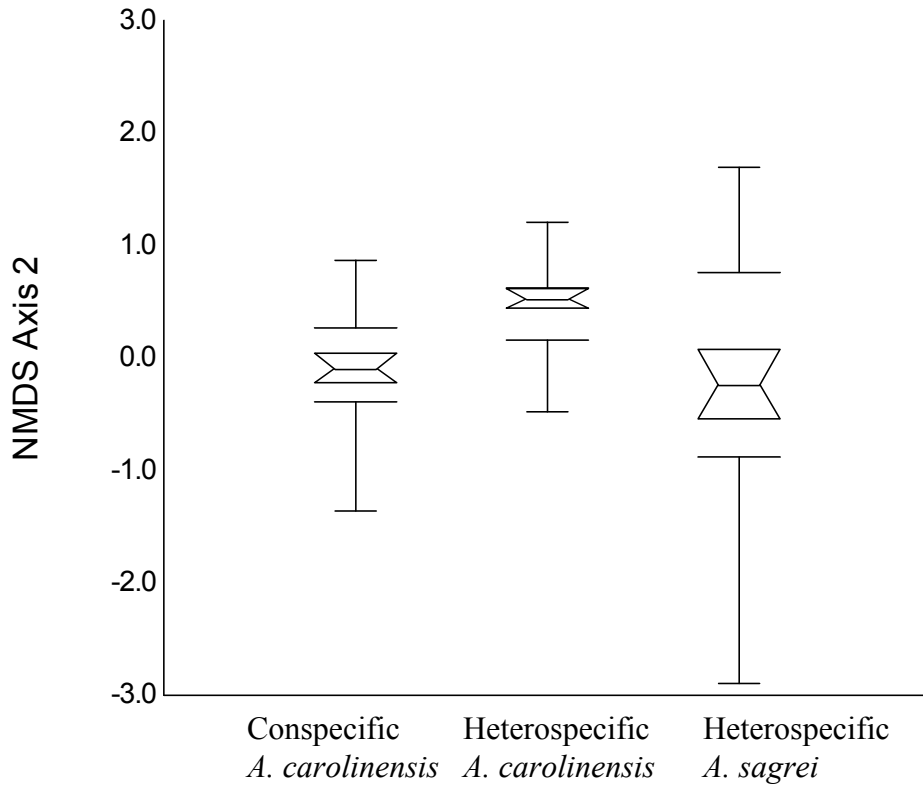


Figure 3.2. Comparison of NMDS ordination Axis 2 scores (negatively correlated with overall rate of display) among juvenile anoles. Non-overlap of notched boxes indicates significant difference in median by nonparametric Bonferroni-corrected multiple comparison Z-test. Inner and outer fences encompass 50th and 75th quantiles, respectively.

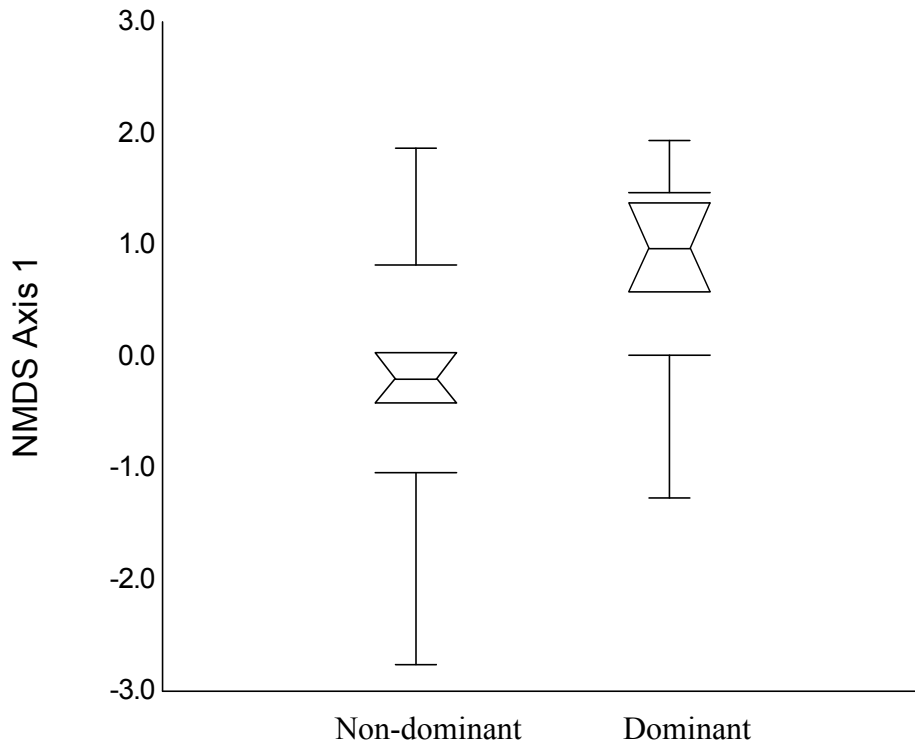


Figure 3.3. Comparison of NMDS ordination Axis 1 scores (correlated with movement in the vicinity of an encountered anole) between all non-dominant and dominant juvenile anoles in all encounters. Non-overlap of notched boxes indicates significant difference in median by nonparametric Bonferroni-corrected multiple comparison Z-test. Inner and outer fences encompass 50th and 75th quantiles, respectively.

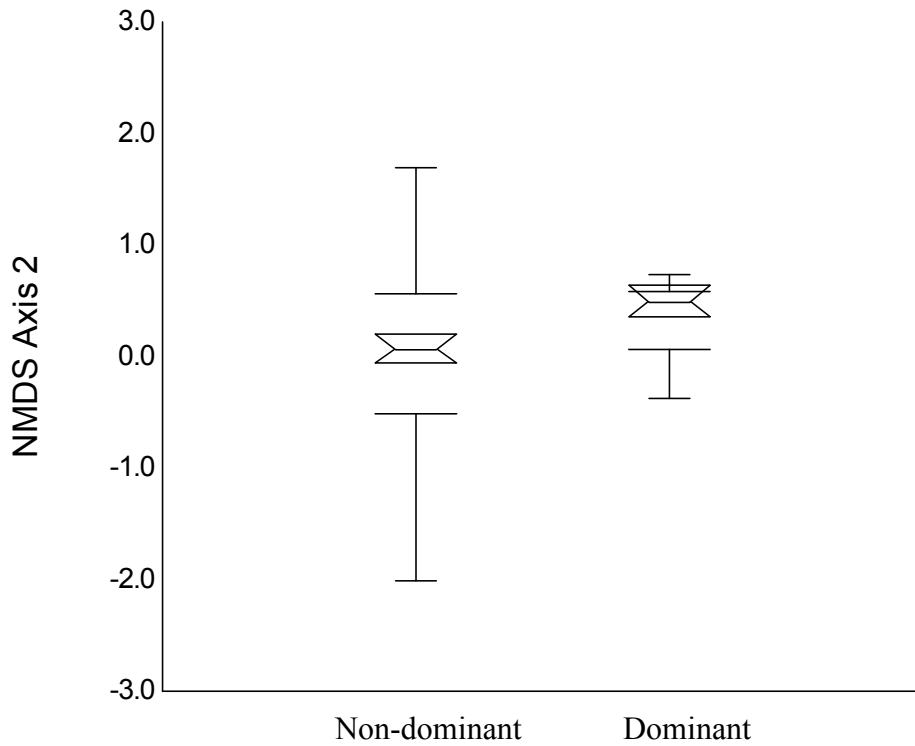


Figure 3.4. Comparison of NMDS ordination Axis 2 scores (negatively correlated with overall rate of display) between all non-dominant and dominant juvenile anoles in all encounters. Non-overlap of notched boxes indicates significant difference in median by nonparametric Bonferroni-corrected multiple comparison Z-test. Inner and outer fences encompass 50th and 75th quantiles, respectively.

