

Article

Differences in Habitat Use, Thermal Ecology, and Behavior of the Semiaquatic Lizard *Anolis aquaticus* at a High- and Low-Elevation Site

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Abstract

For small ectotherms, thermal conditions and habitat structure can drive local adaptations in behavior and habitat use. The water anole, *Anolis aquaticus*, is a semiaquatic lizard occurring along streams in lowland tropical sites, as well as at higher elevations with greater thermal variability. We studied their thermal ecology, habitat use, and behavior at a high- (~1100 m) and low-elevation (~sea level) site in Costa Rica to assess the relationship between thermal environment and behavioral ecology. We measured behavior through focal observations (rates of movement, head turns, and feeding) and recorded the range of environmental temperatures, body temperatures, air and substrate temperatures of perches, and habitat use (perch location relative to water's edge and current, substrate, cover, and visibility). The low-elevation site had higher minimum temperatures and a smaller range of available temperatures. Body temperature and size varied with site and sex: low-elevation males had the highest body temperatures, and high-elevation males were largest. Individuals at the high-elevation site were less active, perched closer to the water's edge (shorter horizontal perch distance), and more often used the ground or rocks near an eddy as a substrate than individuals at the low-elevation site. The temperature and habitat structure of water courses can manifest phenotypic differences in ecology and behavior.

Keywords: body size; body temperature; Costa Rica; environmental temperature; *Norops aquaticus*; riparian



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1. Introduction

For terrestrial ectotherms, temperature can be a driving factor linked to life history, morphology, behavior, and habitat use. Variations in thermal biology can serve as the basis for coexistence in sympatric species and as a link to understanding how species will respond to climate change or habitat destruction [1–3]. Population differences in the thermal

environment can exist and are often associated with behavioral and physiological adjustments [4]. For anoline lizards, significant understanding of their ecology has been achieved by examining thermal requirements and habitat structure [5,6]. Perch characteristics are also important for anoles, which exhibit behavioral preferences for and morphological adaptations to different perch types [7].

As small ectotherms, the thermal environment can drive local adaptations, with some species being active thermoregulators, while others are thermoconformers [8–10]. Limited access to warm areas can be associated with thermal conformity [11–13], but even tropical lizards are sometimes intolerant of high temperatures [9]. Whether a lizard uses behavioral thermoregulation depends on available operative temperatures and the costs and benefits associated with regulation [14]. As a response to thermal constraints, habitat use, activity, and behavior might be adjusted. Similarly, conspecific populations occupying habitats at different elevations are likely exposed to differing thermal regimes, in addition to variations in other environmental conditions. The goal of our study was to characterize aspects of population demographics, habitat features, behavior, and thermal ecology in two populations of a lizard species occupying stream edge habitats at different elevations.

A small number of anoline lizard species are known to be semiaquatic, occurring near and readily entering water [15,16]. Comparative reviews of semiaquatic anoles provided little evidence of morphological convergence among species living in and around water, as aquatic habitats can be used in multiple ways by semiaquatic anoles [15,16], although recent evidence of convergence in skin characteristics of semiaquatic anoles has emerged [17]. Semiaquatic anoles often use a greater range of structural habitats than other anoles [18–21], and their association with bodies of water means that they occur at an ecotone. For most semiaquatic anoles, relevant factors that best characterize their habitat have yet to be clearly identified (but see [16,22]).

The water anole, *Anolis aquaticus*, is a semiaquatic lizard from lowland and premontane slopes of southwestern Costa Rica and southwestern Panama [23] that is restricted to water courses and readily enters water to flee pursuers [24,25]. Habitat selection by water anoles is related to characteristics of the adjacent river [22]. They dive and can remain submerged for extended periods of time [26], with the sexes exhibiting differences in their willingness to do so [27]. Ecomorphologically, water anoles bear traits that are better suited to perching on boulders rather than to vegetation along stream beds [16]. We undertook a comparative study on the ecology in *A. aquaticus*, examining aspects of their thermal biology, habitat use, and behavioral profiles in the field at two sites differing in elevation. We characterized the thermal environment at the two sites, as well as the range of habitat features used by water anoles at each elevation. We hypothesized that their ecology and behavior at the two sites would differ in ways reflecting the thermal environments.

2. Materials and Methods

We studied water anoles living along rivers at two sites differing in elevation and general aquatic characteristics: Las Cruces Biological Station (Estación Biológica Las Cruces), Coto Brus County, Puntarenas, Costa Rica (8°47' N, 82°57' W), and Golfito National Wildlife Refuge (Refugio Nacional Silvestre de Golfito), Golfito County, Puntarenas, Costa Rica (8°39' N, 83°10' W) (Figure 1). At Las Cruces (elevation ~1100 m; = high-elevation site), our study rivers (Java and West Java) were fast flowing and typically > 3 m in width. The river shore varied from steep banks to flat beaches several meters wide. The bordering forest was an advanced secondary or primary tropical premontane wet forest. Trees lined both sides of the river, providing shade but generally not forming a closed canopy over the river (Figure 2). At Golfito (near sea level; = low-elevation site), the two study rivers were narrower and shallower, generally slower flowing, and with fewer cascades and pools than

the rivers in Las Cruces. The Golfito rivers were bordered by secondary tropical lowland forest, providing more of a closed canopy than the high-elevation site (Figure 2).

