ORIGINAL ARTICLE

Age- and sex-specific variations in microhabitat and macrohabitat use in a territorial lizard

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Abstract

Animals should select microhabitats with features that enhance fitness. However, the fitness benefits of different habitats may vary across ages and between sexes. By quantifying microhabitat choice in relation to age or sex, as well as the specific fitness consequences of habitat selection, we can better understand the factors that shape the way organisms distribute themselves across landscapes. Studies of *Anolis* lizards have provided critical insights into population and community structure, but most studies have focused on interspecific variation in habitat use, rather than intraspecific patterns. We quantified habitat use of *Anolis sagrei* at two scales (microhabitat and macrohabitat) for males and females of two distinct age classes (juvenile vs adult). We show that age, sex, size, and macrohabitat have significant effects on how *A. sagrei* utilize available microhabitat and that age, sex, size, and season influence macrohabitat use. In addition, large individuals of both age classes had increased survival during the breeding season. However, body size did not influence overwinter survival, but lizards that used relatively low perches had increased overwinter survival. Overall, this study demonstrates that the complex variation in habitat use by *A. sagrei* is explained by interactions among age, sex, size, season, and habitat scale.

Significance statement

Habitat choice behaviors can have important effects on fitness, yet optimal habitat may vary across ages and between sexes. In this paper, we quantified microhabitat and macrohabitat use of the brown anole lizard (*Anolis sagrei*) and subsequently estimated selection on these behaviors via mark recapture. We show that the complex variation in habitat use by *A. sagrei* is explained by interactions among age, sex, size, season, and habitat scale. In addition, body size influenced survival of both age classes during the breeding season but not over winter. However, lizards that used relatively low perches had increased overwinter survival. These findings provide new insights into the factors that shape the way these organisms distribute themselves across landscapes and provide a rare assessment of selection on behavioral traits.

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Introduction

How an individual uses its habitat can have important fitness consequences. Thus, choices that animals make with regards to habitat characteristics should be under strong natural selection (Munday 2001; King et al. 2006). Indeed, differential survival across large-scale habitat types (e.g., grassland vs

forest habitats) has been well documented for many organisms (Tupper and Boutilier 1995; Ginsberg and Zhioua 1996; Gabbert et al. 1999; Chouinard and Arnold 2007). However, despite the potential for behavioral choice of habitat to affect fitness, relatively few studies estimate fitness consequences associated with small-scale microhabitat use (e.g., perch height) across different macrohabitat types. Nevertheless, habitat characteristics that affect fitness may vary spatially or temporally depending on environmental context or an individual's phenotype. For example, the quality of habitat can depend upon predator density (Schlosser 1987; Heithaus and Dill 2002; Mao et al. 2005), competitor density (Robertson 1996), and resource abundance, and the importance of these factors may vary among individuals depending upon their body size (Ardia and Bildstein 1997; Englund and Krupa 2000). Thus, a broad range of environmental factors and phenotypic variation can synergistically influence how natural selection operates on behaviors associated with habitat use.

Individuals of different age classes often vary in habitat requirements (Stamps 1983; Shine et al. 2003; Vagelli 2004; Montgomery et al. 2011). First, adults and juveniles must satisfy different needs across life history stages. For example, adults may occupy locations that enhance conspicuousness for territorial or sexual communication, despite increased predation risk (Hedrick 2000; Husak et al. 2006). On the other hand, juveniles should choose habitats that minimize predation or maximize growth. Second, juveniles are often at a greater risk of predation because of their small body size and lack of experience (Foster et al. 1988; Werner and Hall 1988) and may use habitats with more shelter (Schlosser 1987; Tabor and Wurtsbaugh 1991; Lindholm et al. 1999). Third, resource needs (Hjelm et al. 2000) or performance (Irschick et al. 2000; Irschick et al. 2005) may change depending on body size and can vary by habitat. Lastly, direct competition between adults and juveniles can force one age class to less preferred habitat (Van Horne 1982; Keren-Rotem et al. 2006).

Life history variation between adult males and females can also lead to differential habitat use. For example, females often use areas that are adequate for parturition or oviposition during certain seasons (Angilletta et al. 2009), whereas males may have more flexibility in choosing habitat (Barten et al. 2001; Blaustein et al. 2004; Barbknecht et al. 2011). For species that exhibit parental care, the sex that cares for young benefits by using habitat that increases offspring growth or survival (Young and Isbell 1991; Barten et al. 2001; Stokke and Toit 2002). In addition, females may forage in different habitats than males due to their greater energetic demands during reproduction (Boinski 1988; Blouin-Demers and Weatherhead 2001). In contrast, males often spend more time defending territories or engaged in social displays (Andrews 1971; Wells 1977; Williams et al. 2004). For example, males

of the arboreal lizard, *Anolis polylepis*, occupy higher perches than females and spend the majority of their time engaged in social interactions (mostly with other males), whereas females spend the majority of their time foraging (Andrews 1971).

