

Lizards on Islands within Islands: Microhabitat Use, Movement, and Cannibalism in *Anolis sagrei* (Brown Anole) and *Anolis smaragdinus* (Bahamas Green Anole)

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Abstract - Inland lakes on larger Bahamian islands often contain small islands. We surveyed 6 such interior islands on Long Island, Bahamas, to determine whether any of the 4 *Anolis* lizard species found on the nearby “mainland” were present. *Anolis sagrei* (Brown Anole), perhaps the most successful overwater disperser and colonizer of all *Anolis* species, was present on all 6 interior islands. Of the 3 other “mainland” species, only *A. smaragdinus* (Bahamas Green Anole) was present on interior islands and only on the 2 islands with mature, closed-canopy coppice forest. To investigate how sympatric Brown Anoles and Bahamas Green Anoles use interior-island habitat, we performed a capture–mark–recapture study on 1 island. We found population-level interspecific perch height partitioning typical of other areas where these species co-occur, yet within both species there is a wide range of intra-individual variation in perch height and diameter. We also report male-biased, within-island dispersal in Brown Anoles over a 5-month period and the first recorded case of cannibalism in the Bahamas Green Anole.

Introduction

The genus *Anolis* contains over 400 species of small, primarily arboreal lizards (anoles) that have become a model for the study of ecology and evolution, particularly as a textbook example of insular adaptive radiation (Losos 2009). To further refine our understanding of the ecological and evolutionary forces that have shaped anoline diversity through time, we must embrace advances in genetics and developmental biology (e.g., Sanger and Kircher 2017), while also building upon decades of observation of inter- and intraspecific interactions in the wild (for general arguments in favor of natural history observations, see Greene 2005, Tewksbury et al. 2014; for their importance in anole research, see Losos 2009). Despite decades of observation, some wild populations of anoles have historically received little attention. On larger Bahamian islands that contain up to 4 sympatric *Anolis* species, inland lakes contain their own small islands. The ecology and natural history of anoles on these “islands within islands”, or interior islands, have been entirely unexplored. Here we report and interpret the first surveys of the distribution of *Anolis* lizards on 6 small, interior islands on Long Island, Bahamas. We also describe a

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detailed study of anole habitat use on 1 interior island and report the first observation of cannibalism in *Anolis smaragdinus* Barbour & Shreve (Bahamas Green Anole).

The Bahamas Archipelago, which stretches >1360 km from northwest to southeast (19°84'–27°30'N; 68°70'–80°54'W, inclusive of the Turks and Caicos Islands), is a complex of large and small carbonate platforms (banks) supporting hundreds of emergent islands. All Bahamian islands contain 0–4 native species of *Anolis* lizards (Buckner et al. 2012), with a total of 6 species found across the archipelago (Schwartz and Henderson 1991). Where these species co-occur, they exhibit classic ecological-niche partitioning, and as many as 4 species can be found in close proximity (indeed, often on the same tree; Schoener 1968). Long Island, a relatively large (596 km²) emergent portion of the Great Bahamas Bank, supports all 4 species of *Anolis* that occur on this bank: Bahamas Green Anole, *A. sagrei* Duméril & Bibron (Brown Anole), *A. distichus* Cope (Bark Anole), and *A. angusticeps* Hallowell (Twig Anole). Like some other large Bahamian islands, Long Island has inland lakes that contain their own small islands. We surveyed 6 such islands to provide the first description of anole distribution across interior islands.

Our initial survey revealed that 1 interior island (Midway Island) contained high densities of 2 anole species, the Brown Anole and the Bahamas Green Anole (Fig. 1), making it suitable for a detailed study of how these species use interior-island habitat. The Brown Anole and the Bahamas Green Anole each belong to a different anole “ecomorph” (Williams 1972) and are morphologically and



Figure 1. Left: *Anolis sagrei* (Brown Anole) male from New Providence, Bahamas (Photograph © R.G. Reynolds). Right: *Anolis smaragdinus* (Bahamas Green Anole) male from Ragged Island, Bahamas (Photograph © Alberto R. Puente-Rolón).

