NEOTROPICAL BIOLOGY AND CONSERVATION

Neotropical Biology and Conservation 21(2): 149–171 (2026)
DOI: 10.3897/neotropical.21.e185618

Research Article

Seasonal variations in spatial ecology, habitat use and habitat selection by San Cristóbal lava lizards *Microlophus bivittatus* in Galápagos

John W. Rowe[1], Jennifer A. Moore[2], Morgan R. Fonley[1], David L. Clark[1], Carlos A. Valle[3]

1 *Biology Department, Alma College, 614 West Superior Street, Alma, Michigan, 48801, USA*
2 *Biology Department, Grand Valley State University, 1 Campus Drive, Allendale, Michigan 49401, USA*
3 *Universidad San Francisco de Quito USFQ, Colegio de Ciencias Biológicas y Ambientales, Galápagos Science Center GSC, Casilla Postal 17-1200-841, Quito, 170901, Ecuador*

Corresponding author: John W. Rowe (rowe@alma.edu)

Abstract

Activity of terrestrial ectotherms in seasonal equatorial environments can be challenging due to temporal variations in temperature and water availability. Social interactions among conspecifics, along with predation risks, can also place limitations on activity patterns and spatial ecology. We studied the spatial ecology, habitat use, and habitat selection in the San Cristóbal lava lizard (*Microlophus bivittatus*) during a hot-wet period (March), and a cool-dry period (August). Overall, lizards used rock faces under canopy more frequently than other microhabitats. Compared to the hot-wet period, lizards increased their use of rock crevices and detritus and were sometimes inactive for several consecutive days during the cool-dry period. Lizards varied in their selection of structural features and thermal characteristics across seasons and throughout the day, relying on open areas for basking (especially during the mornings) during the hot-wet period and shifting to sheltered, cooler microhabitats during the cool-dry season. Within their larger activity areas, each lizard concentrated movements within a single area but occasionally and often repeatedly traveled to peripheral specific areas. While minimum convex polygons and AKDE-95% utility distributions (UDs) overlapped among individuals extensively, AKDE-50% UDs rarely overlapped among individuals that resided adjacent to one another. Lizards showed a reduction in space use metrics by over 50% between the hot-wet and the cool-dry period further indicating seasonal limitations on activity between seasons. Overall, San Cristóbal lava lizards are sensitive to both thermal and structural habitat characteristics and vary their habitat use and activity patterns seasonally.

Key words: Activity, activity area, core area, home range, movements, utility distributions

OPEN ACCESS

Academic editor: Vinícius Sperandei
Received: 18 January 2026
Accepted: 27 April 2026
Published: 21 May 2026

ZooBank: https://zoobank.org/3BAA3854-5171-42BF-AF22-B58CF8645544

Citation: Rowe JW, Moore JA, Fonley MR, Clark DL, Valle CA (2026) Seasonal variations in spatial ecology, habitat use and habitat selection by San Cristóbal lava lizards *Microlophus bivittatus* in Galápagos. Neotropical Biology and Conservation 21(2): 149-171. https://doi.org/10.3897/neotropical.21.e185618

Copyright: © John W. Rowe et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Activity cycles, habitat use, and movements of a species in a particular environment presumably reflect adaptative responses to both abiotic and biotic features of the environment (Dunham et al. 1989). For many ectotherms, spatially and temporally variable and often extreme variations in the thermal environment can have fitness consequences that will ultimately influence habitat

selection (Huey 1991). The risk of predation can strongly influence activity and movements of individuals (Rusch et al. 2023) and along with various density-dependent effects is expected to shape habitat selection (Northrup et al. 2022; Webber et al. 2023). Therefore, the study of habitat selection and spatial ecology should be critical to understanding phenotypic responses of species to their environments.

Movement patterns of an animal are formed by complex interactions among the behaviors of an individual (Fleming et al. 2015). Factors that affect the location and size of a home range (Burt 1943; Powell 2000) include familiarity with foraging areas, escape routes, and hiding places, access to mates (Webber et al. 2023) and thermoregulation sites (Huey 1991; Clement and Roedder 2021). Ectothermic vertebrates in the tropics are subject to seasonality where dry seasons may influence home range size either by increasing it as individuals forage widely for food (Volampeno et al. 2011; Morellet et al. 2013) or decreasing it as individuals become inactive (see Christian et al. 1983; Ariano-Sánchez et al. 2020). Within home ranges individuals may establish core areas that reflect features important to the selection of a microhabitat (Wilson et al. 2010) and therefore represent better estimates of the space used by individuals over time (Tracy and Christian 1986).

Lava lizards (*Microlophus*, Tropiduridae) are a complex of at least 11 species that occupy most of the islands of Galápagos (Benavides et al. 2009; Torres-Carvajal 2024). As essentially coastal species, lava lizards generally occupy arid beaches and rock habitats, but do not occur in the wetter uplands, characterized by lush and dense vegetation (Tanner and Perry 2007). All species are sexually dimorphic in size (males are larger than females) and sexually dichromatic with both males and females displaying distinct and often colorful markings (Clark et al. 2017, 2023; Toyama and Boccia 2021). Lava lizards are omnivorous (Van Denburgh and Slevin 1913; Moore et al. 2017; Hervías-Parejo et al. 2019; Moreno-Buitrón et al. 2024) and some species are cannibalistic (Lewbart et al. 2017). Both male and female lava lizards communicate through visual displays and may engage in physical territorial disputes (Clark et al. 2015). Spatially, lava lizards may maintain well-defined activity areas (Rowe et al. 2019) and distinct activity areas may persist throughout the year (Stone and Baird 2002). Lava lizards appear to effectively thermoregulate by shifting use of different microhabitats under the hot equatorial sun (Stebbins et al. 1967; Rowe et al. 2020). The Galápagos are seasonal with relatively hot (January–May) and cool (June–December) seasons (Trueman and d'Ozouville 2010), and resource limitations for terrestrial lizards may occur during the cool season, which also tends to be relatively dry along the coastal areas (Christian et al. 1983; Jordan and Snell 2002). Despite possessing some degree of cryptic coloration (Mancero et al. 2022), the conspicuous diurnal activities that are associated with social signaling, foraging, and thermoregulation presumably leave lava lizards vulnerable to predation (Jordan et al. 2008; Valle et al. 2024). Predators of lava lizards include Galápagos Racers (Ortiz-Catedral et al. 2019; Valle et al. 2024), various avian predators (Burke et al. 2015), and feral cats (Carrión and Valle 2018).

San Cristóbal lava lizards (*M. bivittatus*) establish relatively small activity areas (minimum convex polygons) that overlap among individuals and that shift over time, possibly in response to seasonal changes in environmental conditions (Rowe et al. 2019). Although the territorial males are significantly larger than females and seasonal rainfall and temperature patterns can be pronounced in

Galápagos, neither intersexual nor seasonal differences in space use have been demonstrated (Rowe et al. 2019). *Microlophus bivittatus* thermoregulate more effectively when environmental temperatures are moderate than during extremely hot or cool periods (Rowe et al. 2020). Thermoregulation by lava lizards entails use of open rock faces during the morning and evening and shaded retreats during the warm afternoon hours (Stebbins et al. 1967; Rowe et al. 2020).

We studied spatial ecology and habitat selection in the San Cristóbal lava lizard during the hot season (February and March) and the cool season (August) using radiotelemetry. We used auto-correlated kernel density analyses (Calabrese et al. 2016; Fleming and Calabrese 2017) and habitat use and selection (Northrup et al. 2022) to determine how *M. bivittatus* utilize their activity areas. We expected lizards to establish relatively large activity areas and move relatively long daily distances during the hot-wet period than during the cool-dry period. Within an individual's activity area, we attempted to identify areas of repeated use by the individual that would imply favorable sites for thermoregulation, foraging, or both, and determine if areas of neighboring lizards appear to overlap, suggesting some degree of territoriality. We expected individuals to avoid open habitats during midday and select microhabitats on rocks with canopy and near or in rock crevices, particularly during the warmest, and potentially wettest, time of year studied at the site to date (March 2016). During the coolest time of year studied at the site to date (August 2016), we expected that individuals would actively select open rock faces during the warmest times of the day (afternoon hours).

Methods

Study site and study grid

Our study site (-0.8920, -89.6110) is on a rocky slope (16 m elevation) along a path that links the Galápagos National Park Interpretation Center and Punta Carola. The eastern half of the site has large, rounded lava boulders with a dense canopy of mostly palo santo trees (*Bursera graveolens*). Smaller, flatter rocks with fewer and smaller trees like Galápagos croton (*Croton scouleri*) and Jerusalem thorn (*Parkinsonia aculeata*), herbaceous shrubs such as stickleaf (*Mentzelia aspera*) and bastardia (*Abutilon viscosum*), and grass-sedge ground cover were the predominant vegetation of the western half of the site. The cacti *Opuntia* spp. and *Jasminocereus thouarsii* are scattered throughout the study site. Weather patterns varied between the two study months with relatively high mean monthly temperature and high monthly precipitation in March when compared to August (Fig. 1). The transition from the hot-wet and cool-dry seasons occurs mostly during May and in 2016, there was an abrupt transition between El Niño and La Niña during May which apparently resulted in the unusually high and variable rainfall patterns during that month.

We used a Trimble Geo7× (Trimble Inc., Westminster, CO, USA) and tape measures to construct a grid (60 × 60 m) using numbered nylon flagging that we tied to vegetation or to wood stakes at regular, 10 m intervals. We placed centrally located flags at the centers of quadrats for finer spatial resolution. Additional reference flags were positioned for lizards that moved beyond the boundaries of the study grid.

