THE EFFECTS OF INTER-AGE CLASS COMPETITION ON HABITAT USE IN A
TERRITORIAL LIZARD

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MASTER OF SCIENCE

ABSTRACT

All organisms have specific habitat requirements that allow them to properly

function in the environment. However, optimal habitats often differ across age classes,

and accordingly, juveniles shift habitat choice as they age. Field observations of the

brown anole lizard (*Anolis sagrei*) suggest that juveniles perch in open-canopy areas on

low vegetation whereas adults reside in forest edges on higher vegetation. I hypothesized

that this age-specific habitat variation is because adults force juveniles to less preferred

habitat. To address these issues, I conducted a series of experiments to examine the role

of inter-age class competition in driving variation in perch use behaviors. In Chapter 1, I

provide a background of relevant literature and briefly discuss the justification and design

of the experiments. In Chapter 2, I altered the density of adult males in mesh enclosures

in the laboratory to examine the response of microhabitat choice by juveniles. I found

that juveniles decreased perch height and had complex density-dependent effects on

perch width and substrate use in the presence of adult males. In Chapter 3, I conducted

two simultaneous field experiments. The first experiment examined how adult male and

female (independently) density affect juvenile microhabitat choice and survival. The

second experiment examined how juvenile presence influences adult microhabitat choice.

I found that high adult male density reduced juvenile survival, yet juveniles did not vary

microhabitat choice in response to either adult male or female density. In addition, adults

did not select against juveniles in a way that would contribute to the observed age-class habitat variation. Neither adult male or female microhabitat choice was influenced by the presence of juveniles. Overall, we show that adults have a sex- and density-dependent effect on juvenile populations. In the lab, we found that juveniles modify microhabitat choice in response to adult males, but we find no evidence for this in the field. This inconsistency in laboratory versus field studies may be explained by the differences of juvenile body size used between experiments (i.e., juveniles in the field experiment were much smaller than those used in the laboratory experiment). Thus, I suggest that the selective pressure from adults and/or other predators is strong enough that hatchlings innately stay low to the ground, whereas larger juveniles are able to shift microhabitat choice plastically depending on environmental context. In addition, juvenile macrohabitat dispersal from areas of high adult male density may contribute to the variation in age-class habitat use.

Keywords: *Anolis*, habitat selection, intraspecific variation, microhabitat

DEDICATION

I would like to dedicate this thesis to my dad, Mike Delaney. I learned how to think about, and developed a passion for, ecology and evolution on our many adventures fishing and hunting. With an understanding of evolution, and enough time in the woods or on the water, life makes a little more sense. Thanks, Dad.

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CHAPTER ONE

BACKGROUND AND JUSTIFICATION

Natural selection should favor individuals that occupy habitats that provide

enhanced performance and satisfy functional requirements (Huey 1991; Lenihan 1999;

Aubret and Shine 2008). However, optimal habitat will vary depending on individual

phenotype (e.g., body size, physiology; Huey 1991; Englund and Krupa 2000) and

environmental context (e.g., level of competition, predation risk; Robertson 1996). For

many organisms, optimal habitats differ across age classes (Dahlgren and Eggleston

2000), and accordingly, individuals shift habitat choice as they age (Stamps 1983; Vagelli

2004; Montgomery et al. 2011). This can be due to age-related differences in resource

needs (Hjelm et al. 2000), predation risks (Foster et al. 1988; Werner and Hall 1988), or

younger individuals may be in direct competition with adults, forcing them to less

preferred habitats. Despite the frequency of ontogenetic habitat shifts for a variety of

taxa, the causal factors driving age specific habitat variation are rarely determined. This

is because most studies document these behaviors using observational approaches rather

than experimentally addressing questions regarding ontogenetic habitat shifts.

Competition for structural habitat has been critical in shaping the adaptive

radiation of the lizard genus *Anolis* throughout the Caribbean (Williams 1983; Losos

2009). Specifically, phylogenetically distant species that use similar microhabitats have

evolved similar morphological (Losos et al. 1998; Beuttell and Losos 1999) and

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ecological (Williams 1972; Losos 1990; Johnson et al. 2008) characteristics. Most notably, species with long limbs perch on thick branches whereas species with short limbs occupy thin branches. This limb length to perch width matching is adaptive, whereby locomotor performance is enhanced on specific branch widths depending upon limb length (Losos and Sinervo 1989; Irschick and Losos 1999). Despite numerous studies on interspecific variation in habitat use in *Anolis* lizards, much less is known about habitat use variation within *Anolis* species. For example, *Anolis aeneus* juveniles occur in open canopy habitats whereas adults reside in more forested areas (Stamps 1983), but it is unknown what drives this variation in age-class habitat use. Understanding niche breadth and the processes that determine a species (rather than just adult) niche are important to fully understand the ecological and evolutionary processes that drive adaptive radiations such as the *Anolis* radiation.

To address these issues, my thesis examined the role of inter-age class competition in generating variation in habitat use behavior in the brown anole lizard (*Anolis sagrei*). This lizard is well suited for addressing these questions for a number of reasons. First, this diurnal lizard often occurs at extremely high densities (Schoener and Schoener 1980; Lee et al. 1989), suggesting competition may influence microhabitat use. Second, *A. sagrei* conspicuously perch on vegetation and have high site fidelity (Schoener and Schoener 1982; Calsbeek 2009). This allows for repeated measurements of microhabitat choice for each individual. Third, field observations suggest that juveniles frequently perch in open-canopy areas on shorter vegetation whereas adults most often reside in forested areas on higher vegetation. These differences in habitat use might be driven by density-dependent interactions between juveniles and adults. For example,

preliminary data demonstrate that juvenile survival is negatively correlated with adult

density, and natural selection on juvenile size is influenced by adult male density (Warner

unpubl.). Indeed, adult *A. sagrei* are cannabalistic on young individuals (Gerber et al.

1999; Cates et al. 2014), although it is unknown how frequently cannibalism occurs.

Thus, not only are adults potential competitors, but they are also predators, which should

place a strong incentive on juveniles to modifiy their behaivors in response to adult

density.

For my thesis research, I conducted a series of experiments that utilized mesh

enclosures that contained artificial trees. These replicate enclosures allowed me to design

treatments that varied in age-class density, while controlling for structural variables. First,

I conducted a laboratory experiment where I altered the density of adult males to test the

response of juvenile microhabitat choice (Chapter 2). Conducting this experiment in the

laboratory allowed me to control for all environmental variables, while altering only the

parameter of interest. Each enclosure contained 6 juveniles and either 0, 1, or 3 adult

males (depending on treatment). Adult males are larger and more territorial than adult

females. Thus, we hypothesized that if age-class competition contributes to habitat use

variation, we would be most likely to observe that with adult males forcing subordinate

juveniles to less preferred habitat.

Following this experiment, I expanded the number of treatments and replication

and conducted two field experiments that occurred simultaneously (Chapter 3).

Conducting these experiments in the field allowed me to assess inter-age class

competition in a more natural setting, yet the field enclosures still allowed me to control

for structural variables. The first field experiment examined how adult male and female

density influence perch use behavior of juveniles, while the second field experiment examined how juvenile presence influences perch use behavior of adults. Each treatment was replicated 6 times for these experiments, enabling a robust assessment of the role of inter-age class competition in driving habitat use behaviors in this territorial lizard.

Natural History of *Anolis sagrei*

The brown anole (*Anolis sagrei*) is native to Cuba and the Bahamas and has been introduced to tropical and subtropical regions around the world (Kolbe et al. 2004). Males and females are dimorphic in body size, dewlap size, and dorsal pattern. Males grow longer (up to 60mm SVL) and heavier, have a considerably larger dewlap, and have a uniformly grey/brown dorsum with darker chevrons running along the mid-dorsum. Females (up to 50mm SVL) have polymorphic dorsal patterns (e.g., diamond or bar shaped) that are typically more conspicuous than male patterns, although the significance of this is unknown.

Anolis sagrei is a generalist in both habitat use and diet. These lizards are trunk-ground ecomorphs, occupying the trunks of trees and the ground, as well as similar anthropogenic habitat. Typical behavior consists of adults basking on tree trunks or low hanging large branches. They detect prey (often on the ground) visually by movement, and then quickly jump and sprint towards it. The prey is then bit and quickly consumed (e.g., see Delaney et al. 2014). Invertebrates are the majority of the prey, but adults occasionally consume small vertebrates such as young *Anolis carolinensis* and conspecific *Anolis sagrei* (Gerber and Echternacht 2000).

Females lay 1 egg clutches every 7 – 10 days through the reproductive period which lasts from about April to October in Florida (Lee et al. 1989). Eggs are laid under cover objects or in leaf litter (Delaney et al. 2013). Hatchlings emerge around 18mm SVL. Both hatchlings and adults are prey to a variety of predators including invertebrates (Spiller and Schoener 1990), conspecifics (Gerber et al. 1999; Cates et al. 2014), other lizards (Schoener et al. 1982), snakes (Calsbeek and Cox 2010), birds, and likely mammals.

Broader Implications

The diversification of the lizard genus *Anolis* is one of the best studied terrestrial radiations. However, we know very little about the role of juveniles in these communities. These experiments provide a comprehensive look at how inter-age class competition can influence how juveniles position themselves in the environment, and how adults can drive population dynamics. Understanding niche breadth and the processes that determine a species (rather than just adult) niche will provide more insight into the ecological and evolutionary processes that drive adaptive radiations such as the *Anolis* radiation.

REFERENCES

Aubret, F., and Shine, R. 2008. Early experience influences both habitat choice and locomotor performance in tiger snakes. The American Naturalist 171:524-531.

Beuttell, K., and J.B. Losos. 1999. Ecological morphology of Caribbean anoles. Herpetological Monographs 13:1-28.

Calsbeek, R. 2009. Sex-specific adult dispersal and its selective consequences in the brown anole, *Anolis sagrei*. Journal of Animal Ecology 78:617-624.

Calsbeek, R., and R.M. Cox. Experimentally assessing the relative importance of predation and competition as agents of selection. Nature 465:613-116.

Cates, C.D., D.M. Delaney, A.M. Buckelew, A.M. Durso, S.S. French, A.M. Reedy, and D.A. Warner. 2014. *Anolis sagrei* (Brown Anole). Cannibalism. Herpetological Review 45:491

Dahlgren, C.P., and D.B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81(8):2227-2240.

Delaney D.M., A.M. Reedy, T.S. Mitchell, A.M. Durso, K.P. Durso, A.J. Morrison, and D.A. Warner. 2013. *Anolis sagrei*. Nest-site choice. Herpetological Review 44(2):314.

Delaney D.M., C.D. Cates, A.M. Buckelew, D.M. Delaney, A.M. Durso, S.S. French, A.M. Reedy, and D.A. Warner. 2014. *Anolis sagrei*. Prey stealing behavior. Herpetological Review 45(2):324-325.

Englund, G., and Krupa, J. J. 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size. Freshwater biology 43:75-83.

Foster, S.A., V.B. Garcia, and M.Y. Town. 1988. Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. Oecologia 74(4):577-585.

Gerber, G.P., 1999. A review of intraguild predation and cannibalism in *Anolis*. Anolis Newsletter 05:28-39.

Gerber, G. P., and Echternacht, A. C. 2000. Evidence for asymmetrical intraguild predation between native and introduced *Anolis* lizards. Oecologia 124(4):599-607.

Hjelm, J., L. Persson, and B. Christensen. 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. Oecologia 122(2):190-199.

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist 137:S91-S115.

Irschick, D.J., and J.B. Losos. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. The American Naturalist 154(3):293-305.

Johnson, M.A., M. Leal, L. Rodriguez Schettino, A. Chamizo Lara, L.J. Revell, and J.B. Losos. 2008. A phylogenetic perspective on foraging mode evolution and habitat use in West Indian Anolis lizards. Animal Behaviour 75:555-563.

Kolbe, J. J., Glor, R. E., Schettino, L. R., Lara, A. C., Larson, A., and Losos, J. B. 2004. Genetic variation increases during biological invasion by a Cuban lizard. Nature 431(7005):177-181.

Lee, J. C., Clayton D., Eisenstein, S., and I. Perez. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. Copeia 1989:930–937.

Lenihan, H. S. 1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. Ecological Monographs 69:251-275.

Losos, J.B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. Univ. of Calf. Press.

Losos, J.B. 1990. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. Animal Behaviour 39(5):879-890.

Losos, J.B., and B. Sinervo. 1989. The effects of morphology and perch diameter on sprint performance of Anolis lizards. Journal of Experimental Biology 145(1):23-30.

Losos, J.B., T.R. Jackman, A. Larson, K. de Queiroz, and L. Rodríguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279(5359):2115-2118.

Montgomery, C.E., K.R. Lips, and J.M. Ray. 2011. Ontogenetic Shift in Height of Sleeping Perches of Cope's Vine Snake, *Oxybelis brevirostris*. The Southwestern Naturalist 56(3):358-362.

Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology 885-899.

Schoener, T. W., and Schoener, A. 1980. Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. The Journal of Animal Ecology 49:19-53.

Schoener, T. W., and Schoener, A. 1982. Intraspecific variation in home-range size in some *Anolis* lizards. Ecology 63:809-823.

Schoener, T. W., Slade, J. B., & Stinson, C. H. 1982. Diet and sexual dimorphism in the very catholic lizard genus, *Leiocephalus* of the Bahamas. Oecologia 53(2):160-169.

Stamps, J.A. 1983. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). Behavioral Ecology and Sociobiology 12(1):19-33.

Vagelli, A.A. 2004. Ontogenetic shift in habitat preference by *Pterapogon kauderni*, a shallow water coral reef apogonid, with direct development. Journal Information 2004(2):364-369.

Werner, E. E., and D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69(5):1352-1366.

Williams, E.E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. Evolutionary Biology 6:47-89.

Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pp. 326–370 in R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), Lizard ecology: studies of a model organism. Harvard University Press, USA.

CHAPTER TWO

ADULT MALE DENSITY INFLUENCES JUVENILE MICROHABITAT USE IN THE
BROWN ANOLE (*ANOLIS SAGREI*)

by

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Format adapted for thesis

ABSTRACT

Habitat choice often has strong effects on organism performance and fitness. For many animals, optimal habitats differ across age classes, and individuals shift habitat choice as they age. Although many studies have documented ontogenetic habitat shifts for various taxa, most are observational and thus cannot identify the causal factor of size-specific habitat variation. Field observations of the brown anole lizard (*Anolis sagrei*) suggest that juveniles perch in open-canopy areas on shorter vegetation whereas adults reside in forested areas on higher vegetation. We hypothesized that this variation is due to adult males forcing smaller juveniles to less preferred habitat. Thus, we manipulated adult male densities in mesh enclosures with artificial trees to examine the response of juvenile microhabitat choice. We found that adult male density had strong effects on juvenile perch height, perch width, and substrate use, suggesting that inter-age class competition contributes to the observed ontogenetic differences in habitat choice in the field. We also found that time of day significantly affected juvenile perch height and substrate use. In many cases, our results suggest that juveniles actively distance themselves from adults by using different microhabitats from those used in our control "no-adult" treatment. However, these findings were often body-size dependent, and varied depending upon time of day. This study highlights the complexity of juvenile perching behavior and demonstrates the role of intra-specific interactions in shaping habitat use by juvenile animals.

INTRODUCTION

All organisms have specific habitat requirements that allow them to properly

function in their environment (Huey 1991; Lenihan 1999; Aubret and Shine 2008). For

mobile organisms, behavioral choices of suitable microhabitat are ecologically important

and should be under strong natural selection (Munday 2001; King et al. 2006). However,

habitat choice behaviors will vary depending upon environmental context (e.g., level of

competition; Robertson 1996) or individual phenotype (e.g., physiology, body size;

Schlosser 1987; Huey 1991; Englund and Krupa 2000;). Moreover, choosing an

appropriate habitat often represents a tradeoff between benefits (e.g., mating or foraging

opportunities) and costs (e.g., predation risk, metabolic costs) (Mittelbach 1981; Gilliam

and Fraser 1987; Lima et al. 2005). Thus, different environmental situations should

influence the behavioral choice of microhabitat and/or affect the way natural selection

operates on this behavior.

Optimal habitats are not necessarily the same for individuals of different age

classes (Dahlgren and Eggleston 2000), and accordingly organisms shift their habitat

choice as they age (Stamps 1983; Shine et al. 2003; Vagelli 2004; Montgomery et al.

2011). Many factors are responsible for ontogenetic shifts in habitat choice. For example,

smaller and younger individuals often have different energetic demands than larger

adults, and therefore young and adults may be spatially separated due to differences in

available resource types across habitats (Hjelm et al. 2000). In addition, younger

individuals are often more vulnerable to predation than adults because of their smaller

size and inexperience (Foster et al. 1988; Werner and Hall 1988). As a result, younger

age classes often reside in habitats that more effectively reduce their predation risk

(Foster et al. 1988; Werner and Hall 1988). In other cases, younger individuals may be in direct competition over space with larger adults, and might adjust their habitat choice accordingly. Such an effect may become even more pronounced in species that are highly territorial and/or occasionally exhibit cannibalism.

Competition for microhabitat has been critical in shaping the adaptive radiation of the lizard genus *Anolis* (Williams 1983; Losos 2009), particularly for species that inhabit the Caribbean Islands. Specifically, phylogenetically-distant species that occupy similar microhabitats have evolved similar morphological (Losos et al. 1998; Beuttell and Losos 1999), as well as behavioral and ecological characteristics (Williams 1972; Losos 1990; Johnson et al. 2008). Species which occupy similar niches on different islands are grouped by their ecomorphologies, whereby their morphologies are specialized for the specific spatial niche they fill. For example, species that occupy habitats with narrow perches have evolved short limb lengths, and those that occupy habitats with wider perches have longer limbs (Williams 1983; Losos 2009). Performance studies show that limb length is adaptively matched to the specific perch structure that each species occupies (Losos and Sinervo 1989; Irschick and Losos 1999). This adaptive limb length evolution is well studied and has arisen many independent times in *Anolis* species throughout the Caribbean (Losos 2009). Remarkably, this same ecomorphological diversification seen across species is reflected across populations of a single species (*Anolis sagrei*; Losos et al 1997).

