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Habitat use and body temperature influence push-up display rate in the tree lizard, *Urosaurus ornatus*

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Abstract

Lizards engage in push-up displays to signal dominance and to secure access to important resources. The rate and patterns of push-up displays have been shown to vary based on both biotic and abiotic factors. We investigated push-up display rate in tree lizards, *Urosaurus ornatus*, to determine contributions from potentially conflicting factors including sex, throat colour, microhabitat usage, social context, and thermal traits. We found that display rate was best described by an interaction between microhabitat and body temperature (T_b). The relationship between display rate and T_b was significantly different between three microhabitats: sunny dead trees, the inner branches of trees, and tree trunks. We suggest that this variation in display rate is driven by shifts in microhabitat temperature over the course of the day and spatial and temporal adjustments being made depending on the probabilities of being detected by both conspecifics and predators.

Keywords

animal communication, displays, lizard, microhabitat use, predation risk, body temperature.

1. Introduction

Visual communication plays a major role in conveying information across multiple contexts among vertebrate species. The information may pertain to mating status, coordination of parental care, predator detection and response, and territorial status (Hartmann et al., 2005; Osorio & Vorobyev, 2008). Many lizard species engage in physical displays that involve postures, exaggerated movements, and colouration as a method of communication between conspecifics (Carpenter & Grubitz, 1960; Martins, 1994; Carpenter & Fergu-

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son, 1997; LeBas & Marshall, 2000; Radder et al., 2006). Displays of male and female lizards include push-ups, head bobs, extension of a dewlap or neck frills, tail movements, and lateral compressions of the body to signal dominance or aggressive intent; these displays may be critical for securing key resources, such as territory and access to potential mating (Martins, 1991, 1994). Males will display when engaged in direct competition with other males in agonistic territoriality encounters, towards females in courtship, and, most often, as a broadcast without an obvious, direct recipient for territory maintenance and courtship advertising (Martins, 1993a).

Among lizard species that engage in displays, substantial variation exists in the patterns and rates of push-up displays, both between species and within populations (Martins, 1993b). Elucidating contextual causes of such variation is of interest due to the ecological role that displays play and because push-up displays are thought to be honest signals that communicate reliable information about the sender (Brandt, 2003). In lizards, males have been found to display more frequently and use different patterns than females (Martins, 1991). The context of a display can also influence display patterns and intensity. For example, the displays in *Sceloporus graciosus* differed depending on whether the sender was engaged with a conspecific (courtship behaviour or agonistic contests) or general broadcasting (Martins, 1993a). Other ecological factors have been shown to influence display rate: brown anoles (*Anolis sagrei*) decrease display rate after a simulated predator attack, which is assumed to reduce the conspicuousness of an individual to a predator (Simon, 2007).

Whereas substantial attention has focused on biotic factors that influence display patterns, abiotic factors, such as temperature and microhabitat, have received scant investigation. Heterogeneity in microhabitats should influence the variability of the thermal landscape as well as the detectability of the signaller (Baird et al., 2020). Just as variation in the thermal environment modulates physiological performance in ectotherms, it has been proposed that temperature should also limit other traits that have a physiological underpinning, such as behaviour (Gunderson & Leal, 2015). As a consequence, the perch site selected by an individual may promote or constrain the vigour of displays, because of the thermal properties of the substrate. In addition, differences in visibility among microhabitats may influence display rate.

Push-up displays are influenced by endurance capacity in lizards (Brandt, 2003). Endurance capacity is sensitive to temperature, indicating that the intensity and duration of push-up displays may also covary with temperature in a manner similar to thermal performance curves. The rate at which physiological functions occur accelerates as temperature increases up to a peak, known as the thermal optimum, after which these traits decline (Huey & Stevenson, 1979). Thermal optima are often at or close to the preferred temperature, that is the body temperatures that lizards select in the absence of ecological costs ($T_{\text{pref},}$ Hertz et al., 1993). In addition, T_{pref} has been demonstrated to influence social interactions in lizards, including direct correlations between T_{pref}, aggression, and courtship in mountain log skinks (*Pseudemoia entrecasteauxii*; Stapley, 2006; Baird, 2013). Hence, individuals with higher T_{pref} values may also display at higher rates. To maximize display rates, individuals may also display at body temperatures that match their T_{pref}.

In one of the few studies that has investigated the thermal sensitivity of display performance, Ord & Stamps (2017) tested three factors that could influence variation in push-up display rates in male *Anolis* lizards. They found that push-up display rate covaried with ambient temperature, with display rates increasing with temperature up to a maximum followed by a rate decrease. Male *Anolis* push-up display rates did not vary based on metabolic rate or the number of potential recipients of the display (Ord & Stamps, 2017).

We were interested in analysing both abiotic and biotic factors as possible determinates of display rate in a model species, the tree lizard (*Urosaurus ornatus*). *Urosaurus ornatus* occurs in a diversity of habitats and can be found on rocks and trees. In populations that are arboreal, lizards may be found on a range of substrates, including tree trunks, branches, and the canopy on both live and dead trees. In addition, both males and females are characterized by a throat colour polymorphism that varies among populations (Hews et al., 1997; Zucker, 1989). Males are characterized by a blue, orange, or yellow throat. In addition, there are mosaic morphs that include an orange or yellow background with a central blue spot. Female *U. ornatus* may have orange, yellow, or white throats (Carpenter, 1995; personal observation). Prior studies of the species have shown that the throat morphs are fixed and have divergent social roles, including variation in dominance status (Hover, 1985; Thompson & Moore, 1991; Hews et al., 1997; Moore et al., 1998, Miles unpublished). The mating system of tree lizards is polygynous, with males having a despotic hierarchy (Zucker, 1989; Deslippe et al., 1990). Males are territorial and perform push-up displays in dominance and courtship interactions. The displays consist of series of push-ups in which all four limbs are extended and the entire body, head, and tail of the lizard are off the perch (Carpenter & Grubitz, 1961). Push-up displays can be accompanied by lateral compression of the body and an extension of the dewlap. In addition, males have bright blue ventral patches that are exposed during displays; by broadcasting their bright ventral and throat badges during push-up displays, male tree lizards become very conspicuous. The pattern of these displays is consistent in *U. ornatus* (Carpenter & Grubitz, 1961).

