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DAILY ACTIVITY PATTERNS AND MICROHABITAT USE OF A HELIOTHERMIC LIZARD, *AMEIVA EXSUL* (SQUAMATA: TEIIDAE) IN PUERTO RICO

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Abstract. Although *Ameiva exsul* is among the most common species of lizard found throughout the Puerto Rican Bank, studies examining the thermal ecology of the taxon remain scarce. In order to better understand the daily activity cycle and thermoregulatory behavior of *A. exsul,* daily activity and microhabitat data were analyzed along with thermal data including weather, air temperature, and relative humidity. A relative significant relationship was found between number of encounters and time of day, month, or weather. However, significantly more individuals were encountered active on the ground during the morning hours, whereas at night more were found sleeping under various substrates. Although no significant relationship between microhabitat, activity, and weather was detected, more individuals were encountered sitting under substrate during clear and cloudy/rainy conditions, whereas during partly cloudy weather lizards were more active. Significantly more individuals were encountered during warmer temperatures with less humidity. There was no significant relationship between air temperature, relative humidity, microhabitat use, and activity. However, there was a significant relationship between temperature and the number of individuals active on the ground. Future studies are needed that examine the physiological ecology of the species more closely, which include other potentially relevant environmental variables such as body temperature and wind velocity. This will provide a more comprehensive analysis on the daily activity patterns and thermal ecology of the species, which may in turn be applicable to other congeners distributed throughout similar environments.

Keywords. Behavior, Ectothermy, Temperature, Thermoregulation, West Indies.

Introduction

Ameiva exsul is a large, abundant, and widespread teiid lizard found throughout Puerto Rico and most of the Virgin Islands, and has been observed at elevations as high as 366 m (Rivero, 1978; Lewis and Saliva, 1987). Along with most members of its family, *A. exsul* is an actively foraging, predominantly diurnal lizard that consumes primarily arthropods (Schwartz and Henderson, 1991; Schell *et al.,* 1993), although *Ameiva* are known to consume a wide variety of prey available to them (Rivero, 1978; Sproston *et al.,* 1999). *Ameiva* also generally tend to be most active during the late morning/early afternoon hours when temperatures are the highest, whereas during cloudy/cooler conditions they seek refuge (Rivero, 1978; Morgan, 1988; Rivera-Vélez and Lewis, 1994; White *et al.,* 2002; Nicholson *et al.,* 2005). Average body temperatures (T_b) for individuals in the genus range from 36°C to 41°C (Morgan, 1988; Sproston *et al.,* 1999). *Ameiva exsul,* like most of its congeners (Schell *et al.,* 1993; White *et al.,* 2002), maintains an internal body temperature significantly higher than its surrounding environment, with critical upper and lower T_b threshold values of approximately 39.5°C and 32.5°C respectively (Rivera-Vélez and Lewis, 1994).

Although *A. exsul* is abundant throughout the entire island of Puerto Rico and surrounding Vieques and Culebra (Rivero, 1978), studies examining the basking behavior and daily activity patterns of this species are limited. Nicholson *et al.,* (2005) found significant correlations between air temperature and relative humidity versus abundance in *A. exsul*. However, they did not incorporate additional potentially significant variables in their analysis or investigate the interactions among thermal variables. For example, does weather condition influence abundance and activity? Is seasonal variation present? How do ambient conditions influence microhabitat selection? What interactions among variables best explain daily activity?

Herein I provide further data pertaining to the diel cycle of *A. exsul*. More specifically, I examine diel variation in activity patterns and microhabitat preference of the species over the course of four months in northeastern Puerto Rico and relate behavior to local environmental conditions.