behaviorally adapted for locomotion in particular structural microhabitats. Brown Anoles, which are most commonly observed on or near the ground, have relatively long limbs that are well-suited for sprinting on broad surfaces such as thick tree trunks (Losos and Sinervo 1989, Williams 1983). Bahamas Green Anoles have relatively short limbs, which confer balance on narrow perches (Losos and Sinervo 1989), and relatively large toepads well-suited for clinging to smooth surfaces such as leaves (Irschick et al. 1996, 2005a). Where they co-occur elsewhere in the Bahamas, these species exhibit classic habitat partitioning, with Bahamas Green Anoles tending to perch higher than Brown Anoles (Losos and Spiller 1999; Mattingly and Jayne 2004; Schoener 1968, 1975). Additionally, male Brown Anoles tend to perch higher than females (Lister 1976, Schoener 1968, Schoener and Schoener 1971). By contrast, between-sex habitat partitioning appears weak or non-existent in both the Bahamas Green Anole (Schoener 1968) and its close relative on the North American mainland, *A. carolinensis* Voight (Carolina Anole; Irschick et al. 2005b, Jenssen and Nunez 1998). Historically, *A. smaragdinus* has frequently been called *A. carolinensis* (Les and Powell 2014) and is occasionally referred to as such in literature cited above. However, the Bahamas Green Anole and the Carolina Anole are currently recognized as distinct species (Glor et al. 2005, Les and Powell 2014).

To investigate how sympatric Brown Anoles and Bahamas Green Anoles use interior-island habitat, we performed a capture–mark–recapture study on Midway Island. We aimed to determine whether males and females of these species partition habitat based on perch height and diameter, similar to patterns observed elsewhere in the Bahamas. We also sought to address 2 questions about anole habitat use for which direct observations are generally lacking: (1) What is the extent of intra-individual variation in perch height and diameter? and (2) within a single population, how consistent are sex-specific trends in adult movement across different time scales?

Although population-level habitat partitioning is well studied in anoles (reviewed in Losos 2009), there are few detailed accounts of intra-individual variation in microhabitat use (Kamath and Losos 2017a). Such data are needed because the extent of individual specialization in resource use can inform predictions about how species may evolve in response to changes in resource availability and interspecific competition (Bolnick et al. 2003, 2010; Roughgarden 1972; Van Valen 1965). Furthermore, studies of anole microhabitat use have historically characterized an individual lizard's perching behavior based on a single observation of that individual. It is not clear whether a single observation per individual is representative and repeatable.

Sex-biased interseasonal dispersal within populations is another important aspect of anole habitat use for which there are few direct observations (but see Andrews and Rand 1983). Dispersal rates influence gene flow between subpopulations and can therefore affect a population's evolutionary trajectory (Clobert et al. 2001). Long-distance movement may carry both risks (e.g., physiological costs, increased visibility to predators) and rewards (e.g., reduced competition for mates or food); thus, the timing and magnitude of such events can be used to generate hypotheses

about what drives an individual to disperse. Adult males of several *Anolis* species, including the Brown Anole, tend to move longer distances than females during the breeding season (intra-seasonally), which typically lasts from March through October at subtropical latitudes (Calsbeek 2009, Jenssen and Nunez 1998, Kamath and Losos 2018, Schoener and Schoener 1982). Microsatellite data suggest persistent male-biased dispersal in at least 2 species of anole (Johansson et al. 2008, Stenson et al. 2002). However, male-biased movement within the breeding season may be only partly responsible for the genetic signature of persistent male-biased dispersal over longer time scales. More direct observations of interseasonal movement, or movement that occurs between the breeding season and non-breeding season, may lead to better-informed hypotheses about the mechanistic drivers and evolutionary consequences of male-biased dispersal.

Methods

Surveying “islands within islands” (interior islands)

Long Island is relatively low-lying (<37 m above sea level) and contains a number of large and small interior lakes (Fig. 2), or bodies of water without epigean connections to the sea. Some of these lakes contain islands. We initially set out to determine which *Anolis* species (if any) occur on such interior islands. We visually