In particular, we investigated whether *U. ornatus* exhibits thermal sensitivity in display rates. We measured preferred body temperatures of each lizard to determine whether individuals selected body temperatures that maximized display rates. We also include additional factors that are relevant to the natural history of *U. ornatus* and are known to alter display behaviour in other species (Baird, 2013). These include sex, throat colour, body size, microhabitat use, and social context (presence/absence of conspecifics within the visual field of the displaying lizard). We tested the following predictions. First, that individuals with higher values of T_{pref} would display at higher rates. Second, that lizards would select for and display at body temperatures that match their T_{pref}. Third, that lizards that displayed at temperatures near their T_{pref} values would display at higher rates.

2. Materials and methods

2.1. Study population

We studied adult tree lizards during the reproductive season, from 5 June–23 July 2018, at the Appleton-Whittell Research Ranch (AWRR) of the National Audubon Society in southeastern Arizona (31.365°N, −110.303°W). The focal population is located within a 2 ha site in a semi-arid grassland. The abundance of the population during the study was estimated at 100 individuals (direct count). Adult female body sizes range from 45–55 mm, while males range from 46–57 mm (personal observation). At our study site adult lizards are arboreal, spending the majority of their time on live oak (*Quercus emoryi*, *Q. arizonica*), mesquite (*Prosopsis velutina*), and standing dead trees (snags). At this site the microhabitats available to lizards differ in frequency: there are ~150 live trees but fewer than 10 snags. While there are fewer snags than live trees, their large size and exposure to the sun offer ample basking opportunities. At this site, males and females show a clustered distribution where multiple males and females occupy the same tree. At AWRR, male throats are yellow, orange, yellow/orange, blue, or yellow/blue. Females had yellow or orange throats.

2.2. *Operative environmental temperature*

We quantified the operative thermal environment (T_e) using Thermochron iButtons (Thermochrons^{tm}, Maxim Integrated Products, Sunnyvale, CA, USA). T_e data characterizes the range of thermal microhabitats available to *U. ornatus* individuals throughout the day over the course of the study, which is important when considering how microhabitat use influences display rate. We placed iButtons in operative temperature models constructed using PVC pipe. Models matched the length and mass of adult *U. ornatus* and were painted to match the reflectivity of the lizards (Gilbert & Miles, 2017, 2019). We placed seven models each on tree trunks, inner branches of trees, outer branches of trees, sun-exposed snags (dead, woody substrates), and snags in shade environments. These microhabitats are used by *U. ornatus* at our site and thermal properties between microhabitats were expected to differ based on sun exposure throughout the day. Each iButton sampled temperature once per hour for the duration of the study, 5 June–23 July 2018.

2.3. *Quantifying display rate*

We recorded push-up display rates by visually scanning trees for lizards during mornings from 07:00–11:00 and using focal animal sampling when individuals were located. Most activity ceased by 11:00 because ambient temperatures exceeded the voluntary body temperatures for activity of lizards (personal observation). All observations were made by the same individual (TMG), who wore grey and brown clothes to avoid any potential influence of brightly coloured clothing on lizard behaviour (Putman et al., 2017). Observations were made at a distance of at least 3 m to avoid influencing the behaviour of the focal individual. Past experience has shown that *U. ornatus* will cease displays and flee when approached to within 1–2 m (Miles, unpublished data). We found no evidence that the presence of an observer at 3 m altered the display behaviour of the focal lizard. We observed lizards until they performed push-up displays or 15 min elapsed without displays. The display behaviour of *U. ornatus* consists of sequences of 3–8 push-ups, which may be repeated multiple times. We counted the number of push-ups and recorded the time elapsed during the display sequence. We continued to observe a lizard until it moved to a new substrate. We quantified display rate as the number of push-ups performed over the time we observed the lizard.

2.4. Field measurements, lizard capture, and husbandry

We captured lizards using a noose as soon as it changed perches to obtain a measurement of its T_b during the display. Lizards that evaded capture for over one minute after displaying were not included because of a potential change in T_b that differed from the value during display. In addition, because different perch types (e.g., trunk, branch, or twig) vary in temperature, we also measured the temperature of the substrate (T_s) used as a perch by the lizard. We measured T_b and T_s where the lizard displayed using an infrared digital thermometer (Amprobe IR-750), which has been validated against a quick-reading cloacal thermometer (Gilbert & Miles, 2019). We recorded the sex of lizards based on the presence/absence of enlarged post-anal scales (present in males) and the colour morph of individuals as described in “study population”. Colour was assessed using visual inspection. Previous studies of tree lizards at this population used spectrometry to verify colour scores of males and females (Lattanzio & Miles, unpublished data). We also recorded the time of capture, microhabitat type at the display site (trunk, inner branch, outer branch, snags in exposed sun, snags within the shade), and social context. To quantify social context, we surveyed the environment surrounding the displaying lizard for the presence/absence of male or female conspecifics within the visual field of the displaying lizard. In arboreal lizards, horizontal and vertical visual exposure must be considered by accounting for tree trunks and branches that obscure the body of potential recipients (Baird et al., 2020). We considered conspecifics present if they were in the visual field of a displaying lizard within 3 m of the individual (Martins, 1993a; Ord & Stamps, 2017). However, conspecific individuals were often much closer to the signaller (within 0.5 m, personal observation). It was clear when the focal individual was displaying towards a conspecific because the individual would orient towards the receiver to enhance ventral and throat colouration during display and move towards the receiver between display sequences. We considered the social context as a challenge display when the receiver matched the sex of the displayer. We considered the social context to be courtship when the receiver was the opposite sex of the displayer. We did not observe any instances of multiple recipient conspecifics. In the absence of conspecifics, we designated the social context of the displaying lizard as general broadcasting (Martins, 1993a). If the recipient conspecific was not marked, it was captured to determine its sex. The behaviour of recipient conspecifics was not recorded

We transported lizards to a laboratory at AWRR. We measured snout-vent length (SVL) and tail length (to the nearest mm) and body mass (to the nearest 0.1 g). We considered males and females larger than SVL $>$ 42 mm as adults (Dunham, 1982; Zucker, 1989). During captivity lizards were housed in individual terraria and provided a thermal gradient with an upper limit at their field active body temperature (36°C) to allow for thermoregulation. Lizards were maintained on a 13 h/11 h light/dark cycle to mimic local photoperiod. Nocturnal temperatures were ambient. Lizards were offered mealworms daily and provided water ad libitum.