Materials and Methods

Sampling

The study site is located in the Río Grande region of northeastern Puerto Rico (18. 2050°N, 65. 4845°W) directly adjacent to the Caribbean

National Forest/Luquillo Experimental Forest (CNF/LEF) (Fig. 1). Annual rainfall in the region is approximately 2640-3524 mm/yr depending on elevation (Garcia-Martino *et al.,* 1996), with the wet season lasting between May and October (Larsen, 2000). The selected study site lies at an elevation of approximately 135 m, with annual rainfall amounts falling at the lower end of the spectrum (Garcia-Martino *et al.,* 1996). Since *A. exsul* is more abundant in coastal and/or disturbed locations (Rivero, 1978; Lewis and Saliva, 1987), the study was conducted in anthropogenically disturbed/pastureland macrohabitat instead of primary rainforest where relative abundance was less (*pers. obs.*). Livestock (sheep) also inhabit and graze throughout the study site, keeping the amount of vegetation minimal.

A 50 × 25 m parcel was constructed and sampled three times a week for *A. exsul.* Due to the potentially disruptive sampling scheme, the plot was not sampled more than once per day or on consecutive days. However, it has been suggested that species habituated to anthropogenic activity, like *Ameiva,* are less likely to alter their behavior in response to human observation (Schell *et al.,* 1993). On each sampling day only one time interval was investigated, either during the morning hours (approximately 0800 h-1200 h), the afternoon (approximately 1200 h-1600 h), or at night (2000-2400 h). The plot was sampled by systematically walking in straight lines up and down the plot until the entire area was sampled, disturbing vegetation and turning over substrate such as rocks and concrete blocks when encountered. Data recorded at each encounter included date, time, substrate, and activity. In addition, each day before sampling, air temperature (T_a), relative humidity (RH), and weather conditions were recorded approximately 1 m off the ground. Sampling commenced 1 March 2007 and lasted until 26 June 2007, with equal sampling of each time interval (1-0 h). No observable difference in T_a and RH were recorded before and after each day of sampling. Thus, values recorded before sampling were used in all statistical analyses.

Individuals were encountered on one of four substrates including ledge/rock, ground, grass/shrub, or under object, generally rocks or concrete blocks. Vegetation (*i.e.* potential cover) was fairly limited throughout the sample plot. Additionally, activity was classified as either active, basking, sitting, or sleeping. Lizards were marked as basking if they were stationary in direct sunlight when encountered (Schell *et al.,* 1993) and marked as sleeping if stationary with eyes shut at time of encounter. No

