

ARTICLES

Herpetological Review, 2016, 47(4), 529–535.
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Differential Range Expansion and Habitat Use Among the Naturalized *Anolis* Lizards of Bermuda

Until the 20th Century, the Bermuda archipelago hosted a single endemic species of lizard: the Bermuda Rock Skink, *Plestiodon longirostris* (formerly *Eumeces longirostris*; Brandley et al. 2005; Wingate 1965). Beginning in the early 1900s, however, both purposeful and apparently accidental introductions of *Anolis* lizards have resulted in three species becoming permanently established (“naturalized”) on Bermuda. These three species—*Anolis grahami*, *Anolis leachii*, and *Anolis extremus* (Fig. 1)—are native to different Caribbean islands and belong to distantly related *Anolis* clades (Poe 2004, Nicholson et al. 2012; Gamble et al. 2014; Helmus et al. 2014).

Anolis grahami was introduced in 1905 (26 males and 45 females) from Kingston, Jamaica to the Botanical Gardens in Paget Parish, and achieved a virtually archipelago-wide distribution at some point between 1935 and 1945 (Wingate 1965). In contrast, *A. leachii* from Antigua and Barbuda, and *A. extremus* from Barbados (all islands in the Lesser Antilles) appear to have been small, unintentional introductions occurring in the 1940s (Wingate 1965; Losos 1996; Macedonia and Clark 2003). *Anolis leachii* first was discovered around 1940 on the north (harbor) shore of Warwick Parish. *Anolis extremus* is thought to have arrived in the Royal Naval Dockyard at the tip of Ireland Island (Sandys Parish) sometime before 1945, although it was not formally documented until 1953 (Wingate 1965). By 1956, *A. extremus* was abundant on Ireland and Boaz Islands, and exhibited a “patchwork distribution” on Somerset Island (Wingate 1965; Losos 1996).

Although *A. grahami* and *A. extremus* are similar in size (SVL: adult males ~65–70 mm, adult females ~50 mm; Macedonia and Clark, 2003 and unpubl. data) and have been reported to exhibit similar structural habitat use, they differ in insolation preference: whereas *A. grahami* is heliophilic, *A. extremus* prefers shade (Wingate 1965; Schoener 1970; Losos 1996). Losos (1996) found

that although males of the substantially larger *A. leachii* (SVL: adult males ~95–100 mm, adult females ~70 mm; Macedonia and Clark, 2003 and unpubl. data) preferred larger perch diameters than did male *A. grahami*, the two species did not differ in use of sun versus shade. In addition, Wingate (1965) noted that despite the introduction of *A. leachii* into habitat already occupied by *A. grahami*, the former’s preference for broader perches and thicker vegetation, as well as spending very little time foraging on the ground, probably reduced competition between these two species.

Unlike the rapid range expansion documented for *A. grahami*, the distributions of *A. leachii* and *A. extremus* were still (virtually) limited to a single parish each in 1963—roughly two decades after they first appeared on Bermuda (Wingate 1965). By the early 1990s, however, *A. leachii* had enlarged its range to encompass the western three-quarters of the archipelago (Losos 1996). In contrast, *A. extremus* extended its range very little (< 2 km) between the early 1960s and early 1990s (Losos 1996). Wingate (1965) suggested that competition arising from similar body size and structural habitat could have resulted in the inability of *A. grahami* to colonize Boaz and Ireland Islands, and the inability of *A. extremus* to expand its range eastward beyond Somerset Island. It was this apparent case of competitive exclusion (e.g., Hardin 1960) that motivated Losos (1996) to conduct his follow-up study of the Bermudian anoles nearly three decades after Wingate’s (1965) original research.

In the present study we replicate and extend the work of these earlier authors on the distribution and ecology of *Anolis* lizards naturalized on Bermuda. First, we update the distributions of each species using data from GPS-tagging cameras. These cameras allowed us to link the geographic position of each lizard with a photographic record for later verification of species identity and age/sex class. Second, we compare perch heights and perch diameters among our study species and between sexes with data accurately gathered using measuring tapes. Last, we follow previous authors in comparing insolation preferences among study species and between sexes, but in addition we compare body surface temperatures using data obtained with laser-sighted thermometer “guns.”

MATERIALS AND METHODS

Sites and Sampling.—We conducted our study during the first two weeks of May 2012. The 40 km-long Bermuda archipelago is arrayed in the shape of a “fishhook” lying in a northeast–southwest orientation, and is divided into nine parishes (Fig. 2).