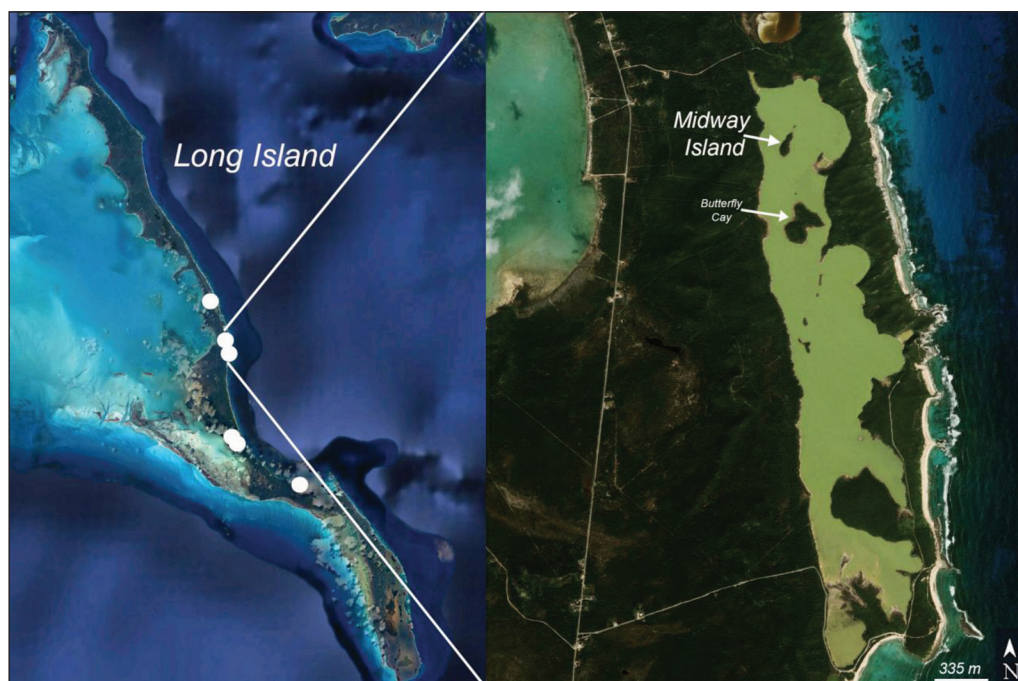


Figure 2. Long Island, Bahamas, with interior islands sampled in this study labeled by white circles. Our focal island, Midway Island (expanded), is shown to the right, along with neighboring Butterfly Cay in an interior brakish lake on Long Island. Other visible islands in this lake are small rocks, barely emergent above the water. Water depths in the lake are ~3–4 m. Imagery from Google Earth Pro® 2017.

surveyed 6 interior islands (Fig. 2) on Long Island with varying amounts of vegetation (from closed canopy coppice to low scrub) during daylight hours on 5 days in May 2016. We accessed islands via kayak and walked slowly through all available habitat types on each island for 30 min–3 h, allowing sufficient time to visually confirm which species were present.

Description of Midway Island

One of the 6 islands we surveyed contained high densities of 2 anole species, the Brown Anole and the Bahamas Green Anole, making it suitable for a detailed study of how these species use interior-island habitat. To distinguish this interior island from the nearby lakeshore “mainland” in which it is nested, we call it Midway Island owing to its location approximately midway between the northern and southern ends of Long Island (Fig. 2). Midway Island is a 0.84-ha island within a relatively large (~1.75 km²) lake on Long Island, Bahamas (Fig. 3; coordinates: 23°16'47.65"N, 75°05'29.04"W). Midway Island’s jagged limestone shoreline is sparsely covered with trees and shrubs, most of which are shorter than 3 m. Its interior is more densely vegetated with tropical dry forest, the canopy height of which is 3–5 m (see Supplemental Table S1, available online at <https://www.eaglehill.us/CANAonline/suppl-files/c187-Herrmann-s1> for a list of plant species recorded). Hereafter, unless otherwise specified, “the island” refers to the study site (Midway Island) and not the whole of Long Island.

Capture–mark–recapture

We began our focused study of Midway Island on 25 July 2016 by constructing a detailed map based on 163 reference trees distributed throughout the island. We labelled each tree and measured the distances between neighboring trees using a Bosch GLM35 laser meter (RL Bosch Ltd., Waltham, MA, USA). We conducted 15 d of focused sampling during daylight hours from 29 July to 22 August, during which we walked slowly throughout the island opportunistically capturing lizards by noose or by hand. In total, we captured 386 individual adult Brown Anoles (169 males, 217 females) and 180 individual adult Bahamas Green Anoles (95 males, 85 females). We recorded each lizard’s perch height, perch diameter, and distance to at



Figure 3. Left: Midway Island in August 2016 as seen from the top of a nearby ridge and right: from the island’s interior.

least 3 nearby reference trees. We used the latter to triangulate each lizard's exact location on the island, which yielded finer horizontal resolution than a handheld GPS unit. We did not assign a perch diameter to lizards sighted on the ground ($n = 10$). We permanently marked all lizards subcutaneously with visible-implant fluorescent alphanumeric tags (Northwest Marine Technology, Inc., Shaw Island, WA, USA). We also marked them temporarily (and superficially) with a unique identifier using a non-toxic marker. We used this mark to identify lizards from a distance, then recorded perch height, perch diameter, and location for every individual that we spotted subsequent to its release (though never more than once per day). We returned lizards to their exact point of capture within 24 h. We revisited the island for 17 d in January 2017 to recapture tagged individuals and again triangulate their location using nearby reference trees. No other data were collected during the second visit.

We estimated population sizes for the Brown Anole and the Bahamas Green Anole using the package *Rcapture* (Baillargeon and Rivest 2007) in R version 3.4.1 (R Development Core Team 2017). We fit various models of population size based on closed-population models implemented in *Rcapture*, then conducted model-selection procedures using Akaike information criterion and Bayesian information criterion scores (AIC and BIC, respectively).