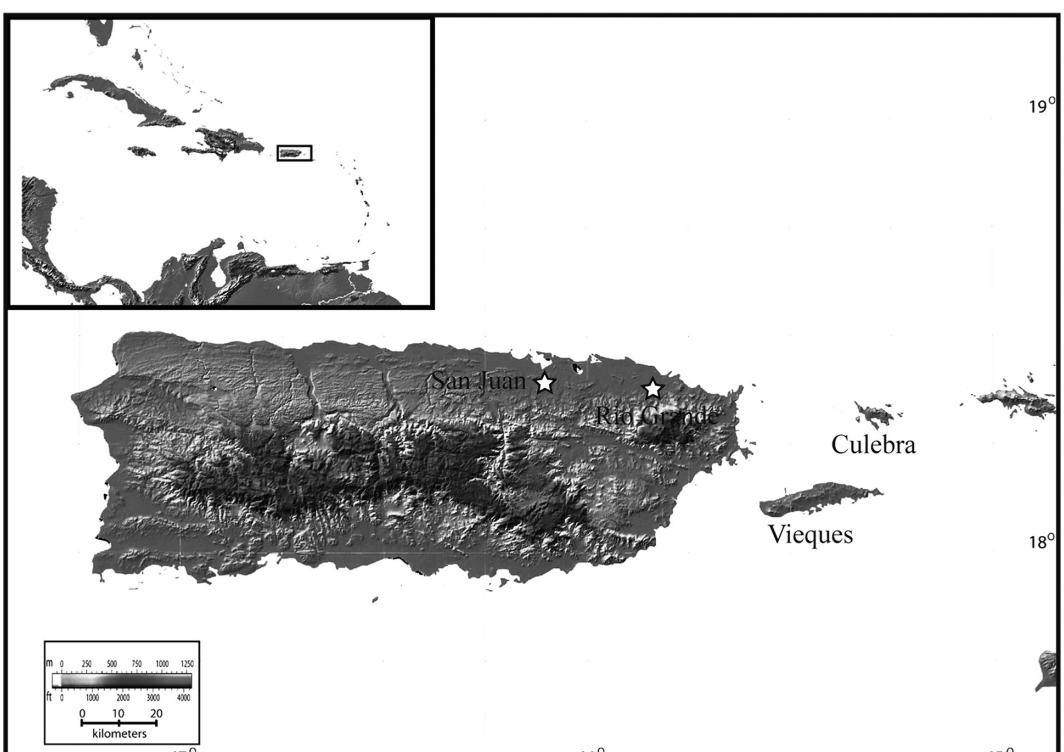

FIGURE 1. Map of the West Indies focusing specifically on the study area in the Río Grande region of northeastern Puerto Rico.

animals were encountered basking with their eyes closed. Weather conditions at the time of sampling were classified as clear, partly cloudy, mostly cloudy, overcast, or overcast/rain. Weather was scored as mostly cloudy during days with approximately 75% or greater cloud-cover.

Data Analysis

Due to the potential interaction between measured variables, a combination of univariate and multivariate statistics were used to investigate the relationships between environmental conditions, microhabitat use, and activity. Analysis of variance (ANOVA) was used to examine seasonal variation in both air temperature and percent humidity. Factorial ANOVA was used to test differences in *A. exsul* encounters due to time interval (morning, afternoon, night), month, and weather. Spearman Rank Correlations were used to examine relationships between air temperature and relative humidity versus number of individuals encountered for each time interval and for all intervals combined. Bonferroni corrections were used for all correlations to account for multiple tests. Factorial regression analysis was then performed to determine if a temperature × humidity interaction significantly influenced number of encounters.

Microhabitat use and activity patterns were analyzed using both factorial regression analysis and multivariate analysis of variance (MANOVA). Factorial regressions were used to determine if there was a significant relationship between air temperature and humidity versus activity and microhabitat use. MANOVA was then used to determine if there were significant relationships between activity and time of day, activity and weather, activity and month, substrate and time of day, and substrate and weather. All statistical analyses were performed using Statistica v.8.0 (StatSoft Inc., 2008) or SAS v.9.0 (SAS Institute Inc., 2002) with an alpha = 0.05.

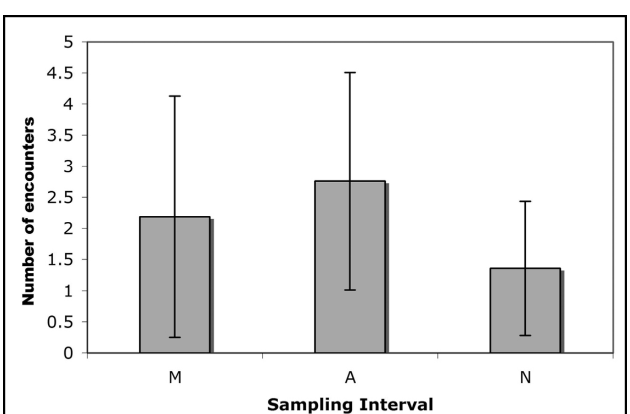

Figure 2. Diel variation in the abundance of *A. exsul.* Data include all sampling days for each time period. Each bar represents the mean (± SE) number of encounters for the corresponding sampling period. M = Morning (0800 h-1200 h); A = Afternoon (1200 h-1600 h); N = Night (2000-2400 h).

