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Activity Patterns of *Stenocercus iridescens* in an Ecuadorian Coastal Agroecosystem: Is Temperature Important?

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Abstract: Circadian rhythms of Neotropical lizards have been poorly studied, which represents a problem when designing ecological studies or monitoring such species based on direct observations. In this work, 1000 m-long transects were established in an agroecosystem area of the Ecuadorian coast region to study the activity patterns of *Stenocercus iridescens*. The number of individuals (as a response variable) was correlated with local weather conditions: temperature, precipitation, and heliophany (duration of the solar brightness). We carried out the study in both dry and rainy seasons, and during different time ranges. The time range in which the transects were performed was the most important predictor, and the activity peak was established between 16:00 h and 18:00 h. Heliophany negatively affected lizard activity, but only on the days with higher heliophany during the dry season, whereas temperature was not a significant predictor. Our results suggest that in an area where temperature is relatively constant and the solar radiation is high, particularly during the dry season, the heliophany (an indirect measure of solar radiation) can affect ectotherm activity patterns more than temperature, particularly in open habitats such as agroecosystems.

Keywords: circadian rhythms; species richness; thermoregulation; agroecosystems; reptiles

1. Introduction

Many reptile populations are declining worldwide due to habitat loss, climate change, invasive species, emerging diseases, or agriculture intensification [1–3]. In the Neotropical region, the ecology of reptiles is poorly known, and most parameters of the ecology of many species (including circadian rhythms) are unknown [4].

Western Ecuador is one of the most threatened and less studied regions of the Neotropical ecoregion, which includes tropical moist forests and tropical seasonal dry forests. It is part of the biodiversity hotspot called the Chocó–Darién–Western Ecuador Hotspot [5]. This region shows high endemism [6] and has high herpetofauna biodiversity [7]. This hotspot is one of the most endangered areas within the Neotropics because of habitat loss and fragmentation due to agricultural practices [8–10], and with the available data it is difficult to assess the impact of agricultural intensification on reptile populations because only a few studies have been conducted to determinate their abundance [11].

Sampling methodologies are frequently developed in temperate regions and later applied in Neotropical environments even though Neotropical lizards could respond differently to environmental conditions than Nearctic or Palearctic lizards, whose environments are where the sampling methodologies were developed. Since lizards are ectotherms, their detectability strongly depends on local environmental conditions, thus affecting their daily activity pattern. Therefore, sampling methodologies based on direct observation should be

adapted to local conditions and consider specific behavioral patterns and environmental factors rather than generic ones.

Meteorological stations of the National Institute of Meteorology and Hydrology (IN-AMHI) have been recording global insolation (Wh/m^2/day) and heliophany, or the duration of solar brightness that corresponds to direct solar radiation (h/day), since 1962. There is, therefore, a direct relationship between global insolation and heliophany [12]. Solar radiation is, in theory, an unlimited resource on Earth, but it can be locally limited. Ectotherm organisms use solar radiation to elevate their body temperatures [13]. Many works have shown how the environmental temperature affects reptile activity patterns, but other variables such as solar radiation have been less explored [13–15]. Reptiles can attain a higher body temperature with a higher solar radiation (measured as Wh/m^2), and therefore, this variable should be also considered in studies on activity patterns. However, in a subtropical environment with a relative constant high temperature, a high insulation level could be a stressful factor.

Behavioral thermoregulation, which occurs mainly by location in the sun or in the shade, enables many ectotherm vertebrates to take advantage of thermal diverse environments and control temperature-sensitive physiological processes [15]. Ectotherm species compensate for changes in their body temperature through behavioral thermoregulation and/or physiological adaptations [16]. For some animals, changing posture or moving to a new location is an adequate method of thermoregulation. For reptiles, sunning or basking is a typical behavior by which the animal exposes its body to as much solar radiation as possible, leading to internal heat gain [13].

The study of species' responses to varying environmental conditions has a long history in biological research [17], but the reptile's ability to compensate has gained particular attention in the face of climate change [18,19]. For example, the upper thermal tolerance limits of many organisms increase (within individuals) as mean body temperatures rise, meaning that physiological adjustments can potentially compensate for the negative consequences of rising habitat temperatures [15]. We therefore expect that lizards synchronize their daily activity patterns to optimize their body temperature according to local conditions [20]. However, daily patterns are influenced not only by temperature but also by water balance, since temperature and hydration are critical factors to optimize metabolism [21,22]. Therefore, not only environmental temperature, but also water and other factors such as heliophany (average sunshine hours), can influence the activity patterns of reptiles.

The aim of this work is to study the activity patterns of *Stenocercus iridescens* in an agroecosystem of Western Ecuador. The climate of Ecuador is characterized by no marked annual changes in temperature, where the temperature does not reach high values, there are two well-defined seasons (rainy season and dry season), and high solar radiation is due to the perpendicular incidence of sunlight [12,23]. Under these climatic conditions, we hypothesize that temperature is not an important factor, and some factors such as time range or heliophany are more significant.