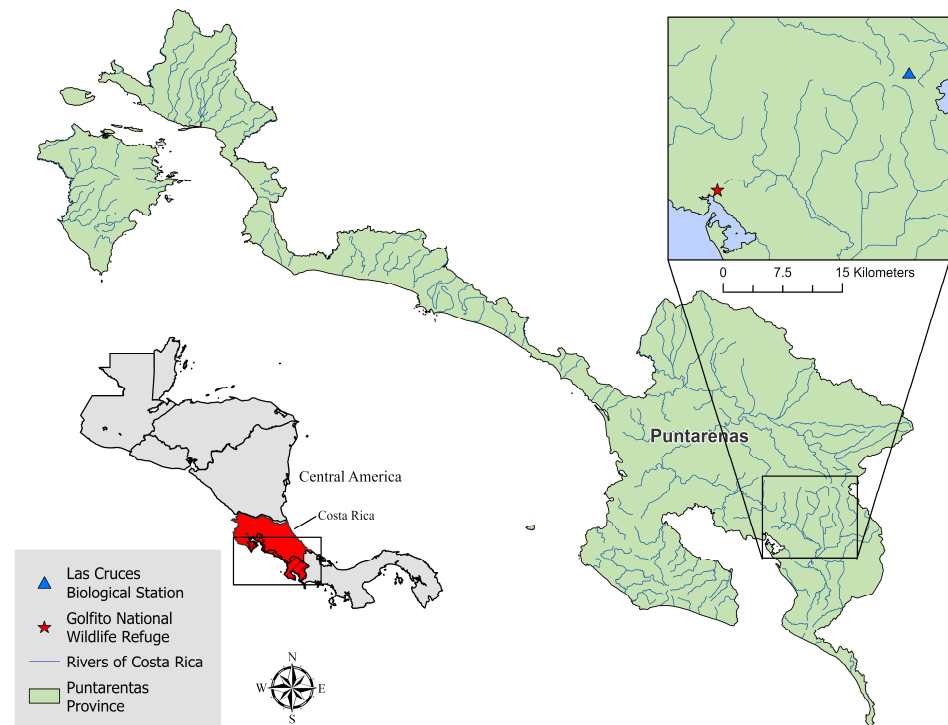


Figure 1. Relative location of the two study sites in Puntarenas, Costa Rica. The low-elevation site was located in Golfito National Wildlife Refuge and the high-elevation site at the Las Cruces Biological Station.



Figure 2. High- (left) and low-elevation (right) sites, illustrating differences in width of the rivers and bank structure.

Lizards at both sites were sampled from 24 June–17 July 2008 between 08:00 and 14:00 h by walking through the middle of the waterway while searching the banks. Once sighted, adult lizards (snout to vent length (SVL) ≥ 54 mm for males or ≥ 52 mm for females; [25] were captured with a lasso attached to the end of an extendable pole or by hand, and body temperatures (T_b) were immediately taken using a Schultheis-Weber cloacal thermometer (Miller and Weber, Inc., Ridgewood, NY, USA; <http://www.millerweber.com/>). Immediately after capture, we also measured air (T_a ; ~3 cm above the perch) and substrate temperatures (T_s) where the lizard was initially sighted. We did not use body temperatures for lizards whose capture was protracted or for whom handling exceeded

15 s prior to T_b being determined. Upon capture, each lizard was measured (SVL using a ruler and mass using Pesola spring scales), uniquely marked with a color code at the base of its tail using non-toxic paint pens, and released at its capture site.

To determine the potential range of environmental temperatures available to water anoles, we installed temperature loggers at both sites (Thermochron iButtons (DS1921H) Maxim Integrated Products, Inc., San Jose, CA, USA, <http://www.mouser.com/maxim-integrated/>; [28,29]). We placed iButtons in a variety of microhabitats, logging temperatures available in full shade and full sun, ensuring our ability to document maximum and minimum temperatures available to the lizards at each study site. We placed 25 iButtons at the low-elevation site from 29 June to 17 July and 24 at the high-elevation site from 27 June to 22 July, each recording temperature every 15 min. To characterize the available thermal environment in the two study sites, we generated mean maximum and minimum temperatures for each 15 min interval (08:00–14:15 h) recorded at each study site for all days that iButtons were in place. In addition, we computed the maximum (T_{max}) and minimum (T_{min}) temperature at the time of capture for each water anole from the temperatures recorded by all iButtons at the high- or low-elevation site during the bracketing 15 min interval for the day of capture. The 4 environmental temperatures associated with each lizard (T_a , T_s , T_{max} , and T_{min}) characterize the thermal environment at the time of capture.