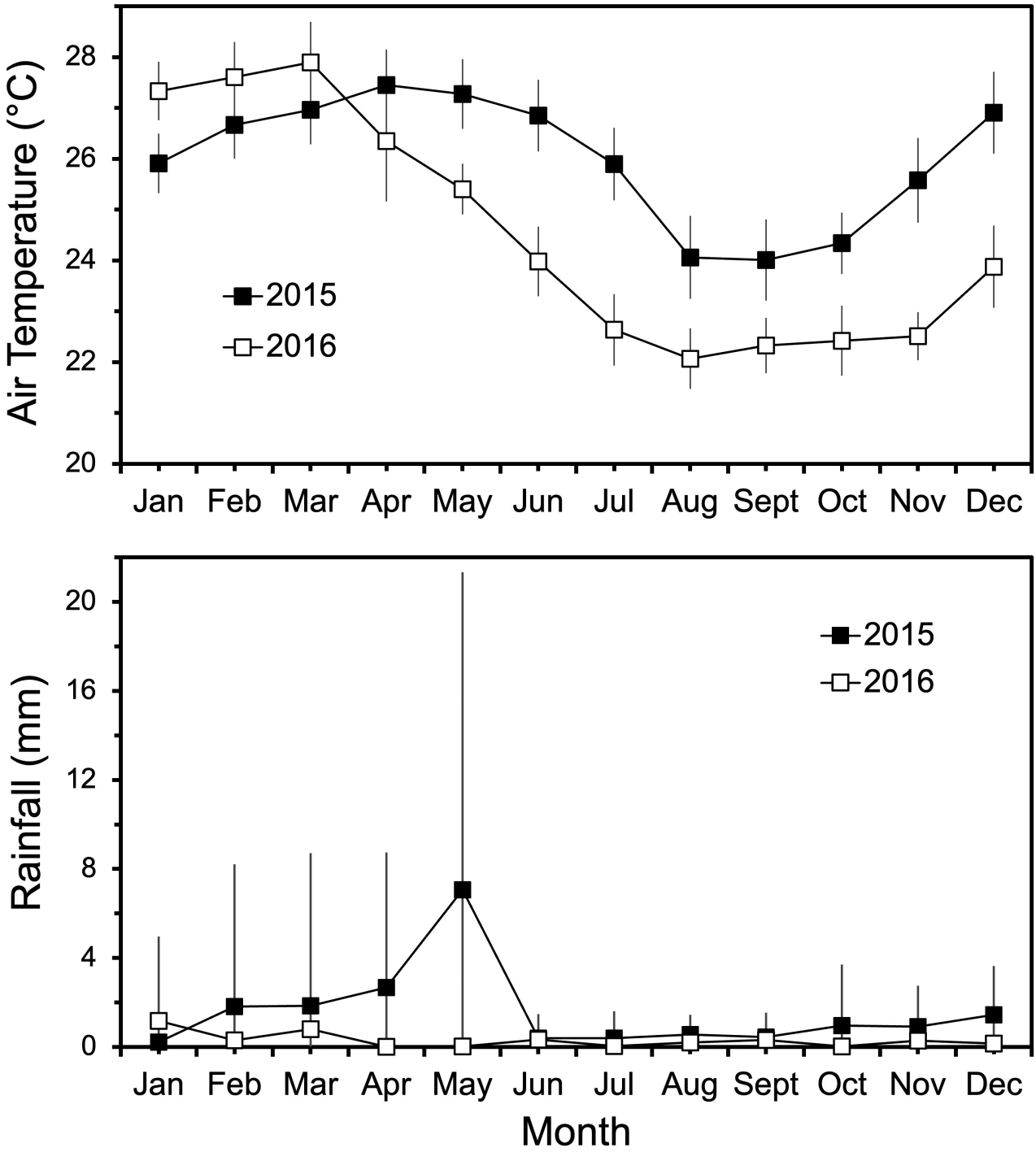

Figure 1. Ambient temperature and rainfall in Galápagos. Mean monthly air temperature and rainfall (± SD, vertical lines) recorded at the Charles Darwin Research Station on Santa Cruz (data courtesy of the Charles Darwin Research Station), Galápagos, Ecuador.

Radiotelemetry

We searched the grid site for lizards and captured them by noose or by hand. Lizards were placed in individual mesh bags and transported to the Galápagos Science Center for processing. We used plastic rulers to measure snout-vent length (SVL) to the nearest 1.0 mm and Pesola scales (either 30 ± 0.5 or 100 ± 1.0 g) to measure body mass. We obtained digital images of the dorsum and ventrum of each lizard for future recognition based on pigmentation patterns of the scales.

We adhered radio transmitters (Model R1615, 0.5 g, 151 mHz, Advanced Telemetry Systems, Isanti, MN) to the dorsal pelvis using epoxy (5 min epoxy, ITW Devcon, Danvers, MA, USA) such that the antenna rested along the dorsum of the tail. Lizards were maintained in plastic containers overnight to allow the epoxy to harden. We released each lizard at their site of capture the following morning. Between 28 February and 3 March 2016, we radio-tagged 6 female and 6 male lizards. Two transmitters (from one M and one F) failed immediately. Transmitters of two females were shed in rock crevices where they could not be recovered. One male was monitored for 6 d before it shed its transmitter, but we recovered it and placed it on a different male that we monitored for 8 d. Body size statistics for those lizards that we included in our analyses are reported in Table 1. Radio-transmitters averaged 5.0% of the body mass and all were below the 10% that impedes mobility in small iguanid lizards (Knapp and Abarca 2009).

We began monitoring lizards on the day following their release at the study site. We used radio-receivers (Advanced Telemetry Systems R410 Receiver) and antennae (RA–23K VHF; Telonics Inc., Mesa, Arizona, USA) to locate lizards. We relocated lizards three times per day, between 0800–1100 h, 1100–1500 h, and 1500–1800 h. The location of the lizard was recorded on a hardcopy of the map relative to grid flags by triangulation and if necessary, we used tape measures to facilitate mapping of the approximate locations of lizards on the grid relative to reference flags.

Spatial ecology

We plotted locations of each lizard from hardcopy maps on electronic maps of our study grid using Trimble Pathfinder Office (Trimble Inc., Westminster, CO). For each lizard, we measured distances (nearest 1 m) that were moved between the three successive radiolocations for each day. Time constraints imposed by radiolocation of focal lizards and by the microhabitat data collection process sometimes precluded radiolocation of all lizards three times daily for every lizard on every day. However, three daily radiolocations were collected for each lizard on over 90% of the total observation days of the study period.

We determined activity areas and utilization distributions (UDs) in two ways. First, we determined minimum convex polygons (MCPs), areas enclosed by the outermost locations representing a convex polygon of an individual without consideration of the utilization distribution of points within the MCP (Mohr 1947). Second, we used autocorrelated kernel density estimation (AKDE) to determine areas of utilization distributions such that biologically relevant clusters

Table 1. Body size statistics for radio-tagged *M. bivittatus* at Frigate Bird Hill 2016.

		Females		Males	
		SVL (mm)	Mass (g)	SVL (mm)	Mass (g)
March	Mean ± SE	63.5 ± 0.9	7.5 ± 0.2 g	81.4 ± 0.3	19.9 ± 2.9
	Min – max	61–66	7–8	74–90	13–32
	N	2	2	5	5
August	Mean ± SE	58.8 ± 0.2	7.2 ± 0.1	71.8 ± 0.4	14.3 ± 0.2
	Min – max	54–62	6–8	65–70	11–19
	N	4	4	4	4

of repetitive use by an individual can be identified (De Solla et al. 1999; Gitzen et al. 2006). We determined MCPs using the built-in R function 'chull' (convex hull) to find their vertices, then computed the corresponding enclosed areas. We determined UD95% and UD50% values by AKDE for each lizard using the Continuous-Time Movement Modeling (ctmm) R package (Calabrese et al. 2015). Because we sometimes had differing numbers of radiolocations for individuals on a given day, we determined UDs using the optimally weighted area-corrected ADKE model (pHREML-fitted wAKDEc; Silva et al. 2022).

Microhabitat use and selection

We did not collect microhabitat data for every lizard each day given the time required to radio-locate each lizard and for the collection of microhabitat data at both lizard and random locations. Rather, in advance of data collection on a given day, we randomly selected lizards for measurement of microhabitat variables during each radiotelemetry period (morning, mid-day, and late afternoon). Microhabitat selection data were collected for each lizard on a similar number of days throughout the study. Based on data from Rowe et al. (2019), we measured 9 variables that we surmised could be important to the ecology of a lizard at both the site of a lizard upon its radiolocation and at a location 20 m from the lizard's location site. We chose to use 20 m between the lizard and random sites because it was the approximate diameter of the average minimum convex polygon and well within the average daily distance moved for lizards at the site (i.e., generally selectable microhabitats would be within 20 m and therefore available and accessible for each lizard in our relatively fine-grained environment, Rowe et al. 2019). The direction (N, NE, E, SE, S, SW, W, or NW) of the random site was randomly determined. Most often, we were able to collect microhabitat data without disturbing the focal lizard. Microhabitat data that we collected at the site of the lizard included percent canopy cover as measured by a Spherical Crown Convex Densiometer (J.C. Doster, Forest Densiometers, Marchianna, FL, USA), substrate temperature, and distances to the closest low shrub or small tree (< 20 cm diameter), a large tree (> 20 cm in diameter), an open rock face (no canopy directly above), a rock face with canopy directly above, a rock crevice, leaf litter (dead leaves and small sticks), and to low ground vegetation cover. We measured substrate temperature with an infrared thermometer (MiniTemp, Raytek®, Wilmington, North Carolina, USA) as a measure of the immediate environmental temperature. We note that substrate temperature does not represent an operative temperature that a lizard might obtain at one place and one point in time (Bakken and Gates 1975). However, operative temperatures are partially determined by conduction between the substrate, and an object and substrate temperature is correlated with other variables such as solar radiation and air temperatures (Bakken et al. 1985; Shine and Kearney 2001).