Habitat structure has clearly played an important role in the diversification of the *Anolis* genus. Moreover, interspecific competition for perches has likely contributed to the spatial partitioning of niches observed in *Anolis* lizards that occur sympatrically

(Pacala and Roughgarden 1982; Salzburg 1984; Stuart et al. 2014). Despite this, however, the effects of intraspecific competition among age classes on behavioral choices of microhabitat are poorly understood. For example, microhabitat differences between juvenile and adult *A. aeneus* have been documented (Stamps 1983), but it is unknown what drives this variation in habitat use. Individuals of different age classes may select different microhabitats to reduce competition and therefore partition resources or one age class may force another to less desirable habitat (Schoener 1974; Polis 1984).

The brown anole lizard (*Anolis sagrei*) is well suited for addressing this issue. First, this diurnal lizard often occurs at extremely high densities (Schoener and Schoener 1980; Lee et al. 1989), suggesting that competition may play a role in habitat use. Second, *A. sagrei* conspicuously perch on vegetation and have high site fidelity (Schoener and Schoener 1982; Calsbeek 2009). This facilitates repeated measurements of microhabitat choice for a given individual. Third, preliminary data (Warner unpubl. data) demonstrate that juvenile survival is negatively related to adult density, suggesting that adults might be an important factor that influences juvenile behavior. This finding suggests significant density-dependent competition between age classes. Indeed, juvenile and adult age classes differ in microhabitat choice in the field; juveniles are found on thinner, lower vegetation, whereas adults are more frequently encountered on thicker, higher vegetation (pers. obs.), possibly due to adult males forcing subordinate juveniles to less preferred microhabitats. Fourth, adult *A. sagrei* occasionally cannibalize young individuals (Gerber et al. 1999; Cates et al. 2014). Thus, not only are adults potential competitors, but they are also predators, which should place a strong incentive on juveniles to modifiy their behaivors in response to adult density. Lastly, because these

lizards thrive in laboratory environments and perform normal behaviors, studies of direct effects of adults on juvenile behaviors are feasible in controlled laboratory experiments.

We conducted a laboratory study to experimentally examine the response of juvenile microhabitat choice to variation in adult male density in *A. sagrei*. In the presence of adult males, we predicted that (1) juveniles would choose lower perches because adults typically occupy high perches to patrol territories; (2) juveniles would choose thinner perches because these narrow perches are rarely occupied by adults; (3) juveniles would be forced off preferred perch substrates (e.g., trunk of tree, horizontal branch, leaf) because adults would outcompete juveniles for those substrates. We also recorded these behaviors during each morning, midday, evening, and night to determine if juveniles alter their behavior throughout the day.

METHODS

Sixty-six *Anolis sagrei* were collected in Flagler County, Florida during October 2013 and transported to the University of Alabama at Birmingham. Lizards were randomly and equally distributed across 9 commercially-available butterfly cages (0.61m x 0.61m x 1.83m; Carolina Biological Supply Co.) constructed of a PVC pipe frame and covered with mesh. Each cage received 2 crickets per lizard twice per week and cages were misted with water daily. A wide range of cricket sizes was provided due to multiple size-classes of lizards in each cage. Ultraviolet reptile lights (Reptisun 5.0 UVB and Tropic Sun 5500K Daylight bulbs from Zoo Med Laboratories Inc.) were placed above each cage and lizards were kept on an 11 hour light – 13 hour dark cycle (lights on at

0700h, off at 1800h). These conditions were kept until the start of the experiment on 18

January 2014.

Experimental Design

On 18 January 2014, all lizards were captured from the enclosures. We measured

snout-vent length (SVL) and tail length (TL) to the nearest mm and mass to the nearest

0.1g. Sex was determined by dorsal pattern and the presence or absence of enlarged post

cloacal scales found on males. Toes were clipped to uniquely mark each individual.

Permanent markers were used to write numbers on the lateral surfaces of each lizard so

they could be visually identified while in the enclosures. Lizards were then randomly

assigned to one of three treatments which varied by the density of adult males; each

treatment had three replicate cages. Each cage contained 6 juvenile lizards and either no

adults (control treatment), one adult male (low-adult density treatment), or three males

(high-adult density treatment) depending on treatment. Although sexual maturity has

been documented to occur at 39mm SVL for males and 34mm SVL for females in

Florida (Lee et al. 1989), we defined lizards ≤ 42mm SVL as juveniles and used adults >

44mm SVL.

Each enclosure contained an artificial tree (~ 1.83m tall) with horizontal perches

that varied in height (42cm, 84cm, 126cm, and 168cm) and width diameter (0.32cm,

0.64cm, 1.27cm, 1.90cm, and 2.54cm) with an artificial leaf glued to the distal end (Fig.

1). Wooden fence posts were used as the trunk of each tree, and horizontal perches were

constructed from 15 cm long dowel rods (branches) that were attached perpendicularly

into the trunk. Perches were radially-arranged (spaced ~5cm intervals) around the trunk,

and the order of the 5 perch diameters was random at each of the 4 heights so that each

height contained perches of each of the five diameters. The floor of each cage was covered with linoleum (0.61m x 0.61m) to prevent the tree from tearing holes in the mesh, and to catch feces. Blinds with small holes cut at various heights were hung so that an observer was able to approach and record behaviors without disturbing lizards. Blinds were also placed between cages so that lizards could not see or interact with lizards from another cage.

Juveniles were placed inside enclosures on 19 January 2014, and allowed two days to acclimate before observations began. Perch height, width, and substrate (i.e., trunk, branch, leaf, base of tree, floor, or other parts of the enclosure) were recorded at four different times each day (i.e., morning – 0800-1000h, midday – 1230-1400, evening – 1600-1730, and night – 1900-2300) during 3 different observation periods. During period 1 we recorded behaviors of juvenile lizards for 7 days in the absence of adults. Adults were then released into enclosures in the low- and high-adult density treatments on 27 Jan 2014. During period 2 we recorded behaviors of juvenile and adult male lizards during the first 8 days following adult introduction. During period 3 we recorded behaviors of juvenile and adult male lizards for 7 days beginning 46 days after adult introduction. During all observation periods, we also recorded behaviors of juveniles in the control enclosures (i.e., no adults present). This design allowed us to examine the change in juvenile perch behaviors immediately after the introduction of adults, and if those behaviors persist after 46 days.

Statistical Analyses

All analyses were performed with SAS software (version 9.3). All statistical tests described below were performed with mixed model analyses using individual ID nested within cage as a random effect.

To test if adults and juveniles chose different perch heights overall, we used a mixed model analysis of variance (ANOVA) with height as the dependent variable and age class as the independent variable. Subsequent analyses of perch height focused only on juvenile behavior. To assess the effects of adult male density on juvenile perch height, we used a mixed model ANOVA with height as the dependent variable and treatment, period, time-of-day (TOD), SVL (covariate), and all 3-way interactions as independent variables. Thus, a treatment x period interaction would test whether the introduction of adults altered juvenile perch height.

To assess the effects of adult male density on juvenile perch width, we calculated the percent of observations an individual was observed on a given perch width. We then used those calculated values (arcsin transformed) as the dependent variable in a mixed model ANOVA. We used perch width, treatment, period, TOD, SVL (covariate), and their interactions as independent variables. Period was not significant in any models; therefore, we removed period 1 (when no adults were present in any treatments) and re-ran the analyses. Time of day was also not significant and was removed from the final model.

To assess the effects of adult male density on juvenile substrate use, we calculated the percent of observations an individual was observed on a given substrate and divided that value by the area available for that substrate. We then used those area-adjusted

values (arcsin transformed) as the dependent variable in a mixed model ANOVA. We used substrate, treatment, period, TOD, SVL (covariate), and their interactions as independent variables.

RESULTS

Perch Height

Adult lizards perched higher than juvenile lizards ($F_{1,1998}$ = 13.07, P = 0.0003; Fig. 2a). Juvenile perch height decreased over time in all treatments (period effect), and this change occurred rapidly when adult males were present (period x treatment; Table 1), particularly in the treatment with three adult males (Fig. 2b). Overall, large juveniles perched higher than small juveniles (P < 0.0001). Small juveniles decreased their perch height over time, whereas large juveniles varied little over time (SVL x period, Table 1; Fig. 3). This pattern was most pronounced in treatments with no adult males and 3 adult males (SVL x period x treatment, Fig. 3). The relationship between SVL and perch height varied little across time of day during daylight hours (i.e., morning, midday, and evening), but at night the slope of this relationship decreased significantly, such that perch height decreased for large juveniles and increased for small juveniles compared to perch heights used during the day (Table 1; supplementary Fig. 1).

Perch Width

All perch widths were used about equally by juvenile lizards when no adults were present, but juveniles used wider perches more frequently when one adult male was present (Table 1). Juveniles that were exposed to three adult males perched more

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frequently on two of the perches of intermediate width than on extremely narrow or wide

perches or middle perch width (Fig. 4). Time of day had no effect on the use of perches

of different widths ($F_{3,646} = 0.30$, $P = 0.8223$).

Substrate Use

Adults used the trunk of the tree during 27.8% of observations while juveniles

used the tree trunks in only 16.3% during daytime observations. Juvenile lizards had a

strong preference for branches and leaves (Table 1; Fig. 5a). Thus, our subsequent

analyses of substrate use focused primarily on these two substrate types. Juveniles

increased leaf use from period 1 to 2 and then dropped back to levels similar to period 1

during period 3. However, juveniles continually increased leaf use over time when one

male was present and decreased leaf use when three males were present ($F_{4,494} = 3.43$, $P

= 0.0089$; Fig. 5b). Density of adult males did not affect juvenile branch use ($F_{4,494} =

0.44$, $P = 0.7767$). The use of leaves, branches and the tree trunk increased with SVL,

whereas the use of the tree base and other parts of the enclosure tended to decreased with

SVL. The increase in leaf use with SVL was most pronounced during night time hours

(Table 1; Supplementary Fig. 2).

DISCUSSION

Competition for habitat has been an important driver of the diversification of the

Anolis genus throughout the Caribbean (Losos 2009). While many studies have examined

interspecific variation in habitat use in *Anolis*, relatively few studies have looked at

intraspecific variation. In addition, most studies on habitat use by different size classes

are observational and thus cannot identify the causal factors of this variation. To address these issues, we experimentally altered the density of adult male *A. sagrei* in laboratory enclosures to examine the response of juvenile microhabitat choice. We hypothesized that adult male density would influence juvenile perch height, perch width, and substrate use. Indeed, we found that juvenile perch height was negatively associated with adult density, and that adult density had unpredicted and complex effects on the use of different perch widths and substrate types.

Perch Height

The density of adult males significantly affected juvenile perch height in a direction consistent with our prediction. Although, perch height decreased over time in all treatments, this decrease happened rapidly (i.e., over 8 days) when adult males were present and persisted for a longer time period (i.e., over the entire experiment) when 3 adult males were present. This decrease in height should increase the distance between adults and juveniles, thus reducing physical interactions. This type of habitat partitioning might benefit juveniles by reducing competition with, and potentially cannibalism by, adult males (Alford and Crump 1982; Hines et al. 1987). We also found that small juveniles decreased their perch height more than large juveniles. A plausible explanation for this size-specific behavior could involve the greater risk of injury or cannibalism in smaller individuals.

In addition to their plastic behavioral response, the threat of predation by adults or other potential predators may be strong enough that juveniles innately stay lower to the ground to avoid risks associated with higher perches. Indeed, behaviors that have been

shaped by selection (e.g., antipredator behaviors) can persist even in the absence of an immediate selective agent (e.g., in the laboratory; Coss 1991; Lahti et al. 2009). Also, performance may be enhanced at heights differentially based on lizard size. For example, there may be more appropriately sized prey near the ground for smaller lizards to forage more efficiently. Such partitioning of habitat to increase foraging efficiency has been suggested for a variety of animals, including insects (Giller and McNeill 1981), fish (George and Hadley 1979; Werner and Hall 1979; Paine et al. 1982; Winemiller 1989; Hyndes et al. 1997), amphibians (Werner et al. 1995), reptiles (Lind and Welsh Jr. 1994), birds (Hunt and Hunt 1973; Davoren et al. 2003), and mammals (Theberge and Wedeles 1989; Kotler et al. 1993; Jones et al. 2001). In our study, however, most prey items remained on or near the floors of the enclosures, yet the height partitioning persisted.

Time of day also had significant effects on perch height. Perch height during daylight observations was fairly consistent. However, larger lizards decreased perch height and smaller lizards increased perch height at night. Smaller juveniles may increase perch height at night to avoid ground dwelling predators, which has been suggested of Amazonian snakes (Martins 1993). Rat predation has also been found to reduce populations of lizard species that occupy the ground at night on islands offshore of New Zealand (Whitaker 1973; McCallum 1986). Thus, microhabitat choice at night may be driven by predation risk rather than competition.

Perch Width

We predicted that juveniles would choose thin perches in the presence of adults because adults would occupy the thick perches and force smaller juveniles to thinner

perches. Although, treatment had significant effects on juvenile perch width use, it was not in the predicted direction. Instead, juveniles selected relatively thick perches in the presence of 1 adult male, and had high use for two of the perches with intermediate widths (0.64cm and 1.90cm) in the presence of 3 adult males. Although juveniles may perform better than adults on thin perches, juvenile performance may still be better on relatively thick perches, thereby allowing them to flee more effectively from adults. Indeed, *Anolis* lizards choose perch widths that enhance sprinting performance (Irschick and Losos 1999), and thicker perches enhance sprint speed (Losos and Sinervo 1989; Losos and Irschick 1996). Perch diameter has also been shown to influence whether anoles sprint or jump when escaping predators (Losos and Irschick 1996), which may be important when adult males are present. When three adult males were present, perch availability for juveniles may have decreased due to the greater amount of space that adults occupy. The observed erratic use of perch widths in the presence of three adult males may be a result of the complexity of interactions occurring within this treatment. For example, competitive interactions likely occurred between the 3 adult males, between the 6 juveniles, and between the age-classes. Such complexity of competitors and predators can lead to complex partitioning of the environment (Schoener 1968; Toft 1985).

Substrate Use

Overall, juveniles had a strong preference for perching on leaves and branches. Although branch use did not vary with adult male density, leaf use was significantly affected but not necessarily in the direction that we predicted. Juvenile leaf use increased over time in the presence of one adult male, but decreased when three adult males were

present. Because adults used the trunk of the tree more often than juveniles, the juveniles

may have shifted their microhabitat choice towards the periphery of the tree (i.e., the

leaves) which would increase their distance from adult males. However, this explanation

does not hold when three adult males were present, as leaf use decreased with greater

density of adult males. In this case, juveniles may have been forced completely off the

tree and onto less preferred substrates when adult density was relatively high. Indeed,

young animals often disperse away from areas of high larger-individual density to reduce

competition and/or cannibalism (Moksnes et al. 1997; Matthysen 2005).

Snout-vent length also had significant effects on substrate use. Large juveniles

were more frequently observed using leaves, branches, and the trunk than smaller

juveniles, whereas small juveniles more frequently used the base of the tree, and other

parts of the enclosure than large juveniles. These findings suggest that large juveniles

used the overall more preferred substrates (i.e., leaves and branches) more often than

small individuals. This pattern may be driven by intra-age-class competition for substrate

use, which larger juveniles out competed smaller individuals for preferred substrates.

Another plausible explanation is that small juveniles perceive adults as a greater threat

than large juveniles, and thus shift to less-preferred substrates. These interpretations are

supported by previous studies that demonstrate that agonistic encounters are typically

won by larger individuals (Caldwell and Dingle 1979; O'Neill 1983; Tokarz 1985;

Schuett 1997), and that small individuals avoid confrontation (Cooper and Vitt 1987; Van

Buskirk 1992; Schuett 1997). Competition between size- and age-classes can be complex

with competition occurring not just between adults and juveniles, but also between

juveniles of different sizes (Van Buskirk 1992; Claessen et al 2000). This is especially

important for animals which have long egg reproductive seasons, which can generate substantial variation in body size of young produced in a single year (e.g., *Anolis sagrei*). Thus, timing of hatching may influence habitat use and have important fitness consequences (Olsson and Shine 1997; Warner and Shine 2007; Wapstra et al. 2010).

Time of day also significantly affected juvenile substrate use. Although juveniles perched on substrates at similar frequencies during daylight hours, they reduced trunk and branch use and increased leaf use at night. Increased leaf use at night has been documented for several *Anolis* species (Clark and Gillingham 1990; Chandler and Tolson 1990; Vitt et al. 2002; Singhal et al. 2007). Perching on hard substrates such as the trunk and branches likely reduces the ability to sense vibrations from approaching nocturnal predators. For example, blunthead tree snakes (*Imantodes cenchoa*; Vitt et al. 2002) and Grenadian tree boas (*Corallus grenadensis*; York et al. 2003) forage from trees other than those the prey is perched on, presumably to reduce vibrations the prey can sense.

Conclusion

Our objectives were to identify a potential driver of variation in habitat use by juvenile *Anolis sagrei*. We show that adult male density had strong effects on juvenile microhabitat choice in terms of perch height, perch width, and substrate use. We also show that TOD significantly influenced juvenile perch height and substrate use. In many cases, our results suggest that juveniles actively distance themselves from adults by using different microhabitats from those used in our control "no-adult" treatment. However, these findings were often body-size dependent, and varied depending upon time of day. This study highlights the complexity of juvenile perching behavior and demonstrates the

role of intra-specific interactions in shaping habitat use by juvenile animals. Although data from free ranging lizards or manipulations in the field will provide greater ecological relevance, experimental designs in the laboratory, such as this study, offer an insightful approach for understanding the factors responsible for how organisms use their environment.

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REFERENCES

Alford, R. A., and Crump, M. L. 1982. Habitat partitioning among size classes of larval southern leopard frogs, *Rana utricularia*. Copeia 1982:367-373.

Aubret, F., and Shine, R. 2008. Early experience influences both habitat choice and locomotor performance in tiger snakes. The American Naturalist 171:524-531.

Beuttell, K., and J.B. Losos. 1999. Ecological morphology of Caribbean anoles. Herpetological Monographs 13:1-28.

Caldwell, R. L., and Dingle, J. 1979. The influence of size differential on agonistic encounters in the mantis shrimp, *Gonodactylus viridis*. Behaviour 69(3):255-264.