We also recorded habitat characteristics at the location where we initially sighted an individual perching. For each lizard we first measured three aspects relative to the water course: (1) perch distance = horizontal distance from the lizard to the nearest water in the river, (2) perch height = vertical distance from the lizard to the river surface, and (3) current = water flow at the nearest point of the river, recorded as either eddy, smooth flowing, or turbulent flowing. Second, we categorized the substrate where we sighted a lizard perching as ground, rock, log (dead wood), tree (live wood), or vine. Third, we defined cover as open, partial, or covered (=any material directly above and ≤ 0.5 m of the lizard's position). Finally, we assessed visual noise, which we defined as the degree to which a perched lizard was exposed to moving water, a potential visual distraction. To measure noise, we held a compass at a perch site, and for each of the four cardinal directions we determined whether moving (either smooth or turbulent) water was visible. The resulting score ranged from 0 (no moving water visible) to 4 (flowing water in all directions) (Figure 3). We considered water to be visible if we saw a direct line from the perch to water that was not obstructed by vegetation or landscape features [30]. Water anoles rely on visual signals during social interactions [31,32] and feed on both aquatic prey and prey that are already dead [24], making perch selection and environmental noise potentially important factors for habitat use.

We conducted focal animal observations from 8 to 17 July 2008, observing individual lizards for 15 min while maintaining a minimal observation distance of 2 m (usually > 5 m). We recorded the number of head turns, head bobs, body movements, eating events (=“feeding”), and, for males, dewlap displays. We observed lizards that had been captured and marked previously or were caught and processed directly after being observed. Individual lizards were observed only once during the study.

Statistical analyses were performed using Minitab 15 (College Park, Pennsylvania, <http://www.minitab.com/>) with a significance level of 0.05, and we tested data for normality. We used general linear models (GLMs) to examine the influence of sex and site on population characteristics (SVL and mass), thermal ecology (T_a , T_b , and T_s), habitat use (perch distance, perch height, current, substrate, cover, and visual noise), and behavior (head turn, move, feeding, head bob, and dewlap display rates). We converted behavioral counts into rates (frequency/min) for analysis. In several instances, we used one-way anal-

ysis of variance (ANOVA) tests, with Tukey’s test for post hoc comparison of demographic classes. We used t-tests for comparing temperatures between sites and Pearson correlations to examine the relationship between temperature variables. To examine habitat use, we used chi-square analyses, examining standardized residuals to aid the interpretation of chi-square results [33]. To evaluate comparisons with low expected values, we applied Fisher exact tests [33].



Figure 3. Depiction of the water flow patterns we used for determining current and noise. The foreground shows smooth flowing water, the upper area has turbulent flowing water, and on the right is an eddy.

3. Results

3.1. Population Characteristics

We collected morphological measurements and thermal information for 182 lizards. Body size was significantly related to both site and sex. Lizards at the high-elevation site were larger than those at the low-elevation site, and males were larger than females (GLM, SVL: site $F_{1,179} = 24.2$, $p < 0.001$, sex $F_{1,179} = 90.4$, $p < 0.001$; MASS: site $F_{1,179} = 52.7$, $p < 0.0001$, sex $F_{1,179} = 27.0$, $p < 0.0001$; Table 1).

Table 1. Mean $\pm$ standard deviation of body size (mass and SVL), temperature, and habitat characteristics for males and females at low- (“low”) and high-elevation (“high”) sites. Perch height and perch distance were determined relative to the river. Visual noise was assessed at perch sites (possible values = 0 (no flowing water visible)–4 (flowing water in all directions)). Samples sizes are provided in parentheses for each site and sex. Significant sex and site differences are indicated by s and l superscripts, respectively. Statistical results are provided in the text.

	Low Males (46)	Low Females (40)	High Males (63)	High Females (33)
SVL (mm) ^{s,l}	64.8 $\pm$ 3.8	58.6 $\pm$ 2.2	67.9 $\pm$ 5.7	61.8 $\pm$ 3.5
Mass (g) ^{s,l}	5.6 $\pm$ 1.1	4.6 $\pm$ 0.5	6.9 $\pm$ 1.7	5.9 $\pm$ 1.1
Air °C ^{s,l}	25.1 $\pm$ 0.6	24.8 $\pm$ 0.6	20.8 $\pm$ 0.6	20.5 $\pm$ 0.7
Substrate °C ^{s,l}	24.9 $\pm$ 0.6	24.6 $\pm$ 0.6	20.5 $\pm$ 0.8	20.3 $\pm$ 0.7
Body °C ^{s,l}	25.4 $\pm$ 0.8	25.0 $\pm$ 0.5	21.0 $\pm$ 1.0	20.4 $\pm$ 1.1
Perch height (cm)	99 $\pm$ 81	92 $\pm$ 68	97 $\pm$ 57	89 $\pm$ 51
Perch distance (cm) ^l	44 $\pm$ 52	38 $\pm$ 41	86 $\pm$ 88	104 $\pm$ 98
Visual noise ^l	2.2 $\pm$ 1.0	2.0 $\pm$ 1.0	1.6 $\pm$ 1.1	1.2 $\pm$ 0.9

3.2. Thermal Ecology

The two study sites represent very different thermal environments. Maximum temperatures were higher at the low-elevation site, while minimum temperatures were lower and the range of temperatures ($T_{\max} - T_{\min}$) was greater at the high-elevation site (Figure 4). For the specific intervals during which lizards were captured, the low-elevation site had significantly higher minimum temperatures than the high-elevation site (mean = 23.7 ± 0.4 vs. 19.0 ± 0.6 °C; $t = 58.3$, $df = 141$, $p < 0.0001$), but the maximum temperatures did not differ significantly between the two sites (mean = 25.9 ± 1.9 vs. 26.0 ± 4.2 °C; $t = 0.2$, $df = 106$, $p = 0.84$; Figure 4). The range of environmental temperatures at the times of capture was significantly greater at higher elevations (mean of ranges = 6.9 ± 4.0 vs. 2.1 ± 1.7 °C; $t = 9.75$, $df = 103$, $p < 0.0001$; Figure 4).

