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E-Natural History Note

A Few Meters Matter: Local Habitats Drive Reproductive Cycles in a Tropical Lizard

Luisa M. Otero,[1,*] Raymond B. Huey,[2] and George C. Gorman[3]

1. Department of Biology, University of Puerto Rico, Rio Piedras, PO Box 23360, San Juan 00931, Puerto Rico;
2. Department of Biology, University of Washington, Seattle, Washington 98195; 3. Paso Pacifico, Ventura, California 93002

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ABSTRACT: Reproductive phenology often varies geographically within species, driven by environmental gradients that alter growth and reproduction. However, environments can differ between adjacent habitats at single localities. In lowland Puerto Rico, both open (sunny, warm) and forested (shady, cool) habitats may be only meters apart. The lizard *Anolis cristatellus* lives in both habitats: it thermoregulates carefully in the open but is a thermoconformer in the forest. To determine whether reproduction differs between habitats, we compared reproductive cycles of females in open versus forest habitats at two localities for over 2 years. Open females were more likely than forest females to be reproductive throughout the year, probably because open females were able to bask and thereby achieve warmer body temperatures. These between-habitat differences in reproduction were especially marked in cool months and are equivalent in magnitude to those between populations separated by elevation. Thus, environmental differences (even on a microlandscape scale) matter to reproduction and probably to demography.

Keywords: habitat, thermal biology, landscape ecology, phenology, reproduction.

Introduction

Reproduction and life history often vary geographically and parallel environmental gradients that drive such variation (Dunham et al. 1989; Grant and Dunham 1990; Adolph and Porter 1993). Environmental variation can occur on micro- as well as macrogeographic scales (Christian et al. 1983; Porter et al. 2002; Sears et al. 2011; Kearney et al. 2014; Dowd et al. 2015). If individual organisms perceive heterogeneous landscapes as coarse grained (Levins 1968; Sears et al. 2011) and thus tend to stay within a given habitat type, then their reproductive cycles might vary on a local scale (that is, microgeographically). However, whether local environmental patchiness affects reproduction and ecology is rarely investigated (Riechert and Tracy 1975; Mitchell et al. 2009; Dowd et al. 2015).

Temperature is a dominant environmental factor influencing the physiology, reproduction, and ecology of terrestrial ectotherms (Gorman and Licht 1974; Huey 1982; Angilletta 2009). Environmental temperatures often vary spatially, even on local scales (Huey 1974; Riechert and Tracy 1975; Grant and Dunham 1990; Logan et al. 2013; Potter et al. 2013; Kearney et al. 2014; Sears and Angilletta 2015). At many Caribbean localities, for example, open habitats, which are sunny and hot, can be adjacent to forest habitats, which are shaded and warm (Huey 1974; Hertz 1992*b*; Logan et al. 2013). Because temperature drives reproduction in some Caribbean anoles (but see Licht and Gorman 1970, 1975; Gorman and Licht 1974; Lister 1981), reproductive cycles of open versus forest lizards might differ, but this has never been investigated.

In the New World tropics, different species of *Anolis* lizards are often restricted to either open or forest habitats (Ruibal 1961; Rand 1964; but see Schoener 1970; Logan et al. 2013). Open-habitat anoles thermoregulate relatively carefully to achieve body temperatures (T_b) that are relatively warm and that overlap with thermal preferences measured in laboratory thermal gradients, whereas forest (below-canopy) species are typically thermoconformers and have lower T_b (Ruibal 1961; Rand 1964; Huey 1974; Lister 1976; Hertz et al. 1999; Gunderson and Leal 2012; Logan et al. 2013). However, some *Anolis* species occur in both types of habitats at single localities (Huey 1974; Huey and Webster 1975, 1976; Lister 1976). Species occupying thermally distinct but adjacent habitats offer special opportunities to evaluate the impact of local environmental variation on reproduction.

Here we evaluate (1) whether reproductive patterns and cycles of female *Anolis cristatellus* differ between adjacent (open, forest) habitats at two sites in lowland Puerto Rico and (2) whether habitat differences in thermal environments and in opportunities for thermoregulation might

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[*] Corresponding author; e-mail: luisinhaotero@yahoo.com.