Habitat use and competition for specific microhabitats are known to be important factors responsible for the diversity seen in many adaptive radiations (Schluter 1994; Rainey and Travisano 1998; Gillespie 2004). *Anolis* lizards across the Caribbean islands provide an excellent example of diversification due to habitat competition (Williams 1983; Losos 2009). Specifically, phylogenetically distant species, that occupy similar microhabitats, have evolved similar ecological (Williams 1972; Losos 1990; Johnson et al. 2008) and morphological (Losos et al. 1998; Beuttell and Losos 1999) characteristics. Most notably, species that occupy narrow perches have evolved short limbs, whereas species that occupy broad perches have longer limbs. Performance studies have shown that this limb-length-to-perch-width matching is adaptive, such that locomotor performance is enhanced (Losos and Sinervo 1989; Irschick and Losos 1999). Furthermore, a number of studies have shown that sympatric species partition habitat (Schoener 1968; Pacala and Roughgarden 1982; Pacala and Roughgarden 1985; Leal and Fleishman 2002; Stuart et al. 2014), likely a consequence of habitat competition.

While many studies have examined interspecific variation in habitat use in *Anolis* lizards, considerably less is known about intraspecific variation, particularly across age classes and between the sexes. Moreover, the age- and sex-specific fitness consequences of habitat choice remain poorly understood. The brown anole (*Anolis sagrei*) is particularly well suited for addressing these issues because they occupy a broad range of habitat types (Schoener 1968), occur in high densities, and strongly compete for territory space (Schoener and Schoener 1980; Tokarz 1985), and age class- and sex-specific habitat use is easily and readily identified. Moreover, anecdotal observations during our field work with *A. sagrei* suggest that juveniles perch on low vegetation, whereas adults use taller and thicker vegetation. We tested these observations by quantifying habitat use at two scales (microhabitat and macrohabitat) for males and females of two distinct age classes (juvenile vs adult). We predicted that adults would use higher/thicker perches than juveniles and would be more frequently found in forested habitat than in open-canopy habitat. We also predicted that adult males would use higher and thicker perches, which would enhance conspicuousness for social interactions, whereas females would use lower perches that may reduce predation risk (Andrews 1971). Age-specific habitat use should also shift through time due to seasonal changes in the relative abundance of offspring/juveniles. Fitness consequences of these habitat choices were then examined via estimates of survival using a mark-recapture study. Because high/thick perches likely increase conspicuousness, we

predicted that lizards using these microhabitats would have reduced survival.

Methods

We studied a population of *A. sagrei* on a small island (Fig. 1) in the Halifax River, in Ormond Beach, Florida. This island was created, along with many others, when the US Army Corps of Engineers dredged the Intracoastal Waterway and piled sediment to the side of the channel from 1953 to 1961. The island consisted of the following three macrohabitats: forest, open-canopy, and an intermediate habitat along the ecotone of the forest and open-canopy habitats (Fig. 1). The periphery of the island consisted primarily of open-canopy habitat with very few trees, and the vegetation consisted of mostly mangrove stems and grasses. The center of the island was forested and had sparse understory growth. We considered the first 5 m of open-canopy outside of the forest edge as the intermediate habitat. The island also contained a small, sparsely vegetated area covered with bare sand in the interior of the forest; relatively few lizards were observed in this area so we did not consider it in this study.

We captured 717 *A. sagrei* from 7 July 2014 to 27 July 2014 during daylight hours using hand and noose techniques. We recorded perch height, perch diameter, and substrate (i.e., ground vs vegetation). Some microhabitat measurements were not taken for some individuals because the lizard's location prior to disturbance from the observer was unknown. Macrohabitat (defined above as forest, open-canopy, or intermediate) was recorded for each lizard. Sex was identified by dorsal pattern and the presence (males) or absence (females) of enlarged post-cloacal scales. Snout-vent length (SVL), tail length (to

nearest millimeter), and mass (to nearest 0.01 g) were measured for each individual. Females less than 34-mm SVL and males less than 39-mm SVL were considered juveniles and those equal to or larger as adults (Lee et al. 1989). Each lizard was marked with a unique toe clip. A subset of the lizards ($n = 281$) were housed in mesh field enclosures ($0.61 \times 0.61 \times 1.8$ m) for 4–8 days for another experiment (Delaney 2015) and then released. Because this experiment had no effect on survival (logistic regression, $P \geq 0.1780$), these lizards were incorporated into the present study. All other lizards were released within 24 h of capture after they had been measured. All lizards were released haphazardly throughout the forested habitat. We returned to the island from 30 September 2014 to 2 October 2014 and again from 21 March 2015 to 25 March 2015 to estimate survival via mark recapture. Survival from the initial capture (July) to the first recapture (October) occurred during the reproductive/activity season, and survival from the first recapture to the second recapture (March) occurred mostly over the winter.