Calsbeek, R. 2009. Sex-specific adult dispersal and its selective consequences in the brown anole, *Anolis sagrei*. Journal of Animal Ecology 78:617-624.

Cates, C.D., D.M. Delaney, A.M. Buckelew, A.M. Durso, S.S. French, A.M. Reedy, and D.A. Warner. 2014. *Anolis sagrei* (Brown Anole). Cannibalism. Herpetological Review 45:491

Clark, D.L., and Gillingham, J.C. 1990. Sleep-site fidelity in two Puerto Rican lizards. Animal Behaviour 39:1138-1148.

Chandler, C.R., and Tolson, P.J. 1990. Habitat use by a boid snake, *Epicrates monensis*, and its anoline prey, *Anolis cristatellus*. Journal of Herpetology 24(2):151-157.

Cooper Jr, W. E., and Vitt, L. J. 1987. Deferred agonistic behavior in a long-lived scincid lizard *Eumeces laticeps*. Oecologia 72(3):321-326.

Coss, R. G. 1991. Context and animal behavior III: the relationship between early development and evolutionary persistence of ground squirrel antisnake behavior. Ecological Psychology 3(4):277-315.

Dahlgren, C.P., and D.B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81(8):2227-2240.

Davoren, G. K., Montevecchi, W. A., and Anderson, J. T. 2003. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. Marine Ecology Progress Series 256:229-242.

Einum, S., Sundt-Hansen, L., and Nislow, K.H. 2006. The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. Oikos 113(3):489-496.

Englund, G., and Krupa, J. J. 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size. Freshwater biology 43:75-83.

Foster, S.A., V.B. Garcia, and M.Y. Town. 1988. Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. Oecologia 74(4):577-585.

George, E. L., and Hadley, W. F. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. Transactions of the American Fisheries Society 108(3):253-261.

Gerber, G.P., 1999. A review of intraguild predation and cannibalism in *Anolis*. Anolis Newsletter 05:28-39.

Giller, P. S., and McNeill, S. 1981. Predation strategies, resource partitioning and habitat selection in Notonecta (Hemiptera/Heteroptera). The Journal of Animal Ecology 50:789-808.

Gilliam J.F., and D.F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:1856-1862.

Hines, A. H., Lipcius, R. N., and Haddon, A. M. 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. Marine Ecology Progress Series 36:55-64.

Hjelm, J., L. Persson, and B. Christensen. 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. Oecologia 122(2):190-199.

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist 137:S91-S115.

Hunt, G. L., and Hunt, M. W. 1973. Habitat partitioning by foraging gulls in Maine and northwestern Europe. The Auk 90(4):827-839.

Hyndes, G. A., Platell, M. E., and Potter, I. C. 1997. Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. Marine Biology 128(4):585-598.

Irschick, D.J., and J.B. Losos. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. The American Naturalist 154(3):293-305.

Johnson, M.A., M. Leal, L. Rodriguez Schettino, A. Chamizo Lara, L.J. Revell, and J.B. Losos. 2008. A phylogenetic perspective on foraging mode evolution and habitat use in West Indian Anolis lizards. Animal Behaviour 75:555-563.

Jones, M., Mandelik, Y., and Dayan, T. 2001. Coexistence of temporally partitioned spiny mice: roles of habitat structure and foraging behavior. Ecology 82(8):2164-2176.

King, D. I., Degraaf, R. M., Smith, M. L., and Buonaccorsi, J. P. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). Journal of Zoology 269:414-421.

Kotler, B. P., Brown, J. S., and Subach, A. 1993. Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. Oikos 67:548-556.

Lahti, D. C., Johnson, N. A., Ajie, B. C., Otto, S. P., Hendry, A. P., Blumstein, D. T., Coss, R. G., Donohue, K., and Foster, S. A. 2009. Relaxed selection in the wild. Trends in Ecology & Evolution, 24(9):487-496.

Lima S.L., N.C. Rattenborg, J.A. Lesku, and C.J. Amlaner. 2005. Sleeping under the risk of predation. Animal Behaviour 70:723-736.

Lind, A. J., and Welsh, H. H. 1994. Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. Animal Behaviour 48(6):1261-1273.

Lee, J. C., Clayton D., Eisenstein, S., and I. Perez. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. Copeia 1989:930–937.

Lenihan, H. S. 1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. Ecological Monographs 69:251-275.

Losos, J.B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. Univ. of Calf. Press.

Losos, J.B. 1990. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. Animal Behaviour 39(5):879-890.

Losos, J.B., and Irschick, D.J. 1996. The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. Animal Behaviour 51(3):593-602.

Losos, J.B., and B. Sinervo. 1989. The effects of morphology and perch diameter on sprint performance of Anolis lizards. Journal of Experimental Biology 145(1):23-30.

Losos, J.B., K.I. Warheit, and T.W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 287:70-73.

Losos, J.B., T.R. Jackman, A. Larson, K. de Queiroz, and L. Rodríguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279(5359):2115-2118.

Martins, M. 1993. Why do snakes sleep on vegetation in central Amazonia? Herpetological Review 24(3):83-84.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28(3):403-416.

McCallum, J. 1986. Evidence of predation by kiore upon lizards from the Mokohinau Islands. New Zealand journal of ecology 9:83-88.

Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62:1370-1386.

Moksnes, P. O., Lipcius, R. N., Pihl, L., and van Montfrans, J. 1997. Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. Journal of Experimental Marine Biology and Ecology 215(2):157-187.

Montgomery, C.E., K.R. Lips, and J.M. Ray. 2011. Ontogenetic Shift in Height of Sleeping Perches of Cope's Vine Snake, *Oxybelis brevirostris*. The Southwestern Naturalist 56(3):358-362.

Munday, P. L. 2001. Fitness consequences of habitat use and competition among coral-dwelling fishes. Oecologia 128(4):585-593.

Olsson, M., and Shine, R. 1997. The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. Journal of Evolutionary Biology 10(3):369-381.

O'Neill, K. M. 1983. The significance of body size in territorial interactions of male beewolves (Hymenoptera: Sphecidae, *Philanthus*). Animal Behaviour 31(2):404-411.

Paine, M. D., Dodson, J. J., and Power, G. 1982. Habitat and food resource partitioning among four species of darters (Percidae: *Etheostoma*) in a southern Ontario stream. Canadian Journal of Zoology 60(7):1635-1641.

Polis, G.A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? American Naturalist 123(4):541-564.

Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology 885-899.

Pacala, S., and Roughgarden, J. 1982. Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. Science 217:444-446.

Salzburg, M. A. 1984. *Anolis sagrei* and *Anolis cristatellus* in southern Florida: a case study in interspecific competition. Ecology 14-19.

Schlosser, I. J. 1987. The role of predation in age-and size-related habitat use by stream fishes. Ecology 651-659.

Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49(4):704-726.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185(4145):27-39.

Schoener, T. W., and Schoener, A. 1980. Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. The Journal of Animal Ecology 49:19-53.

Schoener, T. W., and Schoener, A. 1982. Intraspecific variation in home-range size in some *Anolis* lizards. Ecology 63:809-823.

Shine, R., Shine, T., and Shine, B. 2003. Intraspecific habitat partitioning by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae): the effects of sex, body size, and colour pattern. Biological Journal of the Linnean Society 80(1):1-10.

Singhal, S., Johnson, M. A., and Ladner, J. 2007. The behavioral ecology of sleep: Natural sleeping site choice in three *Anolis* lizard species. Behaviour 144(9):1033-1052.

Stamps, J.A. 1983. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). Behavioral Ecology and Sociobiology 12(1):19-33.

Stuart, Y. E., Campbell, T. S., Hohenlohe, P. A., Reynolds, R. G., Revell, L. J., and Losos, J. B. 2014. Rapid evolution of a native species following invasion by a congener. Science 346:463-466.

Theberge, J. B., and Wedeles, C. H. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Canadian Journal of Zoology 67(5):1285-1290.

Toft, C. A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985:1-21.

Tokarz, R. R. 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). Animal Behaviour 33(3):746-753.

Vagelli, A.A. 2004. Ontogenetic shift in habitat preference by *Pterapogon kauderni*, a shallow water coral reef apogonid, with direct development. Journal Information 2004(2):364-369.

Van Buskirk, J. 1992. Competition, cannibalism, and size class dominance in a dragonfly. Oikos 65(3):455-464.

Vitt, L. J., Cristina, T., Avila-Pires, S., Zani, P. A., and Espósito, M. C. 2002. Life in shade: the ecology of Anolis trachyderma (Squamata: Polychrotidae) in Amazonian Ecuador and Brazil, with comparisons to ecologically similar anoles. Copeia 2002(2):275-286.

Wapstra, E., Uller, T., While, G. M., Olsson, M., and Shine, R. 2010. Giving offspring a head start in life: field and experimental evidence for selection on maternal basking behaviour in lizards. Journal of evolutionary biology 23(3):651-657.

Warner, D.A., and Shine, R. 2007. Fitness of juvenile lizards depends on seasonal timing of hatching, not offspring body size. Oecologia 154:65-73.

Werner, E. E., and Hall, D. J. 1979. Foraging efficiency and habitat switching in competiting sunfishes. Ecology 60(2):256-264.

Werner, E. E., and D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 1352-1366.

Werner, E. E., Wellborn, G. A., and McPeek, M. A. 1995. Diet composition in postmetamorphic bullfrogs and green frogs: implications for interspecific predation and competition. Journal of Herpetology 29(4):600-607.

Whitaker, A. H. 1973. Lizard populations on islands with and without Polynesian rats, *Rattus exulans* (Peale). Proceedings of the New Zealand Ecological Society 20:121-130.

Williams, E.E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. Evolutionary Biology 6:47-89.

Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pp. 326–370 in R. B. Huey, E. R. Pianka, and T. W.

Schoener (Eds.), Lizard ecology: studies of a model organism. Harvard University Press, USA.

Winemiller, K. O. 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan ilanos. Environmental Biology of Fishes 26(3):177-199.

Yorks, D. T., Williamson, K. E., Henderson, R. W., Powell, R., and Parmerlee, J. S. 2003. Foraging behavior in the arboreal boid *Corallus grenadensis*. Studies on Neotropical Fauna and Environment 38(3):167-172.

Table 1. The effects of treatment, period, TOD, SVL, and their interactions on juvenile
perch height, perch width, and substrate use.

Variables	DF	F	P
Perch height			
Treatment	2,2858	1.7	0.1822
TOD	3,2858	11.85	**<.0001**
SVL	1,2858	43.39	**<.0001**
Period	2,2858	45.05	**<.0001**
SVL x Treatment	2,2858	2.14	0.1174
SVL x TOD	3,2858	16.05	**<.0001**
Period x Treatment	4,2858	11.73	**<.0001**
SVL x Period	2,2858	34.61	**<.0001**
SVL x Period x Treatment	4,2858	10.69	**<.0001**
Perch width			
Width	4,671	3.08	0.0158
SVL	1,671	0.23	0.6329
Treatment	2,671	0.07	0.9302
Width x Treatment	8,671	5.52	**<.0001**
SVL x Width	4,671	2.93	0.0203
Perch substrate			
Substrate	5,3212	18.02	**<.0001**
SVL	1,3212	22.25	**<.0001**
TOD	3,3212	3.7	0.0114
Period	2,3212	4.15	0.0159
Treatment	2,3212	0.42	0.6545
Substrate x TOD	15,3212	9.61	**<.0001**
SVL x Substrate	5,3212	36.48	**<.0001**
Period x Substrate	10,3212	2.13	0.0197
Period x Treatment	4,3212	2.58	0.0354
Substrate x Treatment	10,3212	1.18	0.2976
SVL x Substrate x TOD	18,3212	19.12	**<.0001**
Period x Substrate x Treatment	20,3212	2.19	**0.0017**

* Bold values indicate significance after Sequential Bonferroni adjustment for multiple
comparisons.
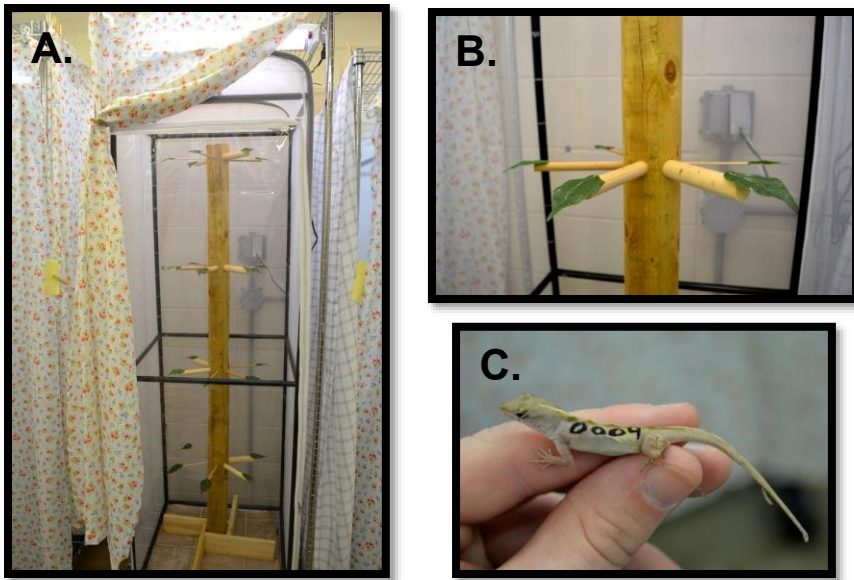
Figure 1. Photographs of the housing conditions used in the experiment: (A) depicts one of the artificial trees inside one of the enclosures, surrounded by blinds on all sides (note, the front blind was pulled back to reveal the tree and cage for photographing), and (B) is a close up of the available horizontal perches. Photograph (C) shows a lizard with its ID number on the lateral body surface for visual identification.
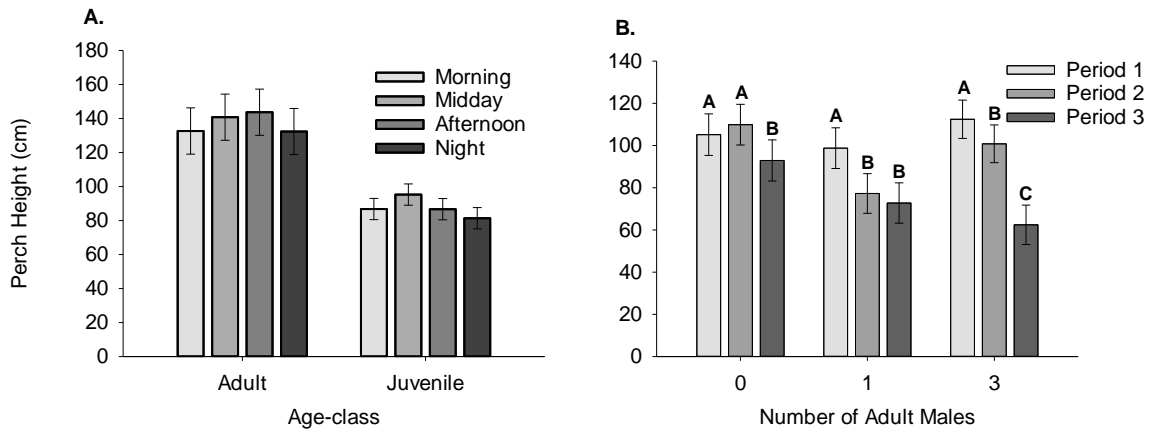
Figure 2. (A) The effect of age-class on perch height at different times of the day. (B) The effect of adult male density on juvenile perch height during each period. Error bars are ± 1 standard error.
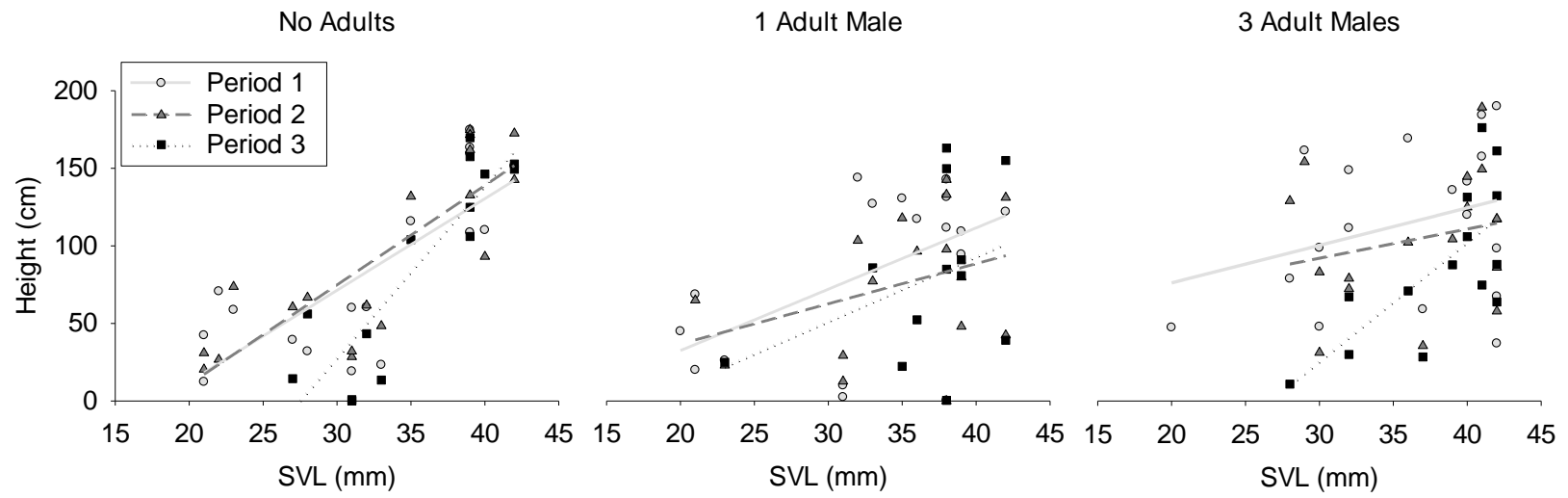
Figure 3. Effect of adult male density and juvenile SVL on juvenile perch height.
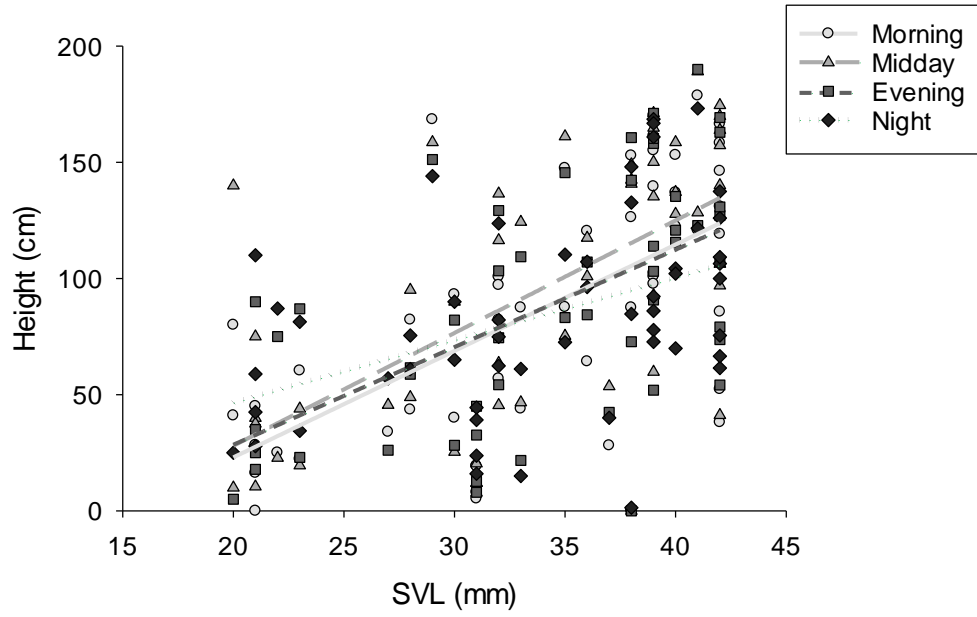
Supplementary Figure 1. The relationship between SVL and TOD on juvenile perch height.