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contribute to observed reproductive differences. We monitored female reproductive condition as well as body and environmental temperatures almost every month for more than 2 years. The percentage of females that were reproductive varied seasonally in both habitats and was highest in summer and lowest in winter. Moreover, forest females were much less likely to be reproductive than were open females in most months, especially during cool months (October–February). In fact, the magnitude of this between-habitat difference in reproduction frequency in winter is large and equivalent to that between lowland versus upland females in winter (Gorman and Licht 1974). To our knowledge, local-scale patchiness in reproductive frequency has not previously been documented in lizards and suggests that the lizards in these habitats—even though separated by only a few meters—probably have very different demographic profiles.

Methods

Study Populations

Anolis cristatellus is a medium-sized, trunk-ground anole that is widely distributed from sea level to midelevation on the Puerto Rico bank (Rand 1964; Williams 1972; Rivero 1998). At lowland sites, it is abundant in both open and forest habitats, but at higher elevations, it is restricted to the open (Schoener and Schoener 1971; Huey 1974; Huey and Webster 1976; Lister 1981; Hertz 1992*b*). Its reproduction (Gorman and Licht 1974; Lister 1981), behavior (Leal and Rodríguez-Robles 1995; Leal 1999), structural niche (Schoener and Schoener 1971), and thermal biology (Rand 1964; Heatwole et al. 1969; Huey 1974, 1983; Huey and Webster 1976; Lister 1981; Hertz 1992*b*; Gunderson and Leal 2012, 2015) are exceptionally well known.

We studied the annual reproductive cycles of female *A. cristatellus* in open and forest habitats (separated by only a few meters) at two localities west of San Juan on the north coast of Puerto Rico: Punta Salinas (18.465°N, 66.189°W, 2 m asl) and Monagas (18.407°N, 66.138°W, 13 m asl). Both sites have well-developed forest and open habitats (photos in appendix; fig. A1; appendix and figs. A1–A4 available online), but the open habitat at Monagas is relatively more open and sunny. Both sites are human-modified parks, and the forest habitats are secondary. We sampled lizards within areas of approximately 12,400 m^2 (open) and 5,000 m^2 (forest) at Punta Salinas and 5,300 m^2 (open) and 7,500 m^2 (forest) at Monagas, respectively. Open trees that we searched were 15–250 m from the section of the forest that we censused but always within 75 m of another section of forest. We did not catch any individual at the forest edge. Because the two sites have somewhat different thermal and physical characteristics and had somewhat different sampling periods, we analyze reproductive data for each separately.

Field Methods and Statistical Analyses

We visited Punta Salinas almost every month from July 2011 through June 2014 and Monagas from February 2012 through June 2014. During each census, we usually captured 15–46 females in each habitat, palpated them to determine reproductive condition, and measured body temperature (T_b; Miller-Weber cloacal thermometer, using standard precautions) and size (snout-vent length [SVL] in millimeters, mass in grams). We separated females into two size classes: small females were shorter than the median SVL (<46.5 mm). We classified females as reproductive if they had either an egg or an enlarged follicle (Gorman and Licht 1974; Lister 1981). (Note: *Anolis* lay single-egg clutches.) L. M. Otero did all palpating: she correctly assigned reproductive status to a test series of 33 female *A. cristatellus* and *Anolis gundlachi* (from several localities) that were killed, preserved, and dissected to assess reproductive condition. We did not monitor male reproduction, because doing so would have required the killing of many individuals. We report T_b data only for females.

For each lizard captured, we recorded habitat (open or forest), time of day, perch height, sun exposure (full sun, partial sun, or shade), and weather (sunny, cloudy, sunny-cloudy, or rainy). We marked all captured individuals with a temporary paint dot so that we would not recapture them during a given census. Identifying dots disappeared within a month, and so we likely recaptured some individuals in subsequent censuses (partial pseudoreplication). However, because the areas we sampled are large (above) and because these anoles are dense (L. M. Otero, unpublished manuscript), recaptures are likely few (see below). Moreover, females are likely laying eggs frequently, at least in warmer seasons; for example, *Anolis carolinensis* lay an egg every 10–14 days under field conditions (see Crews 1973), and *A. cristatellus* lay an egg about every 17 days in the lab at 28°C (J. McGlothlin, personal communication). Thus, pseudoreplication involving reproduction is likely minor (see below). Original and summary data are available in the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.669r8; Otero et al. 2015).