In addition to recapturing marked individuals during our resampling trips, we visually classified non-recaptures as either adult or juvenile and recorded their sex and the macrohabitat where they were captured. We used these data along with demographic data from the initial sample to examine seasonal variation in macrohabitat use between sexes and age classes. A subset of lizards collected during the July sampling period were excluded from analyses of macrohabitat use because we targeted specifically juveniles or adults up to 19 July 2014 for another study; after this period, we collected another 419 individuals without targeting any specific age class. Thus, for analyses on macrohabitat use, we used data from 419, 765, and 905 lizards from the July, October, and March sampling trips, respectively. These lizards were released at the end of each sampling period, thus eliminating

Fig. 1 **a** Aerial photograph of the study island and ground-level photos of the **b** open-canopy and **c** forested habitats. The area between the two *black circles* represents the intermediate habitat. Note the sparsely vegetated area within the forest; lizards were rarely captured in this area, and it was not considered in this study
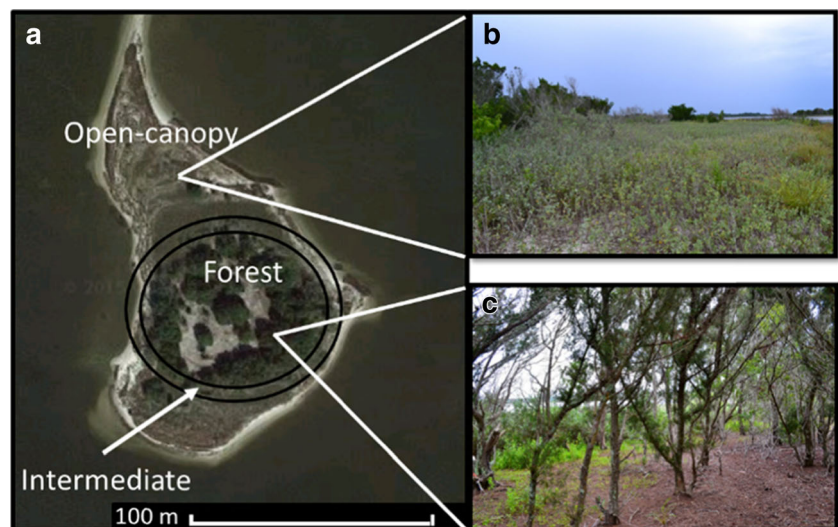
the potential for multiple measurements of the same individual (i.e., pseudoreplication) within each period. It was not possible to record habitat use data blind because our study involved animals of mostly known sex and age classes in the field. Recapture efforts were blind in the sense that we did not know an individual's prior habitat use until data analysis.

Statistical analyses

All analyses were performed with SAS software (version 9.4). The distribution of perch height skewed toward low heights, and transformation did not improve normality. Therefore, Friedman's two-way non-parametric analysis of variance was used to quantify the effects of age class, sex, macrohabitat, and all interactions on perch height. Mann–Whitney U tests were used to evaluate differences among levels for each significant factor. A general linear model (GLM) was used to quantify the effects of age class, sex, macrohabitat, and all interactions on perch diameter (log transformed). We used a logistic regression to quantify the effects of age class, sex, macrohabitat, and all interactions on substrate use (ground vs vegetation). Regressions were used to quantify relationships between SVL and perch height (linear), diameter (log transformed and linear), and substrate (logistic) within each demographic group. A generalized linear model was used to quantify the effects of age class, sex, month, and all interactions on macrohabitat use. The effects of age class, sex, microhabitat, and their interactions on lizard body size were tested with a GLM using SVL as a dependent variable. Only significant interactions that included macrohabitat were kept in the final model.

Logistic regression was used to quantify the strength of directional selection on the continuous behavioral and morphological variables that were measured (Janzen and Stern 1998). Survival was a binomial dependent variable, and the independent variables (perch height, diameter, and SVL) were standardized to a mean of zero and unit variance prior to analysis. In order to normalize perch height (prior to standardization), we removed individuals perched on the ground (i.e., height = 0) and log transformed the remaining height measurements. However, this reduced sample size by 40 % (144/364) for the October recapture and 35 % (33/95) for the March recapture. Therefore, we ran models with height transformed and untransformed. Separate models were run for each recapture period, and adults and juveniles were analyzed separately for the first recapture period (October). Nearly all (88 %) juveniles from the original capture that were recaptured in October had attained adult body size by the October sampling period. Therefore, we did not separate age classes for the analyses that assess phenotypic selection over winter. Lizards that were recaptured in March, but were missed during our recapture efforts in October ($n = 46$), were considered

alive in October. Logistic regression was also used to assess the effects of age class (only up to October 2014), sex, and substrate use on survival. Because we did not release animals to their exact location of capture, we did not test for macrohabitat effects on survival.