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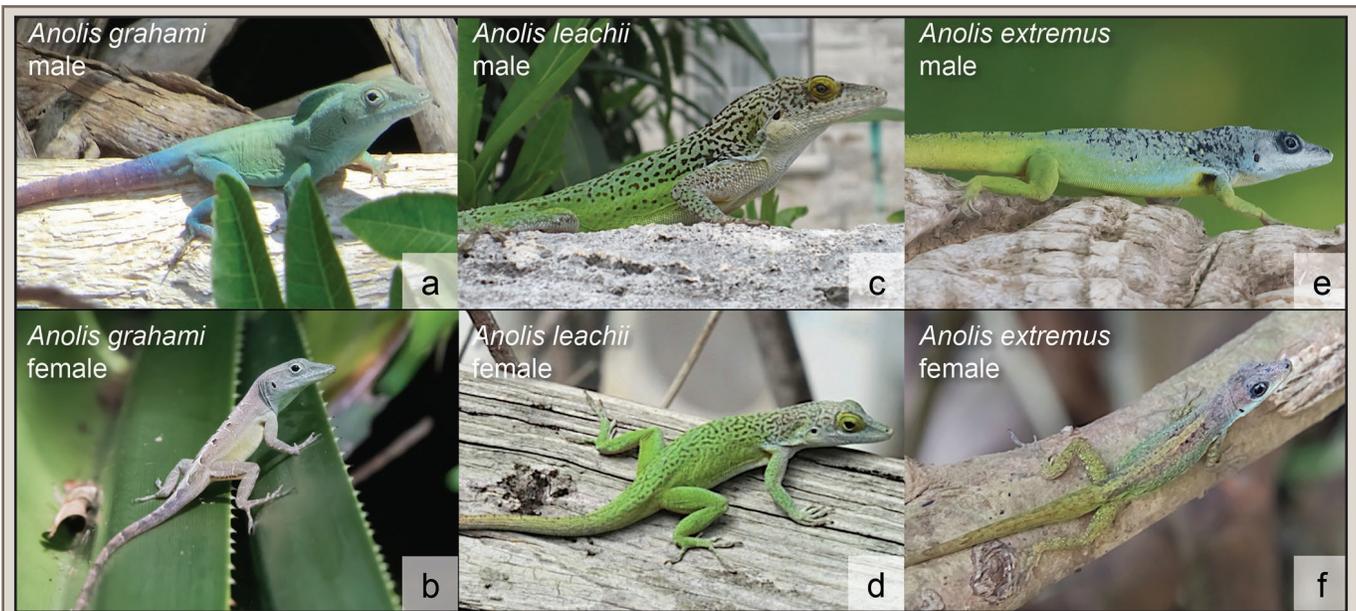


FIG. 1. Representative adult males and females of the three study species on Bermuda. Images not to scale.

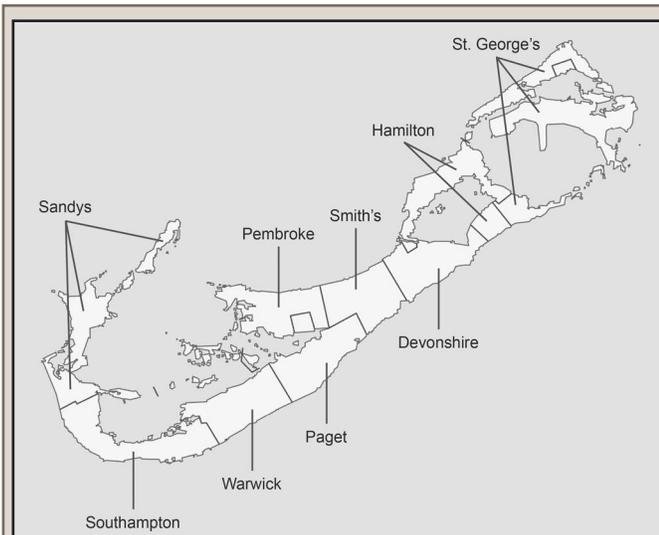


FIG. 2. Map of Bermuda parishes. The three-sided squares in Pembroke and St. George's parishes delineate the City of Hamilton and Town of St. George's, respectively.

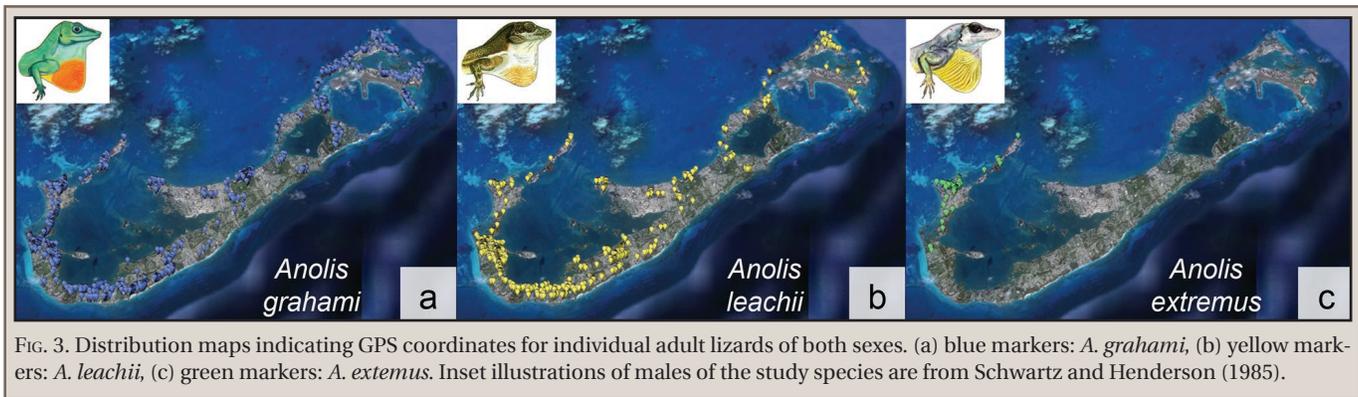
We traveled to different parishes by bus and ferry, and walked predetermined routes while scanning surfaces on which lizards might perch. When a lizard was sighted, it was approached slowly and photographed using a Casio Exilim-H20G camera, which attached a GPS tag to each photo. The GPS longitude/latitude coordinates later were exported as Microsoft Excel files, which were uploaded to Earth Point (Earth Point Corporation, Kuna, Idaho) to create the KML files that plotted each subject's location in Google Earth.