Results

A total of 101 individuals were recorded throughout the study period. T_a and RH values ranged from 20°C to 32.3°C and 52% to 90% respectively. In addition, there was a significant difference in T_a throughout the four study months, with significantly higher temperatures in May and June versus March and April ($F_{3,41} = 2.87$; $P = 0.048$). Relative Humidity values also differed significantly between months, with significantly higher values in March and April versus May and June ($F_{2,28} = 3.53$; $P = 0.043$).

There was no significant diel ($F_{2,44} = 2.78$; $P = 0.073$) or monthly difference ($F_{3,43} = 0.96$; $P = 0.421$) in *A. exsul* encounters throughout the entire study period. However, encounters were slightly greater during afternoon sampling periods (Fig. 2). Furthermore, there was no significant influence of weather on individual encounters ($F_{4,42} = 1.08$; $P = 0.376$) and no significant time × month × weather interaction versus number of encounters ($F_{1,17} = 0.431$; $P = 0.520$). Significant, yet opposite correlations were found between both T_a and RH versus abundance when data were pooled for all three sampling intervals. Conversely, when data were partitioned by sampling interval, mixed patterns were recovered including a positive, although insignificant correlation between RH and abundance during the night samples (Table 1). A significant T_a × RH interaction on abundance was also found ($R^2 = 0.518$; $F_{1,27} = 6.916$; $P = 0.014$).

There was no significant diel variation in substrate use in *A. exsul* (Wilks = 0.707; $P = 0.065$). However, significantly more individuals were encountered on grass ($F_{2,44} = 3.578$; $P = 0.036$) and the ground ($F_{2,44} = 5.005$; $P = 0.034$) during morning and afternoon periods versus night samples (Fig. 3A). Further, weather conditions (Wilks = 0.640; $P = 0.294$) and T_a and RH had no significant effect on microhabitat preference (Table 2). However, there was a significant relationship between the number of lizards encountered on the ground and T_a ($F_{1,27} = 6.820$; $P = 0.014$) as well as a T_a × RH interaction ($F_{1,27} = 5.721$; $P = 0.020$).

Table 1. Spearman Rank Correlations (r_s) showing relationships between thermal variables and abundance of *A. exsul*. Abbreviations are as follows: M = Morning (0800 h-1200 h); A = Afternoon (1200 h-1600 h); N = Night (2000-2400 h); Comb. = All sampling intervals combined; T_a = Air Temperature; RH = Relative Humidity. *Bonferroni corrected.

Interval	Condition	r_s	P*
M	T_a × Ind.	0.571	0.021
A	T_a × Ind.	0.304	0.253
N	T_a × Ind.	0.391	0.187
Comb.	T_a × Ind.	0.478	0.001
M	RH × Ind.	-0.791	0.007
A	RH × Ind.	-0.64	0.034
N	RH × Ind.	0.362	0.305
Comb.	RH × Ind.	-0.6	0.001

Table 2. Factorial regression results showing the relationship between air temperature and relative humidity versus microhabitat use of *A. exsul*. Note that the *P*-value for temperature was bordering significance (0.058).

	Test	Value	*F*	effect df	error df	*P*
intercept	Wilks	0.791	1.583	4	24	0.211
temp	Wilks	0.693	2.653	4	24	0.058
humid	Wilks	0.803	1.475	4	24	0.241
temp × hum	Wilks	0.727	2.254	4	24	0.093

Table 3. Factorial regression results showing the relationship between air temperature and relative humidity versus activity patterns of *A. exsul*.