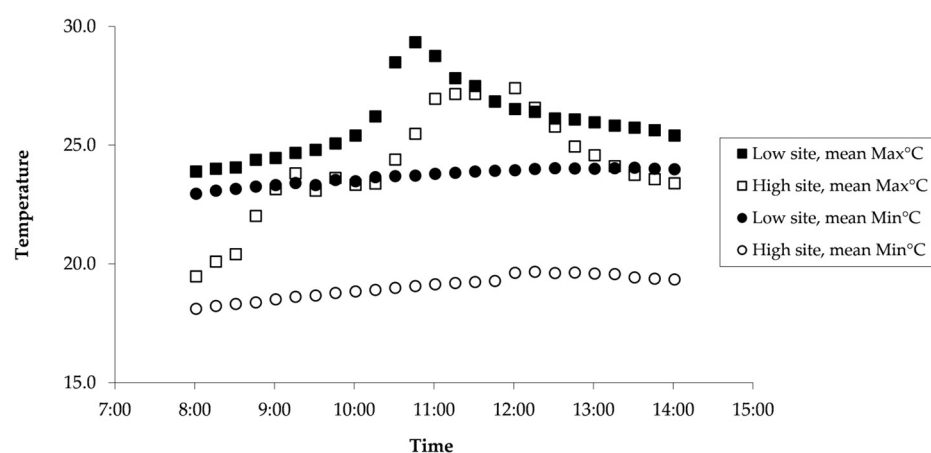


Figure 4. Thermal regime for high- and low-elevation sites, with mean maximum and minimum environmental temperature (°C) recorded by iButtons at each site throughout the lizard's active period. We present the average of the recorded maximum and minimum temperature at 15 min intervals between 08:00 and 14:15 h for each day from 29 June to 17 July at the low-elevation site (19 days) and from 27 June to 18 July at the high-elevation site (21 days).

T_b , as well as T_a and T_s , among observed individuals exhibited significant site and sex variation, with temperatures higher at the low-elevation site and slightly higher for males (GLM, T_b : site $F_{1,167} = 882.10$, $p < 0.001$, sex $F_{1,167} = 20.9$, $p = 0.001$; T_a : site $F_{1,173} = 2060.8$, $p < 0.001$, sex $F_{1,173} = 7.4$, $p = 0.007$; T_s : site $F_{1,170} = 1710.5$, $p < 0.001$, sex $F_{1,170} = 6.3$, $p = 0.013$; Table 2). Within each site, T_b , T_a , T_s , $T_{\max}$, and $T_{\min}$ were significantly positively correlated, although the correlations were always weaker at the high-elevation site (Table 2).

We made paired comparisons for each captured lizard's T_b with its associated T_a and T_s . There was significant variation among groups in the difference between T_b and T_s (ANOVA: $F_{3,167} = 5.02$, $p < 0.002$), as well as between T_b and T_a ($F_{3,169} = 7.12$, $p < 0.001$). Females in the high-elevation site had T_b no different than T_s (paired t : $t = 0.64$, $n = 31$, $p = 0.53$), but $T_b < T_a$ ($t = 2.37$, $n = 31$, $p = 0.025$), whereas all the other groups exhibited $T_b > T_s$ (high-site males $t = 5.80$, $n = 57$, $p < 0.001$; low-site females $t = 7.78$, $n = 39$, $p < 0.001$; low-site males $t = 6.92$, $n = 41$, $p < 0.001$) and T_b no different or greater than T_a (high-site males $t = 1.94$, $n = 57$, $p = 0.057$; low-site females $t = 4.94$, $n = 40$, $p < 0.001$; low-site males $t = 4.24$, $n = 42$, $p < 0.001$). When compared to environmental temperatures at time of capture, T_b 's were closer to $T_{\max}$ at the low-elevation site than at the high-elevation site (GLM: $F_{1,154} = 60.2$, $p < 0.001$, Figure 5) but did not vary with sex (GLM: $F_{1,154} = 0.20$, $p = 0.655$). Differences between T_b and $T_{\min}$ did not vary significantly with site or sex (GLM, site: $F_{1,154} = 0.92$, $p = 0.340$; sex: $F_{1,154} = 0.01$, $p = 0.909$; Figure 5).

Table 2. Pearson correlations (r) among temperatures obtained at the time of capture for each lizard (air (T_a), substrate (T_s), and body (T_b) temperatures, as well as maximum (T_{max}) and minimum (T_{min}) environmental temperatures at the time of capture). For all pairs, $p < 0.001$, except (*) T_b vs. T_{max} , $p = 0.018$ at the high-elevation site.