A. No Adult Males

B. 1 Adult Male

C. 3 Adult Males

Percent of Observations
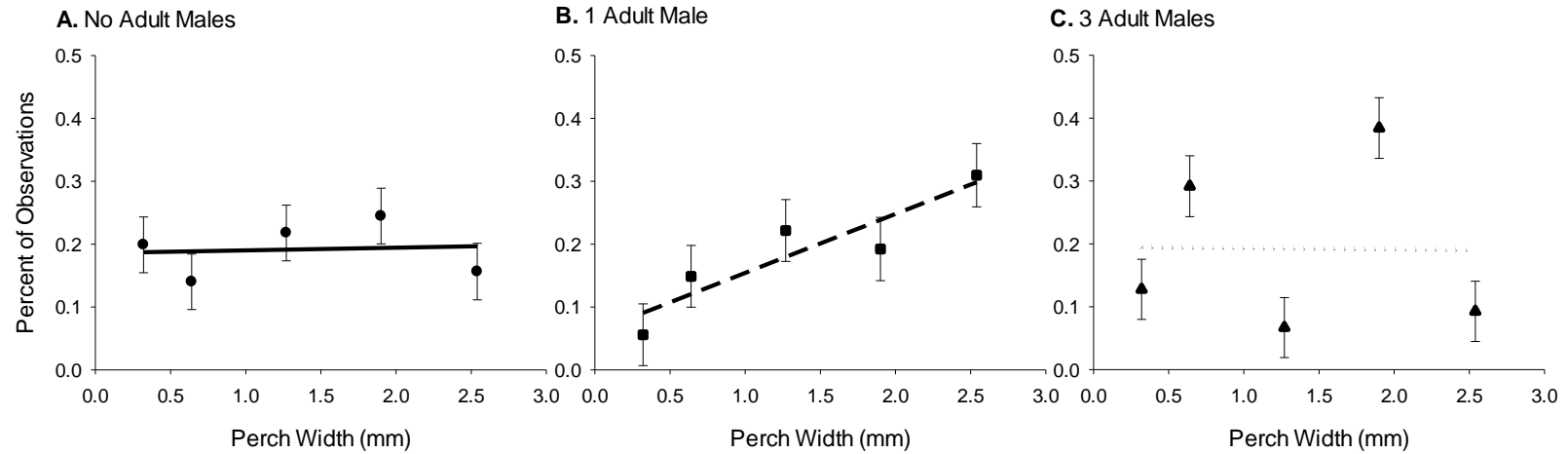
Perch Width (mm)

Figure 4. Percentage of observations on a given perch width for juveniles exposed to (A) no adult, (B) one adult male, and (C) three adult males. Analyses were conducted using the percentage of observations on a given perch width for each individual as the dependent variable. Perch width was used as a categorical independent variable; regression lines are used to show trends and do not indicated that perch width was used as a numerical variable. Error bars are ± 1 standard error.

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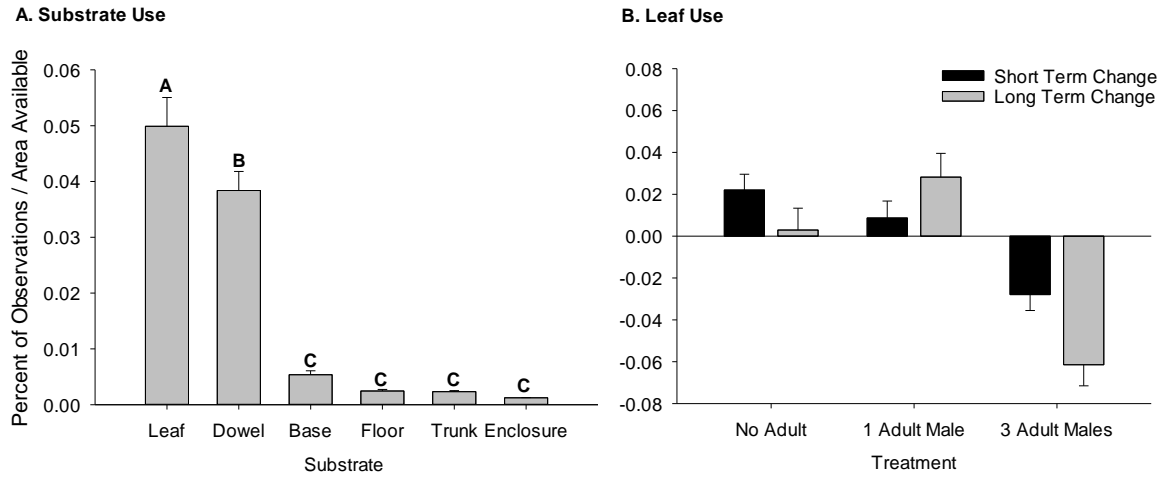
Figure 5. (A) Overall substrate use by juveniles. (B) Effects of treatment and period on leaf use by juvenile lizards. Black bars indicate the short term change in substrate use (i.e., between periods 1 and 2) and grey bars indicate the long term change (i.e., between periods 1 and 3) in substrate use. Error bars are ± 1 standard error.
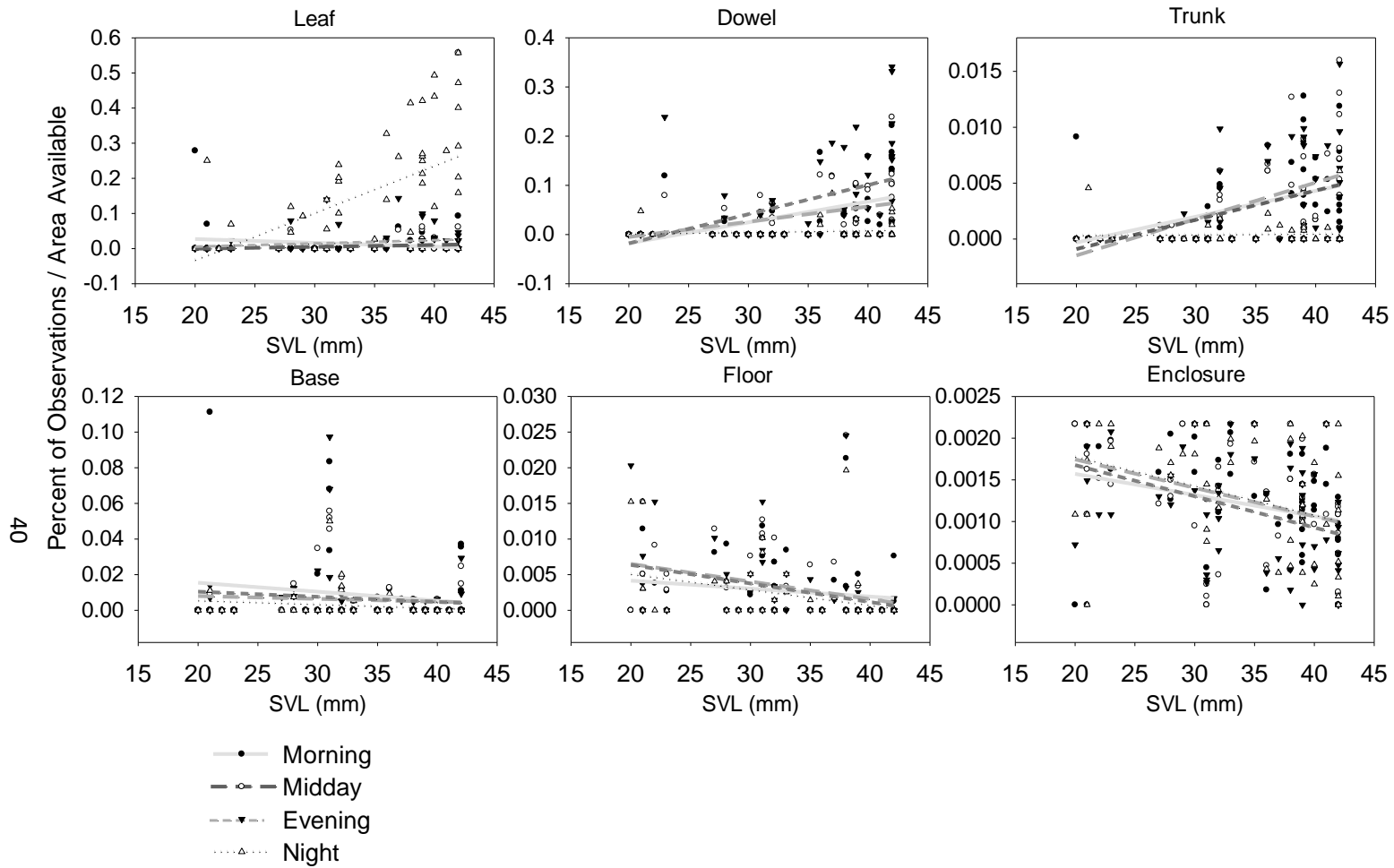
Supplementary Figure 2. The percent of observations a lizard was observed on a given substrate divided by the area available for that substrate as a function of SVL and TOD.

CHAPTER THREE

HIGH ADULT MALE DENSITY REDUCES SURVIVAL, BUT DOES NOT
INFLUENCE MICROHABITAT CHOICE IN JUVENILES OF A TERRITORIAL
LIZARD

by

DAVID M. DELANEY and DANIEL A. WARNER

In preparation for *Animal Behaviour*

Format adapted for thesis

ABSTRACT

All organisms have specific habitat requirements that allow them to properly function in their environment. For many organisms, optimal habitats differ across age classes, and individuals shift habitat choice as they age. Field observations of the brown anole lizard (*Anolis sagrei*) suggest that juveniles perch in open-canopy areas on shorter vegetation whereas adults reside in forest edges on higher vegetation. We hypothesized that this variation is due to adults forcing subordinate juveniles to less preferred microhabitats. We also predicted that adult males and females would exert different influences on juvenile behavior and survival due to sex differences in size and territoriality. We manipulated adult and juvenile densities in mesh enclosures with artificial trees to examine how inter-age class competition influences microhabitat choice. We predicted that juveniles would move to less desired microhabitats as adult density increased (i.e., behavioral plasticity) and/or adults would negatively affect juvenile survival (via competition or cannibalism) in a way that would contribute to the observed age-specific habitat use (i.e., natural selection). Despite our predictions, neither adult male or female density had any effects on juvenile microhabitat choice (i.e., perch height, width, or substrate). However, high adult male density, but not female density, reduced juvenile survival. This suggests adults have a sex- and density-dependent effect on juvenile survival. This experiment also tested if juveniles influence adult microhabitat choice. As predicted, adults did not vary in microhabitat choice in response to juvenile presence. We show that high adult male density reduces juvenile survival, but inter-age class competition does not influence microhabitat choice in *Anolis sagrei*. However, because selection should favor juveniles that occur in areas of low adult male density, we

suggest that variation in age-class habitat use may be driven by juvenile macrohabitat dispersal away from areas of high adult male density.

INTRODUCTION

Organisms benefit by living in habitats that optimize performance and satisfy functional requirements (Huey 1991; Lenihan 1999; Aubret and Shine 2008). Thus, habitat choice is a ubiquitous and ecologically important behavior and should be under strong natural selection (Munday 2001; King et al. 2006). However, optimal habitat will vary depending upon environmental context (e.g., level of competition or predation risk; Robertson 1996) and individual phenotype (e.g., body size, physiology; Huey 1991; Englund and Krupa 2000). Thus, different environmental situations should influence habitat choice and/or the way that natural selection operates on this behavior.

Individuals of different ages often vary in their habitat requirements (Dahlgren and Eggleston 2000), and organisms shift habitat choice accordingly as they age (Stamps 1983; Shine et al. 2003; Vagelli 2004; Montgomery et al. 2011). However, many studies documenting these shifts are observational, and therefore cannot identify the causal factors of this variation. Nevertheless, many factors can be responsible for ontogenetic variation in habitat use. For example, adults and juveniles may vary in resource needs (Hjelm et al. 2000) or performance (Irschick et al. 2000, 2005) which differ across habitat types. Also, young animals are often at a greater risk of predation because of lower levels of experience and smaller body sizes (Foster et al. 1988; Werner and Hall 1988). In

addition, there could be direct competition between adults and juveniles, such that one age class displaces another (Van Horne 1982; Chapter 1).

Intraspecific interactions can be important factors that shape population dynamics (Hamrin and Persson 1986). In particular, competition between age classes can influence foraging efficiency (Milinski 1982; Slowtow and Paxinos 1997), predation risk (Slowtow and Paxinos 1997; Keren-Rotem et al. 2006), and habitat use (Keren-Rotem et al. 2006; Chapter 1). In most cases, juveniles are more likely to be influenced by adults because adults of most species are larger and more dominant (e.g., Van Horne 1982; Smale et al. 2002). In particular, juveniles of species that exhibit cannibalism may be especially motivated to move from habitats that reduce interactions with adults (i.e., behavioral plasticity), and/or selection may favor juveniles that occur in areas of low adult density (i.e., natural selection; Keren-Rotem et al. 2006). However, age class interactions may vary depending upon adult sex because males and females can vary dramatically in behavior (Bjorkqvist et al. 1994), especially in species exhibiting sexual size dimorphism (Perry 1996; Blanckenhorn 2005). Understanding the ecology of each age class, sex, and their interactions will provide more insight into the role of a species in its environment (Selander 1966; Irschick et al. 2005).

Competition for microhabitat has been an important driver of the adaptive radiation of the lizard genus *Anolis* throughout the Caribbean (Williams 1983; Losos 2009). Specifically, phylogenetically distant species that occupy similar microhabitats have evolved similar morphological (Losos et al. 1998; Beuttell and Losos 1999) and ecological (Williams 1972; Losos 1990; Johnson et al. 2008) characteristics. Most notably, species with long limbs occupy thick perches and species with short limbs use

thin perches. Moreover, this limb length to perch width matching is adaptive, whereby locomotor performance is enhanced on specific perch widths depending on limb length (Losos and Sinervo 1989; Irschick and Losos 1999). Remarkably, the limb length evolution observed across the *Anolis* radiation has also been observed in populations of a single species (*Anolis sagrei*) that occur on islands with different microhabitats available (Losos et al. 1997). However, despite extensive work on the interspecific variation in *Anolis* habitat use, much less is known about how individuals within a species partition microhabitat.

The brown anole (*Anolis sagrei*) is well suited for addressing these issues for a number of reasons. First, this diurnal lizard often occurs at extremely high densities (Schoener and Schoener 1980; Lee et al. 1989), suggesting competition may influence microhabitat use. Second, *A. sagrei* conspicuously perch on vegetation and have high site fidelity (Schoener and Schoener 1982; Calsbeek 2009). This allows for repeated measurements of microhabitat choice for each individual. Third, repeated sampling of island populations suggests that juvenile survival is relatively low on islands with high adult densities (Warner unpubl. data). This finding suggests significant density-dependent competition exists between age classes. Indeed, juvenile and adult age classes differ in microhabitat choice in the field (juveniles are typically closer to the ground that adults; pers. obs.) possibly due to adults forcing subordinate juveniles to less preferred microhabitats (Chapter 1). Third, adult *A. sagrei* are cannabalistic on young individuals (Gerber et al. 1999; Cates et al. 2014). Thus, not only are adults potential competitors, but they are also predators, which should place a strong incentive on juveniles to modifiy their behaivors in response to adult density.

We conducted two simultaneous experiments by manipulating adult and juvenile densities in field enclosures to examine the role of inter-age class competition in generating variation in microhabitat use in the lizard *Anolis sagrei*. The first experiment tested the influence of adult sex and density on juvenile microhabitat choice and survival. We hypothesized that adults would, (1) force juveniles to less preferred microhabitat (i.e., behavioral plasticity), and/or (2) be a selective agent against juveniles in a way that would contribute to the observed habitat use variation (i.e., natural selection). Also, because adult males are larger and more territorial, we predicted that adult males would influence juvenile behavior (via plasticity and/or cannibalism) more than adult females. The second experiment assessed the influence of juvenile presence on adult microhabitat choice. Because adults are larger and likely more dominant, we hypothesized that juvenile presence would not influence adult microhabitat use.

METHODS

We assembled 27 mesh enclosures (0.61m x 0.61m x 1.83m; Carolina Biological Supply Co.) constructed of a PVC pipe frame and covered with mesh on an island (Fig. 1, Island A) in the Halifax River, Ormond Beach, Florida from 31 June – 7 July 2014. This island was well suited for this study because the open area in the center of the island was large enough for 27 enclosures, and the central open-area was homogeneous and reduced any variation in ambient conditions among enclosures. In addition, densities of free-ranging lizards were low in the open areas (pers. obs.) and thus free-ranging lizards were less likely to interact with lizards in the enclosures.