	Test	Value	*F*	effect df	error df	*P*
intercept	Wilks	0.844	1.11	4	24	0.375
temp	Wilks	0.743	2.078	4	24	0.115
humid	Wilks	0.841	1.135	4	24	0.364
temp × hum	Wilks	0.763	1.862	4	24	0.15

There was significant diel variation in activity (Wilks = 0.454; $P < 0.001$) with more lizards active during the morning and afternoon ($F_{2,44} = 5.233$; $P = 0.016$), sitting during the afternoon ($F_{2,44} = 5.605$; $P = 0.007$), and sleeping at night ($F_{2,44} = 14.145$; $P < 0.001$; Fig. 3B). No significant relationship was found between either weather condition (Wilks = 0.537; $P = 0.922$) or sampling month (Wilks = 0.686; $P = 0.200$) versus activity. Further, no significant relationship was found

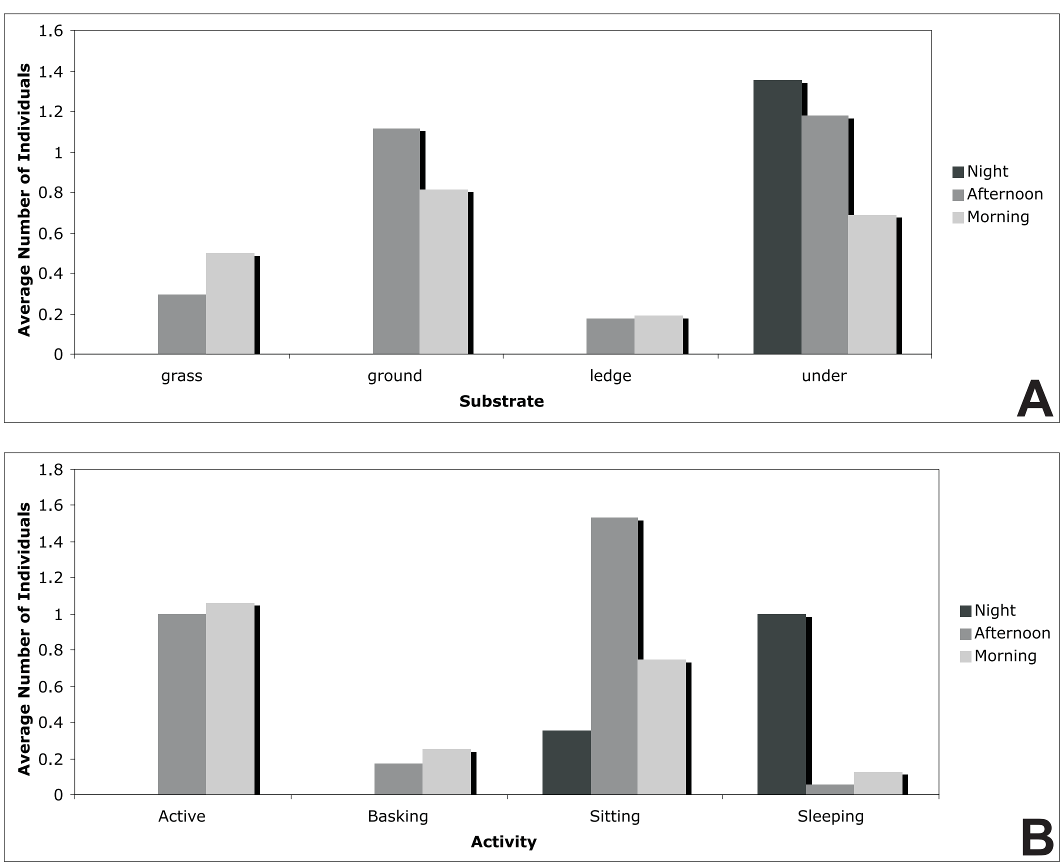

Figure 3. A) Diel variation in microhabitat use for all *A. exsul* encounters averaged over all sampling dates. B) Diel variation in activity for all *A. exsul* encounters averaged over all sampling dates.

between T_a and RH versus activity (Table 3), although significantly more individuals were active at higher temperatures ($F_{1,27} = 3.950$; $P = 0.038$).