Low-Elevation Site				
	Body °C	Air °C	Substrate °C	Max °C
Air °C	0.86			
Substrate °C	0.84	0.92		
Max °C	0.5	0.53	0.51	
Min °C	0.82	0.87	0.85	0.55
High-Elevation Site				
Air °C	0.74			
Substrate °C	0.69	0.72		
Max °C	0.27 *	0.37	0.45	
Min °C	0.62	0.56	0.7	0.42

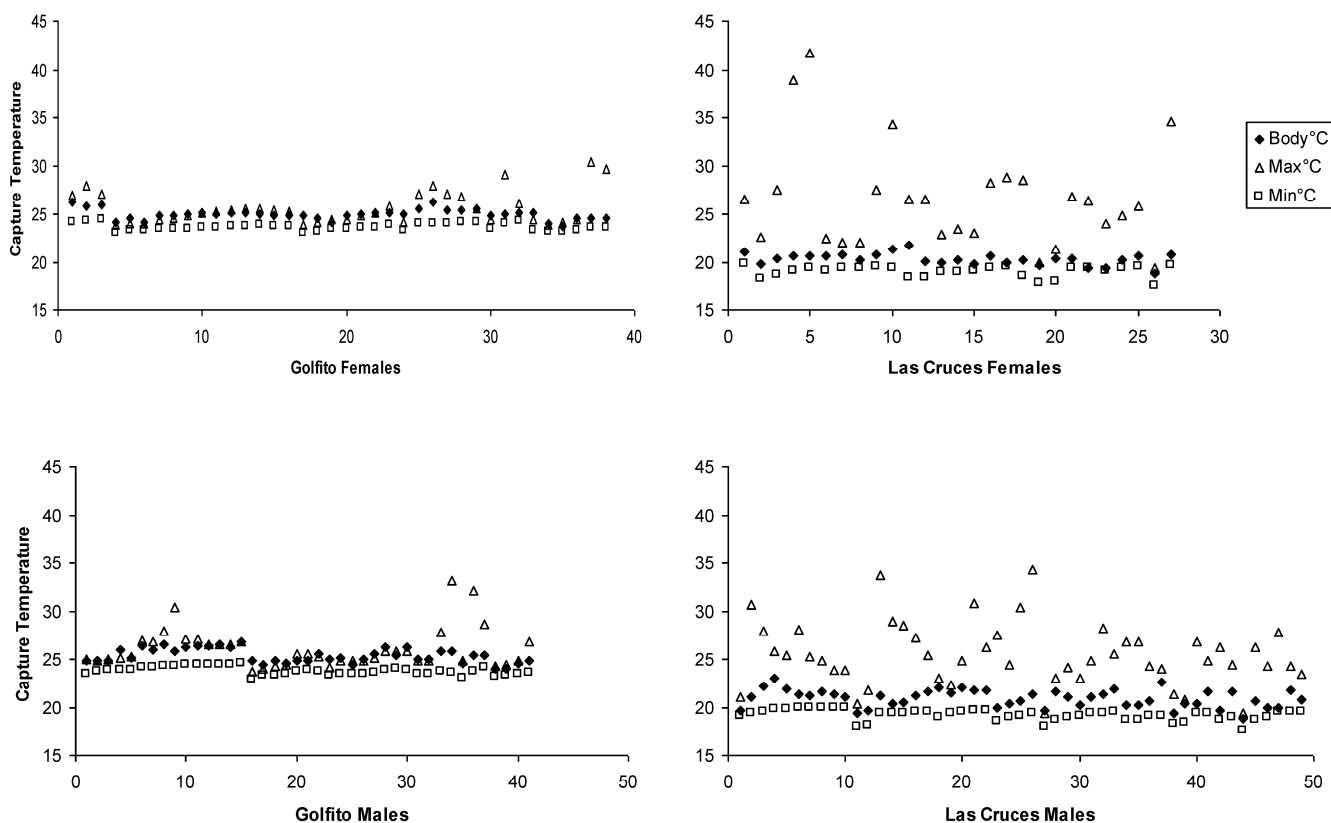


Figure 5. Body temperatures (T_b) along with maximum (T_{max}) and minimum (T_{min}) environmental temperatures at the time of capture for each lizard (vertical triplet of points = 1 individual's capture).

3.3. Habitat Use

Perch distances (i.e., horizontal proximity to water) were shorter at the low-elevation site than at the high-elevation site (GLM: $F_{1,171} = 21.5$, $p < 0.001$) but did not vary with sex (GLM: $F_{1,171} = 0.28$, $p = 0.59$, Table 1). By contrast, perch height (i.e., vertical distance to water) did not vary by site (GLM: $F_{1,170} = 1.00$, $p = 0.32$) or sex (GLM: $F_{1,170} = 0.50$, $p = 0.48$, Table 1) but increased with SVL (GLM: $F_{1,170} = 4.75$, $p = 0.031$). There was significant variation in positioning relative to water current among the four site–sex groupings ($\chi^2 = 19.779$, $df = 6$, $p = 0.003$), but within a site, there were no sex differences (high site: $\chi^2 = 3.10$, $df = 2$, $p = 0.212$; low site: $\chi^2 = 0.03$, $df = 2$, $p = 0.985$). When we combined the sexes at each site,

high-elevation lizards were positioned twice as often near an eddy but only one-third as often near turbulent water compared to low-elevation lizards ($\chi^2 = 17.921$, $df = 2$, $p < 0.001$; proportions (high site vs. low site): eddy 0.41 vs. 0.20, smooth 0.48 vs. 0.46, turbulent 0.11 vs. 0.34).