2.5. *Thermal preference*

To measure T_{pref} of lizard subjects, we constructed a linear photothermal gradient using aluminium flashing on a plywood base (120 × 16 × 20 cm, L × W × H) covered with sand. We had four lanes in the experimental setup. We suspended a 100 W incandescent bulb at one end of the track and a second 60 W bulb in the middle to generate a thermal gradient of 27–45°C. Lizards were placed individually at the gradient centre and allowed to acclimate for 10 min. We then used an infrared digital thermometer to record body temperature every 10 min for 90 min (Gilbert & Miles, 2017). We calculated T_{pref} as the average T_{b} from the 9 measurements and the interquartile range, T_{set}, as the central 50% of selected T_{b} values. Following laboratory experiments, lizards were given unique toe clips for future identification. Toe clipping has been shown to not influence performance or increase individual stress levels in lizards, nor affect survivorship (Borges-Landáez & Shine, 2003; Langkilde & Shine, 2006). Lizards were then released back to their location of capture as determined by GPS coordinates. Individuals were in captivity for no longer than one week.

2.6. *Data analysis*

Each operative temperature model provided hourly T_{e} data for the duration of the study. We generated mean hourly T_{e} values for each of the seven models in the five microhabitats (trunks, inner branches, outer branches, sunny snags, shady snags). We used these values to obtain mean T_{e} values for each microhabitat over a 24 h period.

All statistical analyses were conducted using the R statistical computing environment (v3.5.2, R Core Team, 2019). We calculated summary statistics for T_b, T_pref and T_set. We used t-tests to test for differences in T_pref and T_set between sexes. We used mixed effects models to test for differences in T_b between sexes, using lizard ID as a random effect to account for multiple T_b recordings on individuals. All future mixed effects models (function *lme* in the package *nlme* (Pinheiro et al., 2019)) included lizard ID as a random effect to take multiple observations of individual lizards into account. We measured the repeatability of display behaviour using an the intraclass correlation coefficient using the function *ICC* in the package *ICC* (Wolak et al., 2012). We analysed the relationship between T_b and T_pref using a mixed effects model to determine if lizards displayed at temperatures matching T_pref. We also calculated the difference between T_b and T_pref and used this variable in a mixed effects model to investigate if lizards that were closer to T_pref values in the field displayed at higher rates. We used linear mixed-effects models to assess factors that explain variation in display rate. We built models including sex, throat colour, microhabitat, and social context (challenge, courtship, or broadcasting) as fixed effects. We included T_b, T_s, T_pref, time of day, and SVL as covariates. We checked for multicollinearity between variables using the *vif* function in the package *car* (Fox & Weisberg, 2019) and found no evidence for multicollinearity (VIF for each variable < 5). To compare models we used maximum likelihood and the *model.sel* function in the package *MuMIn* (Bartón, 2022). We used the Akaike information criterion corrected for small sample size (AICc) to determine the best model. We first built and compared models with each variable isolated as a determinate of display rate. Based on this comparison, we constructed more complex models that combined multiple variables, starting with the two most significant variables. When building these models, we included interaction terms based on predicted biological relevance (e.g., microhabitat and T_b). If these interactions were nonsignificant, we built an additional model without the interaction terms. We continued this process by adding one variable at a time to the current best model. This process generated our candidate models. We refit the best model with restricted maximum likelihood and checked the residuals for departures from the main assumptions of GLMM. We used Type II sum-of-square to determine significant terms in the model. Because past studies have demonstrated that T_e

influences temporal and spatial variation in the thermal properties of microhabitats, we investigated the influence of the time of day on display rate and T_b in separate microhabitats using mixed effects models. We expected the thermal sensitivity of display rate to be nonlinear (Huey & Stevenson, 1979), so we analysed the relationship between display rate and T_b using a generalized additive mixed model (GAMM, function *gamm*, package *mgcv* v. 1.8-40; Wood, 2017). We chose to use a GAMM approach because we had multiple observations for each lizard and other nonlinear methods do not allow random effects (see Zajitschek et al., 2012). We anchored the display curve using the critical thermal minimum (CT_{min}) and maximum (CT_{max}) values for *U. ornatus* from Gilbert & Miles (2019). These two traits were measured on lizards from the same population as ours. The critical thermal limits are defined as the lower and upper endpoints for physiological activity. In our analysis the display rate would be 0 for CT_{min} and CT_{max}. We calculated the core statistics of the performance curve, including thermal optima (T_{opt}), and the 90% performance breadth from the display data. We estimated the performance curve with an autoregressive correlation structure to account for within individual variation. Lizard ID was included in the model as a random term.

3. Results

3.1. Microhabitat variation in operative environmental temperatures

The operative temperature models indicated a dynamic thermal profile across microhabitats over the course of the day. Early in the morning, trunks were the warmest microhabitat, though all microhabitats were below the preferred temperature range (T_{set}) of *U. ornatus* (Figure 1). All microhabitats began warming at a rapid rate around 08:00. Near midday, T_e values began showing spatial heterogeneity, with sunny snags being the most exposed and warmest microhabitat. Less exposed microhabitats, such as trunks and inner branches, offered the coolest temperatures (Figure 1).