As we did not capture lizards for this study, we distinguished two adult age/sex classes of subjects from our photos: adult males and adult female-sized lizards. The adult female-sized age/sex class explicitly acknowledges that some small (non-adult) males cannot be distinguished at a distance from adult females (Schoener 1970); we refer to such individuals herein simply as females. Hatchlings and juvenile-sized females were not included in our survey. Subjects' perch heights and perch diameters were

quantified precisely using commercial fabric tape measures. Upon discovering a subject, we noted whether the lizard was located in (1) full sun, i.e., direct, unfiltered sunlight, (2) full shade, or (3) partial shade. We assigned the category of partial shade to a subject if its trunk (i.e., midsection from neck to hind limbs) was (a) entirely in light shade, (b) was in dappled sunlight, or (c) if part of the trunk was in sun and another part in shade. Subjects' body surface temperatures were obtained at a distance (typically 1.5–3 m) by aiming the infrared laser spot of a thermometer "gun" (Etekcity Lasergrip 774 ETC 8380 Temperature Gun Non-contact Digital Laser Infrared IR Thermometer, Etekcity.com) at the subject's trunk. If the trunk was divided unequally by sun and shade, we took our thermal reading within the larger of the two areas (i.e., sun or shade). In cases where a subject's trunk was divided equally by sun and shade, we focused the laser spot at the sun/shade interface. Body surface temperatures were not gathered for all subjects, as some individuals fled before these data could be acquired. Last, we supplemented our small 2012 sample size for *A. extremus* females ($N = 4$) with data from 28 females gathered by James Stroud in 2014 and 2015, as well as with our own additional data from 22 females gathered on 4–5 July 2016.

Statistical analysis.—Statistical tests were conducted in SPSS (v21.0, IBM Inc., Armonk, New York) and VassarStats (Lowry 2014). Prior to analysis, measurement variables were tested for normality with the Shapiro-Wilk test (<http://scistatcalc.blogspot.com/2013/10/shapiro-wilk-test-calculator.html>). Body surface temperature distributions were examined separately for each sex of each species and were found to be normal in all cases. Raw values for perch height and perch diameter were not normally distributed, but conformed to a normal distribution after log transformation. All analyses of perch height and perch diameter used these transformed values. Subjects on the ground were not included in our perch height analyses and were analyzed separately.

For comparisons of measures (e.g., above-ground perch height, perch diameter, and body surface temperature) we used two-way ANOVAs with species and sex as fixed factors. Bonferroni correction was used for post hoc pairwise tests. We conducted between-sex comparisons of proportions of subjects



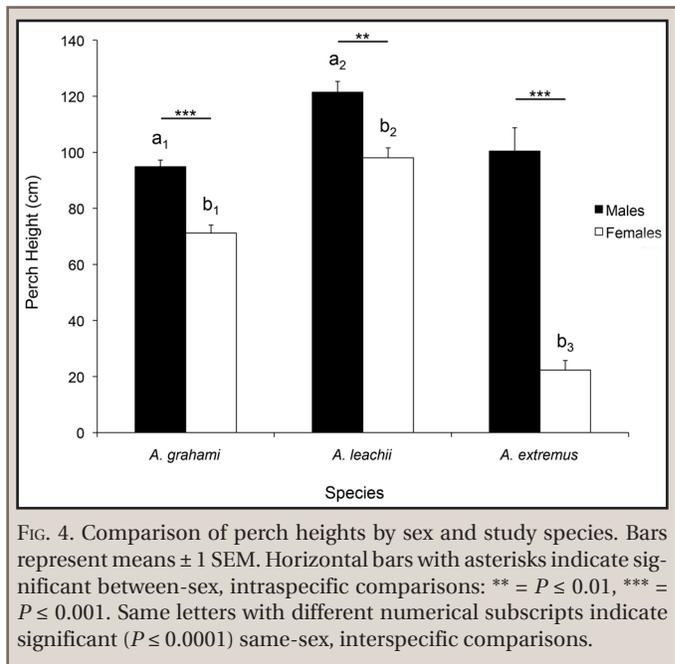
observed on the ground versus above the ground using the z-ratio test for the difference between two independent proportions. For each sex within each species we then compared numbers of subjects occupying different insolation categories using the chi-square goodness-of-fit test. Last, we used the z-ratio test to determine if the proportion of male or female subjects in a given insolation category differed between pairs of species. As Bonferroni correction was not available in SPSS or VassarStats for multiple tests of frequencies or proportions, we used a sequential Bonferroni correction calculator to adjust P -values in such tests (Gaetano 2013). Although significant results of many comparisons in this study exhibited exceedingly small P -values (e.g., $P = 1.0 \times 10^{-10}$), for simplicity we report such values in the text only to $P < 0.0001$, and use the standard convention of asterisks in our figures of * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

RESULTS

Species Distributions.—As anticipated from Losos' (1996) findings, we observed *A. grahami* in all areas that we sampled across Bermuda (Fig. 3a). We also discovered that since Losos' (1996) study, *A. leachii* had extended its range 4.5 km northward from Mangrove Bay to the tip of Ireland Island at the western end of Sandys Parish, and had extended the eastern edge of its range an additional 9 km to the easternmost points of St. George's Parish (Fig. 3b). Thus, *A. leachii* is now the second naturalized anole on Bermuda to achieve an archipelago-wide distribution. Surprisingly, we found no change in the distribution of *A. extremus* (Fig. 3c) from that documented by Losos (1996).