Intraguild ecological analyses

We used multivariate linear models to determine whether Midway Island anoles differed in structural microhabitat use depending on species and sex. We fit each model using a single response-variable (either perch height or perch diameter from the first observation of each lizard) and 3 predictors: species, sex, and their interaction. To describe intra-individual variation in perch height and perch diameter, we calculated the range of these values for each individual observed multiple times in August, and visually displayed the distribution of ranges separately based on species and sex.

To test whether sex-specific trends in adult movement were consistent both within and across seasons, we calculated the distance between locations for all individuals observed multiple times. Re-observed lizards fell into one of 3 categories: (1) observed multiple times in August but not in January, (2) observed once in August and once in January, and (3) observed multiple times in August and once in January. For category 1 individuals, we calculated the maximum distance between any 2 August locations, hereafter, maximum intraseasonal distance. For category 2 individuals, we calculated the distance between the August and January locations, hereafter, interseasonal distance. For category 3 individuals, we calculated maximum intraseasonal distance as above. We also calculated interseasonal distance for these individuals as the distance between their January location and the epicenter of their August locations. We excluded from the original analysis individuals in category 3 ($n = 14$) to avoid resampling because their maximum intraseasonal distance and interseasonal distance represent non-independent data points. However, including distances from category 3 individuals does not qualitatively change the

outcome of our analysis (not presented here but available on GitHub: <https://github.com/NCHerrmann/LizardsofLI/>). Due to uneven sample sizes and non-normally distributed data, we conducted a non-parametric Kruskal–Wallis test to compare the rank order of distances between sexes and across seasons. We used Dunn’s (1964) test of multiple comparisons with a Benjamini–Hochberg (1995) adjustment to P -values to directly compare groups. Owing to small sample sizes for the Bahamas Green Anole, we performed statistical comparisons only for the Brown Anole.

We performed all analyses in R version 3.4.1 (R Development Core Team 2017). Our data and annotated R scripts are available on GitHub (<https://github.com/NCHerrmann/LizardsofLI/>; Hermann 2018).

Results

Surveys of interior islands

Our surveys of interior islands revealed that these islands supported a less diverse herpetofaunal community than “mainland” Long Island, but that all islands had at least 1 species of anole (Table 1). If only 1 species was present, it was always the Brown Anole. Basic habitat features of these 6 interior islands as well as *Anolis* species diversity and approximate relative abundance are noted in Table 1. Brown Anoles are abundant on “mainland” Long Island, and we found that the species was present on all 6 interior islands we surveyed, though with varying abundance (Table 1). Of the 3 other “mainland” anole species, only the Bahamas Green Anole was present on interior islands. We found this species on only the 2 interior islands with mature, closed-canopy coppice forest.

Midway Island herpetofauna

Midway Island had a reduced vertebrate fauna relative to Long Island, and thus represents a somewhat simplified ecological subset of the nearby “mainland”. We estimated a Brown Anole population size on Midway Island of ~3000 individuals (see Supplemental Table S2, available online at <https://www.eaglehill.us/CANAonline/suppl-files/c187-Herrmann-s1>). Though at least several hundred Bahamas Green Anoles were present (based on our observations), we were unable to statistically estimate a population size for this species in *Rcapture*; multiple models fit the data equally well, suggesting high uncertainty in our best estimate of population size (see Supplemental Table S2, available online at <https://www.eaglehill.us/CANAonline/suppl-files/c187-Herrmann-s1>). Bark Anoles and Twig Anoles, while present on “mainland” Long Island, are absent from Midway Island (and all other interior islands we surveyed; Table 1). Midway Island also supports the dwarf gecko *Sphaerodactylus nigropunctatus* Gray, at least 2 individuals of the boid snake *Chilabothrus strigilatus* Cope, and is occasionally visited by wading birds, songbirds, and roosting waterbirds (N.C. Herrmann and R.G. Reynolds, pers. observ.).

Habitat partitioning on Midway Island

Perch height differed based on species ($\beta \pm 1 \text{ SE} = 69.9 \pm 5.9$, $P < 0.001$) and sex ($\beta \pm 1 \text{ SE} = 29.8 \pm 4.7$, $P < 0.001$), with Bahamas Green Anoles perching higher

Table 1. Interior islands situated within lakes surveyed on Long Island, Bahamas, in May 2016. Each island was surveyed during daylight hours for 30 min–3 h to characterize vegetative habitat and document which *Anolis* lizard species from the “mainland” were present. Though present on the “mainland”, we did not observe *Anolis distichus* (Bark Anole) and *Anolis angusticeps* (Twig Anole) on any interior island. We estimated island areas from Google Earth Pro® 2017 imagery.