3.2. Field active T_b and thermal preference

We recorded 88 field active T_b values from 50 individuals that displayed (75 T_b values from 39 males and 13 T_b values from 11 females). The field active T_b values of the lizards when displaying ranged from 29.2–40.1°C with an average of 35.2°C. There was no difference in T_b between males

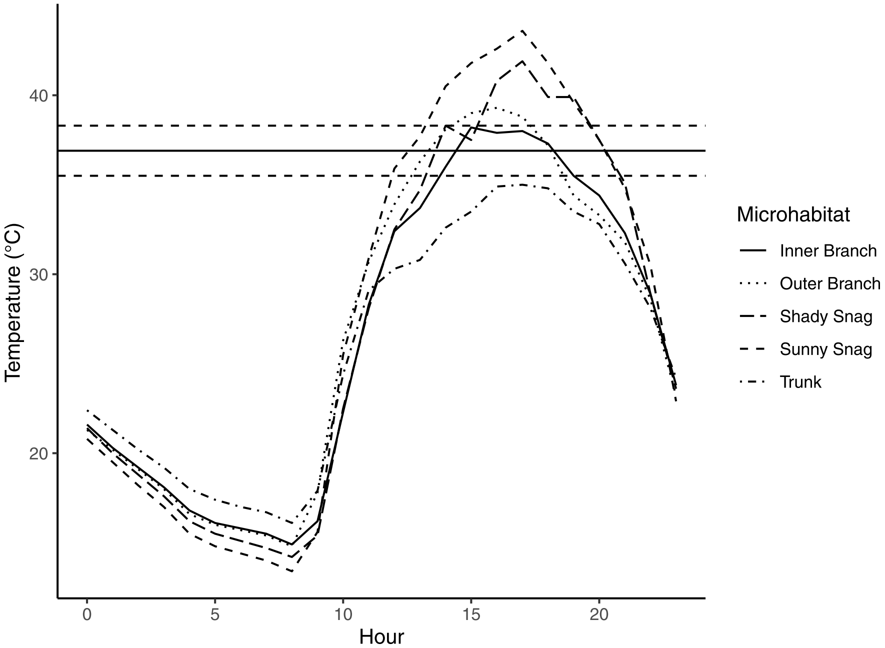

Figure 1. Mean operative temperatures available in five microhabitats known to be used by *Urosaurus ornatus*. Although we provide values for a 24 h period, the activity period of *U. ornatus* is from about 07:00–19:00 over the course of an average day in June. T_{pref} is shown as the solid horizontal line; T_{set} is bracketed within the horizontal dotted lines.

(35.2 ± 0.23°C (mean ± SE), $N = 75$) and females (34.7 ± 0.74°C, $N = 13$; $\chi_1^2 = 0.34$, $p = 0.56$). We measured T_{pref} and T_{set} of the 50 individuals with measurements of display behaviour. Individual T_{pref} values ranged from 34.4–39.3°C with an average of 37.1°C. There was no difference in T_{pref} between males (37.0 ± 0.20°C, $N = 39$) and females (37.5 ± 0.40°C, $N = 11$; $t_{48} = -1.01$, $p = 0.32$). T_{set} values ranged from 0.7–6.4°C with an average of 2.5°C. The T_{set} of males was narrower ($T_{\text{set}} = 2.24 \pm 0.18$°C, $N = 39$) than females ($T_{\text{set}} = 3.35 \pm 0.53$°C; $t_{48} = -2.48$, $p = 0.02$).

3.3. Display rates

We recorded 88 distinct displays from 50 different adult *U. ornatus*: 75 displays from 39 males and 13 displays from 11 females. Because lizards were captured after displaying, repeated observations on the same individual were separated by at least 24 h (mean number of days between repeated observations = 6.7). We measured an average 1.76 display observations per individual. The number of push-ups performed by a lizard ranged from three over 5.6 s to 57 over 81 s. Lizards averaged 0.66 displays/s. There was no difference in display rate between males (0.65 ± 0.007 displays/s, $N = 75$) and females (0.71 ± 0.03 displays/s, $N = 13$; $\chi^2_1 = 2.44$, $p = 0.12$). Display rates among individuals with multiple measurements had low repeatability ($r_{\text{intra}} = 0.02$, $N = 14$).

There was no influence of T_{pref} on display rate ($\chi^2_1 = 1.28$, $p = 0.26$), and individuals did not display at temperatures that matched their preferred body temperatures ($\chi^2_1 = 0.53$, $p = 0.47$; Figure 2). How close a lizard's body temperature was during display to its preferred body temperature (the difference between T_{b} and T_{pref}) also had no impact on display rate ($\chi^2_1 = 0.74$, $p = 0.39$). We found no influence of sex, body size, colour morph, time of day, social context, or substrate temperature on display rate ($p > 0.05$; see Table 1 for summary statistics). The mixed effects model best describing push-up display rate included microhabitat, T_{b}, and the interaction between T_{b} and microhabitat. This model had the lowest AICc (−233.6), the highest Akaike weight (0.39), and a delta AICc of over 2 when compared to the next-best model (2.47; Table A1 in the Appendix). Display rate was influenced by an interaction between T_{b} and microhabitat ($\chi^2_4 = 18.82$, $p < 0.001$; Figure 3). Lizards utilized microhabitats nonrandomly as determined by a chi-square test ($\chi^2_4 = 76.71$, $p < 0.001$), using sunny snags the most ($N = 50$) and outer branches the least ($N = 3$), even though snags were less available than trunks, inner branches, and outer branches (see "study population"). We compared the slopes of the different microhabitats (which represent the interaction between microhabitat and T_{b}) using the Tukey method via *lstrends* in *lsmeans* (Lenth, 2016) and found significant differences between the slopes of sunny snags and trunks ($p = 0.02$) and between inner branches and trunks ($p = 0.006$). There was a positive relationship between T_{b} and display rate on inner branches ($\chi^2_1 = 12.3$, $p < 0.001$, $N = 10$), a negative relationship between T_{b} and display rate on trunks ($\chi^2_1 = 8.7$, $p = 0.003$, $N = 15$), and no relationship between T_{b} and display rate on sunny snags ($\chi^2_1 = 0.18$, $p = 0.67$, $N = 50$) (Figures 3 and 4).