Chapter 4

Niche Differences and the Ontogeny of Habitat Partitioning in Juvenile Anoles

ABSTRACT

Studies of *Anolis* lizards have played a major role in the development of theory concerning the formation and stability of ecological communities and current biological invasions by these species provide an opportunity to test and refine the conclusions of this body of research. I examined the role of interspecific interaction among juvenile anoles in producing the patterns of niche partitioning characteristic of adults in an ongoing invasion. Since its introduction to the southeastern United States, *Anolis sagrei* has steadily expanded its range into that of the ecologically similar native *A. carolinensis*. In this study I compared the behavior and habitat use of *A. carolinensis* juveniles in single-species field enclosures with that of *A. carolinensis* and *A. sagrei* juveniles in two-species enclosures and described changes in the partitioning of space over the first weeks of life. Additionally, I assessed initial behavior and habitat use under both enclosure treatments as predictors of juvenile growth rate in *A. carolinensis* through an information-theoretic model selection approach. Patterns of structural niche partitioning between *A. carolinensis* and *A. sagrei* juveniles mirrored those reported for adults of these species and were evident within a week of hatching. Juvenile *A. carolinensis* in the presence of *A. sagrei* juveniles exhibited an upward shift in mean perch height similar to that seen in reproductive males following experimental imposition of sympatry in adults of these species. Thermal microhabitat partitioning was apparent: *A. carolinensis* juveniles selected perch sites warmer than the mean of all those available and *A. sagrei* on average selected sites cooler than the mean. Over time there was a contraction of space use into volumes largely within vegetation rather than in open sites. Predictive

models of change in body mass indicated this shift to be a positive influence on growth. Despite the shift in structural habitat use of *A. carolinensis* juveniles in the presence of *A. sagrei*, there was no observed consequence of syntopy on growth rate. This study suggests no immediate role of juvenile interactions on numerical declines in *A. carolinensis* following contact with invasive *A. sagrei*.

INTRODUCTION

Age-related changes in the ecological niche and associated interspecific interactions are highly conspicuous in metamorphosing species such as holometabolous insects and amphibians, but in species for which ontogenetic morphological change is manifest primarily through increased body size, shifts in resource use and interspecific resource partitioning can be less obvious. Nevertheless, juveniles of species without major ontogenetic morphological reorganization can differ substantially and even categorically from adults in major aspects of preferred habitat and resource use (Werner & Gilliam 1984). Such ontogenetic niche differences are taxonomically widespread (in invertebrates, Davies et al. 1981; Todd et al. 2006; Blamires et al. 2007; in fishes, Grossman 1980; Robertson 1980; Gratwicke et al. 2006; and in reptiles, Pough 1973, Lind & Welsh 1994; Whitfield & Donnelly 2006); therefore, incorporation of juveniles in the study of competition and the niche is critical to understanding the assembly and structure of ecological communities.

The invasion of ecological communities by exotic species can have profound overall effects on native species (Fritts & Rodda 1998; Mack et al. 2000), in some cases through interspecific interactions that differ in character or intensity according to age or size class (Kupferberg 1997; Gurnell et al. 2004; Webb et al. 2005). Commonly, the interspecific effects documented are those that cross age classes. In size-structured trophic communities, predation by exotic species (Bruno et al. 2005) can impact more native species in their subadult, rather than adult, age classes before these animals reach sizes that exceed the gape-limitation of their consumers (Hambright et al. 1991; Vitt

2000). In other cases, the collective demographic or an undetermined age class of an invasive species exerts a negative influence on juveniles of a native species. For example, although there is no strong evidence that direct interspecific interference between adults is important in the displacement of red squirrels (*Sciurus vulgaris*) by invasive grey squirrels (*S. carolinensis*) in eastern Europe, it does appear that interspecific competition significantly impacts residency and growth rates of juveniles (Gurnell et al. 2004). Experiments explicitly examining population-level mechanisms by which invasive brook trout (*Salvelinus fontinalis*) impose declines in native Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) have shown that survival of juvenile, but not adult, cutthroat trout were affected by density of the invasive species (Peterson et al. 2004), and that biotic interactions at the juvenile stage (Griffith 1972; Novinger 2000) are likely the primary cause of competitive exclusion. Except in regard to animals with larval stages in habitats distinct from those of adults (e.g. anurans, DeBenedictis 1974; Kupferberg 1997; Smith 2005), however, competitive interactions between species *within* early age classes are not often examined, and juvenile interactions are sometimes not considered at all in characterizations of interspecific niche partitioning.

Observational and experimental studies conducted most extensively on adults (but see Schoener 1968) have established the Caribbean *Anolis* lizard assemblages as classic examples of niche partitioning driven by competition (Losos 1994). Independent adaptive radiations have produced a pattern by which *Anolis* species appear as a repeated set of ecological types or “ecomorphs” on each island of the Greater Antilles (Williams 1983; Losos et al. 1998). These morphologically and behaviorally distinct variants of the general arboreal insectivore form are defined in relation to their predominant use of

structural microhabitat. Species representing trunk-ground, trunk-crown, crown-giant, and twig ecomorphs are common to all four islands of the Greater Antilles. In the larger assemblies on Cuba and Hispaniola, sympatric species have been described as partitioning the multidimensional niche predominantly along the structural microhabitat axis and in some communities along body size and thermal microhabitat axes (Schoener 1977). On two-anole islands of the Lesser Antilles partitioning occurs along at least two of these axes (Schoener 1977), and interspecific overlap appears to be minimized by both behavioral avoidance and evolutionary morphological divergence (Pacala & Roughgarden 1982, 1985; Losos 1990; Buckley & Roughgarden 2005). Intraspecific differences have been incorporated into this conceptualization primarily through description of differences between the sexes in adult body size and perch selection (Butler et al. 2000; Butler et al. 2007). Several observational studies have documented intraspecific differences in habitat use between adult male and adult female-sized (females and subadult male) anoles and some have separately considered and described juvenile habitat use (Schoener 1967; Rand 1967; Stamps 1983; Jenssen et al. 1998). Juveniles appear to fit the overall characterization that smaller individuals within species utilize perches of lower height and smaller diameter (Schoener 1977). In complex anole assemblages this results in an interdigitating pattern of species and size class perch dimension ranks and a general maximization of size-dissimilarity between the individuals of species that share microhabitat (Schoener 1977). Experimental studies examining the ontogenetic origins of such resource partitioning and the role of direct interspecific interactions among juvenile anoles are lacking.

The brown anole, *Anolis sagrei*, a trunk-ground ecomorph, is an increasingly widespread exotic species (Losos et al. 1993) and in its invasion from the Caribbean of the southeastern United States (Lee 1985; Kolbe et al. 2004) provides an excellent opportunity to examine the effects of juvenile competition on resource partitioning in the early stages of contact between ecologically similar congeners. The green anole, *A. carolinensis*, a trunk-crown ecomorph, is the only anole native to the United States (Conant & Collins 1998), but it now encounters *A. sagrei* within the portion of its range including Florida and parts of Texas, Louisiana, Georgia, and South Carolina (King et al. 1987; Thomas et al. 1990; Platt & Fontenot 1994; Krusling et al. 1995; Campbell 1996; Turnbough 2006). In the Caribbean, *A. sagrei* appear to limit the distribution and range of habitat utilized by green anole analogs of the “*carolinensis*” species group (Schoener 1975; Losos & Spiller 1999). Experimental introductions suggest that *A. sagrei* imposes an upward shift in the typical perch height of *A. carolinensis* and decreased population densities after only a very short time in sympatry (Losos & Spiller 1999; Campbell 2000). Although niche shifts are apparent in adults, it is not known in what age class these shifts originate.

Anolis carolinensis is ideally suited for mechanistic, experimental study of the role of interspecific competition within early life stages. Under typical conditions, total anole abundance is necessarily highest during seasons in which hatching occurs (but see Schoener et al. 2004), and, therefore, it is juveniles that consistently experience peak population density. Furthermore, all juvenile *A. carolinensis* characteristically use only a limited portion of the total available habitat, that in lower regions of vegetation, most commonly below 1.5m (Jenssen et al. 1998; Lovern 2000). The nutritional requirements

and the demands of growth in reptiles are generally more pronounced in juveniles than they are for adults (Morofka et al. 2000). Juveniles may also be more sensitive to environmental stress such as desiccation (Vitt 2000) and thus incur increased costs in occupying sub-optimal microhabitat. Whereas adult sexual size dimorphism exists in both *A. carolinensis* and *A. sagrei*, and may serve in decreasing overall levels of adult competition (Schoener 1975), no such dimorphism exists in juveniles. Furthermore, survivorship of *A. carolinensis* from the juvenile age class has been estimated to be as low as 5.1% (Gordon 1956). Therefore, securing early access to favorable habitat could be critical. We might therefore expect to see in juveniles a higher intensity of competition for such habitat and a rapid effect of such competition on the realized niche and proximal measures of fitness.

In this study I compare the behavior and habitat use of *A. carolinensis* juveniles in single-species field enclosures with that of *A. carolinensis* and *A. sagrei* juveniles in two-species enclosures. I test the hypothesis that niche differences observed between adults of *A. carolinensis* and *A. sagrei* exist between juveniles of these species and that the characteristic pattern of niche partitioning arises within the first few weeks of life. Additionally I assess initial behavior and habitat use in allopatry and sympatry as factors influencing juvenile growth rate in *A. carolinensis*.