Analyses

We analyzed space-use metrics (MCPs, AKDE-50% and AKDE-95%) and total daily distances moved using General Linear Models with season and sex as main effects. We averaged the total daily distance moved values for all each

individual lizard across all days that each was monitored so that each lizard was represented by a single value in the data set. Sex was included as a main effect in each GLM although, because sex has not been shown to play a role in the spatial ecology of *M. bivittatus* at the site (Rowe et al. 2019) and our sample size for females in March was small (N = 2), we had no a priori expectations for a sex effect. Following natural log data transformations of daily distances moved and of each space-use metric, plots of residuals versus fitted values and normal quantile plots indicated that data were homoscedastic and approximately normally distributed respectively. We assessed the possibility that activity area size was related to variation in durations of radio telemetric monitoring among lizards using Spearman Rank Correlation.

We used conditional (paired) logistic regression to analyze lizard microhabitat selection. The response variable was lizard (1) or random (0) locations. We coded each lizard location and its associated random location (that were measured at approximately the same time, to account for weather conditions and resource availability) as paired strata. To assess multicollinearity among predictor variables, we first examined a Pearson correlation matrix for all continuous predictors (canopy cover, distance to high tree, distance to low tree, distance to rock crevice, distance to closest rock with no canopy, distance to the closest rock under canopy, distance to low ground cover, distance to nearest detritus, and substrate temperature). Based on collinearity, we removed distance to low ground cover, as it was highly correlated with distance to low tree. We also calculated variance inflation factors (VIF) for all multivariate candidate models using an equivalent binomial generalized linear model structure, as VIF cannot be calculated directly from conditional logistic regression objects in R. For models containing interaction terms, we report the generalized VIF (GVIF^(1/(2·Df))) which is comparable to the square root of a standard VIF and accounts for the additional degrees of freedom associated with categorical variables and interaction terms (Fox and Monette 1992). All VIF values were below 1.07 in additive models and below 2.0 in models with interaction terms, indicating no meaningful multicollinearity among predictors. Analyses were conducted in R using the 'car' package. We converted time of day to categories of "morning", "midday", and "afternoon" (0800–1000 h, 1100–1300 h, and 1400–1600 h respectively). Variables were rescaled around a mean of 0 and SD of 1 to improve model performance and make model coefficients more comparable.

We divided the dataset by sampling month (March and August) as resources and environmental conditions are highly variable between the two sampling periods and modelled each dataset separately using the clogit function in the survival package in R (R Core Team 2025). For March and August separately, we constructed a candidate set of 22 models to test the hypothesis that for March, lizards are selecting open canopy rocks early in the morning and late in the afternoon, and during the heat of midday they are selecting closed canopy rocks not necessarily near rock crevices and for August, lizards are remaining close to rock crevices and low trees throughout the day. We included the following variables in univariate or multivariate models (canopy cover, distance to high tree, distance to low tree, distance to rock crevice, distance to closest rock with no canopy, distance to the closest rock under canopy, distance to nearest detritus, and substrate temperature). We also included interaction terms between time of day and rock with no-canopy, rock-canopy and substrate

temperature. We also included interaction terms between time of day and rock with no-canopy, rock-canopy and substrate temperature to assess whether selection of these habitats and temperatures varied throughout the day.

We assessed model fit using Akaike's information criterion corrected for small sample sizes (AIC_c). Important values included the number of parameters in each model including an intercept (K), the delta AIC_c or the difference between the highest ranked model and the model of interest, the AICc weight (ω_i), the cumulative weight, and the log likelihood where smaller values indicate better model fits. To address the potential for overfitting models, we used full model averaging across all candidate models to obtain model-averaged coefficients and relative variable importance (RVI) scores for each predictor (Burnham and Anderson 2002). Model averaging was implemented manually in R as automated functions in the AICcmodavg package were not compatible with our candidate model set.

Test statistics were considered significant at $\alpha = 0.05$. Means are followed by ± SE unless otherwise specified.

Results

General activity patterns

Based on 6–14 radiotelemetry days per individual (165 days total across all lizards) and 15–40 radiolocations per individual (451 total across all lizards), most individual radio-tagged lizards were active on most days during both March and August and moved within irregularly shaped activity centers that varied in size among individuals and between seasons. During March, one female lizard failed to show activity on a single day while all others showed at least some activity on any given day. During August, however, four individuals (two females and two males) failed to show changes in their locations and remained in cover for the day. Of the two females, one was inactive on a single day while another was inactive for two consecutive days. Of the two inactive males, one was inactive for six consecutive days followed by an 11.4 m movement in a single day, then was inactive for a single day with subsequent activity for two days (16 and 2 m moves d^{-1} respectively) and finally inactive for two more consecutive days (Fig. 2). The second male lizard was inactive on three non-consecutive days.

Daily distances moved

Total daily distances moved were variable among individuals and between seasons but not between the sexes. In the GLM of total daily distances with individual ID and day-of-year included as random variables, only the month term was significant (Table 2). Adjusted mean total daily distance moved was significantly greater in March (mean = 14.2 ± 1.3 m, 0–51.5 m, *N* = 7 lizards) than it was in August (mean = 5.8 ± 1.3 m, 0–88.3 m, *N* = 8 lizards) and effect size was relatively large (Cohen's d = 1.39, $CI_{95\%}$ = 0.15–2.58). While most daily distances moved during March were < 30 m d^{-1}, occasional shifts of about 50 m occurred in some individuals (Fig. 2). In contrast, most daily movements during August were < 25 m d^{-1} with shifts more than 40 m d^{-1} observed in one lizard on two oc-

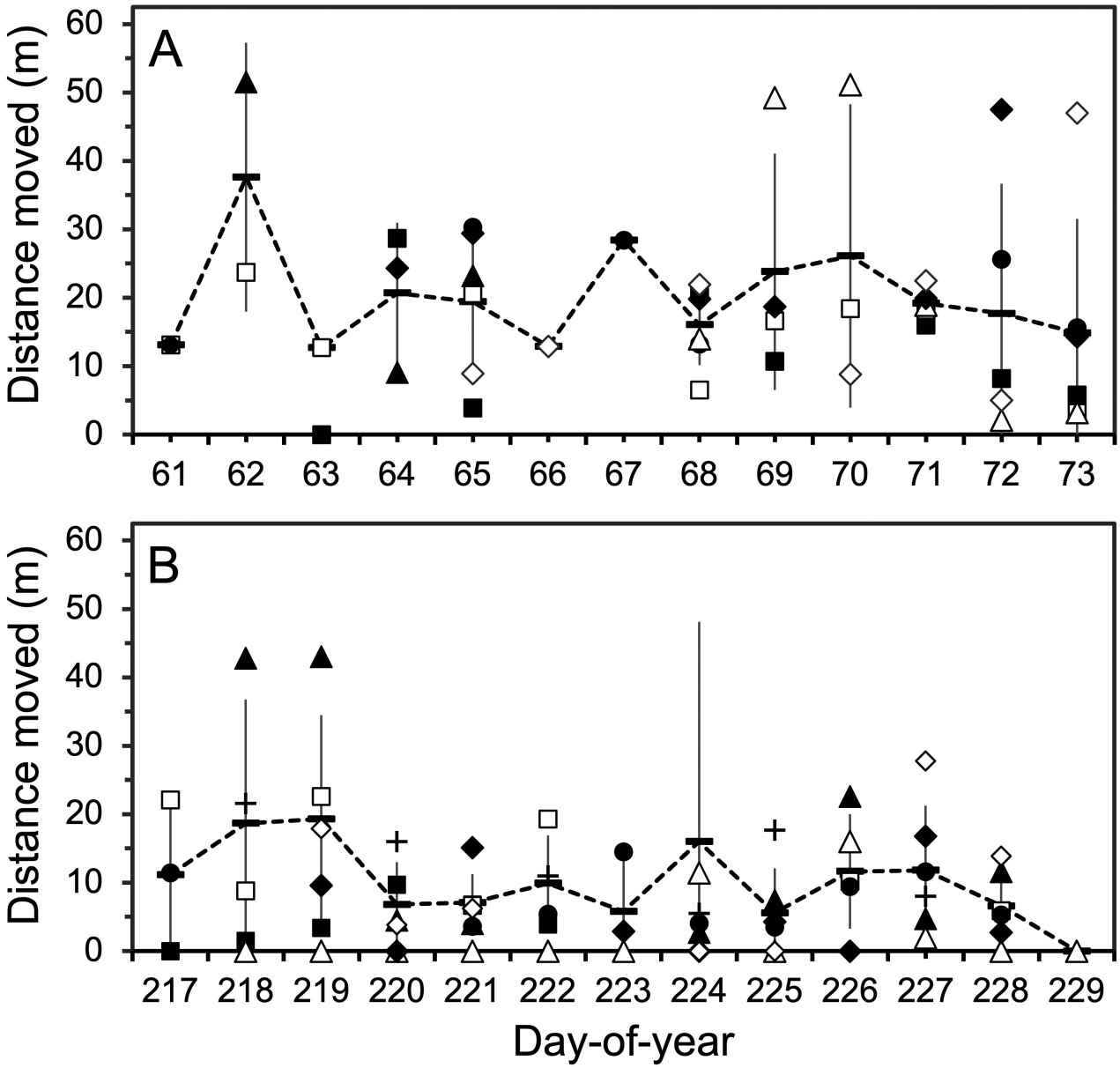

Figure 2. Daily distances traveled by *M. bivittatus* across months. Total daily distances moved for individual *M. bivittatus* (denoted by their radio transmitter frequences) based on combined distances between three radiolocations made during: **A.** March- hot-wet, *N* = 8 lizards; **B.** August- cool-dry, *N* = 8 lizards; symbols represent different individual lizards; females are solid symbols, males are open symbols, horizontal bars are means connected by the dashed line.

casions (Fig. 2). Days where lizards showed little to no activity were also more prominent during August than during March.

Activity area size

Lizards tended to favor a single area within their activity areas with forays that radiated away from the central area (see Fig. 3- lizard 151.202), sometimes repeatedly to the same peripheral area or areas (Fig. 3- lizards 151.262). Radio-tagged lizards with adjacent activity areas made occasional incursions into one another's activity areas resulting in overlapping space use areas (AKDE-50%, AKDE-95%, and MCP). However, we did not observe any cases of completely or mostly superimposed AKDE-50% areas (Fig. 3).