Our sample included some subadult females; thus, before computing the percentage of adult females that were reproductive at each census, we needed to establish the minimum size (SVL) of adult (i.e., reproductive) females. The smallest (SVL) females that were gravid in summer (June–August) were 38 and 39 mm at Punta Salinas and Monagas, respectively, and in winter (December–February) were 40 and 40 mm, respectively. Following Gorman and Licht (1974), we set the minimum size at 2 mm larger than the smallest-observed reproductive female (thus, 40 mm). Sample sizes (per census) of adult females in each habitat in each census were 8–105 in Punta Salinas (median = 24) and 15–27 in Monagas (median = 20). Total captures of adult females were 1,865 at Punta Salinas and 1,112 at Monagas. Sample sizes by census, habitat, and size category are compiled in the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.669r8; Otero et al. 2015).

To compare incidence of reproduction (i.e., percentage of females that were gravid) in forest versus open habitats, we computed the number of monthly censuses in which a higher percentage of females were reproductive in the open than in the forest and then used a sign test to evaluate the overall difference. This binary analysis assumes that reproductive frequencies in adjacent months are independent. In addition, we ran logistic regressions on reproductive state as functions of season, habitat, and size. Nevertheless, to avoid the possibility of pseudoreplication (occasional recaptures of some females; see above), we ran regressions on data collected in only four months (January, April, July, and October samples; appendix; table A1; tables A1–A3 available online). (Despite reduced sample sizes, the resulting patterns are consistent with those derived from the full data.) To illustrate factors influencing reproduction, we used classification tree analyses on the reduced data (ctree in R package party; Hothorn et al. 2006).

To compare T_b of female lizards in the two habitats, we computed the number of censuses in which open females had a higher median T_b than did forest females. We then used a sign test to evaluate difference for each site separately.

To quantify environmental (=operative) temperatures (T_e; Bakken 1992), we set out at least one T_e model (each with two probes) in each habitat and recorded T_e every 15 min (Hobo U23-003) at both localities. Models were PVC (78 mm × 15 mm) painted flat gray. We did not attempt to bracket available T_e. We recorded T_e throughout the year, except when loggers occasionally failed. (Our analyses used time periods only when data from all loggers were available [appendix; fig. A2].) In Monagas, the open probes were positioned on the east and west sides of a tree and thus were exposed to sun at least part of the day. In Punta Salinas, security concerns dictated that open probes be positioned in secluded spots, and thus, these probes were only occasionally exposed to full sun; consequently, open T_e underestimates maximum T_e available at Punta Salinas. Because probes were few in number and rarely moved, and because security concerns prevented our placing more models to bracket the T_e range at both sites, our T_e data should not be interpreted as randomized thermal maps of the two habitats (Bakken and Angilletta 2013) but rather as general indicators of thermal conditions in each. However, to bracket available T_e at Punta Salinas, we deployed eight models in the open and 10 in the forest at Punta Salinas in January 2012 and then monitored T_e over several days (appendix; fig. A3). (Tourists were infrequent in January, and so security concerns were reduced.)

To provide an estimate of the thermal quality of the habitat (Hertz et al. 1993), we computed the percentage of T_e that overlapped with preferred body temperatures (T_p) of *A. cristatellus* (28.6°–30.7°C; see Hertz et al. 1993) in summer (June–August) and in winter (December–February). The T_e in a habitat was considered to be within the T_p range if either of the two probes was within the T_p range or if the two probes bounded the T_p range (such that a shuttling lizard could achieve T_p). Because the number of probes is small, these data should be considered as only a crude reflection of available T_e, especially in the open habitats, which are thermally heterogeneous (figs. A2, A3). In any case, this general approach (Hertz et al. 1993) ignores the spatial distribution of sun and shade (Sears and Angilletta 2015), which differs strikingly between these habitats (Huey 1974).

Results

Reproduction

At both localities, female reproduction varied seasonally and was much higher in summer than in winter (fig. 1; appendix; table A1; both $P < .001$), as in other Puerto Rican anoles (Gorman and Licht 1974). A higher percentage of females were reproductive in the open than in the forest at both field sites (in 28 of 34 monthly samples at Punta Salinas and in 26 of 27 samples at Monagas, both $P \ll .001$; fig. 1). The higher reproduction of open females (vs. forest ones) was especially pronounced in winter (November–February), when 47.9% ($N = 313$) and 59.1% (149) of open females were reproductive in Punta Salinas and Monagas, respectively, but only 5.1% (274) and 8.1% (149) of forest females were reproductive. In effect, forest females were largely nonreproductive for several months in winter (fig. 1).