Lizards occupying sunny snags showed a significant positive relationship between time of day and T_{b} ($\chi^2_1 = 10.5$, $p = 0.001$, $N = 50$; Figure 4). On inner branches, we found a significant positive relationship between time of day and T_{b} ($\chi^2_1 = 12.6$, $p < 0.001$, $N = 10$; Figure 4). There was no relationship between time of day and T_{b} on trunks ($\chi^2_1 = 1.86$, $p = 0.17$,

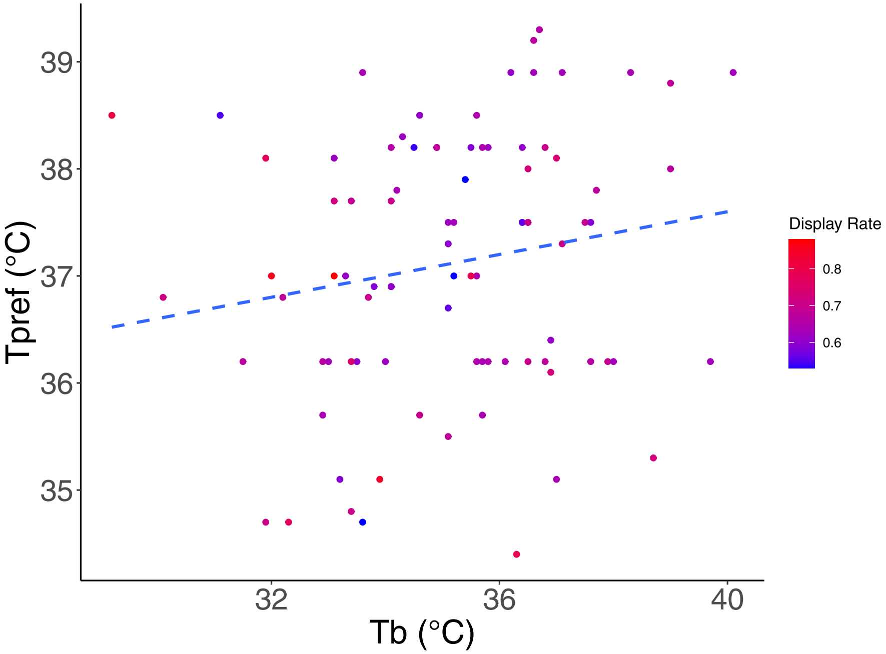

Figure 2. The relationship between a lizard's preferred body temperature (T_{pref}) and its body temperature at the time of display (T_{b}). Lizards did not display at temperatures that matched T_{pref} ($\chi^2_1 = 0.53$, $p = 0.47$). Display rates are represented with a colour gradient, with high rates of display represented with red and low rates represented with blue.

$N = 15$; Figure 4). We also tracked lizard activity, measured as the number of observations of individuals on each microhabitat, over the course of the morning (Figure 5). Among the three microhabitats shown to be significant in our model, activity was highest on sunny snags throughout the day. However, we found activity in the early morning was concentrated on sunny snags and on trunks. Lizard use of inner branches was lower throughout the day (Figure 5).

There was a significant nonlinear relationship between display rate and T_{b} ($F_{2.57,87.4} = 6.82$; $p < 0.001$; $r^2 = 0.27$, $N = 90$). The GAMM showed a relatively high rate of display across a broad range of T_{b} values. The optimal temperature for display was 33.1°C with a maximum display rate of 0.66 displays/s (Figure 6). The 90% thermal performance breadth spanned 16°C, from 23°C to 39°C. Although the optimal temperature for display was below T_{pref} the performance breadth overlapped the interquartile range.

Table 1.
Display rate ± SE of all considered fixed effects: sex, throat colour, microhabitat, and social context.

Parameter	*N*	Display rate (push-ups/s) ± SE
Sex		
Male	75	0.65 ± 0.007
Female	13	0.71 ± 0.03
Throat colour (male)		
Blue	19	0.65 ± 0.02
Blue/Yellow	2	0.66 ± 0.01
Yellow	40	0.64 ± 0.009
Orange	3	0.66 ± 0.02
Yellow/Orange	11	0.68 ± 0.009
Throat colour (female)		
Yellow	4	0.72 ± 0.04
Orange	9	0.70 ± 0.04
Microhabitat		
Sunny snags	50	0.65 ± 0.008
Shady snags	10	0.65 ± 0.02
Trunks	15	0.73 ± 0.03
Inner branches	10	0.63 ± 0.02
Outer branches	3	0.69 ± 0.05
Social context		
Broadcast	75	0.66 ± 0.008
Challenge	3	0.63 ± 0.01
Courtship	10	0.64 ± 0.02

4. Discussion

The goal of this analysis was to identify factors influencing display rate in *U. ornatus*. We did not detect an influence of sex, body size, colour morph, time of day, substrate temperature, or social context (challenge, courtship, or broadcasting) on display rate. However, we found a significant influence of the microhabitat used by an individual for displaying and its T_b. Lizards used microhabitats nonrandomly, and the relationship between display rate and T_b was significantly different among three microhabitats: sunny snags, inner branches, and tree trunks. On sunny snags, display rate was unaffected by T_b and remained at relatively low rates across differing T_b values. On inner branches, display rate increased with T_b. On tree trunks, display rate decreased with T_b. An explicit test of the thermal sensitivity of display rate showed a nonlinear association with body temperature. Two patterns

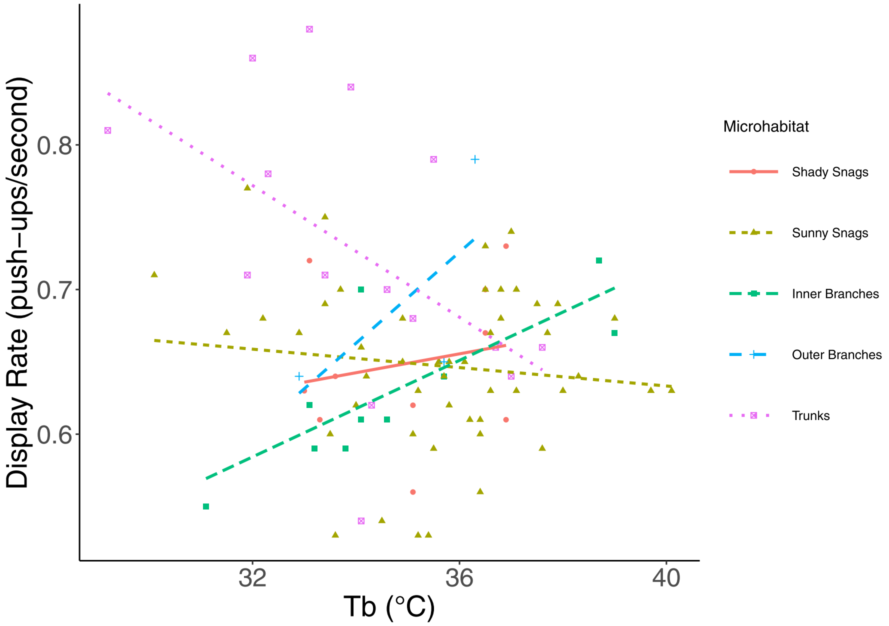

Figure 3. The influence of body temperature on display rate in five different microhabitats. Slopes between sunny dead trees (snags) and trunks ($p = 0.02$) and between inner branches and trunks ($p = 0.006$) are significantly different.