Results

Microhabitat

Adult males perched higher than adult females, but sex did not influence juvenile perch height (Fig. 2a and Table 1). Overall, juveniles used significantly lower (Fig. 2a and Table 1) and thinner (Fig. 2b and Table 1) perches than adults. Similarly, juveniles were found on the ground more often than adults (Fig. 3a and Table 1). However, within the forest, both age classes perched relatively high (Fig. 2c and Table 1) and on thick perches (Fig. 2d and Table 1) compared to lizards in the intermediate or open-canopy macrohabitats. Vegetation was used most frequently in the forest, followed by the open-canopy, and then the intermediate zone (Fig. 3b and Table 1). Males and females did not differ in the perch diameter that they used (Table 1), but females were found on the ground more frequently than males (Fig. 3c and Table 1). Within each demographic group, body size did not influence perch height ($P \geq 0.1222$; Supplementary Table 1). However, large adult males were found more frequently on vegetation, whereas small adult males were located more often on the ground (Supplementary Fig. 1a), and large adult females used thicker perches than small adult females (Supplementary Fig. 1b and Supplementary Table 1). Body size of other demographic
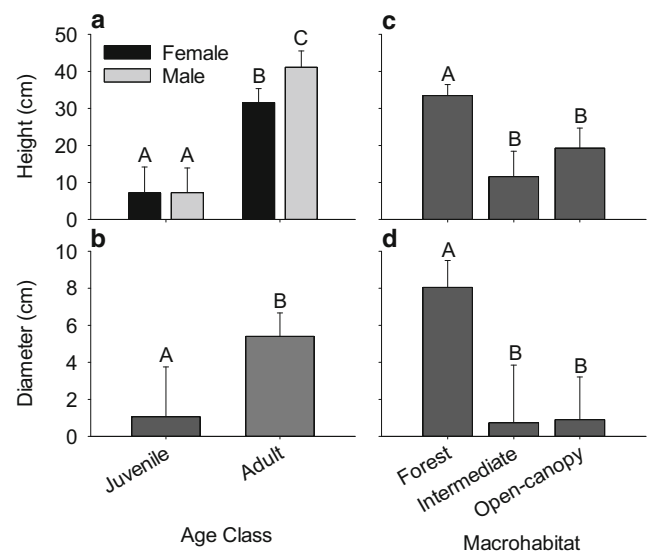

Fig. 2 Effects of age class on **a** perch height and **b** perch diameter and the effects of macrohabitat on **c** perch height and **d** perch diameter. *Error bars* are ±1 standard error. Statistical results are reported in Table 1

Table 1 Effects of demographic variables (age class and sex) and snout-vent length (SVL) on microhabitat (perch height, diameter, and substrate) and macrohabitat use

Variables	df	F value	P value
Perch height			
Age class	1	40.75	<0.0001
Sex	1	1.72	0.1902
Macrohabitat	2	5.24	0.0057
Age class × sex	1	4.64	0.0318
Perch diameter			
Age class	1,215	5.5	0.0199
Sex	1,215	1.2	0.2753
Macrohabitat	2,215	27.35	<0.0001
Substrate			
Age class	1,380	40.43	<0.0001
Sex	2,380	3.58	0.0289
Macrohabitat	1,380	4.73	0.0302
Macrohabitat			
Age class	1, 2000	5.27	0.0218
Sex	1, 2000	8.03	0.0046
Month	2, 2000	11.12	<0.0001
Age class × month	2, 2000	14.87	<0.0001
SVL			
Age class	1,645	2,099.42	<0.0001
Macrohabitat	2,645	10.94	<0.0001
Age class × macrohabitat	2,645	30.39	<0.0001

groups did not influence perch diameter or substrate ($P \geq 0.0549$; Supplementary Table 1).