Effects of season, habitat, and size on female reproduction (appendix; fig. A4) were analyzed via classification trees (fig. 2). At both sites, season was highly significant (fig. 2; both $P < .001$), separating winter from the remaining seasons. At Punta Salinas, summer had higher reproduction than spring and autumn ($P < .001$). At both sites, habitat was also highly significant in all seasons (both $P < .036$). At Punta Salinas, large females were slightly more likely than small females to be reproductive in the open in winter ($P = .024$) and in the forest in spring ($P = .009$). At Monagas, large females had a reproductive advantage only in the open in spring, summer, and autumn ($P < .001$). The patterns of significant factors in these classification trees are very similar to those in logistic regressions on seasonal data (appendix; table A1).

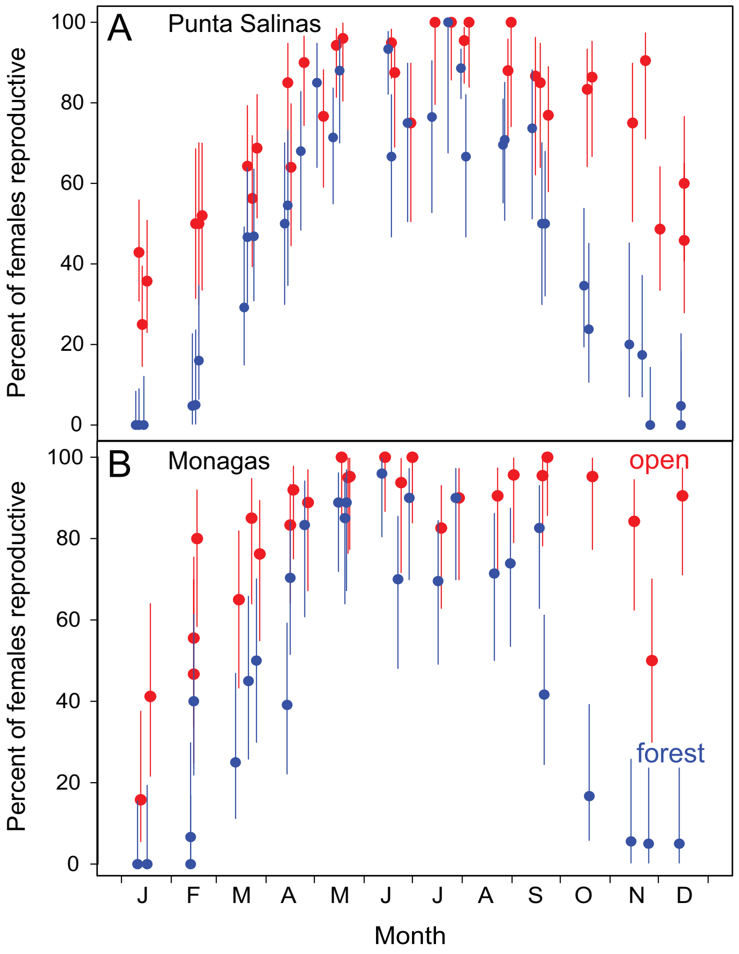

Figure 1: Seasonal patterns of the percentage (with 95% confidence intervals) of females that were reproductive in the open (red) versus in the forest (blue) habitats at Punta Salinas (*A*) and Monagas (*B*), Puerto Rico. Dates for Monagas are shifted by +2 days to eliminate overlap with data for Punta Salinas. Data underlying figure 1 are deposited in the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.669r8; Otero et al. 2015).

A few females—especially open ones—contained two oviductal eggs. At Punta Salinas, gravid females with two oviductal eggs were infrequent in either habitat (5.0% of 576 in open vs. 1.9% of 374 in forest), but even this small difference was significant (χ^2 test, $P = .3313\text{e-}06$). At Monagas (the warmer site), relatively more gravid females in the open had two eggs than did forest females (13.3% of 430 vs. 4.1% of 242, $P = 3.313\text{e-}06$). However, a reviewer cautioned that the statistical significance of this pattern might be inflated if individual females differed in the tendency to have one versus two eggs and if we repeatedly sampled those individuals in the two habitats (thus, pseudoreplication). However, in a single month sample (August 2012) at Monagas, 8 of 23 individual females in the open had two eggs, whereas 0 of 23 in the forest had two eggs (Fisher's exact test, $P = .004$). During the entire study, we caught a total of only 10 females in the forest with two eggs.

Operative Temperatures

The T_e was warmer during the day in the open than in the forest (appendix; figs. A2, A3). In Punta Salinas (or Monagas) during daytime samples (0900 to 1700 hours), an open model was warmer than either of the two forest models in Punta Salinas 94.5% of the time (or 99.7% at Monagas). During that same time interval, a much higher percentage of open T_e overlapped with preferred body temperatures of *Anolis cristatellus* (28.6°–30.7°C; see Huey and Webster 1976) than did forest T_e (Punta Salinas: 41.3% vs. 25.7%; Monagas: 41.3% vs. 23.0%).