Table 2. General linear mixed model analyses for ln transformed total daily distance moved and ln transformed space use metrics (AKDE-50% and 95%, and MCP) for *M. bivittatus* on Frigatebird Hill, San Cristóbal, Galápagos, Ecuador, 2016. * indicates statistical significance.

Metric of distance or area	Model effect	*F*	df	*P*
Total daily distance moved	Sex	0.0494	1,11	0.8281
	Month	6.4084	1,11	0.0279*
	Sex × month	0.2637	1,11	0.6177
AKDE-50%	Sex	0.0019	1,11	0.9357
	Month	15.2951	1,11	0.0024*
	Sex × month	0.9988	1,11	0.3391
AKDE-95%	Sex	0.0009	1,11	0.9768
	Month	9.5393	1,11	0.0103
	Sex × month	0.0064	1,11	0.9377
MCP	Sex	0.0002	1,11	0.5971
	Month	6.9165	1,11	0.0234*
	Sex × month	0.7208	1,11	0.4140

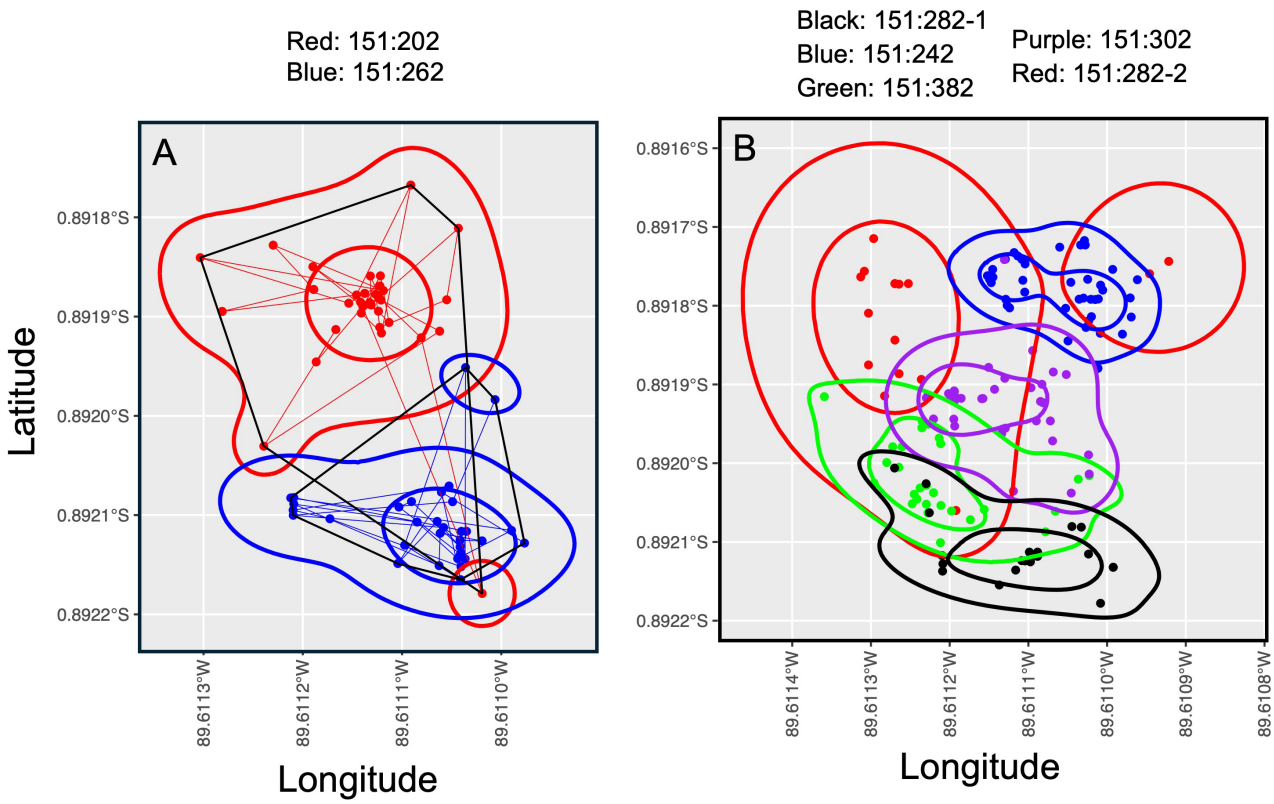

Figure 3. Movements of lizards within their activity areas. **A.** Space use by *M. bivittatus*. Movements for two females monitored during March 2016; points are locations for individuals and narrow lines connect successive location points. Large contours are AKDE-95%, small contours or AKDE-50%, and polygons are minimum convex polygons; **B.** Space use by five males with adjacent activity areas monitored during March 2016; points are individual locations large contours are AKDE-95% and small contours are AKDE-50%; polygons for MCPs were omitted for figure clarity.

Activity area size was not related to variation in durations of radio telemetric monitoring among lizards, and lizards used larger areas in March than they did during August. Although some lizards were tracked on more days than other

Table 3. Space use metrics (AKDE-50% and 95% and MCPs) for *M. bivittatus* on Frigatebird Hill, San Cristóbal, Galápagos, Ecuador, 2016.

Month	Lizard ID	Sex	AKDE Model	AKDE-50% (m^2)	AKDE-50% 95% CI (m^2)	AKDE -95% (m^2)	AKDE -95% 95% CI (m^2)	MCP (m^2)	*N telemetry* d	*N* locations
August	151.201	F	IID anisotropic	42.1	25.3–63.0	208.5	125.5–312.2	120.9	7	21
August	151.221	M	IID anisotropic	84.8	58.7–115.5	589.0	407.9–802.8	586.6	13	36
August	151.241	F	OU anisotropic	27.4	18.5–38.1	140.6	94.7–195.4	95.9	13	35
August	151.261	M	IID	42.0	28.9–57.4	298.5	205.5–408.6	346.6	13	34
August	151.282	M	IID anisotropic	30.9	20.7–43.1	209.1	140.1–291.8	144.2	12	30
August	151.301	M	IID anisotropic	15.6	10.7–21.5	79.9	54.6–109.8	58.1	12	33
August	151.322	F	IID	46.4	30.6–65.4	201.9	133.0–284.8	127.9	11	28
August	151.341	F	OU anisotropic	122.9	65.5–198.0	584.3	311.5–941.6	318.3	10	26
March	151.202	F	OU	140.3	88.6–203.7	964.6	609.0–1400.6	876.2	12	34
March	151.242	M	IID anisotropic	118.5	84.3–158.5	405.6	288.4–542.4	230.4	14	40
March	151.262	M	IID anisotropic	119.1	80.9–164.5	571.6	388.3–789.6	359.6	10	32
March	151.282-1	M	IID	239.7	1263.3–3669.2	2310.8	1563.3–3669.2	919.2	6	15
March	151.282-2	M	IID anisotropic	143.6	86.4–215	597.0	359.4–893.8	298.3	8	20
March	151.302	M	IID	136.6	96.2–184	629.0	442.8–847.2	432.0	14	38
March	151.382	M	OU anisotropic	164.8	101.9–242.5	704.3	435.5–1036.8	388.6	10	29

lizards (Table 5), there were no significant correlations between activity area size (AKDE-50%, AKDE-95%, and MCP) and the number of days monitored, nor with the number of radiolocations obtained per individual over all (P > 0.05 in all Spearman Rank Correlations). There were no significant differences in activity area size between the sexes nor was there an interaction between sex and month in any of the three GLM analyses (Table 1). However, mean activity area adjusted for main effects and interactions in the GLMs were significantly larger in March (AKDE-50%: mean = 150.7 ± 1.3 m^2; AKDE-95%: mean = 749.5 ± 1.3 m^2; MCP: mean = 475.5 ± 1.34 m^2) than they were in August (AKDE-50%: mean = 42.8 ± 1.2 m^2, Cohen's d = 2.14, $CI_{95\%}$ = 0.72–3.50; AKDE-95%: mean = 237.6 ± 1.3 m^2, Cohen's d = 1.69, $CI_{95\%}$ = 0.38–2.95; MCP: mean = 173.0 ± 1.3 m^2, Cohen's d = 1.44, $CI_{95\%}$ = 0.18–2.64; Fig. 4).

Microhabitat use

In March, lizards most frequently used rock faces with or without canopy but shifted to mostly rocks under canopy, detritus, and high trees late in the day (Fig. 5). Rocks under canopy were the most used microhabitat types in March. Throughout the day in August, lizards used rock crevices, detritus or were under low ground cover with about equal frequency with rock faces, with or without canopy (Fig. 5).

Microhabitat selection

Factors affecting habitat selection differed between March and August. The March microhabitat selection analysis found distance to the nearest low tree and substrate temperature as the two best predictors of lizard site selection. The model that included these two covariates received the strongest support (AICc = 92.47, AICc weight = 0.95) with all other models > 6 AICc points high-

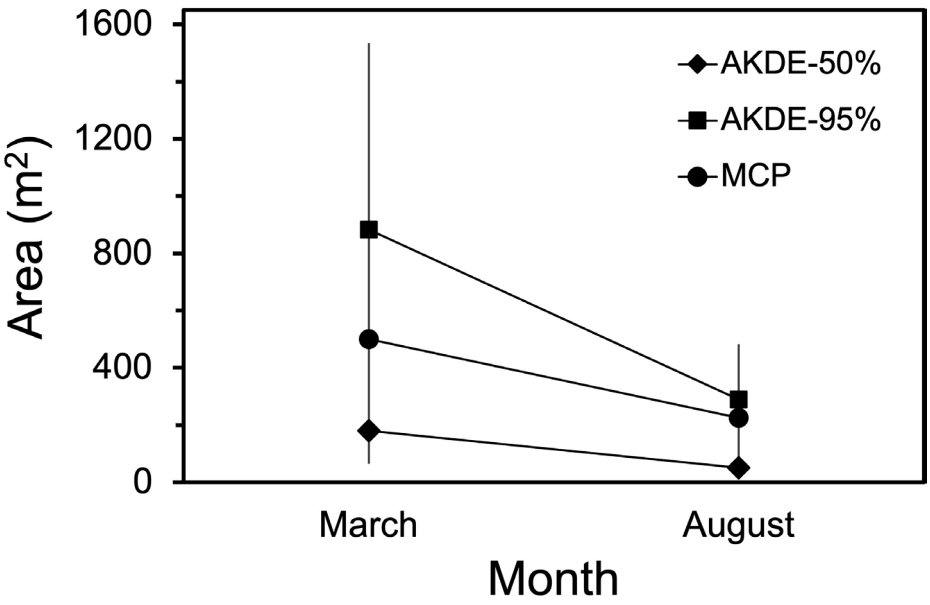

Figure 4. Activity area size of *M. bivittatus*. Space use metrics (mean ± SE) for *M. bivittatus* based on combined distances across three daily radiolocations made during A) March- hot-wet, *N* = 8 lizards and B) August- cool-dry, *N* = 7 lizards.