METHODS

Laboratory Housing and Egg Collection

Juvenile anoles were obtained from eggs laid in the laboratory by wild-caught females as described in Goodman & Walguarnery (2007) and in the previous chapters. Adult, reproductive, female *A. carolinensis* and *A. sagrei* were collected from syntopic populations in Jacksonville, Duval County, Florida during May 2003. These animals were housed under identical laboratory conditions at the University of North Florida (Jacksonville, FL) for up to six weeks. All eggs collected were incubated at 30° C. Upon hatching, juvenile anoles were housed in the laboratory under the same conditions as those for the adult females for no more than three days before being introduced to the field enclosures. During this time, juvenile anoles were provided with an ad libitum supply of flightless fruit flies.

Enclosure and Treatment Design

Ten enclosures for juvenile anoles, each measuring 1.2 x 1.2 x 1.5 m, were constructed on an approximately 900 m² cleared, fenced plot at the University of North Florida. These lizard-proof, predator-proof enclosures were made of frames of 2 x 2 (5 cm x 5 cm) lumber and sides of galvanized aluminum window screening overlapped by chicken wire. Partial shading was provided with 80% shade cloth (see Figure 4.1). The interior of each enclosure was planted with two low shrubs (*Illicium parviflora*) in the

center third and a single small sweet gum tree (*Liquidambar styraciflua*) in one of the remaining thirds. The end third of the enclosure opposite the sweet gum was kept bare of vegetation. A floor of commercial-grade landscaping cloth was covered by a 3 cm layer of soil and leaf litter. This tripartite array of native vegetation, while simple enough to allow for precise standardization across all replicates, encompassed a realistic degree of structural variation in comparison to an equivalent area of natural anole habitat, and permitted movement across the full vertical range commonly occupied by *A. carolinensis* juveniles (Lovern 2000). The vegetation and substrate within each enclosure was sprinkled with 1 L of water each morning (before 0700 hr). Every third day the enclosures were stocked with 25 mL of small domestic crickets in order to maintain a consistent level of potential arthropod prey.

Each enclosure was stocked with six juvenile anoles (≤ 4 days old). Half of the enclosures were each stocked with six *A. carolinensis* juveniles (conspecific enclosures) and the other half were each stocked with three *A. carolinensis* juveniles and three *A. sagrei* juveniles (mixed-species enclosures). Based on the lower range of nearest neighbor distances recorded in the field (Lovern 2000), the total of six individuals to be placed in each enclosure represented a high lizard density without forcing the animals into unnatural proximity to each other. Anoles were assigned randomly to conspecific and mixed-species enclosures with regard to sex and mass. Juvenile *A. carolinensis* of the ages used in this study do not differ by sex in perch selection, home range volume, typical nearest neighbor distance, or display behavior (Lovern 2000). The range of juvenile masses at the time of introduction to the enclosures was representative of the range of masses at hatching. There was no significant difference between the mean body

mass of *A. carolinensis* juveniles in the conspecific enclosures and those in the mixed enclosures at the time of introduction (two-sample T-test, $n = 36$, $p = 0.138$). All six juveniles of each enclosure were introduced simultaneously into the central region of the enclosure at 0700 hrs on the first day on which observations were to be made. One *A. carolinensis* juvenile in a conspecific enclosure died after the first week, and this individual was not replaced. Conspecific and mixed-species enclosures were systematically dispersed on the plot to insure that at all times all enclosures received equal sun exposure and that the temporal and spatial pattern of shading within enclosures did not differ between replicates.

Data Collection

I conducted observations on five days of each week for three weeks. During each hour of an observation day (0800 hr-1800 hr) I collected data from all anoles in one pair of adjacent enclosures (conspecific enclosure and mixed-species enclosure) for 20 min. per enclosure. This observation schedule yielded a complete temporal profile (one observation period per each of the ten hours) for each enclosure per week of the study. Anoles in each enclosure were uniquely marked by toe clipping and with dots of acrylic paint applied to the lumbo-dorsal region so that individuals could be easily distinguished and identified. Positions of all anoles within an enclosure and all agonistic interactions were recorded according to an all-animals scan sampling method. The behavior of each individual participating in an interaction was classified as one of the following: attack, display-attack, display, display-flee, no response, or flee.

Anole positions within enclosures were recorded in reference to a grid system dividing the volume of each enclosure into cubic cells of approximately 15 cm on a side so that any position within the enclosure could be described by the one of 640 cells in which it was contained. In order to facilitate identification of anole positions, visible grids were applied to all sides of the enclosures, and the vertices of the grid were marked on the floor of the enclosures. Observations were made at a distance from the enclosure of no less than 0.5 m. It has been shown that the presence of an unobtrusive, yet completely visible, observer does not influence the activity level and behavior of *A. sagrei* (Sugerman 1990), and preliminary observations prior to commencement of the present study indicated that this was also true for *A. carolinensis*. Observations conducted as part of this study at no time suggested that either species within the space of the enclosures was influenced by the presence of an observer at a distance of 0.5 m. Temperature data loggers (Onset TIDBITs®) recorded the temperature every half hour in four locations within a random sample of three enclosures; 1) within the higher vegetation (tree), 2) within the lower vegetation (shrub), 3) on the ground in the unvegetated region, and 4) on a wall of the enclosure. Each observed position of an anole was assigned the temporally closest mean temperature measurement for the sample of the corresponding substrate.

Pairs of conspecific and mixed-species enclosures were stocked and observations begun on these at different times between June 28, 2003 and July 7, 2003 so that six replicate pairs could be obtained from the total of ten enclosures. The following variables for each individual for each week were used in subsequent analyses: 1) the total positions (15 x 15 x 15 cm volumetric units) in which the anole was observed (TOTAL_POS), 2)

the proportion of TOTAL_POS not also used by another anole in the same enclosure (EXCLUSIVE), 3) the proportion of TOTAL_POS on the ground (GROUND), 4) the proportion of TOTAL_POS on vegetation (VEGETATION), 5) the mean height of TOTAL_POS (HEIGHT), 6) the mean estimated temperature of the observed positions (TEMPERATURE), 7) the mean difference between the temperature of observed positions and the temperature of all substrates at those same times (TEMP_DIFF), 8) the number of interactions in which the anole was observed to participate (INTERACTION), 9) and a sum of display and attack interactions weighted according to aggression (Stamps 1978) so that display-flee = 1, display = 2, attack = 3, and display-attack = 4 (AGG_SCORE). The mass of each anole was measured on the day prior to its introduction to the field enclosure and following the last day on which it was observed so that a tenth variable, the percent change in body mass over the three weeks of the study (MASS_CHANGE), could be calculated.

Data Analyses

Enclosure means of variables 1-9 for three groups, *A. carolinensis* juveniles in conspecific enclosures, *A. carolinensis* juveniles in mixed-species enclosures, and *A. sagrei* in mixed-species enclosures, were compared by repeated measures ANOVA with time period (week 1-3) as a within subject factor. In order to maintain equal sample sizes contributing to the enclosure means for each group, only a randomly selected half of the *A. carolinensis* juveniles in each of the conspecific enclosures were designated as subjects and considered in these analyses. Sequential Bonferroni corrections were

applied across all p-values obtained for tests of main effects group and time differences for the nine response variables in order to control type-I error rate for all tests. Geisser-Greenhouse epsilon F-test p-values, correcting for potential deviations from circularity in the within-subject covariances, were used in identifying significantly different mean responses among time periods. Differences in enclosure means of MASS_CHANGE for the three groups were tested by one-way ANOVA. Following main effects F-tests, Tukey-Kramer multiple comparison tests were used to identify the individual significant differences among factor levels.

As an exploratory analysis of potential early effects on *A. carolinensis* growth rate, linear regression models of MASS_CHANGE were constructed and compared by an information theoretic model selection approach. Individual values of variables 1-9 for the first week were considered as predictors. The full main-effects model, including all of these variables, the 510 models comprised of all possible subsets of these variables, and a null, intercept only model were compared by the $ICOMP_{IFIM}$ model selection criterion (Bozdogan 1987, 1988, 1998) in order to identify the best set of predictors. Like the more commonly used Akaike information criterion (AIC), $ICOMP_{IFIM}$ scores estimated model performance based on a likelihood measure of estimated model lack of fit and a bias-correcting “penalty” term linked to model complexity. Rather than attempting to correct overfitting bias through a penalty based merely on the number of estimated model parameters, as in AIC, $ICOMP_{IFIM}$ penalizes model complexity based on the inverse Fisher information of the actual covariance matrix of model parameter estimates. The relative bias-corrected fit of candidate models can be compared and the best model identified as that yielding the lowest $ICOMP_{IFIM}$ score. In exploratory model

selection scenarios for which a large number of potential approximating models are considered, ICOMP_{IFIM} outperforms AIC criteria in identifying the actual set of generative factors influencing a response variable (Bozdogan 1998). This model selection approach was applied twice, first to the *A. carolinensis* juveniles in mixed-species enclosures and subsequently to the full set of *A. carolinensis* juveniles in all enclosures.