There was significant substrate use variation among the four site and sex groups (Fisher exact test: $p = 0.022$), but there were no sex differences in substrate use within sites (Fisher exact test: high elevation: $p = 0.252$; low elevation: $p = 0.212$). When we combined sexes, there was a significant difference in the use of the five substrate types between sites (Fisher exact test: $p = 0.025$; Figure 6). We more commonly found water anoles on the ground or rocks at the high-elevation site than at the low-elevation site.

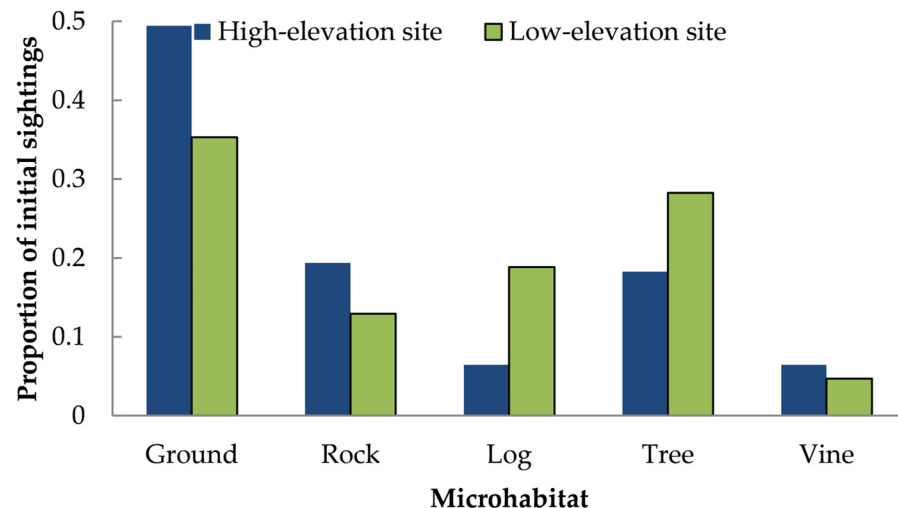


Figure 6. Frequency of microhabitat use by water anoles at high- and low-elevation sites.

Perch cover differed among groups ($\chi^2 = 21.993$, $df = 6$, $p = 0.001$) but was not related to sex ($\chi^2 = 1.64$, $df = 2$, $p = 0.43$). High-elevation individuals were found less than half as often in the open and nearly twice as often under cover compared to low-elevation lizards ($\chi^2 = 18.039$, $df = 2$, $p < 0.001$; proportions, high site vs. low site: open 0.09 vs. 0.22, partial 0.33 vs. 0.47, cover 0.58 vs. 0.31). Finally, visual noise was higher at the low-elevation site (GLM: $F_{1,172} = 27.21$, $p < 0.001$). The visual noise of perches tended to increase with lizard body size (i.e., SVL; GLM: $F_{1,172} = 9.79$, $p = 0.002$) but was not affected by sex (GLM: $F_{1,172} = 0.19$, $p = 0.660$, Table 1).

3.4. Behavioral Observations

Some behaviors only occurred within one sex or on one site—we only observed eating events at the low-elevation site and only observed dewlap displays among males, and while head bobs were occasionally performed by females, we only observed females head bobbing at the low-elevation site (Table 3). Although we detected site differences, there were no sex differences, nor were there any significant interactions between site and sex for any of the behavioral variables (GLM). Lizards at the low-elevation site were more active than those at the high-elevation site, exhibiting higher head turn, movement, and feeding rates (GLM: head turn, $F_{1,77} = 32.1$, $p < 0.001$, Figure 7; moves, $F_{1,77} = 18.9$, $p < 0.001$, Figure 8; feeding, $F_{1,77} = 4.76$, $p = 0.03$; Table 3). We did not observe any significant variation in display behavior between sites (GLM: head bobs: $F_{1,77} = 1.82$, $p = 0.181$; dewlap displays (males only): $t = 0.62$, $n = 53$, $p = 0.537$; Table 3).

Table 3. Behavioral profiles (mean rate $\pm$ standard deviation) obtained for each sex at each site (sample size). Values are given as rates (min^{-1}). Statistical results are given in the text. Significant site differences are indicated by *; sex differences were not detected.