Each enclosure contained an artificial tree (~1.8 m tall) with perches that varied in height (42cm, 84cm, 126cm, and 168cm) and width diameter (0.32cm, 0.64cm, 1.27cm, 1.9cm, and 2.54cm), and had an artificial leaf glued to the distal end (Fig. 2). The mesh enclosures allowed lizards to experience natural ambient conditions. We also tied shade cloth to the top of each enclosure to allow lizards to move between shaded and sunlit areas. The mesh also allowed ample amounts of invertebrates into the enclosures, and all age-classes of lizards were observed feeding on invertebrates. Wooden fence posts were used as the trunk of each tree, and horizontal perches were constructed from 15 cm long dowel rods (branches) that were attached perpendicularly into the trunk. Perches were radially-arranged (spaced ~5cm intervals) around the trunk, and the order of the 5 perch diameters was random at each of the 4 heights so that each perch height contained perches of each of the five diameters. The floor of each cage was covered with linoleum (0.61m x 0.61m) to prevent the tree from tearing holes in the mesh. Blinds with small holes cut at various heights were hung on the north side of each enclosure to allow the observer to approach and record behaviors without disturbing lizards. Enclosures were arranged in locations around the island so that individuals from one enclosure could not interact with individuals from other enclosures.

From 7 – 22 July 2014, two hundred and seventy-six *Anolis sagrei* were collected from a nearby island that was connected by a narrow sandbar (Fig. 1, Island B). Lizards were collected 1 – 2 days before they were needed for the experiments. We measured snout-vent length (SVL) and tail length (TL) to the nearest mm and mass to the nearest 0.01g. Sex was determined by dorsal pattern and the presence or absence of enlarged post-cloacal scales found on males. Toes were clipped to uniquely mark each individual.

Identification numbers were written on the lateral surfaces of adults (using a sharpie marker) so they could be visually identified while in the enclosures without disturbance. Because juveniles were too small to write ID numbers, we placed dots of acrylic paint on their dorsums for unique, visual identification. After lizards were measured and marked, individuals were haphazardly assigned to one of 9 treatments (Table 1) divided among two experiments which occurred simultaneously. The first experiment examined the effects of adult density and sex on juvenile microhabitat choice and survival; the second experiment examined the effects of juvenile presence on adult male and female microhabitat choice. There were three replicate enclosures per treatment. The experiments began on 10 July 2014 (trial 1) and were repeated with another group of lizards on 19 July 2014 (trial 2) to increase replication to six enclosures per treatment (total n = 276). We recorded perch height, width, and substrate (i.e., leaf, branch, trunk, base of the tree, floor, or other parts of the enclosure) for each individual every morning (0730 – 1000 h.), midday (1200 – 1430 h.), evening (1630 – 1900 h.), and night (2230 – 0500 h.) during the experiments. Sunrise occurred about 0700 h and sunset about 1900 h.

Treatments 1-5 (see Table 1) tested the effects of adult density and sex on juvenile microhabitat choice and survival. Six juveniles were placed in each enclosure and microhabitat choice was observed for four days (period 1). Adults were then released into enclosures in treatments 2-5 after the night observation on the fourth day (i.e., middle of the trial). These treatments varied in density and sex of adults, such that there were treatments with 1 adult female, 3 adult females, 1 adult male, and 3 adult males. Treatment 1 served as our control and did not receive any adults. Microhabitat choice was observed for an additional 4 days (period 2). All lizards were collected from the

enclosures after the last observation on the eighth day. We recorded which lizards survived and then released them onto the island that they were originally captured. Comparisons between periods 1 and 2, and our control and treatments with adults, allowed us to see if adult density influences juvenile microhabitat choice and if that varies depending on the sex of adults.

Treatments 2-9 were used to test the effects of juvenile presence and adult density on microhabitat choice and survival of adult males and females (independently of the other sex). Adult lizards were placed in enclosures assigned to treatments 6-9 (Table 1) and microhabitat choice was observed for eight days. These treatments varied in density and sex of adults, such that there were treatments with 1 adult female, 3 adult females, 1 adult male, and 3 adult males. These treatments contained no juveniles, and therefore, allowed us to quantify microhabitat choice for each sex and density in the absence of juveniles. Treatments 2-5 contained juveniles and received adults after the night observations on the fourth day (i.e., they were the same treatments used in experiment 1 described above). We recorded microhabitat choice for these adults for days 5-8 of the experiments. All lizards were collected from the enclosures after the last observation on the eighth day and released onto the island that they were originally captured. No treatment contained adults in the absence of juveniles during period 1 that were then exposed to juveniles in period 2. Thus, we did not make comparisons between periods for this experiment, but instead compare the microhabitat choice of adults in treatments 2-5 during period 2 (juveniles present) with treatments 6-9 during periods 1 and 2 (no juveniles).

Statistical Analyses

All analyses were performed with SAS software (version 9.3). All statistical tests
described below were performed with mixed model analyses using individual ID nested
within enclosure as a random effect.

Effects on juvenile behavior

To test the effects of adult sex and density on juvenile perch height, we used a
mixed model Analysis of Variance (ANOVA) with height as the dependent variable.
Treatment, time-of-day (TOD), juvenile sex, trial, period, SVL (covariate), and all 3-way
interactions were used as independent variables. Thus, a treatment x period interaction
would test whether the introduction of adults altered juvenile perch height. Because
treatment is uninterpretable without period, we only tested treatment interactions that
included period.

To assess the effects of adult sex and density on juvenile perch width, we
calculated the percent of observations an individual was observed on a given perch width.
We then used those calculated values (arcsin transformed) as the dependent variable in a
mixed model ANOVA. Perch width, treatment, TOD, juvenile sex, trial, period, SVL,
and all 3-way interactions that included width were used as independent variables. Time-
of-day, trial, period, and their interactions were not significant and were removed from
the final model.

To assess the effects of adult sex and density on juvenile substrate use, we
calculated the percent of observations an individual was observed on a given substrate
and divided that value by the area available for that substrate. We then used those area-
adjusted values (arcsin transformed) as the dependent variable in a mixed model

ANOVA. Substrate, treatment, TOD, juvenile sex, trial, period, SVL, and all 3-way interactions that included substrate were used as independent variables. Trial, period, and their interactions were not significant and were removed from the final model.

Effects on adult behavior

To test the effects of juvenile presence on adult perch height, we used a mixed model ANOVA with height as the dependent variable. Adult sex, adult density, juvenile presence, TOD, adult SVL, trial, period, and all 3-way interactions were used as independent variables. Trial and its interactions were not significant and were removed from the final model.

To test the effects of juvenile presence on adult perch width, we calculated the percent of observations an individual was observed on a given perch width. We then used those calculated values (arcsin transformed) as the dependent variable in a mixed model ANOVA. Perch width, adult sex, adult density, juvenile presence, TOD, trial, period, adult SVL, and 3-way interactions that included width were used as independent variables. Time-of-day, trial, period, adult SVL, and their interactions were not significant and were removed from the final model.

To test the effects of juvenile presence on adult substrate use, we calculated the percent of observations an individual was observed on a given substrate and divided that value by the area available for that substrate. We then used those area-adjusted values (arcsin transformed) as the dependent variable in a mixed model ANOVA. Perch substrate, adult sex, adult density, juvenile presence, TOD, adult SVL, trial, period, and 3-way interactions that included substrate were used as independent variables. Adult

SVL, trial, period, and their interactions were not significant and were removed from the final model.

Juvenile survival

To test for effects on juvenile survival, we used generalized linear mixed models with individual survival as the dependent variable. The first model tested for the overall effect of treatment, SVL, sex, trial, and 3-way interactions. Sex, trial, and their interactions were non-significant and were removed from the final model. Subsequent analyses focused on the effects of microhabitat choice on survival. We ran different analyses for each microhabitat variable (i.e., perch height, width, and substrate).

To test for the effects of perch height on survival, we used perch height, treatment, juvenile SVL, TOD, juvenile sex, trial, and 2 way interactions that included height as independent variables. Thus, a height x treatment interaction would indicate that adult density and/or sex influenced juvenile survival differentially based on height. Time-of-day, juvenile sex, trial, and their interactions were not significant and were removed from the final model.

To test for the effects of perch width use on juvenile survival, we used a generalized linear model rather than a generalized linear mixed model because the model would not converge with the random effects. We used the calculated percent of observations a lizard was observed on a given perch width (arcsin transformed), width, treatment, and their interactions as independent variables.

To test for the effects of substrate use on juvenile survival, we ran a generalized linear mixed model for each substrate. This analysis also had trouble with model

convergence. To address this, and because the only treatment to significantly reduce juvenile survival was the high adult male density treatment, we focused our analysis on this treatment. We used the calculated percent of observations a lizard was observed on a given substrate divided by the area available for that substrate (arcsin transformed) as the independent variable.

RESULTS

Juvenile behavior

Treatment did not significantly influence juvenile perch height (Table 2). Perch height was similar during morning and midday observations, but significantly decreased in the evening and increased at night (Table 2, Fig. 2). Perch height decreased during period 2 (Table 2). A similar decrease between periods was observed in females, but not males (Table 2, Supplementary Fig. 1B), and during trial 1, but not trial 2 (Table 2, Supplementary Fig. 1A). Despite these interactions, sex and trial were not significant as individual variables (Table 2). Although SVL was not significant after Sequential Bonferroni adjustment for multiple comparisons, large juveniles tended to perch higher than small juveniles (Table 2, Supplementary Fig. 2).

Treatment did not influence juvenile perch width use (width x treatment x period, Table 2). In addition, TOD ($F_{12,391} = 1.42$, $P = 0.1555$), sex (width x sex; Table 2), SVL (width x SVL, Table 2), trial ($F_{4,423} = 1.9$, $P = 0.1098$), and period ($F_{4,391} = 1.68$, $P = 0.1538$) did not have significant effects on juvenile perch width use. Overall, juveniles perched most frequently on thin perches (width; Table 2; Fig. 3)

Treatment did not influence substrate use by juveniles (substrate x treatment x period; Table 2). Juveniles increased leaf use and decreased the use of the base, floor, and trunk at night (Table 2, Fig 4). Period ($F_{5,6302} = 0.24$, $P = 0.9454$) and trial ($F_{5,6307} = 1.21$, $P = 0.3013$) did not affect juvenile substrate use.

Adult behavior

Adult perch height was not significantly influenced by adult density (Table 3), adult sex (Table 3), the presence of juveniles (Table 3), or trial ($F_{1,1762} = 1.19$, $P = 0.2745$). Adults perched higher at night than during the day, and females perched higher than males during evening observations (TOD x sex; Table 3, Fig. 5). Large adults perched higher than small adults, but this trend lessened during morning and night observations (TOD x SVL; Table 3, Fig. 6).

Adult perch width use was not significantly affected by adult density (width x density; Table 3), adult sex (sex x density; Table 3), the presence of juveniles (juvenile presence x density; Table 3), TOD ($F_{12,440} = 1.35$, $P = 0.1873$), SVL ($F_{4,398} = 0.44$, $P = 0.7827$), trial ($F_{4,379} = 0.05$, $P = 0.9948$), or period ($F_{4,393} = 1.36$, $P = 0.2457$). In addition, width of perch by itself did not have a significant effect on adult perch choice (perch width; Table 3).

Adult substrate use was not significantly influenced by adult density (after Sequential Bonferroni adjustment; substrate x density; Table 3), sex (substrate x sex; Table 3), the presence of juveniles (substrate x juvenile presence; Table 3), SVL ($F_{5,3176} = 0.99$, $P = 0.4242$), trial ($F_{5,3165} = 0.1.37$, $P = 0.2316$), or period ($F_{5,3170} = 0.37$, $P = 0.8706$). Adults occupied branches most often during daytime observations. Branch,

trunk, base, and floor use decreased at night, whereas leaf use strongly increased at night (Table 3, Fig. 7).

Juvenile survival

High adult male density, but not female density, reduced juvenile survival ($F_{4,444} = 3.70$, P = 0.0056; Fig. 8). Large juveniles had higher survival than small juveniles ($F_{1,444} = 6.47$, P = 0.0113; Fig. 9). Perch height ($F_{1,484} = 0.36$, P = 0.5461), width (P = 1.0000), substrate (P > 0.05 for all substrates), juvenile sex ($F_{1,442} = 0.02$, P = 0.8955), ($F_{1,441} = 2.93$, P = 0.0874), or any of their tested interactions did not influence juvenile survival.

DISCUSSION

Competition for perch microhabitat has been important in the evolution of *Anolis* lizards. Although many studies have examined interspecific variation in habitat use, much less is known about intraspecific habitat variation in *Anolis* species. Furthermore, despite numerous studies documenting ontogenetic habitat variation for a variety of taxa, most are observational and fail to determine the causal factors responsible for habitat use variation. Field observations of *A. sagrei* suggest that juveniles frequently occur in open-canopy areas on low vegetation whereas adults most often occupy forest edges on higher vegetation. We hypothesized that this age class habitat variation is driven by adults forcing juveniles to less preferred habitats. To address these issues, we conducted two simultaneous experiments by manipulating adult and juvenile densities in field enclosures to examine the role of inter-age class competition in generating variation in microhabitat

use. The first experiment focused on how adults influence juvenile perch behaviors. We hypothesized that adults would, (1) force juveniles to less preferred microhabitat (i.e., behavioral plasticity), and/or (2) be a selective agent against juveniles in a way that would contribute to the observed habitat use variation (i.e., natural selection). For example, juveniles that use high perches may be more likely to be cannibalized by adults, thus selection would favor juveniles that choose low perches. Because adult males are larger and more territorial than females, we hypothesized that they would have a greater effect on juvenile behavior than adult females. The second experiment focused on how juveniles influence adult perch behaviors. We hypothesized that juveniles would not have an effect on adult microhabitat choice because adults are larger and likely to be more dominant.

Juvenile behavior

We predicted that juveniles would be forced to lower perches in the presence of adults. Despite our prediction, neither adult male nor female density significantly influenced juvenile perch height. However, TOD significantly influenced juvenile perch height. Juveniles occupied similar heights during morning and midday observations, but decreased perch height in the evening and increased height at night. Decreasing perch height in the evening may enhance foraging efficiency when crepuscular invertebrates (potential prey) are active (Kunz 1973; Kotler et al. 1993). Aggressive interactions between conspecifics are less likely at night because *Anolis sagrei* are diurnal. Thus, night time perch choice may be driven more by pressures from nocturnal predators than intraspecific competition. Increasing perch height at night may reduce predation risk from

ground nocturnal, dwelling predators. For example, rats have been shown to decrease the number of nocturnal ground dwelling lizards on islands offshore of New Zealand (Whitaker 1973; McCallum 1986). Additionally, some evidence suggests that Neotropical snakes sleep off the ground and on vegetation to reduce predation from nocturnal invertebrates (Martins 1993). Similar factors may be responsible for the observed behaviors in *A. sagrei*.

Body size also had a significant effect on juvenile perch height. Large juveniles perched higher than small juveniles, which matches our field observations. This may be a result of juveniles partitioning microhabitat to reduce competition (Schoener 1974). In addition, smaller individuals often have a higher risk of predation (Stamps 1983). Thus, small individuals may innately stay lower to the ground to avoid risks associated with higher perches (e.g., large adults, birds). Also, performance may be enhanced at heights differentially based on lizard size. For example, appropriately sized prey near the ground might enable smaller lizards to forage efficiently. Such partitioning of habitat to increase foraging efficiency has been suggested for a variety of animals, including insects (Giller and McNeill 1981), fish (George and Hadley 1979; Werner and Hall 1979; Paine et al. 1982; Winemiller 1989; Hyndes et al. 1997), amphibians (Werner et al. 1995), ectothermic reptiles (Lind and Welsh Jr. 1994), birds (Davoren et al. 2003; Hunt and Hunt 1973), and mammals (Theberge and Wedeles 1989; Kotler et al. 1993; Jones et al. 2001). In our study, however, most prey items remained on or near the floors of the enclosures, yet the height partitioning persisted – a pattern similar to that observed in laboratory enclosures (Chapter 2).

In addition, period influenced juvenile perch height and interacted with sex and trial. Specifically, juveniles decreased perch height during period 2, and this effect occurred in females, but not males, and in trial 1, but not trial 2. *Anolis sagrei* may increase perch height when placed into new environments and then decrease height as they acclimate. A decrease in perch height over time has been shown in a previous study using experimental mesh enclosures (Chapter 1). It is unclear why females would be more prone to this than males, but may be a result of aggression or territoriality variation between sexes. The minor difference in perch height between trials may be a result of variation in climate conditions between trials.

We predicted that juveniles would be forced to thinner perches in the presence of adults because adults would prefer and occupy thicker perches. However, neither adult males nor females significantly influenced juvenile perch width use. We also found no evidence that any other variable we measured influenced juvenile perch width use. Despite the importance of perch width in the adaptive radiation of *Anolis* lizards, other microhabitat variables may be more important for juvenile *A. sagrei*.

We hypothesized that juveniles would be forced to less preferred substrates in the presence of adults. Despite our prediction, we found no evidence that adult male or female density changed juvenile substrate use. However, TOD significantly influenced which substrates juveniles chose. Juveniles occupied branches, the base of the tree, and the floor most frequently during daytime observations but reduced base, floor, and trunk use and strongly increased leaf use at night. Other *Anolis* species are known to shift night time substrate use to leaves (Clark and Gillingham 1990; Chandler and Tolson 1990; Vitt et al. 2002; Singhal et al. 2007). Perching on leaves located on the distal ends of branches

likely allows sleeping lizards to sense vibrations as predators attempt to climb towards them. For example, blunthead tree snakes (*Imantodes cenchoa*; Vitt et al. 2002) and Grenadian tree boas (*Corallus grenadensis*; York et al. 2003), presumably to reduce vibrations the lizard could detect.