Discussion

Air Temperature and Relative Humidity

In concordance with previous studies (Nicholson *et al.,* 2005), both T_a and RH were shown to correlate with the presence of *A. exsul,* with more encounters during periods of warmer T_a with less RH (Table 1). However, patterns were significantly different when the data were partitioned by sampling interval, which was not investigated in Nicholson *et al.* (2005). Nicholson *et al.* (2005) also did not correlate temperature and humidity with microhabitat use and activity patterns. Although the multivariate analyses presented here show no significant relationships between T_a and RH and microhabitat preference and activity, significantly more lizards were encountered active on the ground during warmer temperatures. Rivera-Vélez and Lewis (1994) conducted a similar study examining the thermal ecology of *A. exsul,* utilizing a more controlled, manipulation-based approach. They found the species to exhibit a lower variance surrounding the critical thermal maximum value versus the critical thermal minimum. In addition, they found *A. exsul* spent significantly less time thermoregulating in sunlight versus foraging in shade, and attributed the low population numbers of the species at higher elevations (Rivero, 1978) to the inability to maintain an adequate body temperature while foraging in the shade. Similar results were found with congeneric *A. chrysolaema* and *A. festiva* (Schell *et al.,* 1993). Thus, previous studies and the data presented here indicate that the macro- and microgeographic distribution and activity of *A. exsul* and its congeners may be influenced in part by temperature and humidity constraints and that the influence of these two variables on activity patterns might fluctuate throughout the course of the day.

Diel Variation

Although no significant diel differences in *A. exsul* encounters and microhabitat usage were detected, there were significant diel differences in activity, with more individuals found active during the morning, sitting during the afternoon, and sleeping night (Fig. 3B). Further, more individuals were encountered on grass and the ground during morning and afternoon samples. Several researchers have also quantified similar spatiotemporal patterns in lizard activity including *Ameiva* (Heatwole *et al.,* 1969; Rivero, 1978; Lewis and Saliva, 1987; Schell *et al.,* 1993; Rivera-Vélez and Lewis, 1994; Nicholson *et al.,* 2005). The results of this study are concordant with those of previous authors who found *Ameiva* to be more active during the late morning/early afternoon hours. Conversely, Schell *et al.* (1993) found the activity of *A. chrysolaema* restricted during the late morning to early afternoon, coincident with daily maximum temperatures. I suggest *A. exsul* was found to be more active during the morning samples for two reasons. First, individuals may be actively searching for means to obtain their preferred activity temperatures during these hours and second, lizards that have already behaviorally thermoregulated and equilibrated to ambient temperatures may be able to commence activity sooner rather than later due to the increased metabolic rates associated with warmer body temperatures. A third hypothesis, however, would suggest that animals encountered during afternoon samples curtailed their activity to prevent their critical thermal maximum from being reached (Schell *et al.,* 1993).

The fact that more individuals were encountered sitting during the afternoon may be the result of extreme temperatures during this time, although Nicholson *et al.* (2005) found *A. exsul* to be most active during the warmest period of the day. Conversely, Rivera-Vélez and Lewis (1994) found *A. exsul* to seek refuge at a T_b above 39.5°C. Unfortunately, discussions with comparative data cannot be made since T_b was not investigated in the present study. However, these data suggest that during periods of higher temperatures (afternoon samples) more individuals were seeking shelter from direct solar radiation to prevent their critical thermal maximum from being reached.

Weather Influences

No significant relationship was found between weather condition and *A. exsul* encounters, activity, or microhabitat use, although activity seemed to be reduced during both clear and rainy periods. As stated above, more individuals were encountered while sitting during the afternoon, when temperatures were highest. The fact that more lizards were found sitting under substrates during clear conditions may due to similar factors (Rivera-Vélez and Lewis, 1994). More encounters under substrates during cloudy/rainy conditions may be due to the fact that *Ameiva* are generally more active and abundant during times of warmer T_a with some degree of solar radiation (Rivero, 1978; Morgan, 1988). Hillman (1969) found species-specific differences in solar radiation preference for three sympatric species of *Ameiva* in Costa Rica, with *A. quadrilineata* preferring sunnier and warmer habitats than both *A. festiva* and *A. leptophrys.* Similar differences in thermal preferences were also found between other congeners (Sproston *et al.,* 1999) as well as West-Indian species of *Anolis* (Heatwole *et al.,* 1969). Future studies are needed to quantify and compare the thermal preferences of *A. exsul* to other congeners including *A. wetmorei,* whose distribution is restricted to the arid regions of southwestern Puerto Rico (Rivero, 1978). I also hypothesize that more long-term investigations with larger sample sizes would result in a highly significant relationship between weather condition, microhabitat, and activity in *Ameiva.*