	Low-Site Males (27)	Low-Site Females (19)	High-Site Males (26)	High-Site Females (8)
Head turns *	1.89 ± 1.54	1.79 ± 1.10	0.42 ± 0.40	0.49 ± 0.71
Moves *	0.36 ± 0.43	0.25 ± 0.38	0.02 ± 0.04	0.02 ± 0.05
Feeding *	0.02 ± 0.08	0.03 ± 0.06	0.00 ± 0.00	0.00 ± 0.00
Head bobs	0.08 ± 0.17	0.03 ± 0.06	0.04 ± 0.15	0.00 ± 0.00
Dewlap displays	0.03 ± 0.10		0.02 ± 0.06	

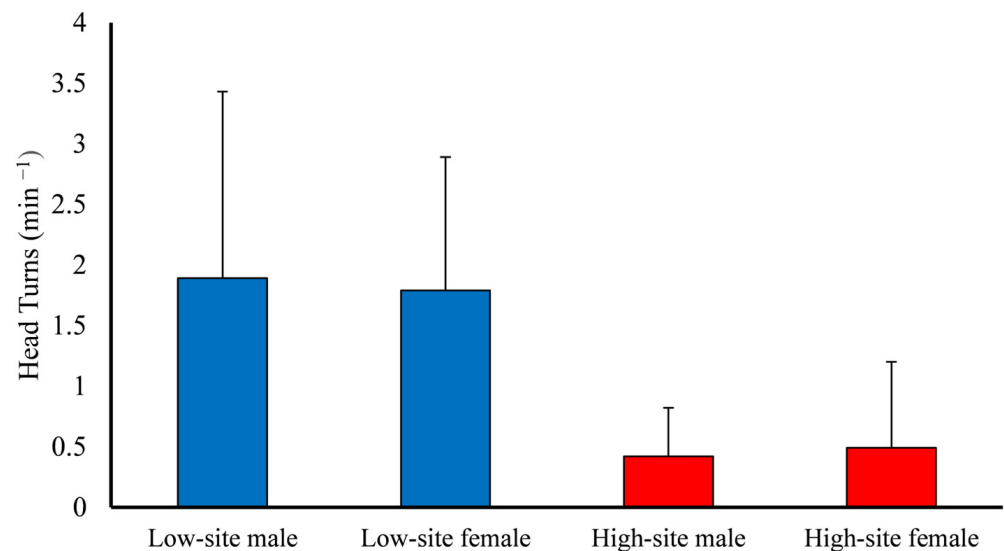


Figure 7. Mean head turns/minute for each sex-site group, with standard deviations shown. Mean and SD values are provided in Table 3 and statistical results (GLM) are in the text.

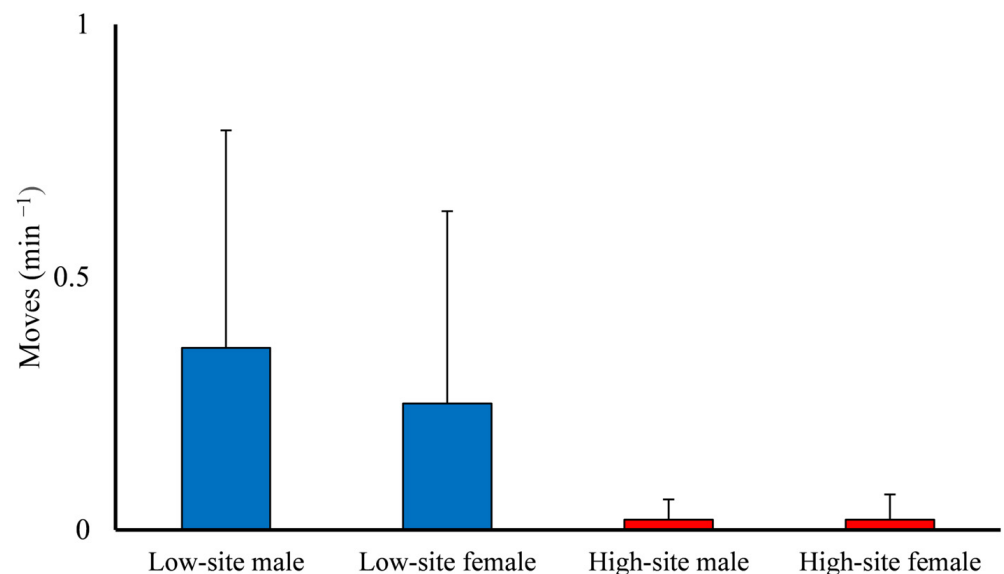


Figure 8. Mean movement rates (moves/min) for each sex-site group, with standard deviations shown. Mean and SD values are provided in Table 3, and statistical results (GLM) are in the text.

4. Discussion

Water anoles living in high- and low-elevation sites experienced very different thermal regimes and habitat structure. Our high-elevation site was cooler (i.e., lower mean

maximum environmental temperature), and lizards there had a much lower T_b than anoles at the low-elevation site, but at the time of capture, water anoles at the high-elevation site had access to environmental temperatures that were higher than their T_b , indicating that through behavioral thermoregulation they could have achieved T_b more closely approximating that of lizards at lower elevations. Some species of anoles behaviorally compensate for elevational changes in thermal regimes [12,13,34,35], showing changes in habitat use, basking, or activity patterns that can minimize elevation-based variation in T_b , whereas others do not [12,34,35]. An absence of behavioral compensation can sometimes be offset by physiological adaptation [36,37]. Behavioral thermoregulation to higher temperatures at the high-elevation site could be too expensive or physiologically unnecessary [12]. Alternatively, if the species is adapted to lower temperatures at higher elevations [38], individuals at lower elevations might be thermally stressed by occupying a habitat that meets or exceeds their preferred operating temperature. A comparison of different high-elevation populations of *A. aquaticus* recorded variations in body temperature and critical thermal maxima [38]. The mean minimum temperature at our low-elevation site was significantly higher than that at our high-elevation site. Future studies investigating the possibility that high-elevation individuals are locally, physiologically adapted to a cooler thermal regime than their low-elevation conspecifics are merited.