Perch Height.—Results of a two-way ANOVA on perch height revealed a significant main effect of species ($F_{2,1963} = 64.82$, $P < 0.0001$) and sex ($F_{1,1963} = 138.87$, $P < 0.0001$), as well as a significant species * sex interaction ($F_{2,1963} = 34.96$, $P < 0.0001$) that arose from differences between the sexes in the among-species relationships of perch heights (see Fig. 4). Between-sex post hoc comparisons showed that males perched significantly higher than females in all three species: *A. grahami* ($N_M = 784$, $N_F = 451$; $P < 0.0001$), *A. leachii* ($N_M = 346$, $N_F = 293$; $P < 0.01$), and *A. extremus* ($N_M = 51$, $N_F = 43$; $P < 0.0001$; Fig. 4). Interspecific comparisons showed that male *A. leachii* perched significantly higher than male *A. grahami* ($P < 0.0001$); no other comparisons among males were significant. Among females, *A. leachii* perched significantly higher than *A. grahami* ($P < 0.0001$) and *A. extremus* ($P < 0.0001$), with female *A. grahami* also perching higher than female *A. extremus* ($P < 0.0001$; Fig. 4).

Between sexes, proportionately more females than males were found on the ground in all three species: *A. grahami* ($z = 7.82$, $P < 0.001$), *A. leachii* ($z = 3.88$, $P < 0.001$), and *A. extremus*



($z = 2.27$, $P < 0.05$; Fig. 5). Between species, proportionately more male *A. grahami* than male *A. leachii* were located on the ground ($z = 3.03$, $P < 0.01$), as were proportionately more female *A. grahami* than female *A. leachii* ($z = 5.20$, $P < 0.001$); no other same-sex interspecific comparisons were significant (Fig. 5).

Perch Diameter.—Results from a two-way ANOVA on perch diameters showed a significant main effect of species ($F_{2,1352} = 21.67$, $P < 0.0001$) and sex ($F_{1,1352} = 54.29$, $P < 0.0001$), as well as a significant species * sex interaction ($F_{1,1352} = 3.31$, $P < 0.05$). This interaction stemmed from a nearly threefold difference in perch diameters between the sexes in *A. extremus*, as compared to less than a twofold difference between the sexes in *A. grahami* and *A. leachii* (Fig. 6). Between-sex post hoc comparisons showed that male perches were significantly greater in diameter than were those of females in all three species: *A. grahami* ($N_M = 525$, $N_F = 286$; $P < 0.0001$), *A. leachii* ($N_M = 259$, $N_F = 214$, $P < 0.0001$), and *A. extremus* ($N_M = 36$, $N_F = 38$; $P < 0.0001$; Fig. 6). Male *A. grahami* perch diameters did not differ significantly from those of the much larger male *A. leachii* ($P > 0.05$), but were greater than those of the similar-sized male *A. extremus* ($P < 0.05$; Fig. 6). Perch diameters of male *A. leachii* also were greater than those of male *A. extremus* ($P < 0.05$; Fig. 6). Although perch diameters did not differ between female *A. grahami* and *A. leachii* ($P > 0.05$), these species exhibited significantly larger

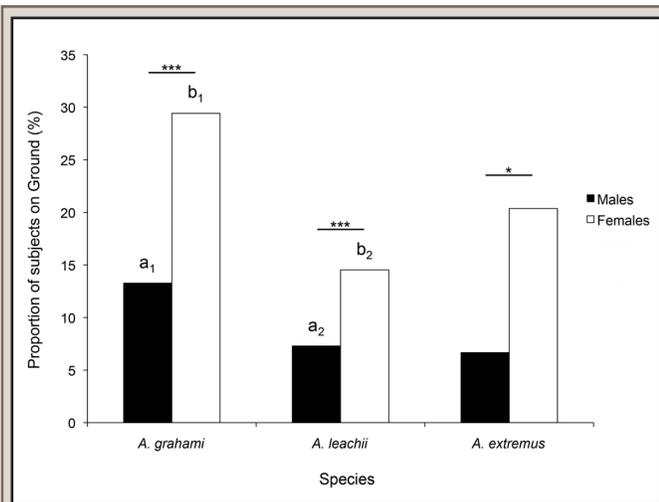


FIG. 5. Comparison of proportions of subjects located on the ground by sex and study species. Horizontal bars with asterisks indicate significant between-sex, intraspecific comparisons: * = $P \leq 0.05$, *** = $P \leq 0.001$. Same letters with different numerical subscripts indicate significant same-sex, interspecific comparisons ($P \leq 0.01$ for males and $P \leq 0.001$ for females).