RESULTS

Microhabitat Selection

The three groups of juveniles, *A. carolinensis* in conspecific enclosures, *A. carolinensis* in mixed-species enclosures and *A. sagrei* in mixed-species enclosures, differed significantly in TOTAL_POS ($F_{2,15} = 36.08$, $p < 0.001$), GROUND ($F_{2,15} = 68.85$, $p < 0.001$), HEIGHT ($F_{2,15} = 333.68$, $p < 0.001$), and TEMP_DIFF ($F_{2,15} = 11.32$, $p < 0.001$) (Table 4.1). By Tukey-Kramer multiple comparison test, the *A. carolinensis* juveniles in conspecific enclosures and those in mixed-species enclosures did not have significantly different means of TOTAL_POS (mean = 32.76 and 33.35 respectively), but these groups both had significantly higher means than that for *A. sagrei* juveniles (mean = 17.17) (Fig. 4.2). The *A. carolinensis* conspecific group and the *A. carolinensis* mixed-species group had substantially and significantly lower means for GROUND (mean = 0.02 and 0.01 respectively) than did the *A. sagrei* group (mean = 0.25) (Fig. 4.5). All three group means of HEIGHT differed significantly (Fig. 4.6). The mean of HEIGHT

for *A. sagrei* was the lowest (mean = 11.2 cm), that for *A. carolinensis* in mixed-species enclosures highest (mean = 57.0 cm), and that for *A. carolinensis* in conspecific enclosures intermediate (mean = 50.4). Although means of TEMPERATURE initially appeared to differ between groups, with the *A. sagrei* mean (30.91) lower than that of the mixed-species and conspecific enclosure *A. carolinensis* (mean = 32.26 and 32.67 respectively), after Bonferroni correction these differences were not significant (Fig. 4.7). Means of TEMP_DIFF, however, did differ significantly according to the same pattern (Fig. 4.8). *A. sagrei* on average selected temperature microhabitats cooler than the mean for all those available, resulting in a mean TEMP_DIFF (-0.21 °C) significantly lower than those for *A. carolinensis* in conspecific or mixed-species enclosures (mean = 0.64 and 0.52 °C respectively).

Significant time effects existed for TOTAL_POS ($F_{2,15} = 11.13$, $p < 0.001$), EXCLUSIVE ($F_{2,15} = 13.29$, $p < 0.001$), and VEGETATION ($F_{2,15} = 10.41$, $p < 0.001$). For each of these effects the significant difference was between the week 1 mean and the means of the subsequent two weeks. By Tukey-Kramer multiple comparison tests, week 2 and 3 means of TOTAL_POS (mean = 25.15 and 26.20 respectively) were significantly higher than the mean TOTAL_POS for week 1 (mean = 31.93) (Fig. 4.2). Week 2 and 3 means of EXCLUSIVE (means = 0.61) were significantly lower than the mean EXCLUSIVE for week 1 (mean = 0.47) (Fig. 4.3). Week 2 and 3 means of VEGETATION (mean = 0.45 and 0.39 respectively) were significantly higher than the mean VEGETATION for week 1 (mean = 0.32) (Fig. 4.4). There were no significant group by time interactions.

Effects on Change in Body Mass

All juveniles increased in body mass over the course of the study. MASS_CHANGE for all subjects ranged from 11.45 to 231.18 with a mean of 114.01. One *A. carolinensis* in a conspecific enclosure died after week 1 and was not included in these analyses. The three groups of juveniles, *A. carolinensis* in conspecific enclosures, *A. carolinensis* in mixed-species enclosures and *A. sagrei* in mixed-species enclosures, did not differ significantly in MASS_CHANGE ($F_{2,51} = 2.21$, $p < 0.001$).

The estimated best predictive model of MASS_CHANGE for *A. carolinensis* juveniles in conspecific enclosures ($n = 35$) was that including GROUND, VEGETATION, and INTERACTION as predictors. By this model, GROUND has a large negative effect on MASS_CHANGE (coefficient = -355.18), VEGETATION has a positive effect (coefficient = 61.55) and INTERACTION has a small positive effect (coefficient = 4.99). This model has an R^2 of 0.27. Comparison of models for the more inclusive sample of all *A. carolinensis* juveniles ($n = 53$) showed the estimated best predictive model again to be that including GROUND, VEGETATION, and INTERACTION as predictors. This model explained slightly more of the variation in MASS_CHANGE ($R^2 = 0.31$) with predictor effects of similar magnitude. Again, by this model, GROUND has a large positive effect (coefficient = -472.21), VEGETATION has a positive effect (coefficient = 83.58) and INTERACTION has a small positive effect (coefficient = 4.10).

The estimated best predictive models each had an $ICOMP_{IFIM}$ score differing from that of the respective second best model by less than one (conspecific *A. carolinensis*

model $\text{ICOMP}_{\text{IFIM}}$ difference = 0.9339, all *A. carolinensis* model $\text{ICOMP}_{\text{IFIM}}$ difference = 0.6679) indicating substantial empirical support for the predictors appearing in these lower ranked models as well (Burnham & Anderson 2002). For both sets, these second best models include the same predictors as the estimated best predictive models and include additionally only TEMPERATURE. TEMPERATURE had a small positive effect on change in body mass (conspecific *A. carolinensis* model coefficient = 1.43, all *A. carolinensis* model coefficient = 0.94) and inclusion of this predictor had little effect on the magnitude of effects from the other predictors.

DISCUSSION

Anolis carolinensis is the only anole present throughout most of its native range but it increasingly encounters *A. sagrei* as this species continues its invasion into North America. The outcome of field enclosure experiments indicate that, in sympatry, juveniles of these species partition structural microhabitat, in part due to a shift imposed by *A. sagrei* on the realized niche of *A. carolinensis*. Following the structural niche characterizations of adults, *A. carolinensis* juveniles in both conspecific and mixed-species enclosures used ground perches as a lesser proportion of their total perch use distribution than did *A. sagrei* juveniles. On average, approximately a quarter of the positions occupied by *A. sagrei* juveniles were on the ground whereas these perches comprised less than two percent *A. carolinensis* positions whether alone or syntopic with *A. sagrei*. Mean perch height differed according to adult characterizations as well. Campbell (2000) noted a shift in *A. carolinensis* males to higher perches on islands

experimentally populated by *A. sagrei*. Results here show this shift to arise on a finer scale in juveniles. In the present study mean perch height of *A. carolinensis* juveniles in the presence of *A. sagrei* juveniles increased significantly to approximately 57 cm, up from approximately 50 cm in the presence of conspecifics alone. Moreover, since there was no time effect on perch height, this shift by *A. carolinensis* occurs as a result of interspecific effects in juveniles of less than a week in age. Although not a categorical shift in habitat, the higher mean perch height of *A. carolinensis* yields a significant and substantial difference from the approximately 11 cm mean perch height of syntopic *A. sagrei* juveniles. These results raise the possibility that previously described patterns of niche partitioning recognized among adults of morphologically similar sympatric species arise primarily in earlier age classes.

A strong direct role of behavioral display interactions and physical aggression among juveniles in space partitioning and niche shifts, however, is not supported. On average juveniles were observed to display approximately twice during the 200 min. set of observations per individual per week. Assuming a temporal uniformity to the distribution of display frequencies, this suggests a mean of at least six display interactions per individual per day. No significant difference was seen among these immediately high display frequencies of *A. carolinensis* juveniles in single-species enclosures and *A. carolinensis* and *A. sagrei* juveniles in mixed-species enclosures, nor was there any change over time in display frequencies. Additionally there seems to be no difference in juvenile aggression between species nor between *A. carolinensis* in syntopy with *A. sagrei* and *A. carolinensis* alone. Aggression showed no change over time. Therefore, although direct behavioral interactions might have influenced specific shifts in the space

use of particular individuals, collectively the interaction rate was not linked to group patterns at the neighborhood level as measured by enclosure means. Staged dyadic interactions between *A. carolinensis* aged less than one week and juvenile *A. sagrei* (unpublished data; previous chapter) show *A. carolinensis* as dominant to *A. sagrei* in first encounters almost without exception, further suggesting a limited direct role of aggression in *A. carolinensis* niche shifts. Likewise, observational and experimental studies of aggression between adults has largely discounted the role of direct behavioral interference as a likely factor precipitating or maintaining niche shifts in *A. carolinensis* (Tokarz & Beck 1987; Brown 1988).