Macrohabitat

We captured 8.9, 11.4, and 13.5 lizards per person per hour in the forest, intermediate, and open-canopy macrohabitats, respectively. Sex ratios were nearly 1:1 in each habitat type, with slightly more males than females captured in the intermediate (54 % male) and open canopy (55 % male), compared to the forest (46 % male; Table 1). Overall, adults were captured more frequently than juveniles across all time periods
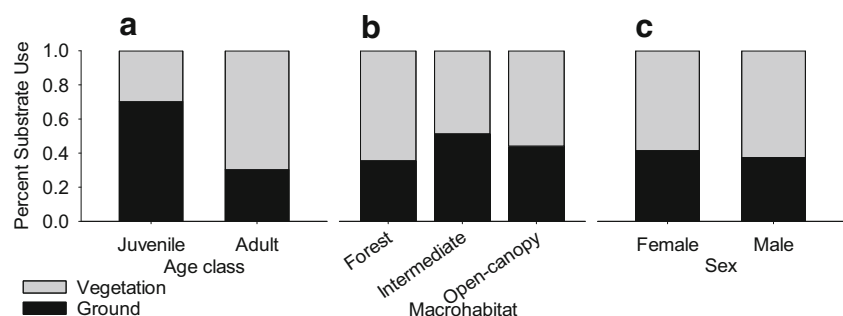
(78 % adults). The relative abundance of juveniles (i.e., juvenile/adult ratio) was highest in October and lowest in March (Fig. 4 and Table 1). In July, relative juvenile abundance was highest in open-canopy habitat, followed by forest, and then intermediate habitat. In October, the relative abundance of juveniles was highest in the open-canopy and intermediate habitats compared to the forest. However, in March, this trend reversed and the relative abundance of juveniles was highest in the forest. Juvenile body size increased in each successional macrohabitat away from the forest (Fig. 5 and Table 1). In contrast, adult body size was smallest in the open-canopy habitat and largest in the forest.

Survival

Adult survival (39 %) was significantly higher than juvenile survival (15 %) from July to October ($\chi^2 = 9.8393$, $P = 0.0017$). During this time, adults (Fig. 6a and Table 2) and juveniles (Fig. 6b and Table 2) experienced significant positive directional selection on SVL. Snout-vent length did not influence survival over winter (Fig. 6c and Table 2). In contrast, perch height (untransformed) did not influence survival over the reproductive season for adults (Fig. 6a and Table 2) or juveniles (Fig. 6b and Table 2). However, lizards experienced significant negative directional selection on perch height over winter (Fig. 6c and Table 2). This pattern remained the same when using transformed height, albeit marginally non-significant ($\chi^2 = 3.3628$, $P = 0.0667$). Sex, substrate, and diameter did not significantly affect survival during either time period (all P values ≥ 0.209).

Discussion

Microhabitat has played an important role in the evolution of *Anolis* lizards (Williams 1972, 1983; Losos 2009). Despite extensive research on interspecific variation in habitat use, relatively little is known about variation in habitat use within a species. To address this, we examined microhabitat and macrohabitat use between age classes and sexes of *A. sagrei*. We found that adults and juveniles vary in perch height, width, and substrate and that males and females differ in perch height

Fig. 3 Proportion of substrate use (vegetation vs ground) with respect to **a** age class, **b** macrohabitat, and **c** sex. Statistical results are reported in Table 1

Fig. 4 Proportion of adults and juveniles captured in each macrohabitat during **a** July, **b** October, and **c** March. Statistical results are reported in Table 1
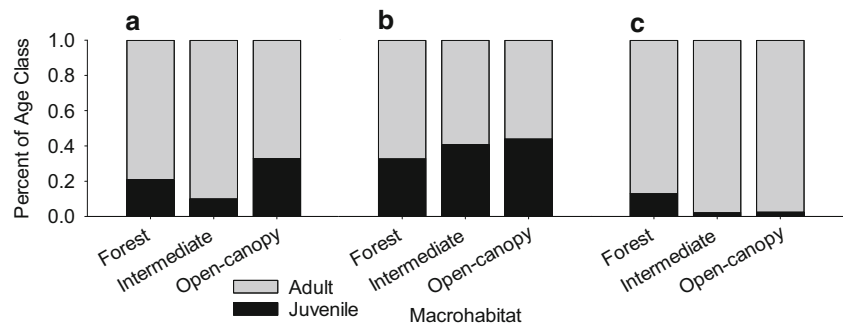
(adults only) and substrate use. Within demographic groups, body size influenced adult female perch width and adult male substrate use. Macrohabitat use varied by sex, age class, size, and across season. Large individuals of both age classes had increased survival during the breeding season, but body size did not influence overwinter survival. In addition, lizards that used low perches had higher overwinter survival. This study also demonstrates complex variation in microhabitat and macrohabitat use by *A. sagrei* that depends upon age, sex, size, and season.