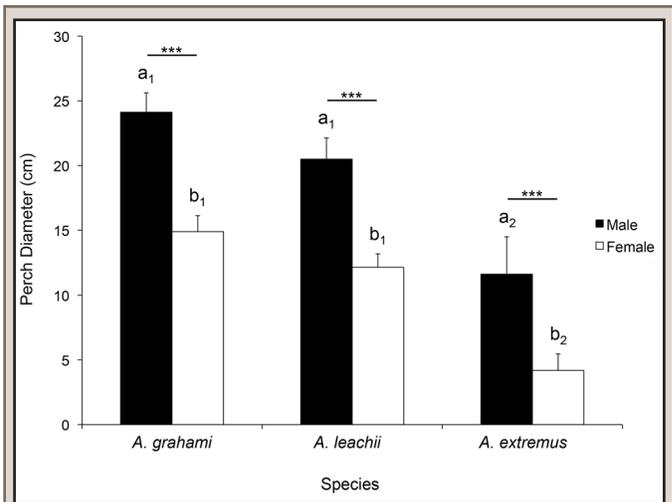


FIG. 6. Comparison of perch diameters by sex and study species. Bars represent means \pm 1 SEM. Horizontal bars with asterisks indicate significant between-sex, intraspecific comparisons: *** = $P \leq 0.001$. Same letters with different numerical subscripts indicate significant same-sex, interspecific comparisons ($P \leq 0.05$ for males and $P \leq 0.0001$ for females).

perch diameters than did female *A. extremus* ($P < 0.0001$ in both comparisons; Fig. 6).

Body Surface Temperature.—Results of a two-way ANOVA on body surface temperatures revealed a significant main effect of species ($F_{2,1437} = 9.45$, $P < 0.0001$) but not sex ($F_{1,1437} = 0.03$, $P > 0.05$). The species \times sex interaction was non-significant ($F_{2,1452} = 0.72$, $P > 0.05$). Posthoc interspecific comparisons showed that *A. grahami* ($N = 947$) body surface temperatures were significantly higher than those of *A. leachii* ($N = 453$, $P < 0.001$) and *A. extremus* ($N = 43$, $P < 0.0001$), and that *A. leachii* body surface temperatures also were significantly higher than those of *A. extremus* ($P < 0.01$; Fig. 7).

Insolation Preference: Intraspecific Comparisons.—Intraspecific within-sex comparisons of the number of subjects observed in each insolation category differed significantly from expected frequencies in all cases (χ^2 goodness-of-fit value range: 20.81–42.78, $df = 2$, $P < 0.0001$ in all tests). Pairwise comparisons ($df = 1$) showed that more *A. grahami* males ($N = 1014$) were observed in full sun than in full shade ($\chi^2 = 14.88$, $P < 0.001$), and that more were located in partial shade than in full shade ($\chi^2 = 20.02$, $P < 0.001$), but the number of *A. grahami* males seen in full sun did not differ from the number in partial shade ($\chi^2 = 0.34$, $P > 0.05$; Fig. 8a). Unlike male *A. grahami*, more male *A. leachii* ($N = 430$) were observed in partial shade than in full sun ($\chi^2 = 28.36$, $P < 0.001$) and in full shade than in full sun ($\chi^2 = 5.76$, $P < 0.05$). In addition, more male *A. leachii* were observed in partial shade than in full shade ($\chi^2 = 8.52$, $P < 0.01$; Fig. 8a). In contrast to *A. grahami* and *A. leachii*, far more male *A. extremus* ($N = 56$) were located in full shade than in partial shade ($\chi^2 = 14.58$, $P < 0.001$) or full sun ($\chi^2 = 22.76$, $P < 0.001$; Fig. 8a). The number of *A. extremus* males observed in partial shade did not differ from those in full sun ($\chi^2 = 0.94$, $P > 0.05$).

Female *A. grahami* and *A. leachii* were more similar in their insolation preferences than were males. Female *A. grahami* ($N = 691$) were found more often in partial shade than in full sun ($\chi^2 = 12.26$, $P < 0.001$) and in full shade than in full sun ($\chi^2 = 19.1$, $P < 0.0001$), but the number of females observed in partial shade did not differ from those in full shade: $\chi^2 = 0.7$, $P > 0.05$; Fig. 8b).

Similarly, female *A. leachii* ($N = 397$) were detected more often in partial shade than in full sun ($\chi^2 = 33.52$, $P < 0.001$) and in full shade than in full sun ($\chi^2 = 37.28$, $P < 0.001$), but the number of females observed in partial shade and in full shade did not differ: $\chi^2 = 0.08$, $P > 0.05$; Fig. 8b). Like males, female *A. extremus* ($N = 26$) exhibited a strong preference for full shade: more females were detected in full shade than in partial shade ($\chi^2 = 8.66$, $P < 0.01$) or in full sun ($\chi^2 = 19.04$, $P < 0.001$); in fact, we failed to observe a single female in full sun (Fig. 8b). A test between female *A. extremus* found in partial shade versus full sun could not be conducted due to expected values < 5 in both cells.

Insolation Preference: Interspecific Comparisons.—Results revealed that proportionally more male *A. grahami* were located in full sun than were male *A. leachii* ($z = 3.0$, $P < 0.001$) or male *A. extremus* ($z = 3.87$, $P < 0.001$), and that proportionally more male *A. leachii* were observed in full sun than were male *A. extremus* ($z = 2.14$, $P < 0.05$; Fig. 8a). Next, proportionately more male *A. leachii* were observed in partial shade than were male *A. grahami* ($z = 2.48$, $P < 0.05$) or male *A. extremus* ($z = 3.57$, $P < 0.001$), and proportionally more male *A. grahami* were observed in partial shade than were male *A. extremus* ($z = 2.75$, $P < 0.01$; Fig. 8a). Last, proportionally more male *A. extremus* were located in full shade than were male *A. grahami* ($z = 6.98$, $P < 0.001$) or male *A. leachii* ($z = 5.49$, $P < 0.001$), and proportionally more male *A. leachii* were found in full shade than were male *A. grahami* ($z = 2.23$, $P < 0.05$; Fig. 8a).