Adult behavior

As predicted, the presence of juveniles did not influence the height that either adult males or females perched. TOD influenced adult perch height similarly to that of juveniles. Night perch sites were higher than daytime perches. Adult males did not differ in perch height throughout the day, but females increased perch height in the evenings. This may represent females moving towards night perch locations sooner than adult males. We also observed that juveniles decreased perch height in the evenings, before moving to higher perches at night (see above). Juveniles may take advantage of reduced competition with adult females for resources low to the ground (e.g., prey) at this time. We also found that large adults chose higher perches than small adults, but this trend lessened during morning and night time observations. Adults may partition perch height based on body size to reduce competition during the day. However, as we previously suggested, night time perch choice is likely to be driven by predation rather than intraspecific competition. Adults may not partition perch height at night because *A. sagrei* is diurnally active, and thus, may not need to compete for as many resources at night.

We predicted that the presence of juveniles would not influence adult perch width use. Indeed, we found no evidence that juvenile presence, or any other parameters,

influenced adult perch width use. Future studies that assess perch structure on adults may benefit from providing greater variation in available perch widths. For example, our thinnest (0.32 cm dia.) and widest perch (2.54 cm dia.) may not have differed enough for adults, which are known to frequent wide surfaces such as tree trunks. Nevertheless, our study design offered a controlled environment with perch structure similar to that found in many environments that *A. sagrei* occurs.

As predicted, the presence of juveniles did not affect adult substrate use. Similarly to TOD effects on juveniles, adults occupied branches most frequently during the day, but shifted to leaf use at night. This night time shift was also accompanied with a decrease in branch, trunk, base, and floor use. As stated for juveniles, this substrate shift likely reduces predation risk from nocturnal, arboreal predators.

<div align="center">Conclusion</div>

We found no evidence that either juveniles or adults shift microhabitat choice plastically in response to the presence of other age classes. Additionally, despite high adult male density reducing juvenile survival, we find no evidence that juveniles are selected against in a way that would contribute to the observed ontogenetic habitat use variation. However, our experimental design only allowed lizards to vary in microhabitat choice, whereas macrohabitat dispersal was limited because of the size of the enclosures. Juveniles may avoid areas of high adult male density by dispersing from these habitats into open-canopy habitats. We show that occurring in an area with high adult male density, even for a short period (i.e., 4 days), reduces juvenile survival. Juvenile microhabitat shifts may not be enough to avoid cannibalism from adult males, which is

supported by our finding that no microhabitat parameter influenced survival (i.e., no microhabitat was safe). We suggest that selection should favor juveniles that avoid or disperse from areas of high adult male density, thus contributing to the observed inter-age class habitat variation.

REFERENCES

Aubret, F., and Shine, R. 2008. Early experience influences both habitat choice and locomotor performance in tiger snakes. The American Naturalist 171:524-531.

Blanckenhorn, W. U. 2005. Behavioral causes and consequences of sexual size dimorphism. Ethology 111(11):977-1016.

Bjorkqvist, K., Osterman, K., and Lagerspetz, K. M. 1994. Sex differences in covert aggression among adults. Aggressive behavior 20(1):27-33.

Cates, C.D., D.M. Delaney, A.M. Buckelew, A.M. Durso, S.S. French, A.M. Reedy, and D.A. Warner. 2014. *Anolis sagrei* (Brown Anole). Cannibalism. Herpetological Review 45:491.

Clark, D.L., and Gillingham, J.C. 1990. Sleep-site fidelity in two Puerto Rican lizards. Animal Behaviour 39:1138-1148.

Chandler, C.R., and Tolson, P.J. 1990. Habitat use by a boid snake, *Epicrates monensis*, and its anoline prey, *Anolis cristatellus*. Journal of Herpetology 24(2):151-157.

Davoren, G. K., Montevecchi, W. A., and Anderson, J. T. 2003. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. Marine Ecology Progress Series 256:229-242.

Englund, G., and Krupa, J. J. 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size. Freshwater biology 43:75-83.

Foster, S.A., V.B. Garcia, and M.Y. Town. 1988. Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. Oecologia 74(4):577-585.

Gerber, G.P., 1999. A review of intraguild predation and cannibalism in *Anolis*. Anolis Newsletter 05:28-39.

George, E. L., and Hadley, W. F. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. Transactions of the American Fisheries Society 108(3):253-261.

Gilliam J.F., and D.F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:1856-1862.

Giller, P. S., and McNeill, S. 1981. Predation strategies, resource partitioning and habitat selection in Notonecta (Hemiptera/Heteroptera). The Journal of Animal Ecology 50:789-808.

Hamrin, S. F., and Persson, L. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. Oikos 47(2):223-232.

Hjelm, J., L. Persson, and B. Christensen. 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. Oecologia 122(2):190-199.

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist 137:S91-S115.

Hunt, G. L., and Hunt, M. W. 1973. Habitat partitioning by foraging gulls in Maine and northwestern Europe. The Auk 90(4):827-839.

Hyndes, G. A., Platell, M. E., and Potter, I. C. 1997. Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. Marine Biology 128(4):585-598.

Irschick, D.J., and J.B. Losos. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. The American Naturalist 154(3):293-305.

Irschick, D. J., Macrini, T. E., Koruba, S., and Forman, J. 2000. Ontogenetic differences in morphology, habitat use, behavior, and sprinting capacity in two West Indian *Anolis* lizards. Journal of Herpetology 34(3):444-451.

Irschick, D. J., VanHooydonck, B., Herrel, A., and Meyers, J. A. Y. 2005. Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population. Biological Journal of the Linnean Society 85(2):211-221.

Johnson, M.A., M. Leal, L. Rodriguez Schettino, A. Chamizo Lara, L.J. Revell, and J.B. Losos. 2008. A phylogenetic perspective on foraging mode evolution and habitat use in West Indian Anolis lizards. Animal Behaviour 75:555-563.

Jones, M., Mandelik, Y., and Dayan, T. 2001. Coexistence of temporally partitioned spiny mice: roles of habitat structure and foraging behavior. Ecology 82(8):2164-2176.

Keren-Rotem, T., Bouskila, A., and Geffen, E. 2006. Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*). Behavioral Ecology and Sociobiology 59(6):723-731.

King, D. I., Degraaf, R. M., Smith, M. L., and Buonaccorsi, J. P. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). Journal of Zoology 269:414-421.

Kotler, B. P., Brown, J. S., and Subach, A. 1993. Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. Oikos 67:548-556.

Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. Journal of Mammalogy 54(1):14-32.

Lima S.L., N.C. Rattenborg, J.A. Lesku, and C.J. Amlaner. 2005. Sleeping under the risk of predation. Animal Behaviour 70:723-736.

Lind, A. J., and Welsh, H. H. 1994. Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. Animal Behaviour 48(6):1261-1273.

Lenihan, H. S. 1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. Ecological Monographs 69:251-275.

Losos, J.B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. Univ. of Calf. Press.

Losos, J.B. 1990. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. Animal Behaviour 39(5):879-890.

Losos, J.B., and B. Sinervo. 1989. The effects of morphology and perch diameter on sprint performance of Anolis lizards. Journal of Experimental Biology 145(1):23-30.

Losos, J.B., K.I. Warheit, and T.W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 287:70-73.

Martins, M. 1993. Why do snakes sleep on vegetation in central Amazonia? Herpetological Review 24(3):83-84.

McCallum, J. 1986. Evidence of predation by kiore upon lizards from the Mokohinau Islands. New Zealand journal of ecology 9:83-88.

Milinski, M. 1982. Optimal foraging: the influence of intraspecific competition on diet selection. Behavioral Ecology and Sociobiology 11(2):109-115.

Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62:1370-1386.

Montgomery, C.E., K.R. Lips, and J.M. Ray. 2011. Ontogenetic Shift in Height of Sleeping Perches of Cope's Vine Snake, *Oxybelis brevirostris*. The Southwestern Naturalist 56(3):358-362.

Munday, P. L. 2001. Fitness consequences of habitat use and competition among coral-dwelling fishes. Oecologia 128(4):585-593.

Paine, M. D., Dodson, J. J., and Power, G. 1982. Habitat and food resource partitioning among four species of darters (Percidae: *Etheostoma*) in a southern Ontario stream. Canadian Journal of Zoology 60(7):1635-1641.

Perry, G. 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. Canadian Journal of Zoology 74(7):1238-1245.

Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology 77(3):885-899.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185(4145):27-39.

Schoener, T. W., and Schoener, A. 1980. Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. The Journal of Animal Ecology 49:19-53.

Schoener, T. W., and Schoener, A. 1982. Intraspecific variation in home-range size in some *Anolis* lizards. Ecology 63:809-823.

Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68(2):113-151.

Shine, R., Shine, T., and Shine, B. 2003. Intraspecific habitat partitioning by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae): the effects of sex, body size, and colour pattern. Biological Journal of the Linnean Society 80(1):1-10.

Singhal, S., Johnson, M. A., and Ladner, J. 2007. The behavioral ecology of sleep: Natural sleeping site choice in three *Anolis* lizard species. Behaviour 144(9):1033-1052.

Slotow, R., and Paxinos, E. 1997. Intraspecific competition influences food return-predation risk trade-off by White-crowned Sparrows. Condor 99(3):642-650.

Smale, L., Frank, L. G., and Holekamp, K. E. 1993. Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with adult females and immigrant males. Animal Behaviour 46(3):467-477.

Stamps, J.A. 1983. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). Behavioral Ecology and Sociobiology 12(1):19-33.

Theberge, J. B., and Wedeles, C. H. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Canadian Journal of Zoology 67(5):1285-1290.

Vagelli, A.A. 2004. Ontogenetic shift in habitat preference by *Pterapogon kauderni*, a shallow water coral reef apogonid, with direct development. Journal Information 2004(2):364-369.

Van Horne, B. 1982. Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in seral stages of coniferous forest. Ecology 63(4):992-1003.

Vitt, L. J., Cristina, T., Avila-Pires, S., Zani, P. A., and Espósito, M. C. 2002. Life in shade: the ecology of *Anolis trachyderma* (Squamata: Polychrotidae) in Amazonian Ecuador and Brazil, with comparisons to ecologically similar anoles. Copeia 2002(2):275-286.

Whitaker, A. H. 1973. Lizard populations on islands with and without Polynesian rats, *Rattus exulans* (Peale). Proceedings of the New Zealand Ecological Society 20:121-130.

Williams, E.E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. Evolutionary Biology 6:47-89.

Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pp. 326–370 in R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), Lizard ecology: studies of a model organism. Harvard University Press, USA.

Werner, E. E., and Hall, D. J. 1979. Foraging efficiency and habitat switching in competiting sunfishes. Ecology 60(2):256-264.

Werner, E. E., and D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 1352-1366.

Werner, E. E., Wellborn, G. A., and McPeek, M. A. 1995. Diet composition in postmetamorphic bullfrogs and green frogs: implications for interspecific predation and competition. Journal of Herpetology 29(4):600-607.

Winemiller, K. O. 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan ilanos. Environmental Biology of Fishes 26(3):177-199.

Yorks, D. T., Williamson, K. E., Henderson, R. W., Powell, R., and Parmerlee, J. S. 2003. Foraging behavior in the arboreal boid *Corallus grenadensis*. Studies on Neotropical Fauna and Environment 38(3):167-172.

Table 1. Distribution of size- and sex-classes per enclosure for each treatment. Treatments 1-5 were used in the first experiment to assess the effects of adult sex and density on juvenile perch use behavior. Treatments 2-9 were used in the second experiment to assess the effects of juvenile presence on adult perch use behavior.

	Treatment								
	1	2	3	4	5	6	7	8	9
Juveniles	6	6	6	6	6	0	0	0	0
Adult males	0	1	3	0	0	1	3	0	0
Adult females	0	0	0	1	3	0	0	1	3

Table 2. Effects on juvenile perch height, width, and substrate. Independent variables are

listed below each dependent variable.

Variables	DF	F	P
Perch height			
TOD	3,2829	129.39	**<.0001**
Period	1,2829	14.27	**0.0002**
SVL	1,2829	11.94	**0.0006**
Treatment	4,2829	2.21	0.0652
Trial	1,2829	2.48	0.1154
Sex	1,2829	0.02	0.8846
Period x Trial	1,2829	7.70	**0.0056**
Sex x Period	1,2829	5.64	0.0177
Treatment x Period	4,2829	0.69	0.5996
Perch width			
Width	4,402	4.81	**0.0008**
Treatment	4,402	0.49	0.7435
Period	1,402	0.00	0.9643
Width x Treatment	16,402	1.65	0.0547
Width x Period	4,402	2.03	0.0889
Treatment x Period	4,402	1.18	0.3185
Width x Treatme x Period	16,402	0.66	0.8337
Perch substrate			
Sex	1,6263	2.03	0.1543
SVL	1,6263	1.68	0.1949
Substrate	5,6263	1.20	0.3077
Treatment	4,6263	0.64	0.6349
Period	1,6263	0.06	0.8114
TOD	3,6263	8.61	**<.0001**
Substrate x Sex	5,6263	2.58	0.0245
SVL x Sex	1,6263	2.42	0.1201
SVL x Substrate	5,6263	2.61	0.023
Treatment x Period	4,6263	0.54	0.7098
Substrate x Period	5,6263	0.23	0.9498
Substrate x Treatment	20,6263	0.54	0.9529
Substrate x TOD	15,6263	28.91	**<.0001**
SVL x Substrate x Sex	5,6263	2.75	0.0174
Substrate x Treatment x Period	20,6263	0.78	0.7466

* Bold values indicate significance after Sequential Bonferroni adjustment for
multiple comparisons.

Table 3. Effects on adult perch height and substrate. Independent variables are listed below each dependent variable. No independent variables had a significant effect on perch width and therefore are not reported here.

Variables	DF	F	P
Perch height			
Period	1,1756	7.68	**0.0056**
SVL	1,1756	6.91	**0.0087**
TOD	3,1756	3.13	0.0249
Density	1,1756	0.99	0.3197
Juvenile presence	1,1756	0.88	0.3483
Sex	1,1756	0.05	0.8179
Sex x TOD	3,1756	5.55	**0.0009**
SVL x TOD	3,1756	3.76	0.0104
Perch width			
Density	1,447	13.35	**0.0003**
Juveniles	1,447	4.13	0.0428
Sex	1,447	1.95	0.1632
Width	4,447	0.51	0.7295
Width x Juvenile presence	4,447	1.59	0.175
Width x Sex	4,447	1.11	0.3524
Width x Density	4,447	0.93	0.4478
Perch substrate			
Substrate	5,3192	33.05	**<.0001**
TOD	3,3192	4.66	**0.003**
Density	1,3192	4.16	0.0414
Sex	1,3192	0.16	0.6883
Juveniles	1,3192	0.00	0.9485
Substrate x TOD	15,3192	20.99	**<.0001**
Substrate x Density	5,3192	2.25	0.0473
Substrate x Sex	5,3192	0.50	0.7773
Density x TOD	3,3192	0.08	0.972
Substrate x Juvenile presence	5,3192	0.10	0.9916
Substrate x Density x TOD	15,3192	1.94	0.0162

* Bold values indicate significance after Sequential Bonferroni adjustment for multiple comparisons.

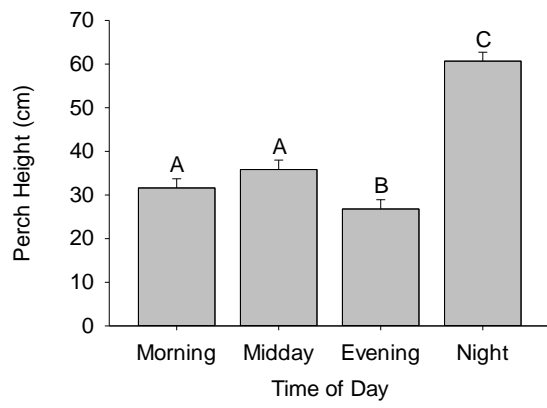Figure 1. Photographs of (A) the islands and (B) an enclosure used in this study.

Figure 2. Effect of TOD on juvenile perch height. Error bars are ± 1 standard error.
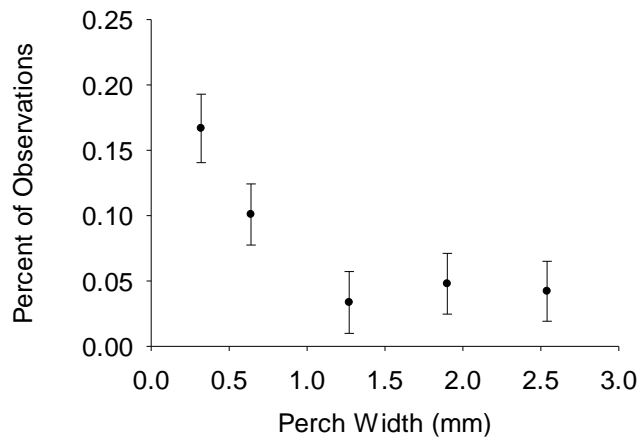
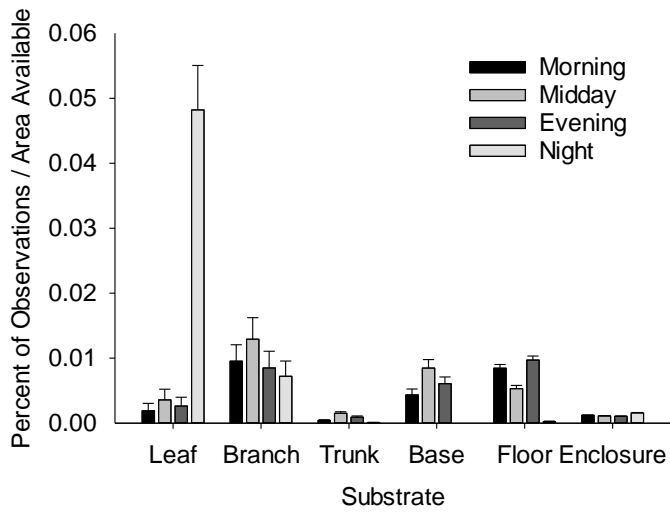Figure 3. Effect of width of perch on juvenile perch use.