In line with our predictions, juveniles perched on significantly lower and thinner perches and used the ground relatively more than adults. Similar shifts in perch height, width, and substrate with age have been reported for *A. carolinensis* (Jenssen et al. 1998), *A. hendersoni* (Moermond 1979), and *A. nebulosus* (Ramírez-Bautista and Benabib 2001), as well as other lizard genera (*Iguana iguana* (Henderson 1974) and *Chamaeleo chamaeleon* (Keren-Rotem et al. 2006)). Juveniles are likely at a greater risk of predation than adults, which may be reduced by occupying the ground or low and thin perches that reduce conspicuousness to diurnal visually oriented predators. The use of low perches may not only enable juveniles to perform well (Moermond 1979) but also to avoid the negative impacts of agonistic interactions with larger adults, as reported in *C. chamaeleon* (Keren-Rotem et al. 2006). Indeed, the small size and short limbs of juveniles
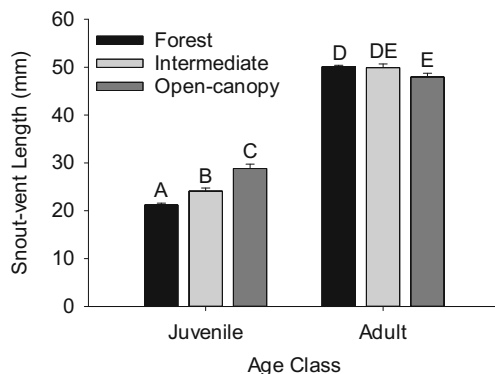
might enable them to outperform adult lizards on low and thin perches, similar to that reported in comparisons of short- vs long-limbed species (Losos and Sinervo 1989; Irschick and Losos 1999; Calsbeek and Irschick 2007). Interestingly, we also found that large adult females used thicker perches than small adult females, which may similarly enhance performance. Alternatively, competition for resources may drive age classes to partition habitat, as suggested for interspecific variation observed among *Anolis* species (Schoener 1968; Pacala and Roughgarden 1982; Stuart et al. 2014). Similar habitat partitioning among age classes has been suggested 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 1994), birds (Hunt and Hunt 1973; Davoren et al. 2003), and mammals (Theberge and Wedeles 1989; Kotler et al. 1993; Jones et al. 2001).

As predicted, adult males perched higher than adult females, which have also been found for other *Anolis* species (*A. cristatellus*, *A. stratulus* (Kolbe et al. 2015), and *A. polylepis* (Andrews 1971)). In addition, females were located on the ground slightly more often than males, and large adult males were observed on vegetation more often than small adult males. The use of high vegetation may enhance a male's ability to interact with conspecifics for social displays. In contrast, females may perch low and on the ground to enhance foraging efficiency or reduce movement when ovipositing eggs in soil (Warner and Shine 2008).

Microhabitat (perch height, diameter, and substrate) use varied substantially across the different macrohabitat types. Lizards in the forest used higher and thicker perches and had lower vegetation use than lizards in the open-canopy or intermediate habitats. These variations in microhabitat use across macrohabitat are likely a result of microhabitat availability. For example, the forested habitat contains taller and thicker vegetation with more horizontal branches than the open-canopy or intermediate habitats because it contains nearly all of the trees on the island. Thus, lizards in the forest are able to utilize microhabitats that are limited in the other macrohabitats. This variation

Fig. 5 Body size variation between macrohabitats for juveniles and adults. *Error bars* are ±1 standard error. Statistical results are reported in Table 1