In contrast to the correspondence between juvenile and adult patterns in structural niche partitioning, thermal microhabitat partitioning between juvenile *A. carolinensis* and *A. sagrei* occurs according to a pattern opposite that seen in adults. Whether in conspecific or mixed-species enclosures, *A. carolinensis* juveniles maintained a higher difference than did *A. sagrei* juveniles between mean selected microhabitat temperature and mean available microhabitat temperature. In fact, *A. carolinensis* on average selected thermal microhabitat warmer than the mean thermal environment, whereas *A. sagrei* selected thermal microhabitat slightly cooler than the mean thermal environment. This pattern in temperature deviations arose despite *A. sagrei*'s much heavier total use of perch sites on the ground, the region with the consistently highest maximum daily temperatures. Clearly, *A. sagrei* juveniles followed a temporal pattern of space use that allowed them to avoid these maximum temperatures. Adult *A. sagrei*, however, have been described as having mean body temperatures among the highest of any *Anolis* species, exceeding 33 °C when in open Caribbean habitats conducive to active

thermoregulation (Lister 1976). *Anolis carolinensis* adults, while largely heliothermic, appear to have substantially lower body temperatures, with means of approximately 31°C (Licht 1968; Clark & Kroll 1974). Mean absolute selected temperatures of juveniles in this study, although themselves not significantly different, mirror the pattern seen in the temperature deviations. The direction of the difference between juveniles in mean selected temperature is concordant with laboratory measures of preferred temperature (unpublished data; previous chapter) that showed *A. carolinensis* juveniles to select median temperatures over 2.5 °C warmer than those of *A. sagrei* juveniles.

The total volumes of habitat used by *A. carolinensis* and *A. sagrei* juveniles differed substantially, with *A. carolinensis* across enclosure treatments occupying a mean volume almost twice that of *A. sagrei*. This difference was largest in the first week and there was a significant time effect by which occupied habitat volume decreased in the second week of observation. Concomitantly, the proportion of space used exclusively increased significantly as did the proportion of total perch sites on vegetation. Collectively, these results suggest a decrease in exploratory behavior, an increase in site fidelity due to territoriality, or both.

Can these shifts in habitat use between the first and subsequent weeks be related to growth rate and thereby potential fitness? Whether trained on the data from conspecific enclosures alone or that from all enclosures, an information-theoretic model selection routine identified proportion of perch sites on vegetation as the highest magnitude positive effect in the estimated best predictive model of *A. carolinensis* percent change in body mass. Therefore, the contraction of space use onto a volume largely within vegetation rather than in open sites appears adaptive. This conclusion is

also supported by the very large negative effect of the proportion of ground perch sites on change in body mass. This detrimental effect of ground site use seems to arise directly as a result of environment, rather than as a result of increased interaction with *A. sagrei*, since ground use appears in the best predictive models based on both the full set and conspecific only scenarios. Indeed, there was no significant difference in growth rate between *A. carolinensis* in conspecific only enclosures and those in enclosures with *A. sagrei*. Furthermore, number of interactions (although not level of aggression) appears in the estimated best predictive model and is actually positively related to growth rate. Beyond structural microhabitat effects, there is some evidence that thermal microhabitat selection has a small effect on growth rate. Mean selected microhabitat temperature appears as a factor in the estimated second best predictive models and has the positive effect expected in reference to temperature-dependent physiological rates in ectotherms.

In agreement with the results of the present study, similar previous enclosure experiments (Gerber 2000) showed there to be no effect of *A. sagrei* juveniles on the growth of *A. carolinensis* juveniles. These experiments, however, did indicate a strong effect of *A. sagrei* juveniles on *A. carolinensis* survival, but only in habitats of low vegetation density. Furthermore, these experiments linked vegetation density and *A. carolinensis* growth rate even in the absence of *A. sagrei* but showed intraspecific density to reduce growth rate across all vegetation density treatments. In the present study I attempted to establish thermal, moisture, and structural complexity conditions representative of suitable natural *A. carolinensis* habitat and to observe space use and behavior under a total juvenile density within the range typical of populations observed in the field. Under these conditions, and excluding potential predators, I observed

extremely low juvenile mortality within the first three weeks after hatching. The results presented here might, therefore, have failed to capture some potential indirect population-level effects of *A. sagrei* on *A. carolinensis* but should be representative of the typical direct competitive interaction between these species. Enclosure studies can jointly be interpreted as suggesting an omnipresent influence of intraspecific competition on proximal measures of fitness in *A. carolinensis* juveniles and an influence of interspecific competition limited only to those habitats that would be of marginal suitability regardless of congener densities.

In summary, the results of this study suggest that interactions within the juvenile age class are likely not contributing to numerical declines in *A. carolinensis* in the presence of *A. sagrei*. Nevertheless, this study does indicate that inclusion of juvenile interactions is necessary for accurate characterizations of niche partitioning in anoles. Significant niche differences between species were apparent in juveniles, and at least along the thermal microhabitat axis were in a direction opposite to that which would be predicted from data on adult habitat use. Importantly, the shift in mean perch height that was predicted from observations of adult anoles actually occurred within the first week after hatching. Furthermore, since there is a suggested influence of immediate microhabitat selection and frequency of behavioral interaction on growth rate, the juvenile abiotic and social environments could have persistent effects that appear in intra- and interspecific interactions in later age classes.

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Appendix: Chapter 4

Table 4.1. Repeated measures ANOVA results for comparison of groups (*A. carolinensis* in conspecific enclosures, *A. carolinensis* in mixed-species enclosures, and *A. sagrei* in mixed-species enclosures) and times (weeks 1-3). Within-subject (time) test p-values are Geisser-Greenhouse epsilon values correcting for potential non-circularity in covariance. The second row p-values for each variable are those given by table-wise sequential Bonferroni correction. Significant Bonferroni-corrected values are highlighted by bold print.

Variable	Group p-value	Time p-value
Total_pos	0.000002 0.000032	0.000463 0.006482
%Exclusive	0.015367 0.169037	0.000079 0.001185
%Ground	<0.000001 0.000002	0.409329 1.000000
%Vegetation	0.140455 1.000000	0.000514 0.006682
Height	<0.000001 0.000017	0.412218 1.000000
Temperature	0.021313 0.191182	0.021261 0.212610
Temp_diff	0.001007 0.012802	0.660433 1.000000
Interactions	0.782610 1.000000	0.980434 1.000000
Agg_score	0.932874 1.000000	0.957551 1.000000



Figure 4.1. South-facing view of field enclosures. Open centers of enclosure tops are covered by bird netting and perimeters are covered by 80% shade cloth.

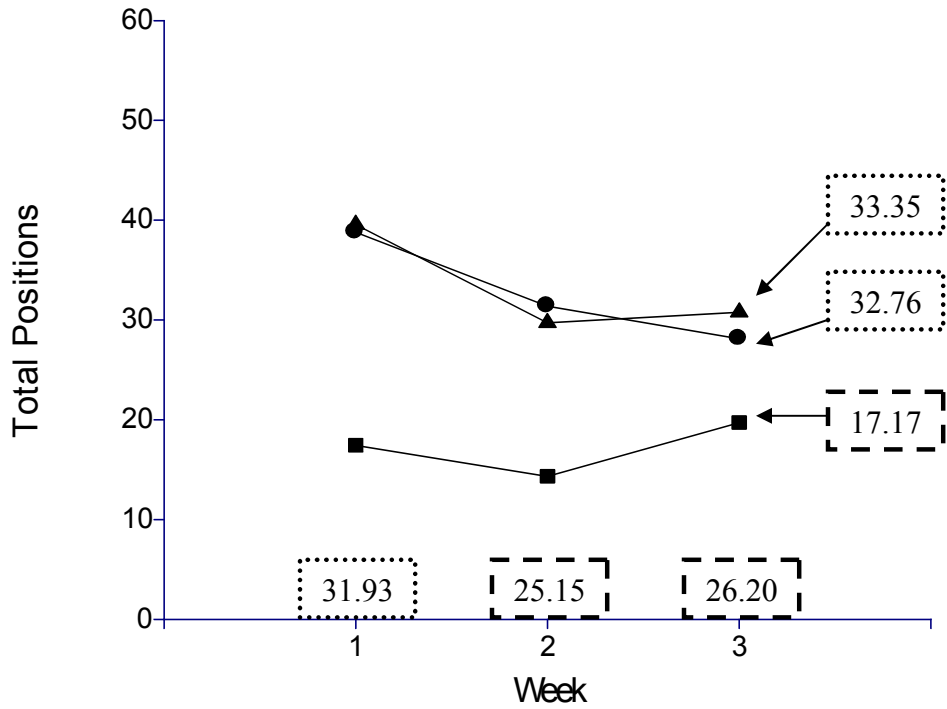


Figure 4.2. Grand mean total number of positions (volumetric units) in which individuals of each group were observed during each week. Means for *A. carolinensis* in conspecific enclosures are shown as circles. Means for *A. carolinensis* in mixed-species enclosures are shown as triangles. Means for *A. sagrei* in mixed-species enclosures are shown as squares. Main-effects factor level means enclosed by different borders are significantly different by Tukey-Kramer multiple comparison test.