Figure 4. Effect of TOD on juvenile substrate use. Error bars are ± 1 standard error.
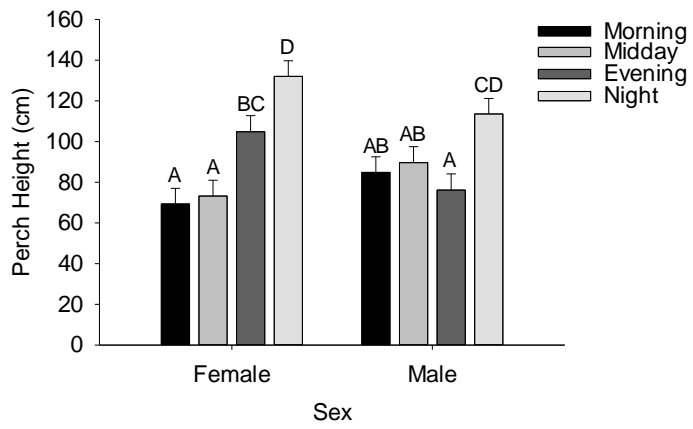
Figure 5. Effect of TOD and sex on adult perch height. Error bars are ± 1 standard error.
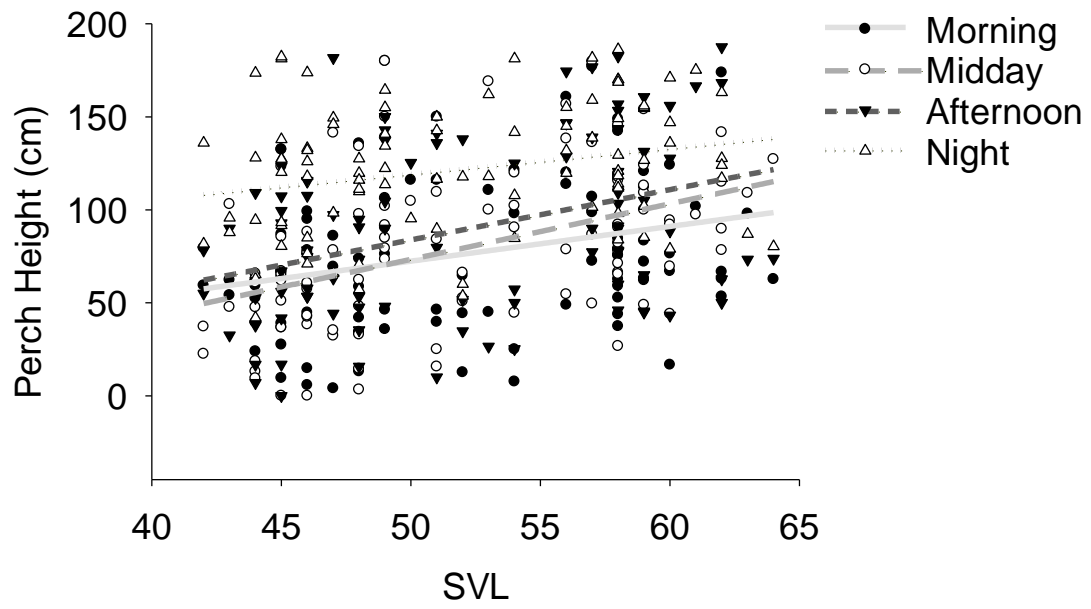
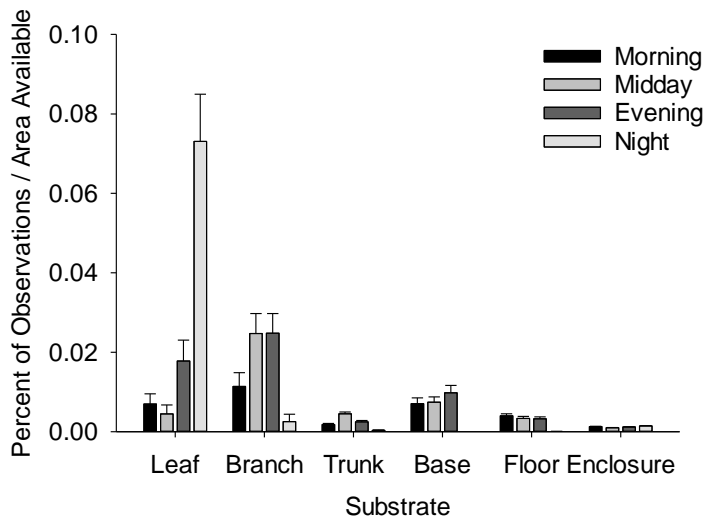Figure 6. Effect of TOD and SVL on adult perch height.

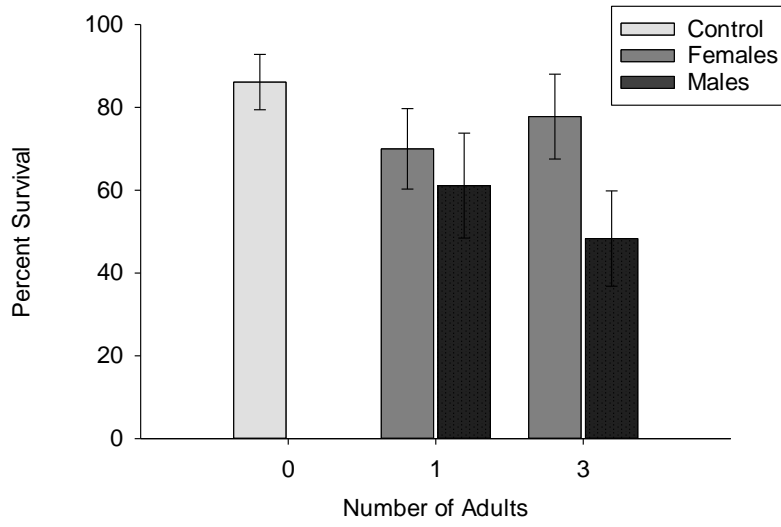Figure 7. Effect of TOD on adult substrate use. Error bars are ± 1 standard error.

Figure 8. Juvenile survival in response to adult male and female density. Error bars are ±

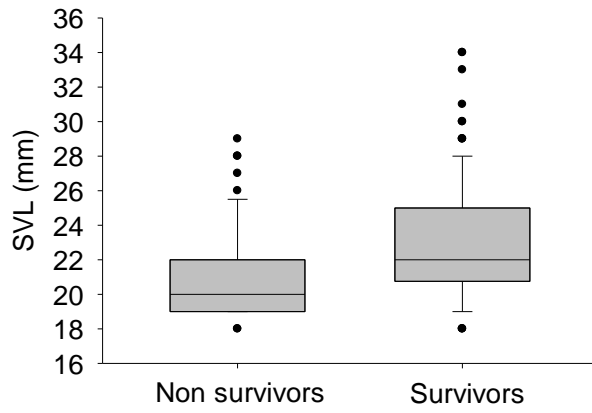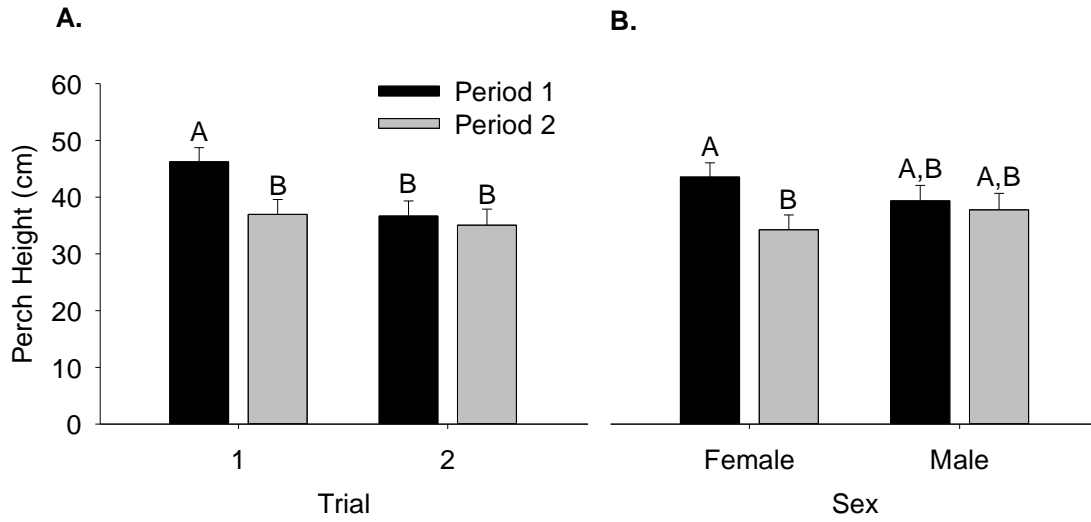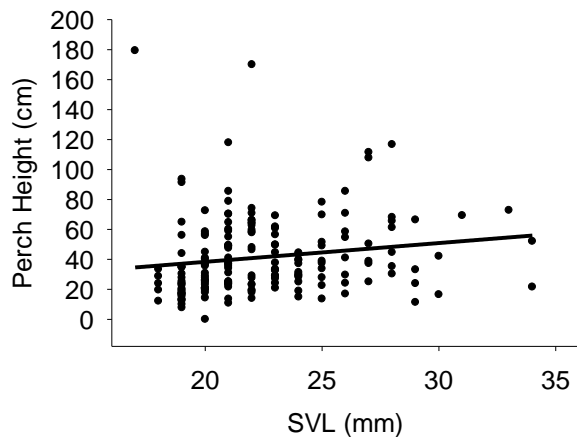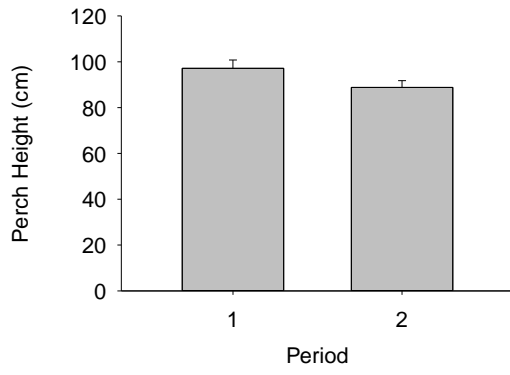1 standard error.

Figure 9. Effect of SVL on juvenile survival. Error bars are ± 1 standard error.

Supplementary Figure 1. Effect of (A) trial and (B) sex on juvenile perch height. Error bars are ± 1 standard error.

Supplementary Figure 2. Effect of SVL on juvenile perch height.

Supplementary Figure 3. Change in perch height for adult lizards between periods. Error

bars are ± 1 standard error.

CHAPTER FOUR

A SYNTHESIS

Habitat choice is an important and ubiquitous behavior that often determines how well organisms function (Huey 1991; Lenihan 1999; Aubret and Shine 2008). However, optimal habitats often differ across age classes, and accordingly, juveniles shift habitat choice as they age (Stamps 1983; Shine et al. 2003; Vagelli 2004; Montgomery et al. 2011). Many studies have documented ontogenetic habitat shifts for a variety of taxa including insects (Giller and McNeill 1981), fish (George and Hadley 1979; Werner and Hall 1979; Paine et al. 1982; Winemiller 1989; Hyndes et al. 1997), amphibians (Werner et al. 1995), reptiles (Lind and Welsh Jr. 1994), birds (Hunt and Hunt 1973; Davoren et al. 2003), and mammals (Theberge and Wedeles 1989; Kotler et al. 1993; Jones et al. 2001). However, despite the frequency of ontogenetic habitat shifts in nature, the causal factors driving age specific habitat variation are rarely determined. This is because most studies observationally document these behaviors rather than experimentally address questions regarding ontogenetic habitat shifts.

Competition for structural habitat has been a major driver in the diversification of the lizard genus *Anolis* (Williams 1983; Losos 2009). While many studies have examined interspecific variation in *Anolis* habitat use, much less is known about intraspecific variation, particularly between age-classes. Yet, there exists many reasons to expect differences in habitat use between adults and juveniles. There are often age-related

differences in resource needs (Hjelm et al. 2000) or predation risks (Foster et al. 1988; Werner and Hall 1988) that result in differential age-specific habitat use. There could also be direct competition between adults and juveniles, such that one age class if forced to less preferred habitat. However, many researchers focus efforts on studying adult biology rather than include juveniles. While this may be most feasible or appropriate for certain questions, studying only one age-class could lead to biased or limited conclusions about the ecology of the species or community.

To address these issues, I conducted a series of experiments that allowed me to examine the role of inter-age class competition in generating variation in microhabitat use in the brown anole lizard (*Anolis sagrei*). Field observations suggest that juveniles perch in open-canopy areas on low vegetation whereas adults reside in forest edges on higher vegetation. I hypothesized that this age-specific habitat variation is because adults force juveniles to less preferred habitat. In Chapter 2, I altered the density of adult males in mesh enclosures in the laboratory to examine the response of juvenile microhabitat choice. I found that juveniles decreased perch height and had complex density-dependent effects on perch width and substrate use in the presence of adult males. In Chapter 3, I conducted 2 simultaneous field experiments. The first experiment examined how adult male and female (independently) density affect juvenile microhabitat choice and survival. I found that high adult male density reduced juvenile survival, yet juveniles did not vary microhabitat choice in response to either adult male or female density. In addition, adults did not select against juveniles in a way that would contribute to the observed age-class habitat variation. The second experiment examined how juvenile presence influences

adult microhabitat choice. As predicted, neither adult male or female microhabitat choice was influenced by the presence of juveniles.

Overall, these experiments highlight the complexity of habitat use in *Anolis sagrei*, and show that microhabitat choice often varies depending on body size, sex, and TOD. I also found that adults are a sex- and density-dependent selective force on juveniles. In the lab, we found that juveniles modify microhabitat choice in response to adult males, but no evidence for this was found in the field. These inconsistent results may be explained by the relatively small juveniles used the field experiment. Thus, I suggest that the selective pressure from adults and/or other predators is strong enough that hatchlings innately stay low to the ground, whereas larger juveniles are able to shift microhabitat choice plastically depending on environmental context. Additionally, the size of the mesh enclosures restricted macrohabitat dispersal away from areas of high adult density, which may also play a role in juvenile habitat use.

The adaptive radiation of the lizard genus *Anolis* is one of the best studied terrestrial radiations. However, we know very little about the role of juveniles in these communities. These experiments show that inter-age class competition can influence how juveniles position themselves in the environment, and how adults can drive population dynamics. Understanding niche breadth and the processes that determine a species (rather than just adult) niche will provide more insight into the ecological and evolutionary processes that drive adaptive radiations such as the *Anolis* radiation.

REFERENCES

Aubret, F., and Shine, R. 2008. Early experience influences both habitat choice and locomotor performance in tiger snakes. The American Naturalist 171:524-531.

Davoren, G. K., Montevecchi, W. A., and Anderson, J. T. 2003. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. Marine Ecology Progress Series 256:229-242.

Foster, S.A., V.B. Garcia, and M.Y. Town. 1988. Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. Oecologia 74(4):577-585.

George, E. L., and Hadley, W. F. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. Transactions of the American Fisheries Society 108(3):253-261.

Giller, P. S., and McNeill, S. 1981. Predation strategies, resource partitioning and habitat selection in Notonecta (Hemiptera/Heteroptera). The Journal of Animal Ecology 50:789-808.

Hjelm, J., L. Persson, and B. Christensen. 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. Oecologia 122(2):190-199.

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist 137:S91-S115.

Hunt, G. L., and Hunt, M. W. 1973. Habitat partitioning by foraging gulls in Maine and northwestern Europe. The Auk 90(4):827-839.

Hyndes, G. A., Platell, M. E., and Potter, I. C. 1997. Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. Marine Biology 128(4):585-598.

Jones, M., Mandelik, Y., and Dayan, T. 2001. Coexistence of temporally partitioned spiny mice: roles of habitat structure and foraging behavior. Ecology 82(8):2164-2176.

Kotler, B. P., Brown, J. S., and Subach, A. 1993. Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. Oikos 67:548-556.

Lind, A. J., and Welsh, H. H. 1994. Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. Animal Behaviour 48(6):1261-1273.

Lenihan, H. S. 1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. Ecological Monographs 69:251-275.

Losos, J.B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. Univ. of Calf. Press.

Montgomery, C.E., K.R. Lips, and J.M. Ray. 2011. Ontogenetic Shift in Height of Sleeping Perches of Cope's Vine Snake, *Oxybelis brevirostris*. The Southwestern Naturalist 56(3):358-362.

Paine, M. D., Dodson, J. J., & Power, G. 1982. Habitat and food resource partitioning among four species of darters (Percidae: *Etheostoma*) in a southern Ontario stream. Canadian Journal of Zoology 60(7):1635-1641.

Shine, R., Shine, T., and Shine, B. 2003. Intraspecific habitat partitioning by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae): the effects of sex, body size, and colour pattern. Biological Journal of the Linnean Society 80(1):1-10.

Stamps, J.A. 1983. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). Behavioral Ecology and Sociobiology 12(1):19-33.

Theberge, J. B., and Wedeles, C. H. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Canadian Journal of Zoology 67(5):1285-1290.

Vagelli, A.A. 2004. Ontogenetic shift in habitat preference by *Pterapogon kauderni*, a shallow water coral reef apogonid, with direct development. Journal Information 2004(2):364-369.

Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pp. 326–370 in R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), Lizard ecology: studies of a model organism. Harvard University Press, USA.

Winemiller, K. O. 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan ilanos. Environmental Biology of Fishes 26(3):177-199.

Werner, E. E., and Hall, D. J. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60(2):256-264.

Werner, E. E., and D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 1352-1366.

Werner, E. E., Wellborn, G. A., and McPeek, M. A. 1995. Diet composition in postmetamorphic bullfrogs and green frogs: implications for interspecific predation and competition. Journal of Herpetology 29(4):600-607.

LIST OF GENERAL REFERENCES

Alford, R. A., and Crump, M. L. 1982. Habitat partitioning among size classes of larval southern leopard frogs, *Rana utricularia*. Copeia 1982:367-373.

Aubret, F., and Shine, R. 2008. Early experience influences both habitat choice and locomotor performance in tiger snakes. The American Naturalist 171:524-531.

Beuttell, K., and J.B. Losos. 1999. Ecological morphology of Caribbean anoles. Herpetological Monographs 13:1-28.

Blanckenhorn, W. U. 2005. Behavioral causes and consequences of sexual size dimorphism. Ethology 111(11):977-1016.

Bjorkqvist, K., Osterman, K., and Lagerspetz, K. M. 1994. Sex differences in covert aggression among adults. Aggressive behavior 20(1):27-33.