Behavioral Thermoregulation and Body Temperature

Lowland *A. cristatellus* are generally active from sunrise to sunset (Huey and Webster 1976; Hertz 1992*b*). Prior

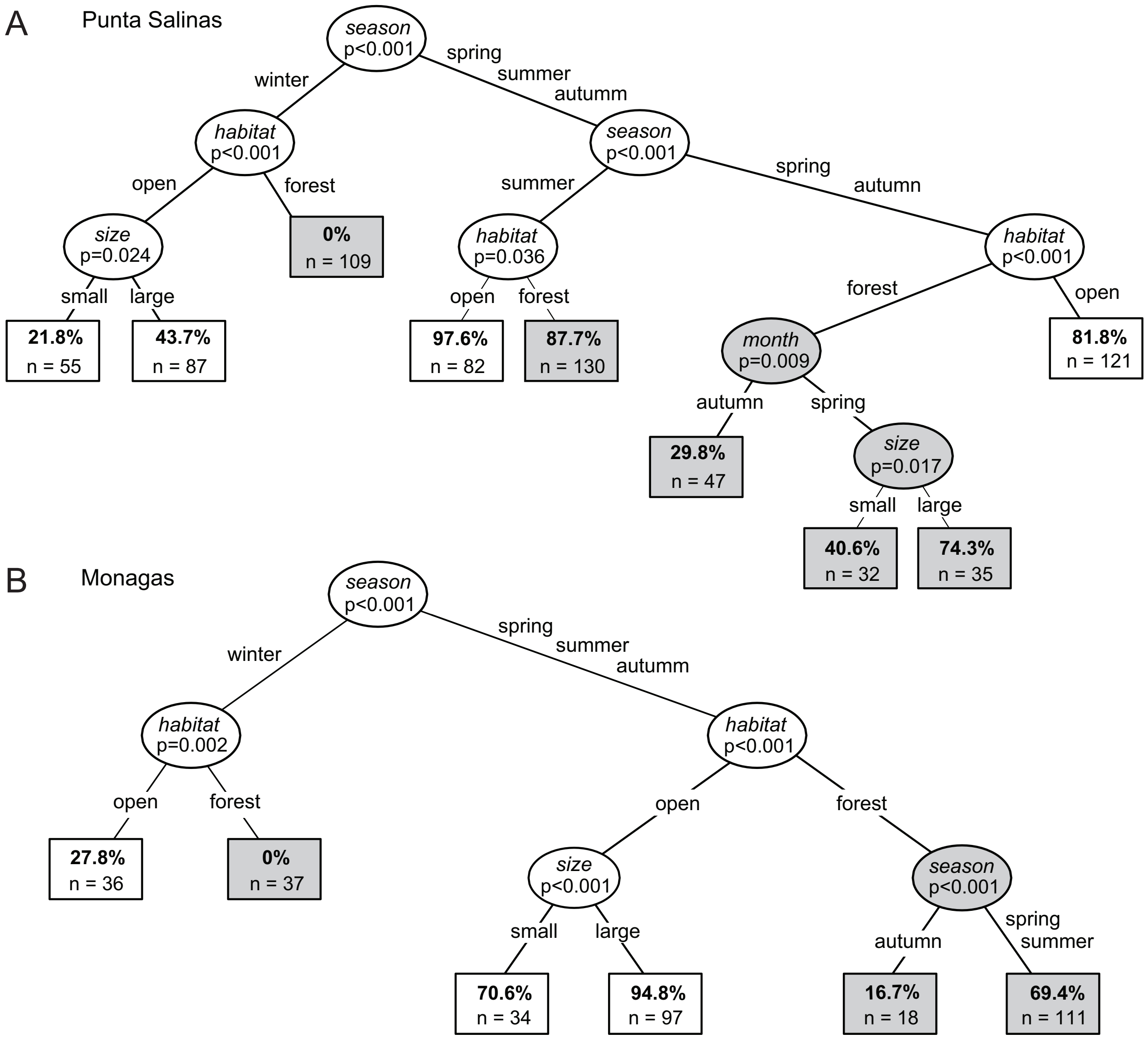

Figure 2: Classification trees for reproduction at Punta Salinas (*A*) and Monagas (*B*), Puerto Rico. At both sites, the root node represents seasonality, showing reduced reproduction in winter relative to other seasons. Lower nodes generally reflect habitat, showing reduced reproduction in forest (shaded) compared to open (unshaded) habitats or differences between other seasons and sometimes reduced reproduction in small females. In the terminal nodes, the percentage of females (and number of individuals) is indicated. Data underlying figure 2 are deposited in the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.669r8; Otero et al. 2015).