Seasonality

No significant relationship was found between month and both *A. exsul* encounters and activity. These results may be due to the fact that the study took place over the course of four months (2 in wet season and 2 in dry season) and not throughout an entire year. The reproductive season of Puerto Rican *A. exsul* and *A. wetmorei* is synchronous with the increasing day lengths found between the summer months (Rodriguez-Ramirez and Lewis, 1991; Censky, 1995). Thus, I suggest that further seasonal sampling would have resulted in significant differences in activity patterns of *A. exsul* due to more males searching for receptive females. Censky (1995) conducted a similar study with *A. plei* from Anguilla and Dog Island, Lesser Antilles and found the species to also exhibit seasonal cycles in reproductive activity, with the reproductive season commencing between May and October, synchronous with increased air temperatures and day length. Seasonal patterns in rainfall also seem to influence the reproductive cycles of *Ameiva,* with reproductive activity significantly reduced during dry conditions (Colli, 1991).

Conclusions

The data presented herein add to our knowledge regarding diel patterns of activity and microhabitat use of an abundant and widespread West Indian lizard and suggest that a variety of thermal variables including air temperature and relative humidity may be contributing, at least partially, to the daily activity cycles of the species. Future studies should employ additional thermal data such as body and ground temperatures along with wind velocity for providing a more comprehensive analysis of the thermal ecology and activity of this and other species that exhibit similar thermal and behavioral regimes. In addition, more precise estimates of temperature and humidity throughout different microhabitats may allow for additional conclusions regarding thermoregulatory behavior to be drawn.

Resumen

Aunque *Ameiva exsul* es una de las especies de lagartijas más comunes de Puerto Rico y las islas aledañas, estudios ecológicos sobre las preferencias termales de esta especie son escasos. Para entender mejor el ciclo de actividad diaria y los comportamientos de termorregulación de *A. exsul,* hemos analizado datos sobre las actividades diarias y de micro hábitats de esta lagartija junto con datos termales incluyendo clima, temperatura del aire y relativa humedad. He encontrado una relación relativamente significativa sobre el número de encuentros con el reptil y la hora del día, etapas del mes o de clima. Significativamente más individuos fueron encontrados activos en el suelo durante las horas de la mañana, mientras que en las noches, más individuos fueron descubiertos durmiendo debajo de varios substratos. Aunque no he detectado una relación significativa entre micro hábitat, actividad diaria de estos reptiles y el clima, he hallado más individuos sentando debajo de sustratos durante días despejados y nublados/lluviosos, mientras que durante días semi-nublados, estas lagartijas estaban más activos. Significativamente más individuos fueron encontrados durante temperaturas más cálidas con menos humedad. No he encontrado una relación significativa entre la temperatura del aire, humedad relativa, uso del micro hábitat y actividad diaria. Sin embargo he hallado una relación significativa entre la temperatura y el número de individuos activos en el suelo. Futuros estudios son necesarios para examinar más detalladamente la ficología ecológica de este reptil, que podría incluir potencialmente otros variables relevantes del medio ambiente como la temperatura del cuerpo y la velocidad de viento.

Esto proveerá un análisis más exhaustivo sobre los patrones de la actividad diaria y la ecología termal de esta especie de lagartijas, información que podría ser aplicada a otros congéneres distribuidos en ambientes similares.

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