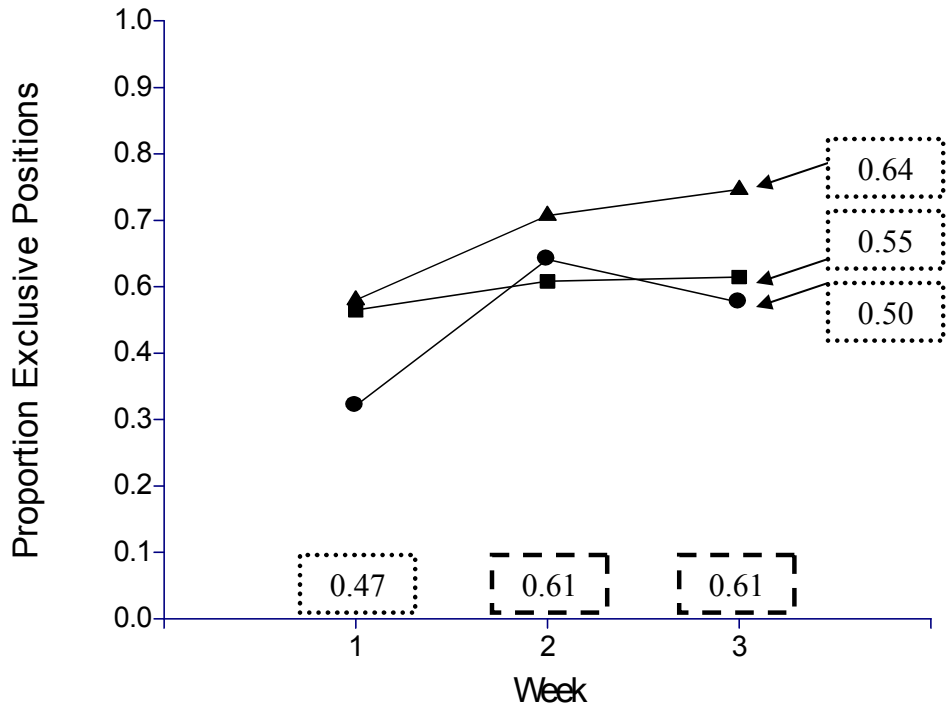


Figure 4.3. Grand mean proportion of total number of positions (volumetric units) in which individuals of each group were observed during each week that were not also occupied by another individual during that week. Means for *A. carolinensis* in conspecific enclosures are shown as circles. Means for *A. carolinensis* in mixed-species enclosures are shown as triangles. Means for *A. sagrei* in mixed-species enclosures are shown as squares. Main-effects factor level means enclosed by different borders are significantly different by Tukey-Kramer multiple comparison test.

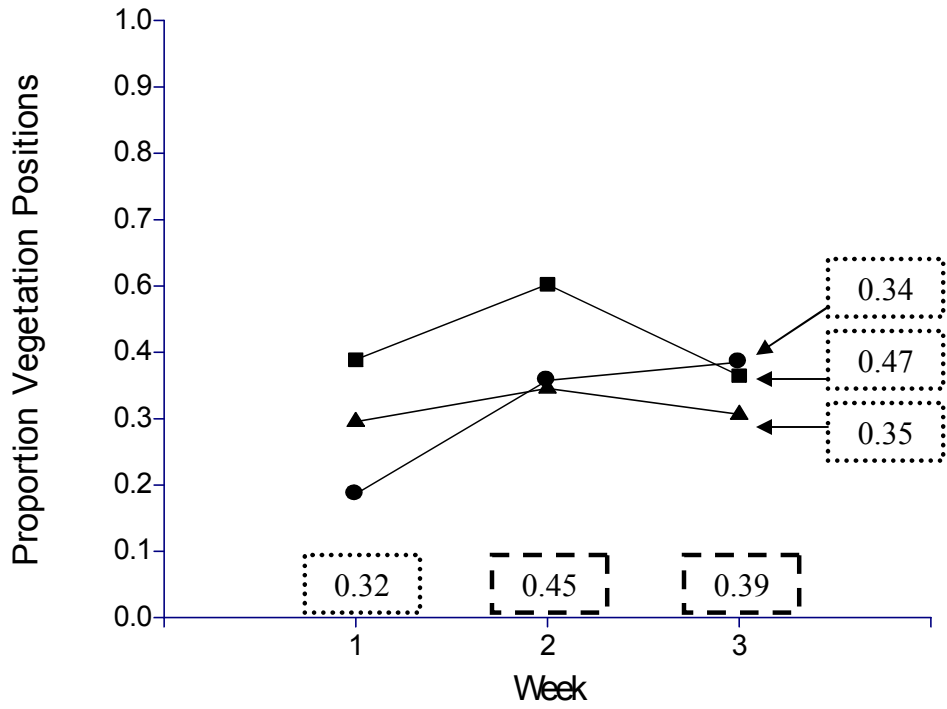


Figure 4.4. Grand mean proportion of total number of positions (volumetric units) in which individuals of each group were observed during each week that were in vegetation. Means for *A. carolinensis* in conspecific enclosures are shown as circles. Means for *A. carolinensis* in mixed-species enclosures are shown as triangles. Means for *A. sagrei* in mixed-species enclosures are shown as squares. Main-effects factor level means enclosed by different borders are significantly different by Tukey-Kramer multiple comparison test.

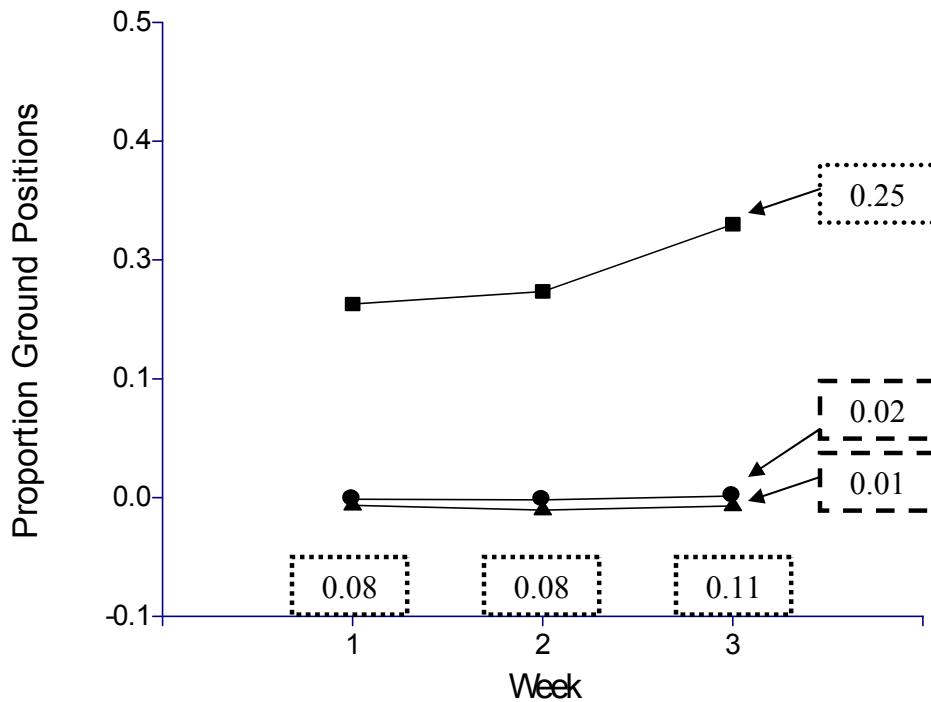


Figure 4.5. Grand mean proportion of total number of positions (volumetric units) in which individuals of each group were observed during each week that were on the ground. Means for *A. carolinensis* in conspecific enclosures are shown as circles. Means for *A. carolinensis* in mixed-species enclosures are shown as triangles. Means for *A. sagrei* in mixed-species enclosures are shown as squares. Main-effects factor level means enclosed by different borders are significantly different by Tukey-Kramer multiple comparison test.