studies based on full-day observations at Punta Salinas (Huey 1974; Huey and Webster 1976) have shown that open *A. cristatellus* bask in the early morning and late afternoon but retreat to shade at midday, whereas forest lizards rarely bask. In our study, we sampled mainly at midday (interquartile range: Punta Salinas = 1138 to 1539 hours; Monagas = 1222 to 1520 hours), when these lizards are typically in shade (Huey 1974; Hertz 1992*b*). Even so, a slightly higher percentage of females were basking (i.e., perched in sun during sunny weather) in the open than in the forest in Punta Salinas (6.4% [$N = 373$] vs. 2.3% [$N = 398$], $P = .0033$, Fisher's exact test, one-tail) and in Monagas (6.5% [$N = 107$] vs. 0% [$N = 60$], $P = .048$).

In prior studies at Punta Salinas (in summer only), body temperatures (T_b) of open lizards were warmer than those of forest lizards (Huey 1974; Huey and Webster 1976). This pattern holds for all-year samples of female data (Punta Salinas: open median $T_b = 29.3°C$ [$N = 662$]; forest = 28.0°C [$N = 662$], $P < 2.2\text{e-}16$; Monagas: open median $T_b = 30.5°C$ [$N = 417$], forest = 28.5°C [$N = 384$], $P <$

2.2e-16). In paired comparisons at each monthly census (fig. 3), open females almost always had warmer T_b than did forest lizards (Punta Salinas: 29 of 31 censuses, $P =$ 4.629e-07; Monagas: 24 of 26 censuses, $P =$ 1.049e-05), and the median difference was +1.8°C for both Punta Salinas and Monagas. However, our samples were largely midday, and thus, we rarely sampled T_b in the morning, when open lizards bask and have T_b 3°–4°C higher than forest lizards (Huey 1974).

The preferred temperature range for lowland *A. cristatellus* is 28.6°–30.6°C (Hertz et al. 1993). In summer, open females were more likely than forest females to have T_b that was warmer than T_p at both localities, especially at Monagas (appendix; table A2; Huey 1974). In winter, however, open females were more likely than forest females to have T_b that was within the T_p range (30.8% vs. 2.9% at Punta Salinas; 37.3% vs. 3.3% at Monagas). In fact, almost all forest females in winter had T_b below the T_p range (Punta Salinas = 96.8%; Monagas = 95.9%). In spring and fall, females in the two habitats had relatively similar T_b patterns. Thus, open females appear too hot in summer, but forest ones appear too cold in winter.