Table 4. Results from paired logistic regression models of lava lizard habitat selection for March 2016 including Akaike's Information Criterion, adjusted for small sample sizes (AICc), rescaled AICc (delta AIC), AIC weight and cumulative weight, and log-likelihood.

	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
lowtree+subtemp	2	92.47	0	0.94	0.94	-44.2
detritus+subtemp	2	99.25	6.78	0.03	0.97	-47.59
Lowtree	1	100.52	8.06	0.02	0.99	-49.25
hightree+subtemp	2	101.92	9.45	0.01	1	-48.92
subtemp*day	5	108.47	16.01	0	1	-49.06
rocknocan+subtemp	2	109.72	17.26	0	1	-52.83
Subtemp	1	110.49	18.02	0	1	-54.23
rockcan+subtemp	2	111.2	18.74	0	1	-53.57
Detritus	1	111.7	19.23	0	1	-54.84
rockcrev+subtemp	2	112.13	19.66	0	1	-54.03
canopy+subtemp	2	112.37	19.91	0	1	-54.15
Hightree	1	119.66	27.19	0	1	-58.82
Canopy	1	120.64	28.17	0	1	-59.31
Rockcan	1	121.35	28.89	0	1	-59.67
Rockcrev	1	121.44	28.98	0	1	-59.71
Rocknocan	1	122.03	29.57	0	1	-60
rocknocan + rockcrev	2	122.67	30.21	0	1	-59.3
rockcan + rockcrev	2	122.81	30.35	0	1	-59.37
rockcan*day	5	123.82	31.35	0	1	-56.73
rockcan*day + rockcrev	6	125.96	33.49	0	1	-56.73
rocknocan*day	5	127.8	35.33	0	1	-58.72
rocknocan*day + rockcrev	6	128.74	36.27	0	1	-58.12

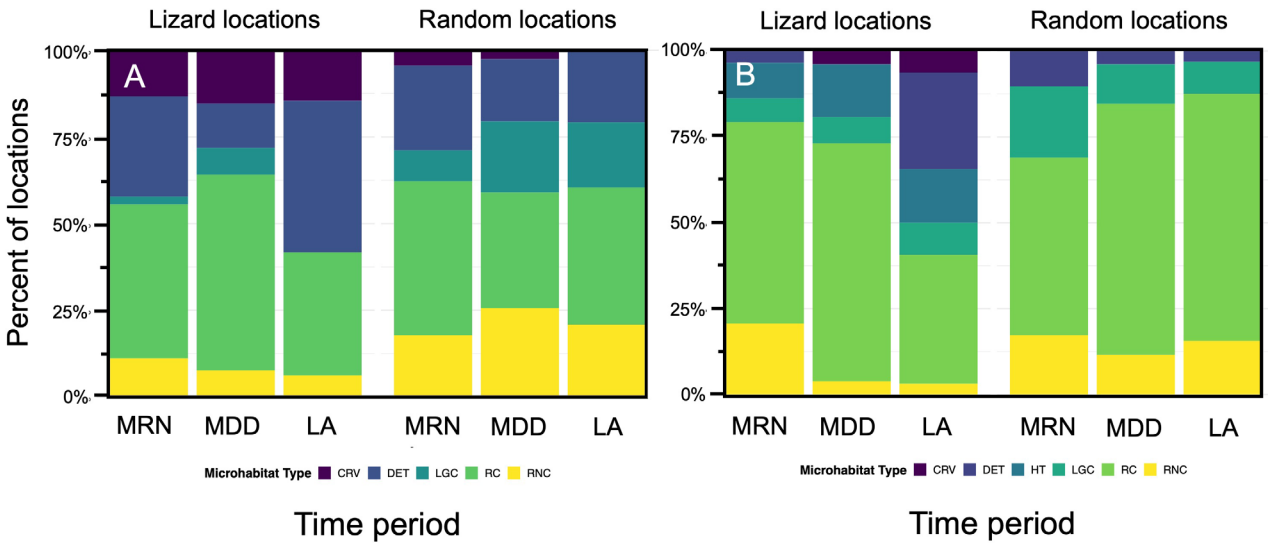

Figure 5. Habitat use by *M. bivittatus*. Percentages of total observations at lizard locations and random locations in: **A.** March; **B.** August, during different time periods of the day (MRN 0800–1100 h; MDD 1100–1500 h; LA 1500–1800), 2016. Microhabitat types include rock crevices (CRV), detritus (DET), low ground cover (LGC), high tree (HT), rock face under canopy (RC) and rock face not under canopy (RNC).

Table 5. Results from paired logistic regression models of lava lizard habitat selection for August 2016 including Akaike's Information Criterion, adjusted for small sample sizes (AICc), rescaled AICc (delta AIC), AIC weight and cumulative weight, and log-likelihood.

	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
rocknocan + rockcrev	2	170.97	0	0.44	0.44	-83.46
rockcrev+subtemp	2	172.56	1.59	0.2	0.64	-84.26
Canopy	1	174.88	3.91	0.06	0.7	-86.43
canopy+subtemp	2	175.16	4.19	0.05	0.76	-85.56
Rockcrev	1	175.38	4.41	0.05	0.8	-86.68
rockcan + rockcrev	2	175.58	4.6	0.04	0.85	-85.77
hightree+subtemp	2	175.99	5.01	0.04	0.88	-85.97
subtemp*day	5	176.05	5.07	0.03	0.92	-82.91
rocknocan*day + rockcrev	6	177.08	6.1	0.02	0.94	-82.37
detritus+subtemp	2	177.62	6.65	0.02	0.95	-86.79
rockcan*day + rockcrev	6	178.7	7.73	0.01	0.96	-83.19
Hightree	1	178.97	8	0.01	0.97	-88.48
Subtemp	1	178.99	8.02	0.01	0.98	-88.49
rocknocan+subtemp	2	179.52	8.55	0.01	0.99	-87.74
rockcan+subtemp	2	180.23	9.25	0	0.99	-88.09
lowtree+subtemp	2	180.61	9.64	0	0.99	-88.28
Detritus	1	180.91	9.94	0	1	-89.45
Rocknocan	1	182.47	11.5	0	1	-90.23
Rockcan	1	183.75	12.78	0	1	-90.87
Lowtree	1	184.16	13.19	0	1	-91.07
rockcan*day	5	186.19	15.22	0	1	-87.98
rocknocan*day	5	189.23	18.26	0	1	-89.5

er (Table 4). Model averaging across all 22 candidate models also revealed strong and consistent support for both distance to low tree and substrate temperature. Substrate temperature had the highest relative variable importance (RVI = 0.983) and a negative model-averaged coefficient (β = -0.68, 95% CI: -1.17, -0.19; OR = 0.51), indicating lizards selected microhabitats with cooler substrate temperatures compared to random sites. Distance to low tree also received strong support (RVI = 0.96; β = 0.87, 95% CI: 0.33, 1.41; OR = 2.38), indicating lizards selected sites that were approximately 2.4 times further from low trees than the random sites (Table 4). Throughout the day, lizards selected sites that were relatively far from trees in the morning, but lizards moved closer to trees as the day progressed (Fig. 6A). Lizards also selected relatively warm sites in the morning and relatively cool sites throughout the rest of the day (Fig. 6B) which is consistent with their frequent use of open rock faces in the morning. All remaining predictors had RVI values below 0.04 and confidence intervals that overlapped zero.

The August microhabitat selection analysis, in contrast, did not show strong or consistent support for any predictors of habitat selection. The top two models in the set both contained distance to rock crevice, with distance to rock with no canopy also in the top model (AICc = 170.97, weight = 0.44) and substrate temperature also in the second-best model (ΔAICc = 1.59, weight = 0.20) (Table 5). However, based on model averaging, no predictor received strong or consistent support across models. Distance to rock crevice had the highest RVI (0.76) but its confidence interval overlapped zero (β = -0.35, 95% CI: -0.80, 0.10; OR = 0.704), suggesting a tendency for lizards to select sites that were closer to rock crevices, but this was not robust across models. All other predictors had RVI values below 0.47 and confidence intervals overlapping zero (Table 6).