Fig. 6 Standardized selection surfaces for snout-vent length (SVL) and perch height. Probability of survival for **a** adults from July to October, **b** juveniles from July to October, and **c** adults over winter in relation to standardized SVL (*left column*) and perch height (*right column*). Nearly all juveniles from the original capture that were recaptured in October had attained adult body size. Thus, we did not separate age classes for the analysis of overwinter survival. The selection surfaces were estimated using cubic splines (Schluter 1988). *Dashed lines* represent standard errors calculated with Bayesian methods. *Open circles along the top and bottom axes* represent individual lizards. Statistical results are reported in Table 2
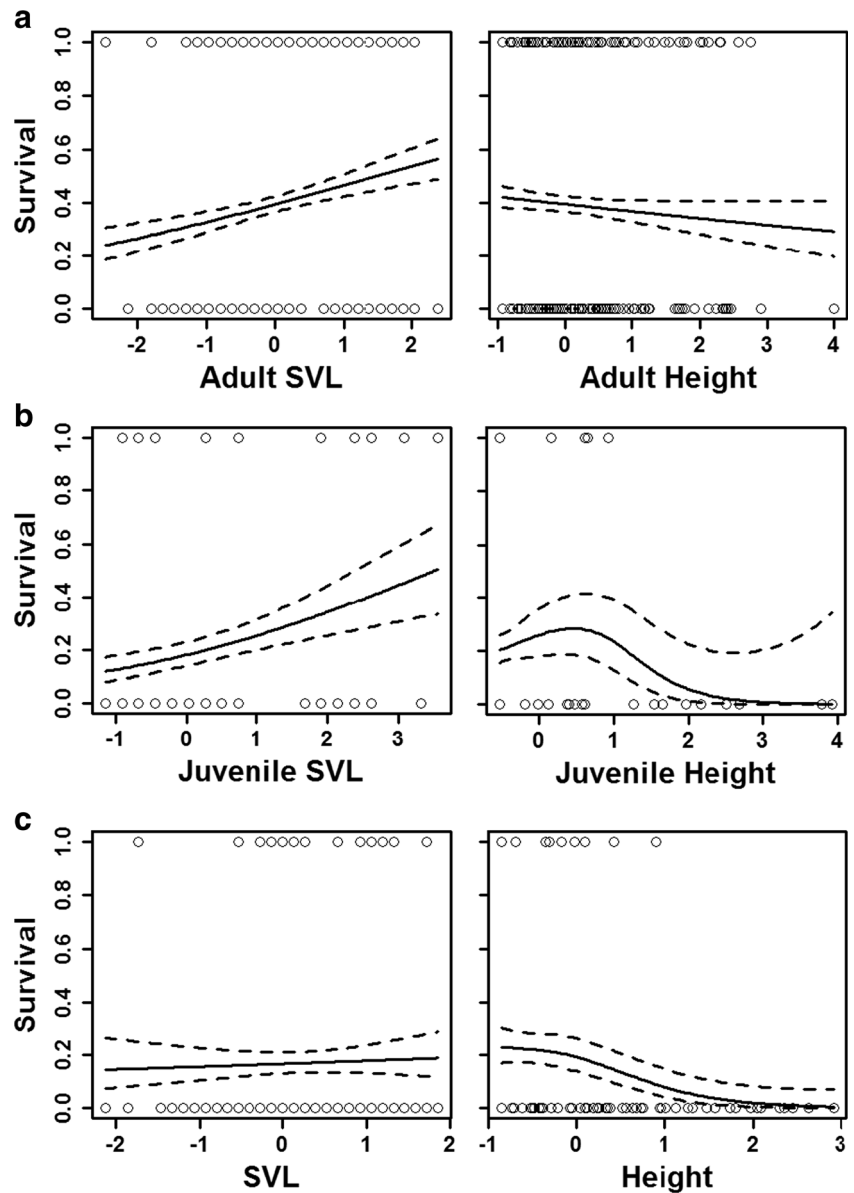

Table 2 Effects of snout-vent length (SVL) and perch height on survival from July to October and over winter

Variables	Average selection gradient (β)	SE	χ^2	P value
July–October survival				
Juvenile SVL	0.4476	0.2154	4.3188	0.0377
Juvenile height	−0.3448	0.3828	0.8113	0.3677
Adult SVL	0.1850	0.0736	6.3109	0.0120
Adult height	−0.0926	0.0766	1.4611	0.2268
Overwinter survival				
SVL	0.1267	0.1280	0.9804	0.3221
Height	−0.3041	0.1532	3.9420	0.0471

Adults and juveniles were analyzed separately for the July–October period. However, nearly all individuals recaptured in October had attained adult body size. Thus, we did not separate age classes for the analysis of survival over winter

in microhabitat availability and use between macrohabitats could have important consequences for foraging efficiency, predator avoidance, and/or conspecific interactions (Nielsen 1992; Mysterud and Ims 1998).

Females were more frequently encountered in the forest than males, and males were observed slightly more than females in the open-canopy and intermediate habitats. On Bahamian islands, high female density was suggested to be indicative of high-quality habitats, with higher female/male sex ratios (Schoener and Schoener 1980). Peripheral, poorer quality habitats had lower female/male sex ratios and likely experienced a "spillover" effect from the good quality habitats. Males likely distribute further apart because of increased territoriality among males, whereas females tolerate higher densities (Calsbeek 2009). In addition, adult females need access to suitable nesting locations, which may be more prevalent in the forest which had more organic soil than the sandy ground in the open-canopy and intermediate habitats. Moreover, the open-canopy and intermediate habitats are sometimes inundated with water during high tide (personal observations), which may place eggs at risk in these habitats (even if *A. sagrei* eggs can tolerate immersion in saltwater for short periods; Losos et al. 2003).