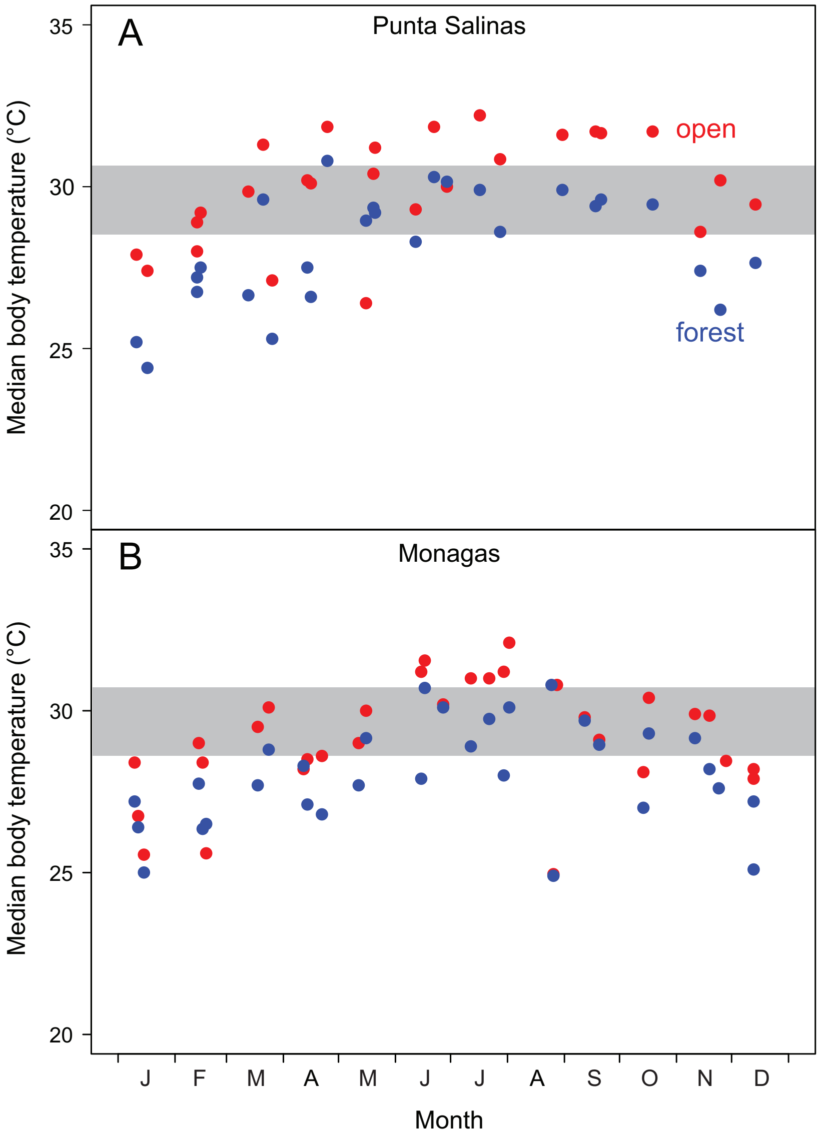

Figure 3: Median body temperatures of *Anolis cristatellus* in open (red) and in forest (blue) habitats at Punta Salinas (*A*) and Monagas (*B*), Puerto Rico. The shaded rectangle indicates the preferred body temperature range for this species. Data underlying figure 3 are deposited in the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.669r8; Otero et al. 2015).

Discussion

To our knowledge, this is the first study documenting the fact that *Anolis* reproductive cycles (or any lizard's cycles) can differ dramatically at a microgeographic scale. Females in shaded forests were significantly less reproductive than were females in open habitats at two localities in lowland Puerto Rico (figs. 1, 2, A4; table A1). We suspect that this pattern will be observed in other tropical ectotherms that live in both open and forest habitats (Huey 1974; Huey and Webster 1975, 1976; Lister 1976; Lee 1980) or possibly in forest lizards living next to a treefall gap (R. Andrews, personal communication). However, in sites with many species of anoles, different species tend to occur in forest versus open habitats (Rand and Humphrey 1968; Rodríguez Schettino et al. 2010); potentially, the habitat-specific patterns in reproductive cycling hold but involve different species (Ruibal 1961; Rodríguez Schettino et al. 2010; R. Andrews, personal communication).

The magnitude of these between-habitat differences in reproduction was large in most months but was especially pronounced in cooler months (October–February; fig. 1). In fact, the magnitude of these between-habitat differences in percentage of reproduction at this time of the year is equivalent to that of open females at localities separated by several hundred meters of elevation (Gorman and Licht 1974).

The magnitude of the difference in reproduction between habitats—and also between months—appears large compared to expectations from thermodynamics. Typically, physiological rates increase two- to threefold with a 10°C increase, and thus, open females might have a 1.4-fold greater incidence of reproduction than forest females, given a +3°C difference in T_b (V. Savage, personal communication; see appendix). However, the observed difference between open versus forest females in Monagas in November 2012 was 18-fold (90.5% vs. 5% reproductive in open and in forest, respectively, and with median T_b difference of <3°C). Seasonal shifts within habitats are also huge relative to the change in T_b (figs. 1, 3).

What accounts for these microscale differences in reproduction? *Anolis* require warm temperatures for reproduction (Licht 1973), and Gorman and Licht's (1974) and Lister's (1981) analyses strongly suggest that environmental temperatures drive seasonal and macrogeographic differences in reproduction in Puerto Rican *Anolis* (see also Licht and Gorman 1975). Do the different environmental temperatures of open versus forest habitats at our sites (figs. 2, A2, A3) and thermoregulation by the lizards themselves contribute to the conspicuous between-habitat differences in reproduction (fig. 1)? The percentage of reproduction in a month is indeed correlated with the median T_b of the lizards (Punta Salinas: $r = 0.6066$; Monagas: $r = 0.677$; both $P \ll .001$). In winter, the low frequency of reproduction—especially of forest females (fig. 1)—very likely relates at least in part to the relatively low T_e (figs. A2, A3) and to the low T_b of those females (fig. 3). As temperatures increase in spring, the percentage of reproductive females increases in both habitats and is somewhat higher in the open than in the forest (fig. 1), consistent with warmer T_b in the open than in the forest at this time (fig. 3; table A2). In summer, open females often had T_b above the T_p range (fig. 3; table A2), consistent with behavioral observations suggesting heat stress at midday in summer (Huey 1974; Gunderson and Leal 2015); nevertheless, most open females continue to reproduce, so the elevated T_b of open females does not appear to be reproductively stressful (fig. 1).