Results of interspecific pairwise comparisons for females showed that proportionately more female *A. grahami* were observed in full sun than were female *A. leachii* ($z = 2.83$, $P < 0.01$; Fig. 8b). The proportion of *A. extremus* females in full sun could not be tested against *A. grahami* due to the requirement that each cell contain at least 5 observations. Although the proportions of female *A. grahami* and *A. leachii* located in partial shade both were greater than the proportion of female *A. extremus* in partial shade, neither test was significant following sequential Bonferroni correction (Fig. 8b). Finally, the proportion of female *A. extremus* found in full shade was greater than that for female *A. grahami* ($z = 4.64$, $P < 0.001$) as well as *A. leachii* ($z = 3.88$, $P < 0.001$), and

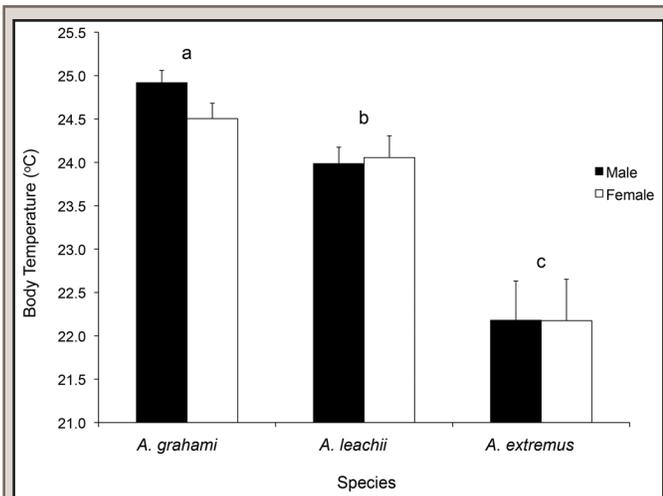


FIG. 7. Comparison of body surface temperatures by sex and study species measured between May 2 and May 12, 2012. Bars represent means \pm 1 SEM. As sexes within a species did not differ in body surface temperature, sexes were pooled for this analysis. Different letters above bars indicate significant ($P \leq 0.01$) between-species comparisons.

the difference between *A. grahami* and *A. leachii* females closely approached significance ($z = 1.94$, $P = 0.0527$; Fig. 8b).

DISCUSSION

Our aim in this study was to replicate and extend Losos' (1996) report on the range expansion, structural habitat use, and thermal ecology of the naturalized anoles of Bermuda. Below we discuss each of these topics in turn, and then focus on the matter of why, in contrast to its congeners, *A. extremus* has increased its range so little over the past half century.

Species Distributions.—Wingate (1965) reported in his 1963 survey that between 30 and 40 years following its introduction in 1905, *A. grahami* could be found everywhere on Bermuda (including several offshore islands) except for the 2.5 km distance between "The Lagoon" on South Ireland Island and the far end of North Ireland Island. By the time Losos (1996) conducted his study in 1991, *A. grahami* had achieved complete coverage of the Bermuda archipelago. We found no differences in the distribution of *A. grahami* from that documented by Losos (1996). Excluding a single observation that Losos (1996) considered to be an outlier, he determined that *A. leachii* had extended its range ~8 km westward and ~13 km eastward from the range limits reported by Wingate (1965). Our results show that *A. leachii* has continued to expand its range both eastward and westward and has achieved an archipelago-wide distribution.

In contrast to dramatic range expansions of *A. grahami* and *A. leachii*, Losos (1996) reported that *A. extremus* had increased its range only ~1.25 km in Sandys Parish since Wingate's (1965) study. In fact, we found no difference in the range limits of *A. extremus* from that reported by Losos (1996). We can rule out the possibilities that abrupt environmental change or unsuitable intervening habitat (e.g., Glor and Warren 2011) are barriers to *A. extremus* dispersal, as the easternmost location in which we found this species (Woodlawn Road in Hog Bay, Sandys Parish) was no different than much of Bermuda: highly developed (e.g., suburbs).

Perch Height.—We found that males perched higher than females, and were found less frequently on the ground than were

females (Figs. 4, 5). These results are consistent with those of Schoener (1970), in which he found that male *A. grahami* and *A. extremus* perched higher than females of their respective species (he did not report on *A. leachii*). We also found for males as well as females that *A. leachii* perched higher than *A. grahami*. In contrast, Losos (1996) did not find interspecific differences in male perch heights (he did not report results for females).

Perch Diameter.—Schoener (1970) reported that, within species, male *A. grahami* and *A. extremus* used significantly larger-diameter perches than did females (he did not report results for *A. leachii*). We found the same outcome for *A. grahami*, *A. extremus*, and *A. leachii*. Previous interspecific comparisons have shown that *A. extremus* (Schoener 1970) and *A. leachii* (Losos 1996) used larger-diameter perches than *A. grahami*. In contrast, we found that diameters of male *A. grahami* perches were larger (though not significantly so) than those of male *A. leachii*, and perches used by male *A. extremus* were significantly smaller than those of *A. grahami* and *A. leachii* (Fig. 6). Our results could reflect, at least in part, a relatively greater use of broad tree trunks as perches by male *A. grahami* than by male *A. leachii* or *A. extremus*.