Relative frequencies of juveniles to adults across all habitat types were highest in October, which is near the end of the reproductive season. Because females lay one egg every 7 to 10 days throughout the reproductive period (April to October in Florida; Lee et al. 1989), juvenile density should increase throughout the summer as eggs hatch. The large decline in the relative number of juveniles in March was probably due to growth to adulthood by this period. Another contributing factor could be that juveniles hatching late in the season may be less likely to survive winter conditions (Olsson and Shine 1997; Shine and Olsson 2003; While and Wapstra 2008; Wapstra et al. 2010). The variations in age- and sex-specific macrohabitat use could have important ecological implications. For example, *A. cristatellus* and *A. sagrei* experience higher body temperatures in open-canopy habitats than they experience in forested habitats (Huey 1974; Lister 1976; Lee 1980), and adult female *A. cristatellus* located in open-canopy habitats are gravid more frequently than females in forested habitats (Otero et al. 2015).

We found that juvenile body size increased across macrohabitat away from the forest, and this trend was reversed for adults, although to a lesser degree. As argued above, females are more likely to lay eggs in the forest, where hatchlings subsequently emerge. Indeed, we observed a number of nest sites in the forest but none in the intermediate or open-canopy habitats. After hatching, many juveniles might disperse to open-canopy habitat to mature, and large adults then migrate back to the forest. A similar ontogenetic shift in habitat use has been observed in *Anolis aeneus*, where juveniles hatch in forested areas, migrate to clearings, and then return to forested areas as adults (Stamps 1983). Predation risk from a larger sympatric congener that occurs in forested areas is suggested to drive the habitat shift in *A. aeneus*. A similar habitat shift in *A. sagrei* could be driven by predation from a sympatric congener, *A. carolinensis*. Alternatively, conspecific adults, especially males, may also pose a predation risk because they occur at high densities and cannibalize juveniles (Gerber 1999; Cates et al. 2014). The open-canopy habitat has smaller and denser vegetation, such as grasses, bushes, and mangroves which may increase retreat sites and reduce predation risk.

Adults had higher survival than juveniles during the reproductive season (July to October), and both age classes experienced positive selection on body size during this time. However, body size had no effect on overwinter survival. Positive selection on *A. sagrei* body size has been found on islands with large predatory lizards (*Leiocephalus carinatus*; Losos et al. 2004) and high conspecific density (Calsbeek and Cox 2010). Despite size differences between the sexes, we found no evidence that males and females differ in survival for either age class. The cost of reproduction may be similar for male and female *A. sagrei* in terms of parasitism and energy stores (Reedy et al. 2016), which may lead to similar survival rates, despite our findings of differential habitat use between sexes (i.e., perch height, substrate, and macrohabitat).

Perch height had no effect on survival from July to October, but lizards experienced negative selection on perch height over winter. High perches are likely to be more exposed which could increase predation risk. In addition, increased exposure may lead to conspecific interactions, some of which are likely to be agonistic. These interactions could directly affect survival if killed or indirectly if the cost (e.g., injury and energy loss) of the interaction leads to reduced physiological or behavioral function (Semlitsch 1990; Wilson 1992; Niewiarowski et al. 1997). We found no effect of substrate or perch diameter on survival. These microhabitat characteristics may not be as important for avoiding diurnal predators or during agonistic interactions with conspecifics.

Importantly, however, one major assumption of our analyses of selection on behavior is that a single observation of a given individual is representative of its general perch use. Unfortunately, this assumption could not be appropriately tested with the data collected here, and it is possible that our behavioral data may not be indicative of an individual's general microhabitat use (i.e., repeatable at the individual level and thus, potentially heritable). This is problematic for predicting adaptive responses to selection. Nevertheless, although we do not assess the repeatability or heritability of microhabitat use, the short dispersal distance (Calsbeek 2009), small home-range size (Schoener and Schoener 1982), and high territory defense (Tokarz 1985; Paterson 2002; Calsbeek and Marnocha

2006) of adult *A. sagrei* suggest that repeatable microhabitat use may be likely.

Conclusion

The influence of habitat use on ecological and evolutionary patterns in *Anolis* lizards is well documented. However, how habitat use varies with respect to age, sex, and season within a species, as well as the consequences of such variation, remains relatively understudied. Our objectives were to examine age- and sex-specific variations in habitat use and assess the effects of habitat use on survival. We show that age, sex, size, and macrohabitat have significant effects on how *A. sagrei* utilize available microhabitat and that age, sex, size, and season influence macrohabitat use. We observed positive directional selection on body size during the reproductive season. Interestingly, however, body size did not influence overwinter survival, but rather, low perching lizards had higher overwinter survival. This study highlights the complexity in microhabitat and macrohabitat use of *A. sagrei* that depend upon both intrinsic (e.g., age, sex, and size) and extrinsic factors (e.g., season). Several other factors could be responsible for the age- and sex-specific habitat variations observed in this species. However, future experimental approaches are needed to fully understand the causal factors contributing to this variation.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed. The University of Alabama at Birmingham Institutional Animal Care and Use Committee approved this project (140410081).

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