Patterns in fall are complex. Reproduction of forest females dropped precipitously in October and November at both sites (fig. 1). Even so, forest females maintained relatively high T_b until November (fig. 3), and many forest females in October and November had T_b within the T_p range (Punta Salinas = 47.6% [$N = 84$], Monagas = 31.7% [$N = 41$]; table A2). Thus, reproduction began dropping before activity T_b did.

Temperature is, of course, not the only environmental factor that influences lizard reproduction. Vitamin D titers might be too low in forest populations (Ferguson et al. 2005). Photoperiod influences female reproduction in *Anolis carolinensis* (Licht 1973), but open females experienced the same photoperiods as forest females while still maintaining high reproduction through late fall (fig. 1). Potentially, food levels are higher in the open—especially in fall. However, physiological interactions between food ration and temperature can be complex (Brett 1971; Huey 1982). A study that monitors feeding as well as net energy gain and reproduction (between habitats, between seasons) would be informative.

Independent of whether habitat-specific reproductive patterns are driven by temperature, food, and other factors, the forest habitats of lowland Puerto Rico appear reproductively suboptimal for *Anolis cristatellus*, though still clearly adequate for them to maintain dense populations. This habitat effect probably influences other life-cycle stages. For example, Schlaepfer (2003) experimentally compared the egg survival of *Anolis limifrons* in two adjacent habitats in Costa Rica: eggs in the pasture had a shorter incubation period and higher survival than did eggs in the forest; the temperature regimes for these two habitats were different (pastures were warmer), as were predation rates.

Other life-history traits (e.g., growth, survival) can be environmentally sensitive (Angilletta 2009) and thus may also show local-scale variation. What are the consequences of such microscale differences in reproduction for *A. cristatellus* populations? Likely, lizards in these two habitats have different demographic profiles. Lizards in the open probably reach maturity faster and reproduce more frequently than do lizards in the forest, implying different recruitment rates in the two habitats, though potential differences in food and predation/parasitism risk could modify these predictions. A demographic (mark-recapture) study at Punta Salinas is under way and will evaluate some of these issues (L. M. Otero, unpublished manuscript; see below).

Some movement between habitats is expected, given that the habitats are separated only by meters. However, male *A. cristatellus* are highly territorial, so they are unlikely to move frequently (Clark and Gillingham 1990; Jenssen 2002; M. Leal, personal communication). Interestingly, only one of 11 recaptured individuals that had moved between habitats at Punta Salinas was male. Overall, about 8% of recaptured lizards had moved between habitats but showed no obvious directional bias (e.g., forest to open; L. M. Otero, unpublished data). Such movements should have reduced the between-habitat differences in reproduction but obviously did not eliminate those differences (fig. 1).

Overall, our data show that a few meters can matter, specifically, environmental variation on a microgeographic scale can profoundly affect body temperatures and reproduction of lizards and by extension the demography of lizards in patchy localities such as Punta Salinas and Monagas. Although forest females currently appear to be at a thermal disadvantage (especially in winter), this disadvantage should be reduced with climate warming. Thus, even modest winter warming will likely benefit forest females. In contrast, warming in summer might induce stress on open females, at least by restricting midday activity (Huey 1974; Gunderson and Leal 2015). However, we see no evidence of lowered reproduction in open females in summer (figs. 2, A4), and *A. cristatellus* are currently thriving in xeric habitats warmer than Punta Salinas (Huey and Webster 1976; Hertz 1992*a*; Gunderson and Leal 2012). Thus, lizards at Punta Salinas and Monagas appear to have a thermal buffer from summer warming.

Finally, many landscapes in Puerto Rico and elsewhere are being modified and fragmented at different spatial scales (Foster et al. 1999; Peters et al. 2013), greatly altering patterns of sun and shade and thus of habitat suitability. A lesson emerging from this study is that landscape changes that alter the thermal environment—even at small spatial scales—are likely to dramatically modify physiology and life history (Kearney 2013).

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