Body Surface Temperature and Insolation.—Although we found no significant differences in body surface temperature between the sexes, these temperatures differed significantly among species: *A. grahami* exhibited the highest body surface temperatures, *A. extremus* the lowest, and *A. leachii* was intermediate (Fig. 7). Unsurprisingly, insolation preferences among our study species mirrored results for body surface temperatures: *A. grahami* males preferred full sun more than males of the other two species, *A. extremus* males strongly preferred full shade, and *A. leachii* males were found most often in partial shade (Fig. 8). Consistent with our findings, both Schoener (1970) and Losos (1996) found male *A. grahami* in the sun more often than the other study species, and found male *A. extremus* most commonly in the shade.

Differential Range Expansion Among Bermudian Anoles.—From the point of their release at the Bermuda Botanical Gardens in Paget Parish in 1905, *A. grahami* achieved a virtually archipelago-wide distribution in 30 to 40 years (Wingate 1965). With no native arboreal lizards to exert competition, apparently little stood in the way of *A. grahami* range expansion. By comparison, roughly 20–25 years post-introduction, *A. leachii* remained restricted almost solely to Warwick Parish (Wingate 1965). Although a dramatic difference must have existed between the known large number of *A. grahami* introduced to Bermuda and the likely small number of *A. leachii* colonists, it also is worth considering that *A. grahami* was well established in Warwick Parish in the 1940s when *A. leachii* first arrived (Wingate 1965). Differences in arthropod prey size preferences and structural habitat probably reduce within-sex interspecific competition between *A. leachii* and *A. grahami* (e.g., Wingate 1965; Schoener 1967), but similar body sizes (SVLs) of female *A. leachii* and male *A. grahami* may increase inter-sexual competition for food, which in turn may have contributed to the initially slow range expansion of *A. leachii*.

Other factors, including reduction in tree cover and low tolerance for cold temperatures, also may have played a role in the marginal range expansion of *A. leachii* during its first few decades on Bermuda (Wingate 1965; Losos 1996). For example, Wingate (1965) reported that numerous *A. leachii* would be found dead following severe winter storms (which never was the case for *A. grahami*). Nevertheless, in the 28 years between the

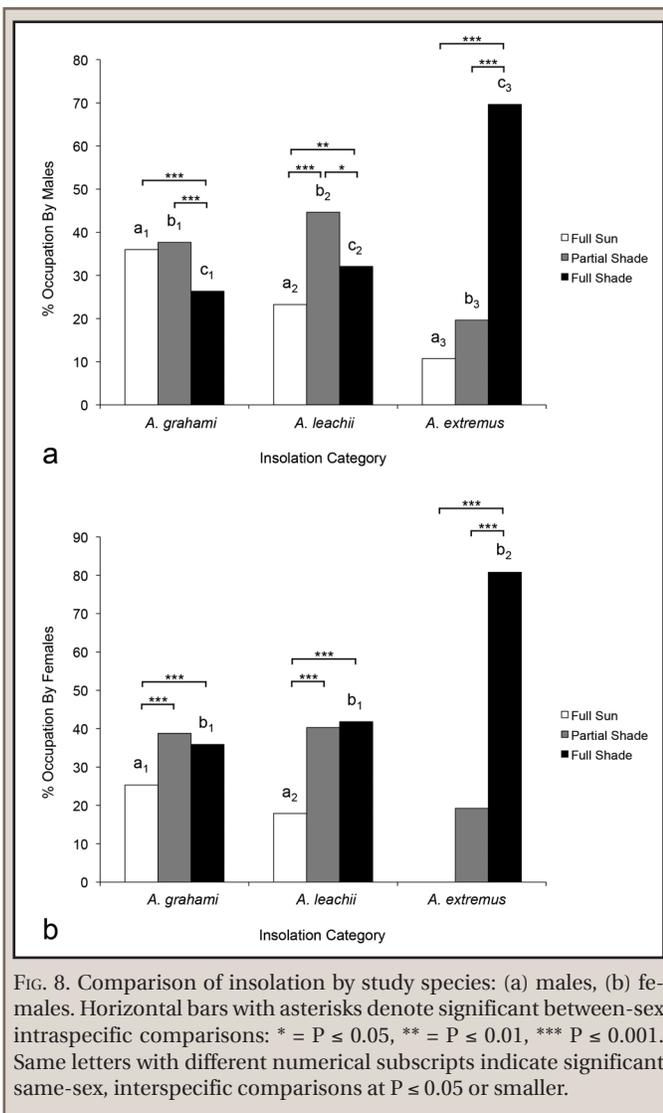


FIG. 8. Comparison of insolation by study species: (a) males, (b) females. Horizontal bars with asterisks denote significant between-sex intraspecific comparisons: * = $P \leq 0.05$, ** = $P \leq 0.01$, *** $P \leq 0.001$. Same letters with different numerical subscripts indicate significant same-sex, interspecific comparisons at $P \leq 0.05$ or smaller.

data gathered in 1963 by Wingate (1965) and in 1991 by Losos (1996), *A. leachii* had expanded its range to include all parishes except St. George's and St. David's in northeastern Bermuda. By the time we conducted our study in 2012, *A. leachii* was present throughout the archipelago. Losos (1996) pointed out that increased vehicle traffic, the ornamental plant industry (i.e., transportation of lizards and their eggs), and purposeful (undocumented) translocations of *A. leachii* by humans beyond Warwick Parish might explain the escalated range expansion in this species over the past several decades. Although these variables may have contributed to the slow-then-rapid range expansion of *A. leachii*, it remains perplexing why *A. extremus* has not experienced a similar sudden accelerated rate of dispersal.