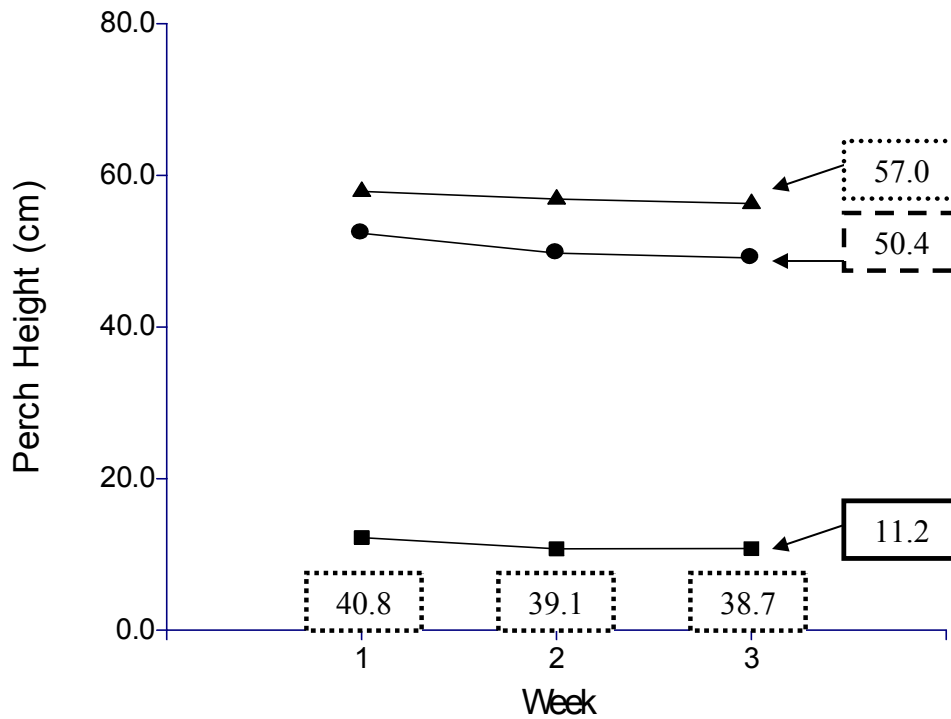


Figure 4.6. Grand mean perch height of individuals of each group during each week. Means for *A. carolinensis* in conspecific enclosures are shown as circles. Means for *A. carolinensis* in mixed-species enclosures are shown as triangles. Means for *A. sagrei* in mixed-species enclosures are shown as squares. Main-effects factor level means enclosed by different borders are significantly different by Tukey-Kramer multiple comparison test.

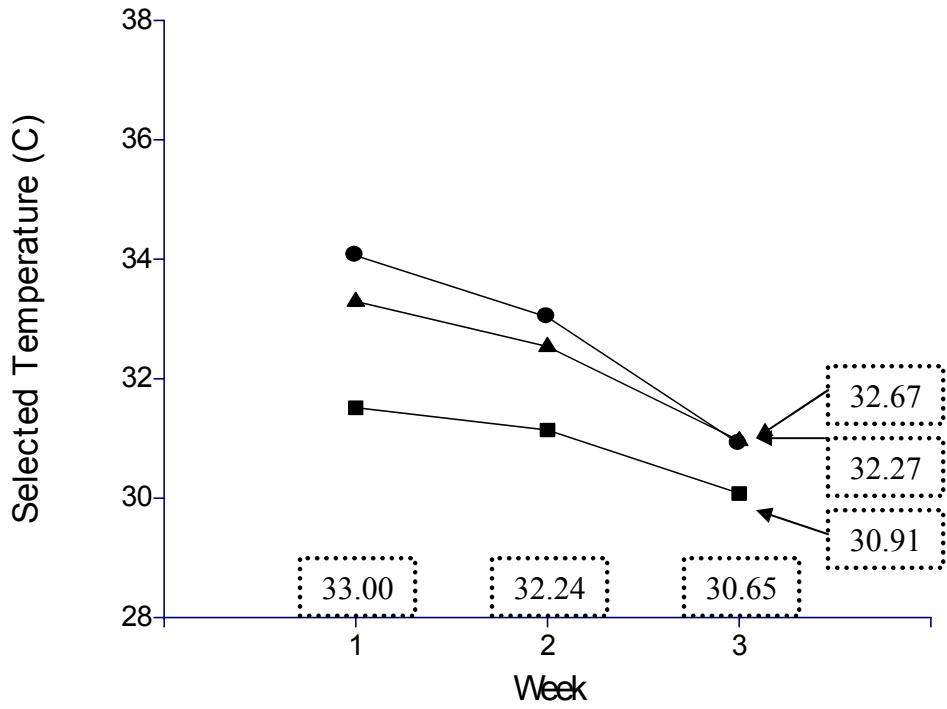


Figure 4.7. Grand mean of environmental temperatures selected by individuals of each group during each week. Means for *A. carolinensis* in conspecific enclosures are shown as circles. Means for *A. carolinensis* in mixed-species enclosures are shown as triangles. Means for *A. sagrei* in mixed-species enclosures are shown as squares. Main-effects factor level means enclosed by different borders are significantly different by Tukey-Kramer multiple comparison test.

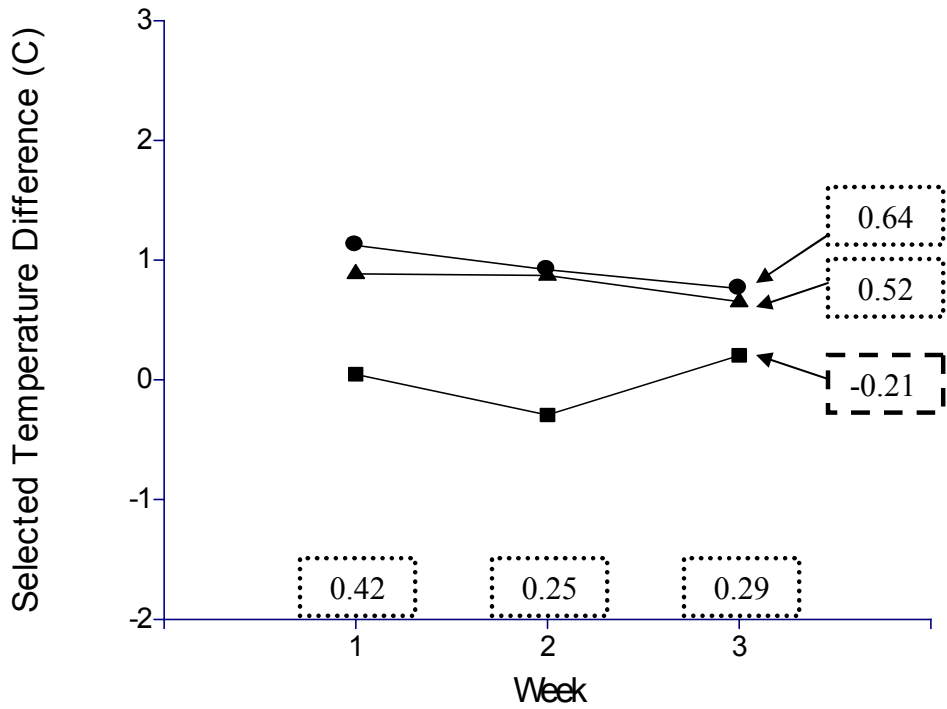


Figure 4.8. Grand mean of differences between selected and available environmental temperatures for individuals of each group during each week. Means for *A. carolinensis* in conspecific enclosures are shown as circles. Means for *A. carolinensis* in mixed-species enclosures are shown as triangles. Means for *A. sagrei* in mixed-species enclosures are shown as squares. Main-effects factor level means enclosed by different borders are significantly different by Tukey-Kramer multiple comparison test.

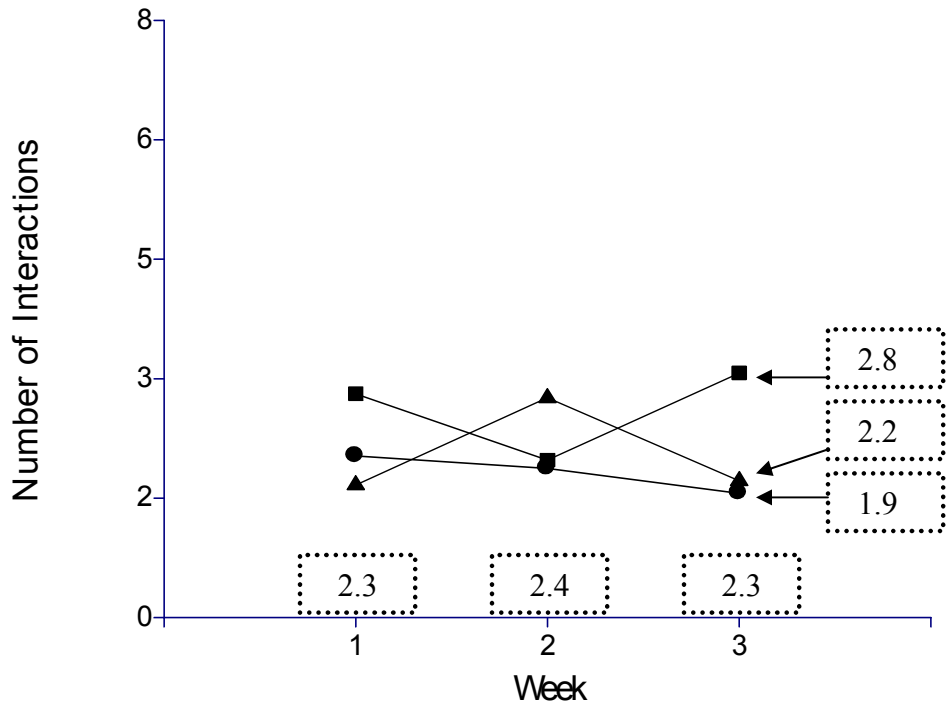


Figure 4.9. Grand mean number of interactions for individuals of each group during each week. Means for *A. carolinensis* in conspecific enclosures are shown as circles. Means for *A. carolinensis* in mixed-species enclosures are shown as triangles. Means for *A. sagrei* in mixed-species enclosures are shown as squares. Main-effects factor level means enclosed by different borders are significantly different by Tukey-Kramer multiple comparison test.