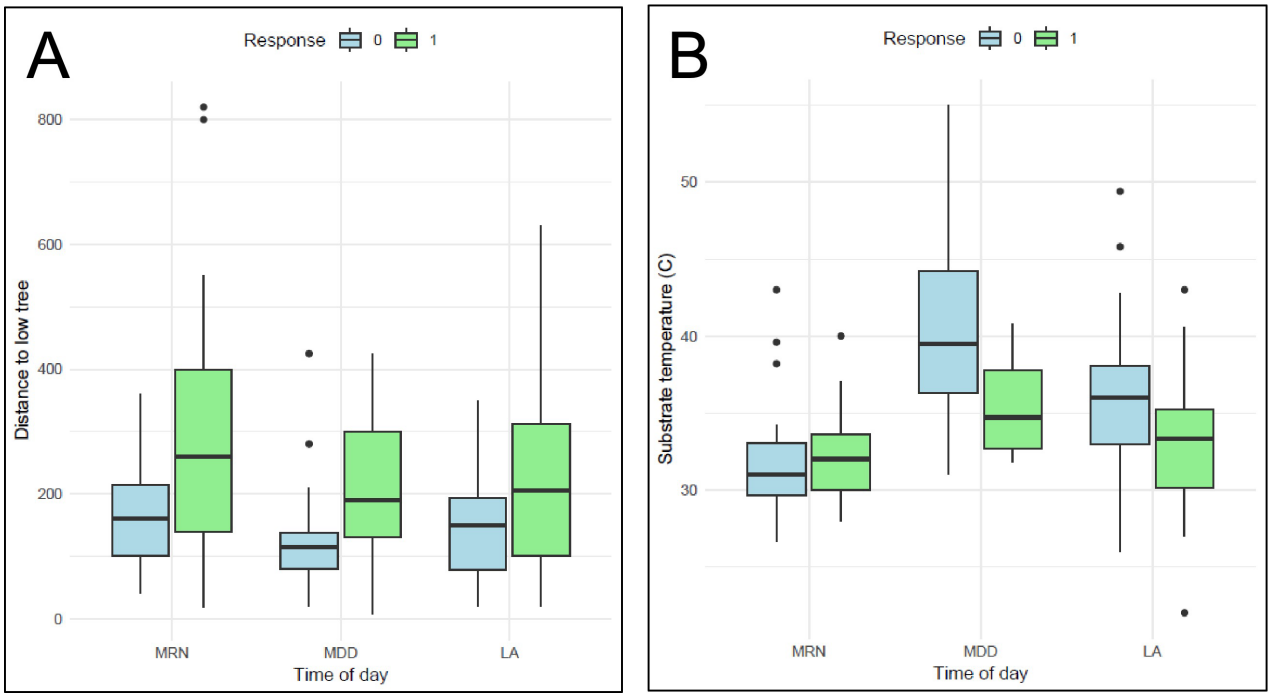

Figure 6. Habitat selection by *M. bivittatus*. Boxplots for lizard (1) and random (0) sites, by time of day in March. Midline is the median, box represents 50% of the data, whiskers indicate the range, and points are outliers. **A.** Distance to low tree – March; **B.** Substrate temperature.

Table 6. Model averaged results of conditional logistic regression models of habitat selection for March and August data for *M. bivittatus* including model averaged estimates (MA), standard errors, relative variable importance (RVI), standard errors, 95% confidence intervals, and odds ratios (OR).

Predictor	MA Estimate	Uncond SE	RVI	Lower 95CI	Upper 95CI	Odds Ratio	OR Lower CI	OR Upper CI
MARCH								
canopy	0	0	0	0	0	1	1	1
hightree	0.005	0.01	0.008	-0.015	0.025	1.005	0.985	1.025
lowtree	0.869	0.274	0.959	0.332	1.406	2.384	1.393	4.078
rockcrev	0	0	0	0	0	1	1	1
rocknocan	0	0	0	0	0	1	1	1
rockcan	0	0	0	0	0	1	1	1
detritus	0.027	0.054	0.032	-0.079	0.134	1.028	0.924	1.144
subtemp	-0.679	0.25	0.983	-1.169	-0.189	0.507	0.311	0.827
AUGUST								
canopy	0.045	0.083	0.116	-0.118	0.208	1.046	0.889	1.231
hightree	-0.013	0.026	0.044	-0.064	0.038	0.987	0.938	1.039
lowtree	0	0.001	0.004	-0.002	0.002	1	0.998	1.002
rockcrev	-0.351	0.229	0.761	-0.799	0.097	0.704	0.45	1.102
rocknocan	0.154	0.187	0.468	-0.212	0.52	1.166	0.809	1.682
rockcan	-0.008	0.019	0.058	-0.046	0.03	0.992	0.955	1.03
detritus	-0.005	0.01	0.019	-0.024	0.015	0.995	0.976	1.015
subtemp	-0.129	0.223	0.361	-0.566	0.308	0.879	0.568	1.36

Discussion

We found significant differences in habitat use and selection, as well as in spatial use, in *M. bivittatus* between the hot-wet and cool-dry periods. Generally, active lizards were mostly found on rock faces under canopy but, during the cool-dry period, frequently used rock crevices and detritus and sometimes remained inactive for several consecutive days. Lizards favored core areas within their larger activity areas and moved more during the hot-wet period than during the cool-dry period.

General activity patterns of *M. bivittatus* during our study fundamentally differed from that previously observed at the site (2015) when lizards were under less extreme weather conditions. Lizards were most frequently observed on open rock faces from morning through late afternoon in February-March and during late morning and early afternoon hours in August in 2015 (Rowe et al. 2019). During 2016, lizards used rock faces under tree canopy throughout the day during both seasons. A possible explanation for the observed differences in use of rock faces with and without canopy across years might be the differences in operative temperatures that would occur in the direct sunlight of the rock faces without canopy. Thermal quality of microhabitats can vary sharply across relatively short distances and have significant impacts on the ability of individuals to thermoregulate (Sears and Angilletta 2015; Sears et al. 2016; Llanos-Garrido et al. 2023). During both February-March and August of 2015, average operative temperatures on the open rock faces attained values within the lizards' preferred body temperature, or their T_{set} range ($T_{set\text{-}min}$ = 36 °C,

$T_{set\text{-}max}$ = 40 °C) or above $T_{set\text{-}max}$ by 4 °C or less during the midday hours (Rowe et al. 2020). Average operative temperatures of rock faces under canopy were just below or above $T_{set\text{-}min}$ by about 1 °C during the afternoon hours. Lizards could therefore attain body temperatures within the T_{set} range relatively easily by shuttling between open rock faces and rocks under tree canopy. In contrast, during March of 2016, average $T_{set\text{-}min}$ operative temperatures in direct sunlight attained values that exceeded $T_{set\text{-}max}$ by about 8 °C while average operative temperatures of rock faces under canopy were just below, or just within $T_{set\text{-}min}$. Lizards could attain body temperatures within T_{set} largely by remaining on shaded rock faces. During the coolest month studied, August 2016, operative temperatures in direct sunlight and under canopy were approximately equivalent and fell just within the T_{set} range only during the late morning and early afternoon hours (Rowe et al. 2020). It is not clear why, when operative temperatures of open rock faces and those under canopy, albeit mostly leafless canopy, were equivalent during the coolest month, lizards overwhelmingly used rock faces under canopy. During cool years, lizards could adjust body temperature through thermal conduction from rock surfaces (Meek and Luiselli 2022), even in shade. Remaining under canopy could reduce the risk of predation (Huey and Slatkin 1976; Luppi et al. 2020) by numerous avian predators or by visually oriented snakes (Valle et al. 2024).

Microlophus bivittatus at our site established activity areas that persisted throughout the duration of our monitoring periods. Within a minimum convex polygon, *M. bivittatus* did not move uniformly but rather clustered their movements within one or more core areas as indicated by AKDE-50% contours, occasionally moving back and forth to more peripheral locations. Consequently, during March and August, utilization distributions (UDs) as determined by AKDE-95% were 43.3% and 22.2% larger than their associated MCP values respectively. Utilization distribution-AKDE-50% values represented only 20.4% and 17.8% that of UD-AKDE-95% values. Why lizards sometimes moved away from a core area (here defined as UD-AKDE-50%) is unclear but would likely be related to employing active search for prey, establishing temporary prey ambush locations, or monitoring the activity of potential mates or rival conspecifics. Such a dynamic use of foraging sites within an activity area might result from temporal changes in arthropod prey availability from one location to the next or induced by competitive interactions with conspecifics for basking or foraging areas (Paterson and Blouin-Demers 2017). Lizards of both sexes and across a broad range of sizes show aggressive behavior (e.g. pushup displays, chasing, biting, wrestling; personal observations but also see Rowe et al. 2019). While incursions by individuals into the UDs of conspecifics occurred, we found very little to no overlap in UD-AKDE-50% among lizards. It seems reasonable to conclude that UD-AKDE-50% represent relatively small territories within larger activity areas. We acknowledge that not all lizards were radio-tagged at the study site and so the degree of spatial overlap among all local individuals is incomplete. Nonetheless, it would be interesting to determine whether UD-AKDE-50% areas are more vigorously defended than are UD-AKDE-95% areas.

Temporal variations in environmental conditions appeared to affect activity area size and daily movements in *M. bivittatus* possibly indicating effects of temporal variations in resource availability or abilities to thermoregulate effectively. We found that *M. bivittatus* maintained larger activity areas during a period

(March) when temperature was warm, and precipitation levels were high relative to the relatively cool and dry period several months later in August. The mean (±SE) MCP found in our study in March (500.6 ± 105.5 m^2) was nearly twice that found in August 224.8 ± 63.5 m^2). Minimum convex polygon values previously reported for *M. bivittatus* at the same study location (February–March females: 462.3 ± 168.2 m^2, males: 502.3 ± 33.6 m^2; August females: 203.9 ± 34.3 m^2, males 395.2 ± 69.3 m^2; Rowe et al. 2019) were not significantly different between seasons, nor between the sexes, but were roughly like values reported here. Peak mating activities also occur during the March period which might have also contributed to the greater movements during that time when compared to August. The significant inter-seasonal difference in MCP values in our study likely occurred at least in part because individual lizards tended to remain inactive on some days which was rarely observed in the previous study (Rowe et al. 2019). We predict that, with relatively large sample sizes (more lizards tracked) and monitoring over a relatively long period of time, inter-seasonal differences in both daily movements and activity areas could be detected in most years.