Island	Coordinates	~Area (m ²)	Brown Anole	Bahamas Green Anole	Habitat
Midway Island*	23°16'47.65"N, 75°05'29.04"W	8400	Present, high density	Present, high density	Mature whiteland coppice
Butterfly Cay	23°16'31.58"N, 75°05'25.59"W	33,500	Present, high density	Present, unknown density	Mature whiteland coppice
Clarencetown Hole	23°05'51.20"N, 74°58'59.74"W	6940	Present, low density	Absent	Low scrub
Goat Island 1	23°09'07.81"N, 75°04'33.00"W	4700	Present, low density	Absent	Low scrub
Goat Island 2	23°09'05.76"N, 75°04'30.85"W	1575	Present, low density	Absent	Thorny scrub, some hardwoods
Pink Flats Island	23°19'34.56"N, 75°06'26.66"W	7000	Present, low density	Absent	Thorny scrub, some hardwoods

*Focal island chosen for a detailed, observational study of how sympatric Brown Anole and Bahamas Green Anole use interior island habitat.

than Brown Anoles, and males perching higher than females (Fig. 4). The interaction term ($\beta \pm 1 \text{ SE} = -25.3 \pm 8.4$, $P = 0.003$) suggests that Brown Anole males and females were more dissimilar in their perch heights than Bahamas Green Anole males and females. Indeed, analyzing Bahamas Green Anoles alone revealed no between-sex perch-height partitioning in this species ($\beta \pm 1 \text{ SE} = 4.5 \pm 8.8$, $P = 0.61$). Overall, the 2-species model explained over 30% of the variance in perch height ($F_{3,557} = 81.2$, $R^2 = 0.30$).

Perch diameter also differed by species ($\beta \pm 1 \text{ SE} = 3.7 \pm 1.4$, $P = 0.01$), with Brown Anoles using wider perches than Bahamas Green Anoles (Fig. 4), although the model explained less than 2% of the variance in perch diameter ($F_{3,547} = 2.89$, $R^2 = 0.016$). Neither sex ($\beta \pm 1 \text{ SE} = -1.8 \pm 1.1$, $P = 0.11$) nor the interaction term ($\beta \pm 1 \text{ SE} = 2.8 \pm 2.0$, $P = 0.16$) were significant predictors of perch width. When we removed the interaction term from the model, parameter values for both species ($\beta \pm 1 \text{ SE} = -2.3 \pm 1.0$, $P = 0.02$) and sex ($\beta \pm 1 \text{ SE} = -0.94 \pm 0.95$, $P = 0.31$) shifted only marginally.

A separate linear regression of perch diameter on perch height for all lizards revealed that these 2 measures of structural-microhabitat use were negatively correlated ($\beta \pm 1 \text{ SE} = -0.014 \pm 0.003$, $P < 0.001$). In other words, lizards observed on higher perches tended to also be on narrower perches.

Intra-individual variation in microhabitat use

Throughout our 15 sampling days in August 2016, we made multiple observations of 101 Brown Anoles (62 males, 39 females) and 25 Bahamas Green Anoles (18 males, 7 females), accumulating 2–7 observations per individual (means:

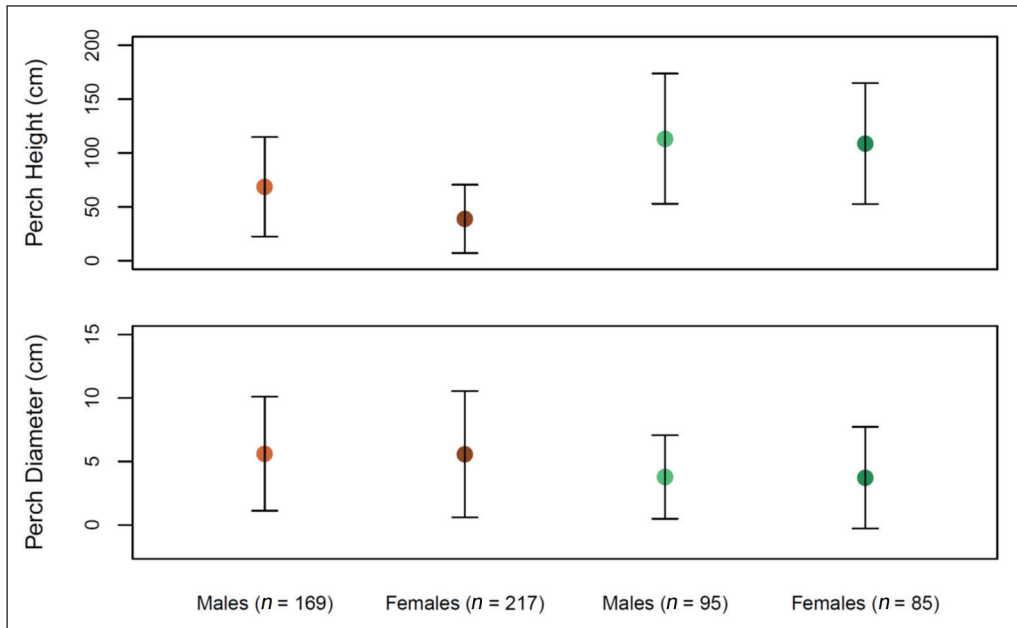


Figure 4. Mean perch height and perch diameter ± 1 SD for male and female Brown Anoles (brown dots, left) and Bahamas Green Anoles (green dots, right).