One factor that may have contributed to the arrested dispersal of *A. extremus* on Bermuda is ecological niche incumbency (Algar et al. 2013). Niche incumbency is a form of competitive exclusion (e.g., Hardin 1960) in which a species is prevented from expanding its range into an area already occupied by a species to which it is ecologically very similar (e.g., Algar et al. 2013; Williams 1965). Several authors (Wingate 1965; Schoener 1970; Losos 1996) have argued that, aside from thermal preference, *A. grahami* and *A. extremus* differ very little in prey size choice or structural habitat use. For example, both Schoener (1970) and

Losos (1996) reported that *A. grahami* and *A. extremus* tend to occupy the same perches at different times of the day: sunny when occupied by *A. grahami* and shady when occupied by *A. extremus*.

It therefore seems relevant that a recent phylogenetically-focused study of ecological interactions among members of three Cuban *Anolis* clades showed, within clades, that similarly sized species (i.e., same structural niche) with differing thermal preferences were more likely to coexist in local assemblages, as were species with the same thermal niche but different structural niches (Cádiz et al. 2013). Likewise, using phylogenetic comparative methods Hertz et al. (2013) showed that recently diverged *Anolis* species differed more often in climatic niche (i.e., thermal and insolation preferences) than in structural niche, and that divergence in thermal niche has often followed diversification in structural niche. Results of these studies suggest not only that thermal preferences may be more plastic in anole evolution than morphological divergence, but also that differences in thermal niche facilitate coexistence via reduced competition.

It therefore is curious that, despite *A. grahami* having achieved nearly complete coverage of Bermuda over three to four decades in the absence of congeners, this species still was unable to invade much of the *A. extremus* stronghold of the Ireland Islands as late as 1963 (Wingate 1965; Losos 1996). The incumbency of *A. extremus* in this location is consistent with the prospect that its presence prevented invasion of the Ireland Islands by *A. grahami* for at least 20 years after the two species came into contact. Yet, given that *A. grahami* eventually colonized the Ireland Islands, and that *A. leachii* eventually expanded its range beyond Warwick Parish, niche incumbency seems unlikely to be responsible for *A. extremus* extending its distribution less than two kilometers over the past half century.

Currently we do not know if subtle attributes of vegetation structure or microclimate that might be unique to Sandys Parish have made it difficult for *A. extremus* to expand its range eastward. Alternatively or in addition, genetic constraints may be limiting the dispersal of *A. extremus*. Gorman et al. (1976) estimated heterozygosity for 24 allozymes of *A. extremus* on Bermuda to be only 16% of that present in this species on its native island of Barbados—a quantity considerably lower than the 56% heterozygosity in *A. leachii* and 82% in *A. grahami* on Bermuda, as compared to their source populations. We therefore cannot discount the possibility that the genetic bottleneck experienced during colonization of Bermuda has compromised this species' ability to disperse in the presence of competition from congeners. Moreover, new mutations that are correlated with phenotypic or life history variation can have an impact on range expansion (e.g., Burton et al. 2010). Hypothetically, such mutations could have contributed to the ability of *A. leachii* to expand its range after the early 1960s, or could have facilitated invasion of the Ireland Islands by *A. grahami* following an apparent standoff with *A. extremus* there for at least two decades.

Future Directions.—Insight into the limited dispersal of *A. extremus* might be gained through a quantitative study of habitat structure and microclimate properties and/or detailed investigations into species-specific biotic interactions (e.g. agonistic relationships) that may have influenced dispersal patterns. Moreover, an experimental removal/introduction study (e.g., Schoener and Schoener 1983; Kalmath et al. 2013; Stuart et al. 2014) is imaginable, in which species introduction order and timing is controlled. Bermuda harbors a number of very small

islands (e.g., in Harrington Sound and the Great Sound) where such an experiment might be carried out.

Finally, it has been over a half century since dietary studies of Bermudian anoles were conducted (Simmons 1958; Wingate 1965), at which time there was no area on Bermuda where all three species were sympatric, and where sympatry between species pairs was limited to Warwick and Sandys Parishes. Such data might provide further clarification of the mechanisms permitting species coexistence, and could be instructive with regard to the recent discovery of the highly invasive *Anolis sagrei* on Bermuda. The presence of *A. sagrei* was first noted by Macedonia (Losos 2012), and since has been studied in the context of ecological and geographical overlap with the critically endangered *Plestiodon longirostris* (Stroud et al., *in press*). In conclusion, we hope that future studies will utilize a range of observational, experimental, and genetic techniques to better understand the dynamics of colonization and range expansion in the naturalized (and newly invasive) *Anolis* lizards of Bermuda.

Acknowledgments.—We thank J. Nisbett, DVM, Government Veterinary Officer, for permission to conduct this research on Bermuda. R. W. Henderson kindly granted us permission to use David Leber's watercolor illustrations (from Schwartz and Henderson 1985) in our figures. The manuscript was greatly improved by comments from Michael Logan, James Stroud, and an anonymous reviewer. We are grateful to our undergraduate assistants from Florida Southern College and Alma College in 2010 and 2012, particularly Bryan Barrows, for help in gathering data. We also thank James Stroud for sharing his unpublished data on *A. extremus* females. Alexandra Jenkins assisted with our supplemental data collection on *A. extremus* females in July 2016. We have complied with appropriate animal care guidelines, and no animals were harmed in this study.

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