The decline in movements between hot-wet and cool-dry periods is likely related to both biotic and abiotic factors. Actively foraging reptiles, that have high energetic needs, may show reduced movement and activity area size during the dry season when compared to a wet season when resources are at their peak (Verwaijen and Van Damme 2008). For instance, Guatemalan Beaded Lizards (*Heloderma charlesbogerti*) reduced their home range sizes by about 90% during dry periods, when resources were presumably low, relative to the wet season (Ariano-Sánchez et al. 2020). Various lizard species lie along a continuum between purely sit-and-wait and active foraging modes depending on phylogenetic history, intrinsic properties of their prey, and social structure (Perry 1999; Verwaijen and Van Damme 2008). *Microlophus bivittatus* show a combination of active and sit-and-wait foraging strategies (Valle et al. 2024) and so could be expected to show at least some differences in movements between wet and dry seasons. During August 2016, the Palo Santo Trees and Jerusalem Thorn, which are by far the most common trees at the site, had few to no leaves leaving primary production to the less common evergreen shrubs, grasses, and sedges. Palo Santo fruits and leaflets of Jerusalem Thorn are at least occasional sources of food for *M. bivittatus* at the site with arthropods being consumed very frequently (Moore et al. 2017). Therefore, both primary and secondary productions would have been relatively low during August. Consequently, limits on energy access might cause energy conservation behavior through inactivity as we observed for some individual lizards during August. Reduced access to water directly, or to water in food, might stress lizards causing reduction of movements or inactivity altogether. Whether the inability to thermoregulate effectively during the cool months, such as what we observed in the August 2016 period (Rowe et al. 2020), affects activity and movements in an equatorial species of lizard remains to be determined.

Habitat selection by *M. bivittatus* appears to be related to both structural and thermal microsite characteristics and varies in response to the extreme seasonal variation in environmental conditions and resource availability that our lizards experience. The study site at Frigatebird Hill is potentially thermally heterogeneous given its irregular lava rock topography and areas of both open and closed canopy. Therefore, opportunities for effective thermoregulation

could be expected (Sears and Angilletta 2015; Sears at al. 2016). Physiological or ecological limitations on activity and movement, however, appeared to dictate spatial ecology at our site. Lizards' adjustment of microhabitat use, from exposed rock faces and trees during the hot-wet season to refugia during the cool-dry season, further reflect the probable thermal constraints and reduced foraging opportunities during the extreme cool-dry season (August) of 2016. As is reflected in their reduced movement during August, avoiding open rock faces and remaining closer to rock crevices or under vegetation could be a response to increased predation risk and a potential inability to rapidly flee (Vanhooydonck and Van Damme 2003). Decreased prey escape speeds can result in increased predation rates (as seen in coral reef fish; Allan et al. 2015). Water availability may also influence habitat selection, causing lizards to reduce basking and seek sheltering microhabitats during times of water scarcity (Crowley 1987; Chabaud et al. 2023). Poorly hydrated animals may seek lower body temperatures, perhaps in shaded microhabitats (Sears and Angilletta 2015). Our results indicate that during the cool-dry season, when resources, water, and ultimately energy acquisition are limited, lizards may rely more on structural refuges that buffer against heat, water loss and predation risk, with a consistent preference for cooler microrefugia throughout the day.

Conclusions

Our observed temporal variations in spatial ecology of *M. bivittatus* between hot-wet and cool-dry conditions are consistent with resource and thermal influences that would be imposed during each period. We note that the monitoring durations of our study are relatively short and offer only snapshots into the spatial ecology of a relatively small number of individual lizards. While we are confident that we identified an important temporal effect, we were unable to evaluate the dynamics of changes in space use. Year-long or even multi-year investigations into variations in food and water availability, thermal constraints on activity, changes in vulnerability to predation, and changes in social environments that result from immigration and emigration patterns, as well as how various combinations of factors affect spatial ecology would seem appropriate.

Acknowledgments

We thank J.P. Muñoz and S. Sotamba, of the Galápagos Science Center, Isla San Cristóbal, for their assistance with permitting and logistics. We conducted our research under a permit (PC-13-16) issued to Carlos Valle and under Grand Valley State University IACUC permit no. 16-06-A.

References

Allan BJM, Domenici P, Munday PL, McCormick MI (2015) Feeling the heat: the effect of acute temperature changes on predator-prey interactions in coral reef fish. Conservation Physiology 3(1): cov011. https://doi.org/10.1093/conphys/cov011

Ariano-Sánchez D, Mortensen RM, Reinhardt S, Rosell F (2020) Escaping drought: Seasonality effects on home range, movement patterns and habitat selection of the Gua-

temalan Beaded Lizard. Global Ecology and Conservation 23: e01178. https://doi.org/10.1016/j.gecco.2020.e01178

Bakken GS, Gates DM (1975) Heat transfer analysis of animals: some implications for field ecology, physiology, and evolution. In: Gates DM, Schmerl RB (Eds) Perspectives of Biophysical Ecology. Springer Press, Berlin, Heidelberg, New York, 255–290. https://doi.org/10.1007/978-3-642-87810-7_16

Bakken GS, Santee WR, Erskine DJ (1985) Operative and standard operative temperature: tools for thermal energetics studies. American Zoologist 25(5): 933–943. https://doi.org/10.1093/icb/25.4.933

Benavides E, Baum R, Snell HM, Snell HL, Sites Jr JW (2009) Island biogeography of Galápagos lava lizards (Tropiduridae: *Microlophus*): species diversity and colonization of the archipelago. Evolution 63(6): 1606–1626. https://doi.org/10.1111/j.1558-5646.2009.00617.x

Burke RL, Figueras M, Calle PP (2015) *Microlophus bivittatus* (Lava Lizard). Predation. Herpetological Review 46(4): e632.

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: A practical information-theoretic approach. Springer New York, New York. https://doi.org/10.1177/0049124104268644

Burt WH (1943) Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24(3): 346–352. https://doi.org/10.2307/1374834

Calabrese JM, Fleming CH, Gurarie E (2016) ctmm: An R package for analyzing animal relocation data as a continuous-time stochastic process. Methods in Ecology and Evolution 7(9): 1124–1132. https://doi.org/10.1111/2041-210X.12559

Carrión PL, Valle CA (2018) The diet of introduced cats on San Cristobal Island, Galapagos: Cat feces as a proxy for cat predation. Mammalian Biology 90: 74–77. https://doi.org/10.1016/j.mambio.2018.02.004

Chabaud C, Lourdais O, Decencière B, Le Galliard J-F (2023) Behavioural response to predation risks depends on experimental change in dehydration state in a lizard. Behavioral Ecology and Sociobiology 77(7): 1–90. https://doi.org/10.1007/s00265-023-03362-2

Christian KA, Tracy CR, Porter WP (1983) Seasonal shifts in body temperature and use of microhabitats by Galápagos land iguanas (*Conolophus pallidus*). Ecology 64(3): 463–468. https://doi.org/10.2307/1939965

Clark DL, Macedonia JM, Rowe JW, Stuart MA, Kemp DJ, Ord TJ (2015) Evolution and discrimination of species-typical displays in Galápagos lava lizards: Comparative analyses of signalers and robot playbacks to receivers. Animal Behaviour 109: 33–34. https://doi.org/10.1016/j.anbehav.2015.08.002

Clark DL, Macedonia JM, Rowe JW, Kamp K, Valle CA (2017) Responses of Galápagos lava lizards (*Microlophus bivittatus*) to manipulation of female nuptial coloration on lizard robots. Herpetologica 72(4): 47–54. https://doi.org/10.1655/Herpetologica-D-16-00056

Clark DL, Macedonia JM, Neyer EE, Mish AME, Rowe JW, Valle CA (2023) Display responses of Galápagos lava lizards (*Microlophus bivittatus*) to manipulation of male shoulder epaulets on conspecific-mimicking robots. Herpetologica 79(1): 37–47. https://doi.org/10.1655/Herpetologica-D-22-00026

Clement VF, Roedder D (2021) Playing favourites-a review and discussion on the allocation of vertebrate orders and foci in home range and habitat selection studies. North-Western Journal of Zoology 17(1): 134–148. http://biozoojournals.ro/nwjz/index.html

Crowley SR (1987) The effect of desiccation upon the preferred body temperature and activity level of the lizard *Sceloporus undulatus*. Copeia 1987: 25–32. https://doi.org/10.2307/1446033

De Solla SR, Bonduriansky R, Brooks RJ (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. Journal of Animal Ecology 68(2): 221–234. https://doi.org/10.1046/j.1365-2656.1999.00279.x

Dunham AE, Grant BW, Overall KL (1989) Interfaces between biophysical and physiological ecology and the population biology of terrestrial vertebrate ectotherms. Physiological Zoology 62(2): 335–355. https://doi.org/10.1086/physzool.62.2.30156174

Gitzen RA, Millspaugh JJ, Kernohan BJ (2006) Bandwidth selection for fixed-kernel analysis of animal utilization distributions. Journal of Wildlife Management 70(5): 1334–1344. 10.2193/0022-541X(2006)70[1334:BSFFAO]2.0.CO;2

Hervías-Parejo S, Heleno R, Rumeu B, Guzman B, Vargas P, Olesen JM, Traveset A, Vera C, Benevides E, Nogales M (2019) Small size does not restrain frugivory and seed dispersal across the evolutionary radiation of Galápagos lava lizards. Current Zoology 65(4): 353–361. https://doi.org/10.1093/cz/zoy066

Huey RB (1991) Physiological consequences of habitat selection. The American Naturalist 137: S91–S115. https://doi.org/10.1086/285141

Huey RB, Slatkin M (1976) Cost and benefits of lizard thermoregulation. The Quarterly Review of Biology 51(3): 363–384. https://doi.org/10.1086/409470

Fleming CH, Calabrese JM (2017) A new kernel density estimator for accurate home-range and species-range area estimation. Methods in Ecology and Evolution 8(5): 571–579. https://doi.org/10.1111/2041-210X.12673

Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM (2015) Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology 96(5): 1182–1188. https://doi.org/10.1890/14-2010.1

Fox J, Monette G (1992) Generalized collinearity diagnostics. Journal of the American Statistical Association 87(1992): 178–183. https://doi.org/10.1080/01621459.1992.10475190

Jordan MA, Snell HL (2002) Life history trade-offs and phenotypic plasticity in the reproduction of Galápagos lava lizards (*Microlophus delanonis*). Oecologia 130: 44–52. https://doi.org/10.1007/s004420100776

Jordan MA, Hollis JL, Stone PA, Snell HL (2008) Habitat as a source of intrapopulational variation of ornament size in Galápagos lava lizards (*Microlophus albemarlensis* complex). Amphibia-Reptilia 29(2): 278–283. https://doi.org/10.1163/156853808784125081

Knapp CR, Abarca JG (2009) Effects of radiotransmitter burdening on locomotor ability and survival of iguana hatchlings. Herpetologica 65(4): 363–372. https://doi.org/10.1655/09-003.1

Lewbart GA, Valle CA, Munoz-Perez JP (2017) *Microlophus indefatigabilis*: Diet. Herpetological Review 48: 851–852.