emerged from the display performance curve. First, lizards can maintain a high display rate over a broad range of temperatures. Second, the optimal temperature for display rate was below both mean active body temperature and mean thermal preference. We predicted that individuals with higher T_{pref} values would display at higher rates, that lizards would select for and display at body temperatures that match their T_{pref}, and that lizards that displayed at temperatures near their T_{pref} values would display at higher rates. We found no support for these hypotheses.

We propose that the variation in display rate is driven by shifts in microhabitat temperature over the course of the day as described by the interaction between microhabitat and T_{b}. In addition, the cost of displaying in more open environments may influence display rate. As in many other mating or territorial behaviours, push-up displays are performed in locations to increase the detection by receiver individuals. The combination of colour signals with variation in dewlap colouration and brilliant blue belly patches combined with overt and exaggerated patterns of movement enhance the con-

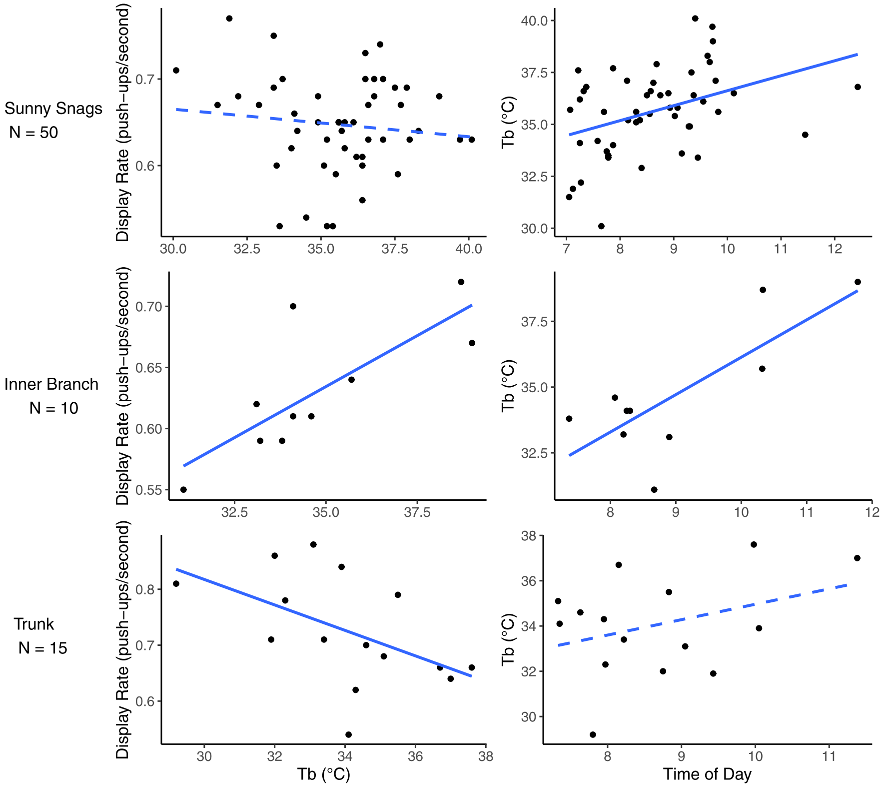

Figure 4. Relationships between display rate, T_b, and time of day on sunny dead trees (snags), inner branches, and trunks. Significant relationships are designated by solid trendlines; insignificant relationships are designated by dotted trendlines. In sunny snags: $T_b \sim$ time of day $\chi_1^2 = 10.5$, $p = 0.001$. In inner branches: display rate $\sim T_b \chi_1^2 = 12.3$, $p < 0.001$; $T_b \sim$ time of day $\chi_1^2 = 12.6$, $p < 0.001$. In trunks: display rate $\sim T_b \chi_1^2 = 8.7$, $p = 0.003$.

spicuousness of a displaying individual. One cost of being conspicuous is the potential to attract the attention of predators (Husak et al., 2006). One of the main predators of *U. ornatus* is a visual hunting snake, the coachwhip (*Masticophis flagellum*) (Goerge & Miles, unpublished observations). When sexually selected traits such as bright colouration and intense bouts of displays attract predators, the force of sexual selection on the traits is often counteracted by reduced survivorship (Kotiaho et al., 2002), and occupancy of microhabitats that carry a high risk of predation can affect courtship behaviour (Candolin, 1997). Lizards have been shown to be capable of adjusting display rate as a response to perceived predation threat (Simon,