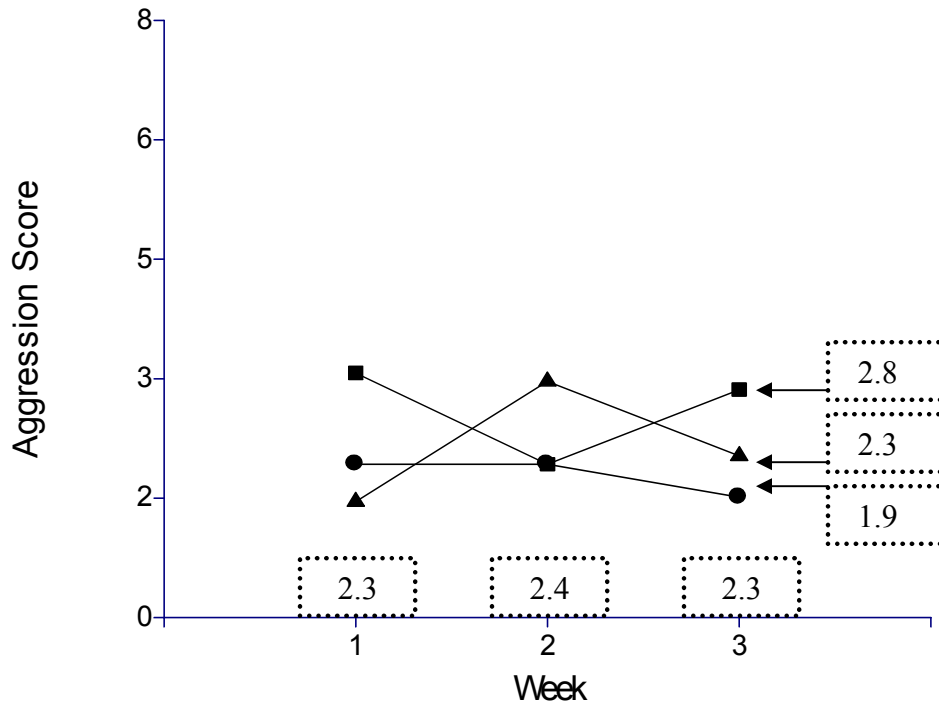


Figure 4.10. Grand mean aggression score for individuals of each group during each week. Means for *A. carolinensis* in conspecific enclosures are shown as circles. Means for *A. carolinensis* in mixed-species enclosures are shown as triangles. Means for *A. sagrei* in mixed-species enclosures are shown as squares. Main-effects factor level means enclosed by different borders are significantly different by Tukey-Kramer multiple comparison test.

Chapter 5

Summary and Conclusions

The ecological influence of introduced *Anolis sagrei* on native *A. carolinensis* in the southeastern United States has been investigated in regard to physiological, behavioral, and ultimate numerical effects. Initially anecdotal links between *A. sagrei* invasion and subsequent rapid declines in *A. carolinensis* density have been supported by experimental replication of the invasion on small islands (Campbell 2000). Sympatry with *A. sagrei* appears to affect *A. carolinensis* in the same way that it affects the closely related and ecologically similar *A. carolinensis* analogs in the eastern Caribbean (Schoener 1975; Schoener & Schoener 1980; Losos & Spiller 1999). Collectively, comparative observational and experimental studies suggest a decrease in density and an exclusion of *A. carolinensis* from open sites and the lowest perches within the vegetation when in sympatry with *A. sagrei* (Campbell 2000; Vincent 2002). Supported mechanisms by which population depression might occur include prey exploitation competition (Campbell 2000), density-dependent reproductive suppression (Vincent 2002), and asymmetric predation on congeneric juveniles (Gerber & Echternacht 2000). Aggression between adult males is of insufficient intensity and opposite direction of asymmetry to indicate any detriment to *A. carolinensis* through interference competition with *A. sagrei* (Tokarz & Beck 1987; Brown 1988).

My investigation of juvenile aggression in staged dyadic encounters (Chapter 3) revealed a pattern similar to that in adults. Most first encounters between juveniles involved display behavior, although *A. carolinensis* was less likely to display towards *A. sagrei* than towards conspecifics. In heterospecific encounters, *A. sagrei* were more likely than *A. carolinensis* to display, but were actually less likely to be dominant, and

almost never displaced *A. carolinensis*. Overall, these data suggest that dominance in juvenile *A. carolinensis* is predicted by whether an individual initiates an interaction and whether the individual with which it interacts is a conspecific. A juvenile *A. carolinensis* initiating an interaction with a juvenile *A. sagrei* has a predicted probability of dominance of over 0.70, whereas an *A. carolinensis* juvenile encountering a conspecific has less than a 0.15 probability of dominance regardless of which individual initiates an interaction. Surprisingly, although body size asymmetry is known to consistently influence dominance in agonistic encounters between adult anoles, there was no strong evidence for an effect of body size in juvenile encounters. This suggests that the observed agonistic advantage of *A. carolinensis* juveniles should hold in nature where the long breeding seasons and high iteroparity of anoles produce juvenile assemblages of variously-sized individuals. Clearly there is also a lesser immediate tendency towards exclusion of conspecifics than of heterospecifics, a disparity that should facilitate *A. carolinensis* juveniles in occupying preferred microhabitat when in sympatry with *A. sagrei*.

Observation of site selection by isolated juvenile anoles on laboratory thermal gradients (Chapter 2) indicated that, controlling for other environmental variables, juvenile *A. carolinensis* will predominantly use warmer microhabitat than *A. sagrei* juveniles. Because juvenile anole body temperatures equilibrate with the temperature of their immediate environment at extremely rapid rates, ready access to sites within the preferred temperature range could be critical. Despite significant differences in the central tendencies of the selected temperature distributions of *A. carolinensis* and *A. sagrei*, the shapes of these distributions describe substantial overlap and show both

species to voluntarily occupy environments of broad temperature range. It appears unlikely, therefore, that species-specific differences among juveniles in the fundamental thermal niche alone are adequate to produce spatial separation of juvenile *A. carolinensis* and *A. sagrei* under natural conditions. Furthermore, given their apparent dominance in dyadic encounters, it would seem unlikely that *A. carolinensis* juveniles would shift thermal microhabitat in response to the presence of *A. sagrei* juveniles.

Neighborhood-level assemblages of juveniles in experimental field enclosures (Chapter 4) exhibited species differences in the use of thermal microhabitat in the directions predicted by the laboratory temperature selection observations, and, indeed, *A. carolinensis* showed no shift in this regard in the presence of *A. sagrei* juveniles. There was, however, an immediate and significant upward shift in mean perch height of *A. carolinensis* juveniles when enclosed with *A. sagrei* juveniles. This result suggests that the characteristic niche shift described for adult *A. carolinensis* in the presence of *A. sagrei*, if not actually due to juvenile interactions, at least appears in similar form among juveniles and arises within the first week of life. In the absence of any apparent direct behavioral exclusion by *A. sagrei*, however, the proximal mechanistic origin of this shift remains unclear, and it remains possible that intraspecific, rather than interspecific, density plays a role. This study does suggest that any further inquiry into this question need address factors acting not only on adults but on the very youngest anoles as well.

In summary, it appears that apparent population displacement of *A. carolinensis* by *A. sagrei* is not influenced by direct interspecific interactions within the juvenile age class. Rather, this study shows juveniles of these species to exhibit significant behavioral and habitat niche differences similar to those characterizing adults, but with thermal

microhabitat preferences potentially differing in direction. Hence, previously demonstrated interspecific effects across age classes, namely predation by adults on juveniles in open habitats (Gerber 2000) and reduced egg production in the presence of *A. sagrei* (Vincent 2002), account for any observed declines in *A. carolinensis* population density. This conclusion is consequential to the ultimate impact of invasive *A. sagrei* because it suggests that in areas of high prey abundance and structural habitat complexity (i.e. undisturbed areas of the southeastern United States) *A. carolinensis* populations will persist and partition resources according to patterns similar those of ecologically analogous *Anolis* on the larger islands of the Carribean.

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