To best document thermoregulation, the frequency distribution of operative temperatures, which account for environmental temperatures as well as factors affecting heat exchange by an animal, should be measured [39]. Because water anoles occupy a large range of substrates, determining proportions of available habitat or the distribution of operative temperatures is difficult. Although some studies attempt to generate mean operative temperatures (e.g., [35]), we simply attempted to document the range of environmental temperatures available to water anoles at our study sites. Future studies using operative temperature models could provide more detail of the environmental differences between sites [40]. Furthermore, indices of habitat quality, such as sun vs. shade, can be misleading when, for example, a lizard displays in full sunlight while being doused by the spray of a waterfall. Because T_b more closely mirrors T_{min} than T_{max} in both populations, we argue that water anoles undergo thermoregulatory compensation to actively maintain a low body temperature.

Water anoles did not seem to be very heat tolerant in either site—handling animals while measuring them was sometimes enough to observe signs of thermal stress. The anole *A. gundlachi* also exhibits elevation-related variation in T_b and a limited ability to tolerate warm temperatures [37]. In a treatment of neotropical lizards, habitat was strongly associated with basking behavior, with open and edge species basking more than those living in forests [2]. Some lizards at that elevation consequently could benefit from global warming [2]. However, our study species, *A. aquaticus*, is an edge species that does not bask and is not likely to benefit from a warmer climate.

Thermal conditions can be closely tied to habitat [38]. The riparian habitat used by water anoles is a complex physical and thermal environment. Not only can temperature vary with perch location due to insolation, but proximity to the water can affect thermal conditions for a perching water anole. In addition, positions along the watercourse vary in their exposure to predators and utility in allowing communication and social interaction. Differences in habitat use between sites, although significant, might in part reflect site differences in habitat availability. As with temperature, labeling substrate-use differences between sites as preferences should be accompanied by a characterization of the available habitat. Although we recorded notable physical differences in the two habitats, differences in habitat use between sites might or might not reflect preference, as we could not assess availability. Our high-elevation rivers were wider and contained more of a bank and rocks

along the shore, while perch height, a characteristic not strictly tied to substrate type, was the same at both sites. Two of the habitat variables we measured were positively related to body size: perch height and visual noise. We initially viewed visual noise as an environmental characteristic that individuals might seek to minimize but later surmised that this metric (and possibly perch height) could reflect the effectiveness of vantage points. Studies focused on habitat preferences that include availability and on the social behavior of *A. aquaticus* are needed to understand why individuals within a population can differ in habitat use.

The slight sex differences in body and capture temperatures (i.e., T_b , T_a , and T_s) we recorded could be due to differences in thermal preferences or the result of sex-based habitat variability. Male water anoles at our high-elevation site occupy more exposed microhabitats than females [22], which might indicate a sex-specific preference for different thermal environments. Thermal preferences remain to be examined, as does a determination of whether changes in T_b affect ecological performance. Sex differences in lizard T_b are not common [41] but could be biologically important [42].

Water anoles in the two populations exhibited site-specific differences in behavior. Lizards at the low-elevation site were more active—they moved more frequently and scanned their environment more often. Temperature can be an important influence on lizard performance [43,44], with lower temperatures potentially restricting general activity. The behavioral differences we recorded could be attributed to differences in environmental temperatures. However, environmental temperature differences between sites also were associated with habitat differences and biotic differences. For example, our general impression was that both food and predators were more common at the low-elevation site, and activities such as long-distance signaling were more feasible at the high-elevation site. Head turns can vary with predation risk [45–47] but serve other functions as well. Further studies are needed to separate temperature from habitat and biotic variables that can affect behavior. Although we were able to identify differences between individuals living at two sites and attribute those differences to variations in thermal regimes at the sites, a more rigorous study involving replicate sites at high and low elevations is required to confirm the importance of the differences we observed and to rule out other possible site-specific explanatory factors.

5. Conclusions

The water anole populations we examined at two different elevational sites differed in their ecology and behavior. The sites differ in their thermal environments, with the high-elevation site having lower temperatures and a greater range of temperatures. Higher-elevation water anoles were larger (SVL and mass), and body temperature varied by site and sex, being highest for low-elevation males. Habitat use by anoles at the two sites varied, with lizards at the low-elevation site spending more time in the open and closer to the water's edge than those at the high-elevation site. Activity levels also varied by site, with low-elevation individuals feeding more frequently as well as being more active and vigilant. The sites differed qualitatively in canopy cover, bank composition, forest maturity, and width of the water course. Such structural differences in the habitat are likely tied to differences in the thermal environment and also could account for the differences we recorded in habitat use and behavior. Site differences in water anole ecology and behavior likely reflect both biotic and abiotic factors that co-occur with differences in thermal environments. Future work characterizing details of habitat use vs. availability at the two sites would help distinguish thermal and habitat constraints for water anoles.

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Data Availability Statement: Data that support the findings of this study are available from the corresponding author upon reasonable request.

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