Brown Anole = 2.9, Bahamas Green Anole = 2.3). Perch height and perch diameter were relatively consistent in some individuals and highly variable in others (Fig. 5).

Movement within and across seasons

We calculated intraseasonal distances for all Brown Anoles observed 2–7 times in August but not in January (46 males, 26 females). We also calculated interseasonal distances for all Brown Anoles observed once in August and once in January (10 males, 28 females). These distances are displayed in Figure 6. Following a significant Kruskal–Wallis test ($\chi^2 = 17.8$, $df = 3$, $P < 0.001$), post-hoc comparisons revealed that males were displaced farther than females both intraseasonally (means = 8.1 m for males vs. 6.0 m for females; $Z = -2.94$, $P = 0.003$) and interseasonally (means = 16.2 m for males vs. 4.3 m for females; $Z = -3.02$, $P = 0.007$). However, maximum intraseasonal distances were statistically indistinguishable from interseasonal distances for both males ($Z = -1.43$, $P = 0.18$) and females ($Z = -0.38$, $P = 0.70$). These trends were largely mirrored in our limited observations of Bahamas Green Anoles, but we did not test them statistically due to small sample size. One notable outlier was a female Bahamas Green Anole observed 60 m away (half the length of the island) from her original August location recorded just 7 days earlier.

Cannibalism in the Bahamas Green Anole

In August 2016, we captured an adult female Bahamas Green Anole with a conspecific juvenile in its mouth. The juvenile was whole except for a missing tail. The specimen has been accessioned into Harvard’s Museum of Comparative Zoology (R-194189).

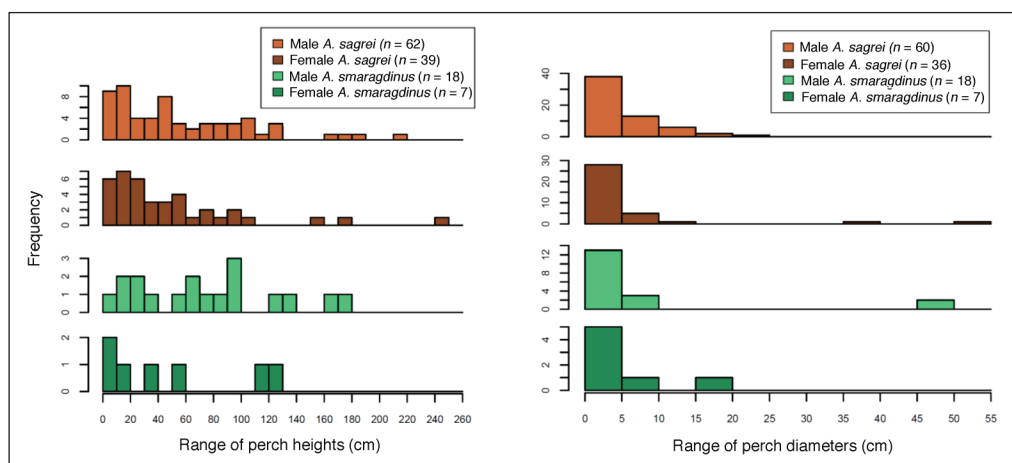


Figure 5. Frequency histograms for the (left) range of perch heights and (right) perch diameters used by individual *A. sagrei* (Brown Anole) and *A. smaragdinus* (Bahamas Green Anole) observed multiple times in August 2016 (2–7 observations per individual). Sample sizes on the right are smaller because observations of lizards on the ground were not assigned a perch diameter.

Discussion

Though Bahamian Island populations of *Anolis* lizards have long been studied, we are not aware of any previous effort to assess *Anolis* occurrence, species richness, or density on Bahamian interior islands. Islands are often used as model study-sites in ecology and evolution, because their discrete boundaries and generally reduced ecological complexity relative to mainland habitats facilitate in situ studies (Losos and Ricklefs 2009). Our islands within islands, with their further reduced community diversity in an even smaller area, represent yet another step down in this hierarchical community organization.