Llanos-Garrido A, Santos T, Díaz JA (2023) Negative effects of the spatial clumping of thermal resources on lizard thermoregulation in a fragmented habitat. Journal of Thermal Biology 115: e103604. https://doi.org/10.1016/j.jtherbio.2023.103604

Luppi M, Gentilli A, Bogliani G (2020) Microhabitat selection of the Western green lizard *Lacerta bilineata*. Natural History Sciences 7(2): 3–10. https://doi.org/10.4081/nhs.2020.451

Mancero EJ, Valle CA, Rowe JW, Moore JA, Clark DL (2022) Sexual selection in San Cristóbal lava lizards (*Microlophus bivittatus*): A test of male body size using lizard robots. Herpetologica 78(2): 93–101. https://doi.org/10.1655/Herpetologica-D-20-00058

Meek R, Luiselli L (2022) Living in patchy habitats: substrate selection by basking sympatric lizards in contrasted anthropogenic habitats in western France. Russian Journal of Herpetology 29(4): 227–236. https://doi.org/10.30906/1026-2296-2022-29-4-227-236

Mohr CO (1947) Table of equivalent populations of North American small mammals. American Midland Naturalist 37: 223–249. https://doi.org/10.2307/2421652

Moore JA, Rowe JW, Wessels D, Plivelich M, Valle C (2017) *Microlophus bivittatus* (San Cristóbal lava lizard). Diet. Herpetological Review 48: e851.

Morellet N, Bonenfant C, Börger L, Ossi F, Cagnacci F, Heurich M, Kjellander P, Linnell JD, Nicoloso S, Sustr P, Urbano F (2013) Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. Journal of Animal Ecology 82(6): 1326–1339. https://doi.org/10.1111/1365-2656.12105

Moreno-Buitrón IJ, Boada-Viteri E, Guayasamin JM, Guerra-Correa ES, Becdach-Mesia I, Betancourt-Cargua L, Román AC, Ramón-Cabrera GK (2024) Aliens on the menu: High prevalence of introduced ants in the diet of Galápagos lava lizards, *Microlophus* spp. Biological Invasions 26(11): 3929–3945. https://doi.org/10.1007/s10530-024-03421-3

Northrup JM, Vander Wal E, Bonar M, Fieberg J, Laforge MP, Leclerc M, Prokopenko CM, Gerber BD (2022) Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. Ecological Applications 32(1): e02470. https://doi.org/10.1002/eap.2470

Ortiz-Catedral L, Christian E, Skirrow MJ, Rueda D, Sevilla C, Kirtana K, Reyes EM, Daltry JC (2019) Diet of six species of Galapagos terrestrial snakes (*Pseudalsophis* spp.) inferred from fecal samples. Herpetology Notes 12: 701–704.

Paterson JE, Blouin-Demers G (2017) Do ectotherms partition thermal resources? We still do not know. Oecologia 183(2): 337–345. https://doi.org/10.1007/s00442-016-3762-7

Perry G (1999) The evolution of search modes: ecological versus phylogenetic perspectives. American Naturalist 153(1): 98–109. https://doi.org/10.1086/303145

Powell RA (2000) Animal home ranges and territories and home range estimators. In: Pearl MC (Ed.) Research Techniques in Animal Ecology. Columbia University Press, New York, Chichester, West Sussex, 65–110. https://doi.org/10.1093/9780191949142.003.0002

R Core Team (2025) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://doi.org/10.32614/r.manuals

Rowe JW, Martin CE, Clark DL, Valle-Castillo C, Vintemilla C (2019) Habitat use and spatial ecology of three lizards of the genus *Microlophus* from Ecuador. Herpetological Review 50(1): 43–51.

Rowe JW, Martin CE, Clark DL, Valle-Castillo C (2020) Diel and seasonal variations in the thermal biology of San Cristobal lava lizards (*Microlophus bivittatus*). Journal of Thermal Biology 88: e102518. https://doi.org/10.1016/j.jtherbio.2020.102518

Rusch TW, Sears MW, Angilletta MJ (2023) The structure of the thermal landscape determined behavioural and physiological responses to simulated predation risk. Functional Ecology 37(11). https://doi.org/10.1111/1365-2435.14429

Sears MW, Angilletta Jr MJ (2015) Costs and benefits of thermoregulation revisited: Both the heterogeneity and spatial structure of temperature drive energetic costs. The American Naturalist 185(4): E94–E102. https://doi.org/10.1086/680008

Sears MW, Angilletta Jr MJ, Schuler MS, Borchert J, Dilliplane KF, Stegman M, Rusch TW, Mitchell WA (2016) Configuration of the thermal landscape determines thermoregu-

latory performance of ectotherms. Proceedings of the National Academy of Sciences 113(38): 10595–10600. https://doi.org/10.1073/pnas.1604824113

Shine R, Kearney M (2001) Field studies of reptile thermoregulation: how well do physical models predict operative temperature? Functional Ecology 15(2): 282–288. https://www.jstor.org/stable/2656513

Silva I, Fleming CH, Noonan MJ, Alston J, Folta C, Fagan WF, Calabrese JM (2022) Autocorrelation-informed home range estimation: A review and practical guide. Methods in Ecology and Evolution 13(3): 534–544. https://doi.org/10.1111/2041-210X.13786

Stebbins RC, Lowenstein JM, Cohen NW (1967) A field study of the lava lizard (*Tropidurus albemarlensis*) in the Galapagos Islands. Ecology 48(5): 839–851. https://doi.org/10.2307/1933742

Stone PA, Baird TA (2002) Estimating lizard home range: the rose model revisited. Journal of Herpetology 36(3): 427–436. https://doi.org/10.2307/1566187

Tanner D, Perry J (2007) Road effects on abundance and fitness of Galápagos lava lizards (*Microlophus albemarlensis*). Journal of Environmental Management 85(2): 270–278. https://doi.org/10.1016/j.jenvman.2006.08.022

Torres-Carvajal O (2024) A new species of lava lizard (Iguanidae: Tropidurinae: *Microlophus*) from the Galápagos. Zootaxa 5428(1): 58–74. https://doi.org/10.11646/zootaxa.5428.1.2

Toyama KS, Boccia CK (2021) Sexual size dimorphism and life history traits in an island-mainland system: an overview of the lizard genus *Microlophus*. Amphibia-Reptilia 42(4): 511–517. https://doi.org/10.1163/15685381-bja10065

Tracy CR, Christian KA (1986) Ecological relations among space, time, and thermal niche axes. Ecology 67(3): 609–615. https://doi.org/10.2307/1937684

Trueman M, d'Ozouville N (2010) Characterizing the Galapagos terrestrial climate in the face of global climate change. Galapagos Research 67(26): 26–37.

Valle CA, Zapata MB, Basso EAV, Quiñonez F, Mena CF, Rowe JW (2024) Predation of the San Cristóbal lava lizard (*Microlophus bivittatus*), Peters, 1871. Herpetology Notes 17: 9–12.

Van Denburgh J, Slevin JR (1913) Expedition of the California Academy of Sciences to the Galapagos Islands, 1905–1906. IX. The Galapagoan lizards of the genus *Tropidurus* with notes on iguanas of the genera *Conolophus* and *Amblyrhynchus*. Proceedings of the California Academy of Sciences, Series 4, 2: 133–202.

Vanhooydonck B, Van Damme R (2003) Relationships between locomotor performance, microhabitat use and antipredator behaviour in lacertid lizards. Functional Ecology 17(2): 160–169. https://doi.org/10.1046/j.1365-2435.2003.00716.x

Verwaijen D, Van Damme R (2008) Foraging mode and locomotor capacities in Lacertidae. Amphibia-Reptilia 29(2): 197–206. https://doi.org/10.1163/156853808784124965

Volampeno MSN, Masters JC, Downs CT (2011) Home range size in the blue-eyed black lemur (*Eulemur flavifrons*): A comparison between dry and wet seasons. Mammalian Biology 76: 157–164. https://doi.org/10.1016/j.mambio.2010.04.005

Webber QM, Albery GF, Farine DR, Pinter-Wollman N, Sharma N, Spiegel O, Vander Wal E, Manlove K (2023) Behavioural ecology at the spatial–social interface. Biological Reviews 98(3): 868–886. https://doi.org/10.1111/brv.12934

Wilson RR, Hooten MB, Strobel BN, Shivik JA (2010) Accounting for individuals, uncertainty, and multiscale clustering in core area estimation. Journal of Wildlife Management 74(6): 1343–1352. https://doi.org/10.1111/j.1937-2817.2010.tb01256.x

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

Funding

Funding was provided by the Alma College Biology Department, Student Research Endowment at Alma College, and a grant to Alma College from the Dow Foundation, and Grand Valley State University.

Author contributions

John Rowe was the lead investigator along with Jennifer Moore. Morgan Fonely conducted spatial analyses and David Clark and Carlos Valle contributed to logistics and manuscript review.

Author ORCIDs

J.W. Rowe https://orcid.org/0000-0002-3981-5042
M.R. Fonley https://orcid.org/0000-0003-3387-0240
C.A. Valle https://orcid.org/0000-0002-5523-634X

Data availability

All of the data that support the findings of this study are available in the main text