Caldwell, R. L., and Dingle, J. 1979. The influence of size differential on agonistic encounters in the mantis shrimp, *Gonodactylus viridis*. Behaviour 69(3):255-264.

Calsbeek, R. 2009. Sex-specific adult dispersal and its selective consequences in the brown anole, *Anolis sagrei*. Journal of Animal Ecology 78:617-624.

Calsbeek, R., and R.M. Cox. Experimentally assessing the relative importance of predation and competition as agents of selection. Nature 465:613-116.

Cates, C.D., D.M. Delaney, A.M. Buckelew, A.M. Durso, S.S. French, A.M. Reedy, and D.A. Warner. 2014. *Anolis sagrei* (Brown Anole). Cannibalism. Herpetological Review 45:491

Clark, D.L., and Gillingham, J.C. 1990. Sleep-site fidelity in two Puerto Rican lizards. Animal Behaviour 39:1138-1148.

Chandler, C.R., and Tolson, P.J. 1990. Habitat use by a boid snake, *Epicrates monensis*, and its anoline prey, *Anolis cristatellus*. Journal of Herpetology 24(2):151-157.

Cooper Jr, W. E., and Vitt, L. J. 1987. Deferred agonistic behavior in a long-lived scincid lizard *Eumeces laticeps*. Oecologia 72(3):321-326.

Coss, R. G. 1991. Context and animal behavior III: the relationship between early development and evolutionary persistence of ground squirrel antisnake behavior. Ecological Psychology 3(4):277-315.

Dahlgren, C.P., and D.B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81(8):2227-2240.

Davoren, G. K., Montevecchi, W. A., and Anderson, J. T. 2003. Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. Marine Ecology Progress Series 256:229-242.

Delaney D.M., A.M. Reedy, T.S. Mitchell, A.M. Durso, K.P. Durso, A.J. Morrison, and D.A. Warner. 2013. *Anolis sagrei*. Nest-site choice. Herpetological Review 44(2):314.

Delaney D.M., C.D. Cates, A.M. Buckelew, D.M. Delaney, A.M. Durso, S.S. French, A.M. Reedy, and D.A. Warner. 2014. *Anolis sagrei*. Prey stealing behavior. Herpetological Review 45(2):324-325.

Einum, S., Sundt-Hansen, L., and Nislow, K.H. 2006. The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. Oikos 113(3):489-496.

Englund, G., and Krupa, J. J. 2000. Habitat use by crayfish in stream pools: influence of predators, depth and body size. Freshwater biology 43:75-83.

Foster, S.A., V.B. Garcia, and M.Y. Town. 1988. Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. Oecologia 74(4):577-585.

George, E. L., and Hadley, W. F. 1979. Food and habitat partitioning between rock bass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. Transactions of the American Fisheries Society 108(3):253-261.

Gerber, G.P., 1999. A review of intraguild predation and cannibalism in *Anolis*. Anolis Newsletter 05:28-39.

Giller, P. S., and McNeill, S. 1981. Predation strategies, resource partitioning and habitat selection in Notonecta (Hemiptera/Heteroptera). The Journal of Animal Ecology 50:789-808.

Gilliam J.F., and D.F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:1856-1862.

Hamrin, S. F., and Persson, L. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. Oikos 47(2):223-232.

Hines, A. H., Lipcius, R. N., and Haddon, A. M. 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. Marine Ecology Progress Series 36:55-64.

Hjelm, J., L. Persson, and B. Christensen. 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. Oecologia 122(2):190-199.

Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist 137:S91-S115.

Hunt, G. L., and Hunt, M. W. 1973. Habitat partitioning by foraging gulls in Maine and northwestern Europe. The Auk 90(4):827-839.

Hyndes, G. A., Platell, M. E., and Potter, I. C. 1997. Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: implications for resource partitioning. Marine Biology 128(4):585-598.

Irschick, D.J., and J.B. Losos. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. The American Naturalist 154(3):293-305.

Irschick, D. J., Macrini, T. E., Koruba, S., and Forman, J. 2000. Ontogenetic differences in morphology, habitat use, behavior, and sprinting capacity in two West Indian *Anolis* lizards. Journal of Herpetology 34(3):444-451.

Irschick, D. J., VanHooydonck, B., Herrel, A., and Meyers, J. A. Y. 2005. Intraspecific correlations among morphology, performance and habitat use within a green anole lizard (*Anolis carolinensis*) population. Biological Journal of the Linnean Society 85(2):211-221.

Johnson, M.A., M. Leal, L. Rodriguez Schettino, A. Chamizo Lara, L.J. Revell, and J.B. Losos. 2008. A phylogenetic perspective on foraging mode evolution and habitat use in West Indian Anolis lizards. Animal Behaviour 75:555-563.

Jones, M., Mandelik, Y., and Dayan, T. 2001. Coexistence of temporally partitioned spiny mice: roles of habitat structure and foraging behavior. Ecology 82(8):2164-2176.

Keren-Rotem, T., Bouskila, A., and Geffen, E. 2006. Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*). Behavioral Ecology and Sociobiology 59(6):723-731.

King, D. I., Degraaf, R. M., Smith, M. L., and Buonaccorsi, J. P. 2006. Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). Journal of Zoology 269:414-421.

Kolbe, J. J., Glor, R. E., Schettino, L. R., Lara, A. C., Larson, A., and Losos, J. B. 2004. Genetic variation increases during biological invasion by a Cuban lizard. Nature 431(7005):177-181.

Kotler, B. P., Brown, J. S., and Subach, A. 1993. Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. Oikos 67:548-556.

Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. Journal of Mammalogy 54(1):14-32.

Lahti, D. C., Johnson, N. A., Ajie, B. C., Otto, S. P., Hendry, A. P., Blumstein, D. T., Coss, R. G., Donohue, K., and Foster, S. A. 2009. Relaxed selection in the wild. Trends in Ecology & Evolution, 24(9):487-496.

Lima S.L., N.C. Rattenborg, J.A. Lesku, and C.J. Amlaner. 2005. Sleeping under the risk of predation. Animal Behaviour 70:723-736.

Lind, A. J., and Welsh, H. H. 1994. Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. Animal Behaviour 48(6):1261-1273.

Lee, J. C., Clayton D., Eisenstein, S., and I. Perez. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. Copeia 1989:930–937.

Lenihan, H. S. 1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. Ecological Monographs 69:251-275.

Losos, J.B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. Univ. of Calf. Press.

Losos, J.B. 1990. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. Animal Behaviour 39(5):879-890.

Losos, J.B., and Irschick, D.J. 1996. The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. Animal Behaviour 51(3):593-602.

Losos, J.B., and B. Sinervo. 1989. The effects of morphology and perch diameter on sprint performance of Anolis lizards. Journal of Experimental Biology 145(1):23-30.

Losos, J.B., K.I. Warheit, and T.W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 287:70-73.

Losos, J.B., T.R. Jackman, A. Larson, K. de Queiroz, and L. Rodríguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science 279(5359):2115-2118.

Martins, M. 1993. Why do snakes sleep on vegetation in central Amazonia? Herpetological Review 24(3):83-84.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28(3):403-416.

McCallum, J. 1986. Evidence of predation by kiore upon lizards from the Mokohinau Islands. New Zealand journal of ecology 9:83-88.

Milinski, M. 1982. Optimal foraging: the influence of intraspecific competition on diet selection. Behavioral Ecology and Sociobiology 11(2):109-115.

Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62:1370-1386.

Moksnes, P. O., Lipcius, R. N., Pihl, L., and van Montfrans, J. 1997. Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. Journal of Experimental Marine Biology and Ecology 215(2):157-187.

Montgomery, C.E., K.R. Lips, and J.M. Ray. 2011. Ontogenetic Shift in Height of Sleeping Perches of Cope's Vine Snake, *Oxybelis brevirostris*. The Southwestern Naturalist 56(3):358-362.

Munday, P. L. 2001. Fitness consequences of habitat use and competition among coral-dwelling fishes. Oecologia 128(4):585-593.

Olsson, M., and Shine, R. 1997. The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. Journal of Evolutionary Biology 10(3):369-381.

O'Neill, K. M. 1983. The significance of body size in territorial interactions of male beewolves (Hymenoptera: Sphecidae, *Philanthus*). Animal Behaviour 31(2):404-411.

Pacala, S., and Roughgarden, J. 1982. Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. Science 217:444-446.

Paine, M. D., Dodson, J. J., and Power, G. 1982. Habitat and food resource partitioning among four species of darters (Percidae: *Etheostoma*) in a southern Ontario stream. Canadian Journal of Zoology 60(7):1635-1641.

Perry, G. 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. Canadian Journal of Zoology 74(7):1238-1245.

Polis, G.A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? American Naturalist 123(4):541-564.

Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology 885-899.

Salzburg, M. A. 1984. *Anolis sagrei* and *Anolis cristatellus* in southern Florida: a case study in interspecific competition. Ecology 14-19.

Schlosser, I. J. 1987. The role of predation in age-and size-related habitat use by stream fishes. Ecology 651-659.

Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49(4):704-726.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185(4145):27-39.

Schoener, T. W., and Schoener, A. 1980. Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. The Journal of Animal Ecology 49:19-53.

Schoener, T. W., and Schoener, A. 1982. Intraspecific variation in home-range size in some *Anolis* lizards. Ecology 63:809-823.

Schoener, T. W., Slade, J. B., & Stinson, C. H. 1982. Diet and sexual dimorphism in the very catholic lizard genus, *Leiocephalus* of the Bahamas. Oecologia 53(2):160-169.

Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68(2):113-151.

Shine, R., Shine, T., and Shine, B. 2003. Intraspecific habitat partitioning by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae): the effects of sex,

body size, and colour pattern. Biological Journal of the Linnean Society 80(1):1-10.

Singhal, S., Johnson, M. A., and Ladner, J. 2007. The behavioral ecology of sleep: Natural sleeping site choice in three *Anolis* lizard species. Behaviour 144(9):1033-1052.

Slotow, R., and Paxinos, E. 1997. Intraspecific competition influences food return-predation risk trade-off by White-crowned Sparrows. Condor 99(3):642-650.

Smale, L., Frank, L. G., and Holekamp, K. E. 1993. Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with adult females and immigrant males. Animal Behaviour 46(3):467-477.

Stamps, J.A. 1983. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). Behavioral Ecology and Sociobiology 12(1):19-33.

Stuart, Y. E., Campbell, T. S., Hohenlohe, P. A., Reynolds, R. G., Revell, L. J., and Losos, J. B. 2014. Rapid evolution of a native species following invasion by a congener. Science 346:463-466.

Theberge, J. B., and Wedeles, C. H. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Canadian Journal of Zoology 67(5):1285-1290.

Toft, C. A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985:1-21.

Tokarz, R. R. 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). Animal Behaviour 33(3):746-753.

Vagelli, A.A. 2004. Ontogenetic shift in habitat preference by *Pterapogon kauderni*, a shallow water coral reef apogonid, with direct development. Journal Information 2004(2):364-369.

Van Buskirk, J. 1992. Competition, cannibalism, and size class dominance in a dragonfly. Oikos 65(3):455-464.

Van Horne, B. 1982. Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in seral stages of coniferous forest. Ecology 63(4):992-1003.

Vitt, L. J., Cristina, T., Avila-Pires, S., Zani, P. A., and Espósito, M. C. 2002. Life in shade: the ecology of Anolis trachyderma (Squamata: Polychrotidae) in Amazonian Ecuador and Brazil, with comparisons to ecologically similar anoles. Copeia 2002(2):275-286.

Wapstra, E., Uller, T., While, G. M., Olsson, M., and Shine, R. 2010. Giving offspring a head start in life: field and experimental evidence for selection on maternal basking behaviour in lizards. Journal of evolutionary biology 23(3):651-657.

Warner, D.A., and Shine, R. 2007. Fitness of juvenile lizards depends on seasonal timing of hatching, not offspring body size. Oecologia 154:65-73.

Werner, E. E., and Hall, D. J. 1979. Foraging efficiency and habitat switching in competiting sunfishes. Ecology 60(2):256-264.

Werner, E. E., and D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 1352-1366.

Werner, E. E., Wellborn, G. A., and McPeek, M. A. 1995. Diet composition in postmetamorphic bullfrogs and green frogs: implications for interspecific predation and competition. Journal of Herpetology 29(4):600-607.

Whitaker, A. H. 1973. Lizard populations on islands with and without Polynesian rats, *Rattus exulans* (Peale). Proceedings of the New Zealand Ecological Society 20:121-130.

Williams, E.E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. Evolutionary Biology 6:47-89.

Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pp. 326–370 in R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), Lizard ecology: studies of a model organism. Harvard University Press, USA.

Winemiller, K. O. 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan ilanos. Environmental Biology of Fishes 26(3):177-199.

Yorks, D. T., Williamson, K. E., Henderson, R. W., Powell, R., and Parmerlee, J. S. 2003. Foraging behavior in the arboreal boid *Corallus grenadensis*. Studies on Neotropical Fauna and Environment 38(3):167-172.
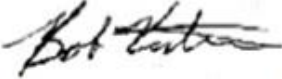
APPENDIX A

CHAPTER TWO IACUC APPROVAL

THE UNIVERSITY OF ALABAMA AT BIRMINGHAM

Institutional Animal Care and Use Committee (IACUC)

NOTICE OF APPROVAL

DATE: September 17, 2013

TO: DANIEL A WARNER, Ph.D.
CH -100
(205) 934-9674

FROM:

Robert A. Kesterson, Ph.D., Chair
Institutional Animal Care and Use Committee (IACUC)

SUBJECT: Title: Perch Site Selection Behavior in the Brown Anole Lizard
Sponsor: Internal
Animal Project_Number: 130909975

As of September 17, 2013 the animal use proposed in the above referenced application is approved.
The University of Alabama at Birmingham Institutional Animal Care and Use Committee (IACUC)
approves the use of the following species and number of animals:

Species	Use Category	Number In Category
Lizards	A	175

Animal use must be renewed by September 16, 2014. Approval from the IACUC must be obtained
before implementing any changes or modifications in the approved animal use.

**Please keep this record for your files, and forward the attached letter to the appropriate granting
agency.**

Refer to Animal Protocol Number (APN) 130909975 when ordering animals or in any correspondence
with the IACUC or Animal Resources Program (ARP) offices regarding this study. If you have concerns
or questions regarding this notice, please call the IACUC office at (205) 934-7692.

Institutional Animal Care and Use Committee (IACUC) | Mailing Address:
CH19 Suite 403 | CH19 Suite 403
933 19th Street South | 1530 3rd Ave S
(205) 934-7692 | Birmingham, AL 35294-0019
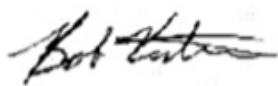FAX (205) 934-1188

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THE UNIVERSITY OF ALABAMA AT BIRMINGHAM

Institutional Animal Care and Use Committee (IACUC)

MEMORANDUM

DATE: September 17, 2013

TO: DANIEL A WARNER, Ph.D.
                CH -100
                (205) 934-9674

FROM:

Robert A. Kesterson, Ph.D., Chair
Institutional Animal Care and Use Committee (IACUC)

SUBJECT: NOTICE OF APPROVAL - Please forward this notice to the appropriate granting
                agency.

The following application was approved by the University of Alabama at Birmingham Institutional Animal
Care and Use Committee (IACUC) on September 17, 2013.

Title: Perch Site Selection Behavior in the Brown Anole Lizard
Sponsor: Internal

This institution has an Animal Welfare Assurance on file with the Office of Laboratory Animal Welfare
(OLAW), is registered as a Research Facility with the USDA, and is accredited by the Association for
Assessment and Accreditation of Laboratory Animal Care International (AAALAC).

Institutional Animal Care and Use Committee (IACUC)
CH19 Suite 403
933 19th Street South
(205) 934-7692
FAX (205) 934-1188

Mailing Address:
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Birmingham, AL 35294-0019
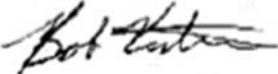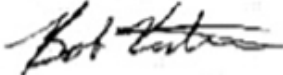
APPENDIX B

CHAPTER THREE IACUC APPROVAL

THE UNIVERSITY OF ALABAMA AT BIRMINGHAM

Institutional Animal Care and Use Committee (IACUC)

NOTICE OF APPROVAL

DATE: April 23, 2014

TO: DANIEL A WARNER, Ph.D.
              CH -100
              (205) 934-9674

FROM:

Robert A. Kesterson, Ph.D., Chair
Institutional Animal Care and Use Committee (IACUC)

SUBJECT: Title: How is Juvenile Perch Use Behavior Affected by Adult Densities in a Territorial
               Lizard
               Sponsor: Internal
               Animal Project_Number: 140410081

As of April 23, 2014 the animal use proposed in the above referenced application is approved. The
University of Alabama at Birmingham Institutional Animal Care and Use Committee (IACUC) approves
the use of the following species and number of animals:

Species	Use Category	Number In Category
Lizards	A	336

Animal use must be renewed by April 22, 2015. Approval from the IACUC must be obtained before
implementing any changes or modifications in the approved animal use.

**Please keep this record for your files, and forward the attached letter to the appropriate granting
agency.**

Refer to Animal Protocol Number (APN) 140410081 when ordering animals or in any correspondence
with the IACUC or Animal Resources Program (ARP) offices regarding this study. If you have concerns
or questions regarding this notice, please call the IACUC office at (205) 934-7692.

THE UNIVERSITY OF ALABAMA AT BIRMINGHAM

Institutional Animal Care and Use Committee (IACUC)

MEMORANDUM

DATE: April 23, 2014

TO: DANIEL A WARNER, Ph.D.
CH -100
(205) 934-9674

FROM:

Robert A. Kesterson, Ph.D., Chair
Institutional Animal Care and Use Committee (IACUC)

SUBJECT: **NOTICE OF APPROVAL - Please forward this notice to the appropriate granting agency.**

The following application was approved by the University of Alabama at Birmingham Institutional Animal Care and Use Committee (IACUC) on April 23, 2014.

Title: How is Juvenile Perch Use Behavior Affected by Adult Densities in a Territorial Lizard
Sponsor: Internal

This institution has an Animal Welfare Assurance on file with the Office of Laboratory Animal Welfare (OLAW), is registered as a Research Facility with the USDA, and is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care International (AAALAC).

Institutional Animal Care and Use Committee (IACUC)
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