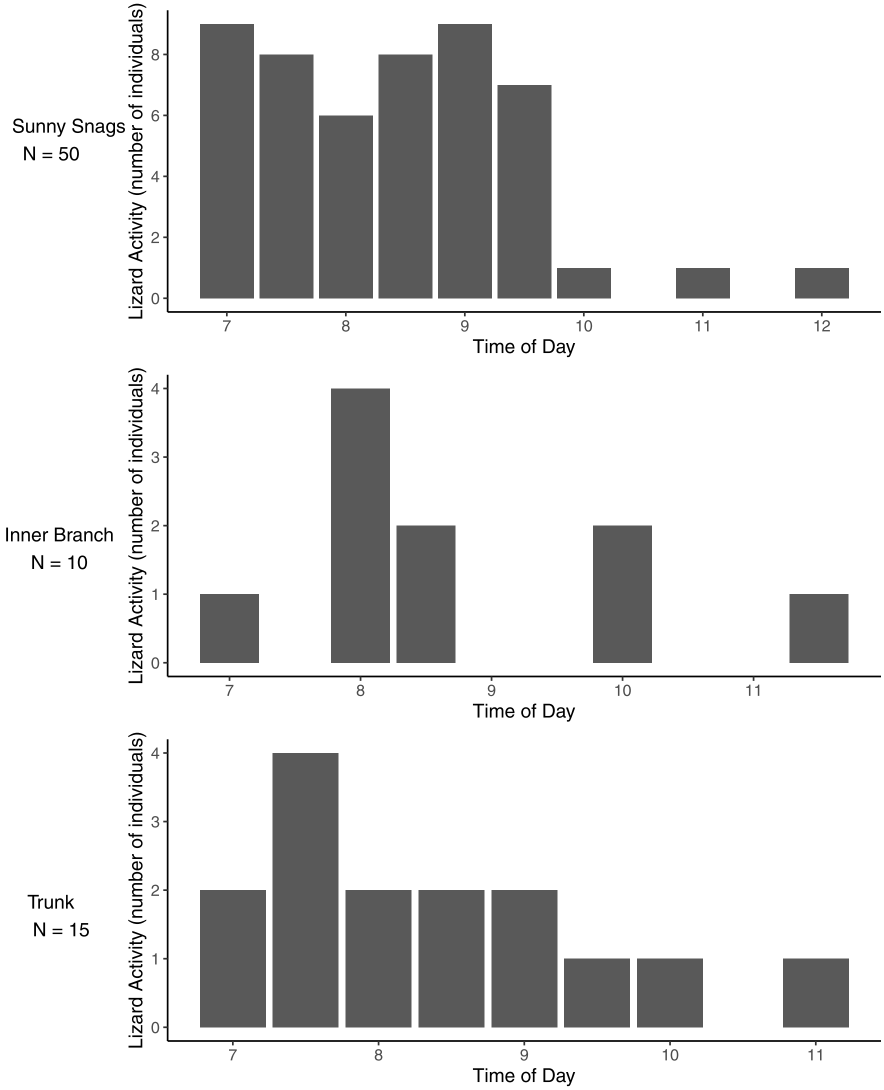

Figure 5. Lizard activity on sunny dead trees (snags), inner branches, and trunks over the course of the morning.

2007). Rather than displaying at maximum capacity, tree lizards might adjust display rates depending on the probabilities of being detected by both conspecifics and predators. This could explain the lack of relationship between display rate and T_b observed on sunny snags and the inverse association

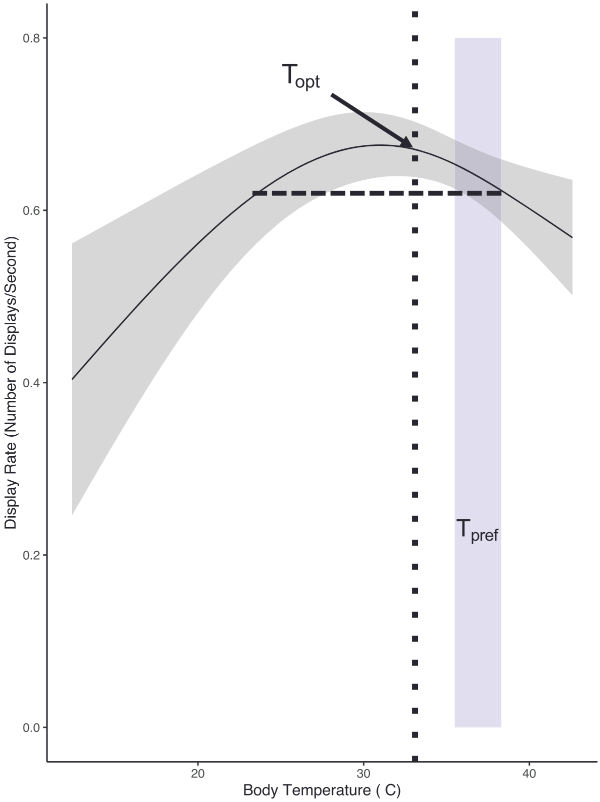

Figure 6. Thermal sensitivity of push-up display rate for *Urosaurus ornatus* based on a GAMM. The vertical dotted line portrays the optimal temperature for display rate (T_{opt}), the horizontal dashed line is the thermal performance breadth (B_{90}), and the shaded rectangle is the thermal preference interquartile range. B_{90} represents the temperatures at which performance is 90% of maximum.

of display rate and T_{b} on tree trunks. Sunny snags had the highest rate of lizard activity across all microhabitats, largely driven by the early hours of the morning during which lizards were basking to increase T_{b}. As the most exposed microhabitat, the T_{e} of sunny snags favours basking behaviour in the morning but becomes too warm for individuals by 10:00 (Figure 1). Despite lizard T_{b} increasing over the course of the day on sunny snags, display rate remained constant and at a lower rate than other microhabitats. The pattern of displays on open microhabitats (snags) may reflect a strategy of lizards to transmit information to conspecifics without attracting the attention of visual hunting predators. As opposed to displaying towards conspecifics within a close visual field, *U. ornatus* in this study engaged in general broadcasting displays in 74/88 (84%) instances, a rate comparable to similar studies (e.g., 88%, Martins, 1993a). Although social context was not significant when modelling display rate, overall lizard movement across microhabitats over the course of the day may have influenced display behaviour of broadcasting individuals (Table A2 in the Appendix).

We observed an inverse relationship between display rate and T_b on tree trunks. During early mornings many individuals of *U. ornatus* will use trunks as a basking site. The high display rate on trunks at low T_b may be a consequence of the ability to signal to multiple conspecifics. We therefore propose that display rate is highest at low temperatures on trunks because this is when more conspecifics are present, making social broadcasting more beneficial, as later in the afternoon trunk occupancy decreases. Ord & Stamps (2017) did not find evidence of *Anolis* lizards adjusting display rate based on the number of nearby conspecifics; however, they also found that display rates were dependent on ambient temperature. Our thermal performance curve showed that lizards could maximize display rates over a broader range of $\mathrm{T_b}$ values, indicating that the drivers of display behaviour may differ between species or systems. Indeed, other taxa have been shown to alter the rate of advertisement signal production based on potential receivers (Aiken, 1982; Wellendorf et al., 2004; How et al., 2008). For example, *Sceloporus* species alter display patterns based on the presence (or absence) of males or females in the immediate vicinity (Martins, 1993a). Display rates on tree trunks at low temperatures is high compared to other microhabitats. Tree trunks are also exposed to conspecifics and predators, but unlike sunny snags, offer easy and accessible refuge via individuals running up into dense tree branches when approached (personal observation). This access to shelter could provide higher degrees of predator safety to vigorous displayers, and this combination of high visibility with relative safety could result in the high observed display rates relative to sunny snags and other microhabitats.