Given what we know about the 4 anole species present on the Long Island “mainland”, we can speculate about the factors driving their distribution across interior islands. The interior islands we surveyed represent a range of habitat types. We found Brown Anoles on all interior islands, even those with little vegetation. This result is unsurprising given the species’ ubiquity on the “mainland”, coupled with its success at colonizing small islands from nearby source populations via overwater dispersal (Schoener 2001a). We found Bahamas Green Anoles only on interior islands with well-developed coppice forest, as might be expected for a canopy anole species. This finding is consistent with experimental evidence suggesting that the Bahamas Green Anole is a less successful colonizer

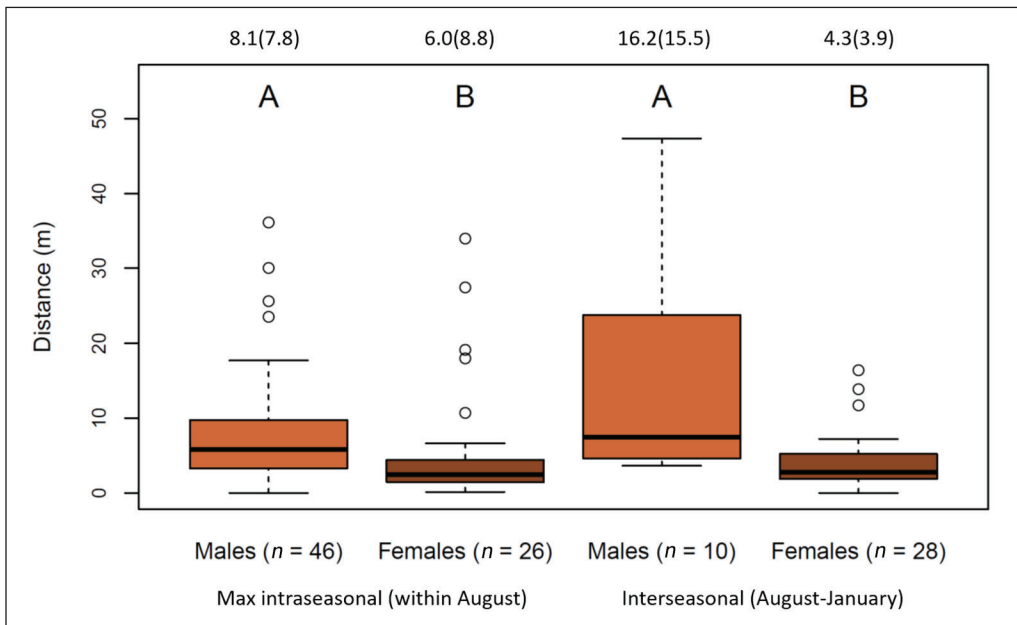


Figure 6. Boxplot illustrating distances between observed locations of the same individual Brown Anole. Maximum intraseasonal distances (left) are based on 2–7 observations per individual. Interseasonal differences (right) are for individuals observed exactly once in August and once in January. Letters below the top border represent post-hoc differentiation between groups following a Kruskal–Wallis rank-order test. Numbers above the border represent mean distance and SD (in parentheses) for each group. Circles represent outliers.

of small islands in general than the Brown Anole, in addition to being competitively disadvantaged to the Brown Anole in habitats that lack a well-defined tree canopy (Losos and Spiller 1999). That we did not observe Bark Anoles or Twig Anoles suggests that these species might be incapable of living on smaller interior islands, particularly those that are already inhabited by Brown Anoles. This limitation is perhaps true for islands dominated by scrubby vegetation, but not for islands with well-developed forest, such as Midway Island, where there appears to be sufficient habitat for accommodating all 4 anole species in sympatry. Thus, the absence of Bark Anoles and the Twig Anoles from some interior islands may be due to poor dispersal or colonization ability, in addition to exclusion by congeneric competitors. The relative importance of these factors requires further study.

Midway Island

On a single interior island with sympatric Brown Anoles and Bahamas Green Anoles, we performed the first detailed observational study of how these species use interior island habitat. We used capture–mark–recapture to evaluate interspecific and between-sex habitat partitioning, intra-individual variation in microhabitat use, and sex-specific trends in adult movement across multiple time scales. We also incidentally observed the first recorded instance of cannibalism in the Bahamas Green Anole.

Patterns of both interspecific and intraspecific between-sex habitat partitioning for these species on Midway Island are similar to those documented elsewhere in the Bahamas. Specifically, Bahamas Green Anoles tend to perch higher than Brown Anoles (Losos and Spiller 1999; Mattingly and Jayne 2004; Schoener 1968, 1975), and males tend to perch higher than females within Brown Anoles but not Bahamas Green Anoles (Lister 1976, Schoener 1968, Schoener and Schoener 1971). Although interior islands are notable for their controlled isolation from the “mainland” despite being nested within it, well-developed coppice forest is not unique to Midway Island. Thus, provided vegetation with sufficient canopy, Brown Anoles and Bahamas Green Anoles can co-occur on an interior island by partitioning habitat in a similar manner as observed elsewhere.