During the warmer hours of the day lizards spend more time in cooler (but within their T_set) microhabitats such as inner tree branches. As with trunks, the interplay between T_b, time of day, and high density of conspecifics on a common microhabitat is a potential driver of the positive relationship between display rate and T_b on inner branches. Display rate is likely low at low temperatures on inner branches because the probability of interaction with conspecifics is also low. As conspecifics shift their perch selection into inner branches during the warmer hours of the day, display rate increases with T_b.

Unlike other studies on display patterns and rates, we were surprised to find no evidence that sex, throat morph, or social context (territoriality vs. courtship vs. broadcasting) influenced display rate (Martins, 1991, 1993a, 1994). These and other studies (e.g., Partan et al., 2011) report differences in the relative frequencies of full push-ups, head bobs, dewlap extensions, and lateral compressions depending on sex and social context. We observed limited variation among the sexes in display pattern. Males, regardless of during broadcasting, territory disputes, or courtship, displayed using similar patterns consisting of 3–8 distinct push-ups accompanied by simultaneous lateral compressions and raised tails. Females exhibit similar display behaviours but with far less lateral compression, likely due to the absence of ventral colouration (or when present pale).

We found display rate to be driven by ecological contexts, similar to the findings by Simon et al. (2007), who showed that individuals altered display rate based on perceived predation threat. Gunderson & Leal (2015) proposed a model under which physiological constraints would limit display rate production, and Ord & Stamps (2017) found that *Anolis* lizards displayed at rates predicted by the influence of temperature on physiological performance. Our data also showed thermal sensitivity in display rate. However, the optimal temperature for displays was 4°C below T_pref (33.1–37.1°C). The thermal performance breadth for display rates exhibited a broad temperature range (23–39°C), which overlapped the range of preferred T_b values. We note that the majority of displays were at temperatures outside the T_set of *U. ornatus* (60/88 T_b values below the mean T_set range of 35.9–38.4°C). Our results are concordant with the patterns observed in Ord & Stamps (2017). Whereas Ord & Stamps found that T_opt for display rate was within the range of peak performance in *Anolis*, our results showed that *U. ornatus* could display at high levels below T_pref. These differences may be due to differences in the thermal ecology of *Anolis* and *U. ornatus*. *Anolis* occupying forest environments tend to be thermoconformers (Hertz et al., 1993); hence, Ord & Stamps (2017) used air temperature as a proxy for T_b rather than the actual T_b of lizard the lizard. In contrast, *U. ornatus* are thermoregulators (Gadsden et al., 2020). We therefore used body temperature rather than air temperature, and to ensure that our recorded display rate matched the lizard's body temperature at the time of display, stopped recording when lizards moved to thermally distinct locations. This presumably resulted in shorter recording times than those used in Ord & Stamps (2017) which could play a role in the differing results. Our findings could also be a result of differences in the thermal environment. For instance, in arid climates where ambient temperatures are often above T_{pref} and CT_{max}, the cost of thermoregulation may be low. Hence, lizards may have the capacity of displaying early in the morning at temperatures below T_{pref} because the risk of predation is low and the information being broadcasted may involve resource holding potential rather than seeking mates. Thus, lizards avoid the need to use perches that may exceed T_{pref} and CT_{max} to use visual displays to convey dominance. Given our findings, we suggest that future studies would benefit by considering the influence of microhabitat and season when dissecting how display rates may be affected by temperature.

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Table A1.
Candidate models for describing display rate in *U. ornatus*.

Fixed Effects	AICc	Delta AICc	Weight
T_b×Microhabitat	−233.6	0.00	0.394
T_b×Microhabitat+Sex	−231.1	2.47	0.115
T_b×Microhabitat+T_s	−230.8	2.71	0.102
T_b×Microhabitat+SVL	−230.8	2.72	0.101
T_b×Microhabitat+T_{pref}	−230.8	2.75	0.100
T_b×Microhabitat+Context	−229.8	3.74	0.061
T_b×Microhabitat+Time	−229.0	4.52	0.041
T_b×Microhabitat+Sex×T_b	−228.5	5.07	0.031
Microhabitat	−227.2	6.32	0.017
Microhabitat+Sex	−226.9	6.63	0.014
T_b*Microhabitat+SVL×Sex	−225.5	8.05	0.007
Sex	−224.0	9.51	0.003
Tb	−223.1	10.43	0.002
T_b×Microhabitat+T_{pref}×Microhabitat+T_{pref}×T_b	−223.1	10.46	0.002
T_b×Microhabitat+Morph	−223.0	10.53	0.002
T_{pref}	−222.9	10.62	0.002
T_b×Microhabitat+T_{pref}×T_s+T_s×T_b	−222.7	10.83	0.002
T_s	−222.0	11.50	0.001
Time	−221.8	11.75	0.001
SVL	−221.6	11.91	0.001
T_b×Microhabitat+T_b×Time+T_s×Time+Time×Microhabitat	−220.5	13.10	0.001
Context	−220.0	13.51	0.000
Morph	−215.4	18.16	0.000

All models shown also included lizard ID as random effect. '×' represents each term individually and an interaction between them, while ':' represents just the interaction (e.g., T_b×Microhabitat = T_b + Microhabitat + T_b:Microhabitat).

Table A2.
The relationships between microhabitat use and social context when a lizard was displaying.

Microhabitat	*N*	Broadcasting	Challenge	Courtship
Sunny snags	50	45	3	2
Shady snags	10	8	0	2
Trunks	15	13	0	2
Inner branches	10	7	0	3
Outer branches	3	2	0	1