Although we detected population-level habitat partitioning between species and between sexes, substantial variation in perch use is unexplained by our models, particularly for perch diameter. Several species of *Anolis* are known to engage in different behaviors at different perch heights (Andrews 1971, Kamath et al. 2013, Paterson 1999), suggesting that some of the unexplained variation in perch use is related to whether an animal was foraging, displaying, or merely scanning its surroundings. Furthermore, population-level measures based on single observations of individuals cannot capture intra-individual variation in resource use, rendering them incomplete at best and misleading at worst (Bolnick et al. 2003). Although we lacked the sample size required to make strong inferences about the extent of individual specialization within our study populations (Bolnick et al. 2002, Kamath and Losos 2017a), our data suggest, importantly, that some individuals use a wide range of perch heights and diameters. Before characterizing an individual lizard’s

perching behavior based on a single observation, future studies should evaluate the extent to which one observation is representative and repeatable.

Our observations of adult movement are largely in agreement with those reported in several studies showing that males of several *Anolis* species, including the Brown Anole, tend to move longer distances than females during the breeding season, which typically lasts from March through October at subtropical latitudes (Calsbeek 2009, Jenssen and Nunez 1998, Kamath and Losos 2018, Schoener and Schoener 1982). However, we are aware of only 1 study that directly recorded the dispersal of adult anoles over a longer time period than in our study (Calsbeek 2009; for studies of anole dispersal throughout ontogeny see Andrews and Rand 1983, Stamps 1983).

Working with adult Brown Anoles, Calsbeek (2009) measured distances between spring (March–April) and fall (September–October) locations for over 200 individuals in the Exuma Islands, Bahamas. This 6-month time period between observations is comparable to the 5-month period in our study, but our 2 observation windows landed squarely inside and outside of the breeding season rather than entirely within the breeding season, as in Calsbeek (2009). When the breeding season ends, competition for mates should cease, increasing the relative importance of competition for other resources (such as food). Thus, we might expect habitat-selection criteria for anoles to differ substantially inside versus outside of the breeding season, particularly if 1 or both sexes compete intensely for mates. Combining the interseasonal male distances observed during this study with the distances observed by Calsbeek (2009), we recorded 4 of the 5 longest distances, even though our work contributed substantially fewer observations (10 vs. 112). The same pattern is less striking but still evident for females; 2 of the 6 largest distances came from our study (our study: $n = 28$; Calsbeek 2009: $n = 126$). Based on these observations, we hypothesize that shifts into and out of breeding season are associated with more frequent long-distance dispersal events relative to equivalent intraseasonal periods. If so, depending on spatial environmental heterogeneity, the selective contexts that individuals face inside versus outside of the breeding season may change in previously unexplored and perhaps unpredictable ways. Future efforts to evaluate this hypothesis should sample over sufficient space and time to capture the full breadth of individual space use (Kamath and Losos 2017b, 2018). In summary, direct observations of anole movements, in concordance with genetic data from other studies (Johansson et al. 2008, Stenson et al. 2002), suggest that male-biased dispersal occurs both intra- and interseasonally. However, the mechanistic drivers of this bias across time scales and its consequences for selection require further study.

Our observation of cannibalism adds the Bahamas Green Anole to the list of at least 20 West Indian *Anolis* species known to eat conspecifics (Powell and Watkins 2014). Anoles are relatively well-studied, and cannibalism is rarely observed in the wild (Gerber 1999), suggesting that its ecological relevance is minimal. Indeed, experiments have indicated that intraguild predation (when an anole from one species eats an individual from another) is more likely to occur than cannibalism (Gerber

1991, Gerber and Echternacht 2000).

Conclusions

We advocate for the exploration and detailed study of “islands within islands”, which are excellent systems in which to examine the ecology and natural history of subsets of *Anolis* communities. Iconic experimental work on the anoles of small, low-lying, open-ocean Bahamian islands has transformed our understanding of how evolutionary trajectories are dictated by resource availability (Losos et al. 1997), predation (Losos et al. 2004, 2006), and founder effects (Kolbe et al. 2012). However, these island communities are frequently disrupted by hurricanes, some of which create a storm surge large enough to wipe out entire island populations (Schoener et al. 2001a, 2001b, 2004, 2017; Spiller et al. 1998). Like open-ocean islands, “islands within islands” are tractable natural systems for observational and experimental studies of ecology and evolution. Unlike open-ocean islands, they are relatively well protected from the violent storm surges caused by hurricanes, and thus might make excellent long-term research sites.

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