2. Materials and Methods

2.1. Study Area

The fieldwork was carried out from September 2015 to June 2016, near Calceta in the province of Manabí in the coastal region of Ecuador (0°49′10′′ S, 80°10′40′′ W; WGS-84 and 15 m above mean sea level), in the ecotone between seasonal dry forests and tropical rain forests of the Chocó-Darién-Western Ecuador Hotspot (Figure 1). The climate has an average annual temperature of 26 °C. During the dry season the temperature ranges between 21 °C and 32 °C, whereas in the rainy season it ranges from 21 °C to 30 °C. The wet season approximately extends from January to April, and the dry season from May to December. The month with the highest rainfall is February, with a monthly average precipitation of 196 mm, whereas in the dry season rainfall ranges from 6 mm to 13 mm. These conditions determinate a significant variation in relative humidity, which reaches 100% in March and 48% in September [14,23].

Figure 1. The location of the study area (black spot) in the province of Manabí (green area) in Ecuador. The location of the five transects are represented by the green spots. Map showing the location of Calceta (Ecuador). Google Earth, earth.google.com/web/ (20 March 2022).

The sampling effort was equal in both dry and rainy seasons. In the study area, 5 transects were established. They were separated to be at least 400 m from one another to ensure independence of the samples. The study area was characterized by a homogeneous agroecosystem with small corn crops and remains of grasslands. Additionally, there were small patches of native shrubby vegetation and a few scattered trees.

2.2. Lizard Sampling

The diurnal activity of *Stenocercus iridescens* was assessed by walking transects three times per week [24] during the dry season and the rainy season. Transects were 1000 m long and 4 m wide, spaced at least 400 m apart [24]. Lizards were counted by direct observation in each transect on each side of the survey line. Potential reptile microhabitats were searched, including rocks and leaf litter, woody debris, and tree trunks [25,26]. To determinate activity pattern, we established four different time ranges, from 7:00 h to 10:00 h, from 10:00 h to 13:00 h, from 13:00 h to 16:00 h, and from 16:00 h to 18:00 h. Transects were surveyed for one hour within this time range.

Air temperature (°C), daily precipitation (mm), and heliophany were taken hourly from the ESPAM MFL meteorological station, which is connected to the official Ecuadorian network of meteorological stations of the National Institute of Meteorology and Hydrology. This station is located less than a kilometer from the study area.

2.3. Statistical Analysis

Two generalized linear mixed models (GLMMs) were applied separately for the dry and wet season using the number of individuals of *Stenocercus iridescens* in each transect as a response variable, which fitted a Poisson distribution with a log-link function. In the initial full model, the time range, precipitation, temperature, heliophany (all of them calculated hourly), and the double interactions among them were included as independent variables, whereas the transect site was included as random factor. The full arrangement of models (all possible combinations) was performed, and model selection was selected by the best subset approach using the Akaike information criterion corrected for a small sample size (AICc) [27]. The generated models were ranked according to AICc values, where the model with the lowest AICc is the best one. The variance inflation factor (VIF) was used to check for collinearity among the predictors, and those models including predictors with VIF > 3 were discarded. Finally, a post hoc test within a mixed analysis was carried out to

check for differences among the levels of categorical variables. Statistical analyses were performed using InfoStat software [28].

3. Results

In the study area, 847 individuals of *Stenocercus iridescens* (Günther, 1859) were registered; 438 in the dry season, (mean per transect $\pm$ SD = 3.62 $\pm$ 1.33); and 409 in the wet season (3.12 $\pm$ 3.01). Heliophany and air temperature were not correlated in our study site (ρ = $-$0.01; *p*-value = 0.783).

The time range was the most important predictor of the number of *Stenocercus iridescens* individuals, since this variable was included in all the best candidate models (Tables 1 and 2), both in the dry and wet season. The post hoc test within the mixed model showed that the highest number of individuals was detected between 13:00 h and 16:00 h and between 16:00 h and 18:00 h (Figure 2). The heliophany was also an important predictor since it was included in many candidate models (Tables 1 and 2). However, the heliophany had a greater effect in the dry season models (Table 2), showing a negative association between the heliophany and the number of recorded individuals in the dry season, whereas in the wet season there was a slightly positive effect (Figure 3).

Table 1. Best candidate models explaining the number of individuals according to the AIC criteria for the dry and wet season separately. Only candidate models (ΔAIC < 2) are shown. k = number of parameters.

Candidate Models	k	AICc	ΔAICc
Dry Season			
Null model	0	578.81	
Time range $\times$ Heliophany	2	493.63	0.00
Time range $\times$ Heliophany $\times$ Temperature	3	494.46	0.83
Time range $\times$ Heliophany $\times$ Precipitation	3	495.50	1.77
Time range	1	495.79	2.16
Wet Season			
Null model	0	536	
Time range	1	486.67	0.00
Time range $\times$ Heliophany	2	486.83	0.16
Time range $\times$ Heliophany $\times$ Precipitation	3	488.62	1.92
Time range $\times$ Temperature	2	488.62	1.95
Time range $\times$ Heliophany $\times$ Temperature	3	488.72	2.05

Table 2. Results of the best candidate models explaining the number of individuals of *Stenocercus iridescens* for the dry and the wet season separately.

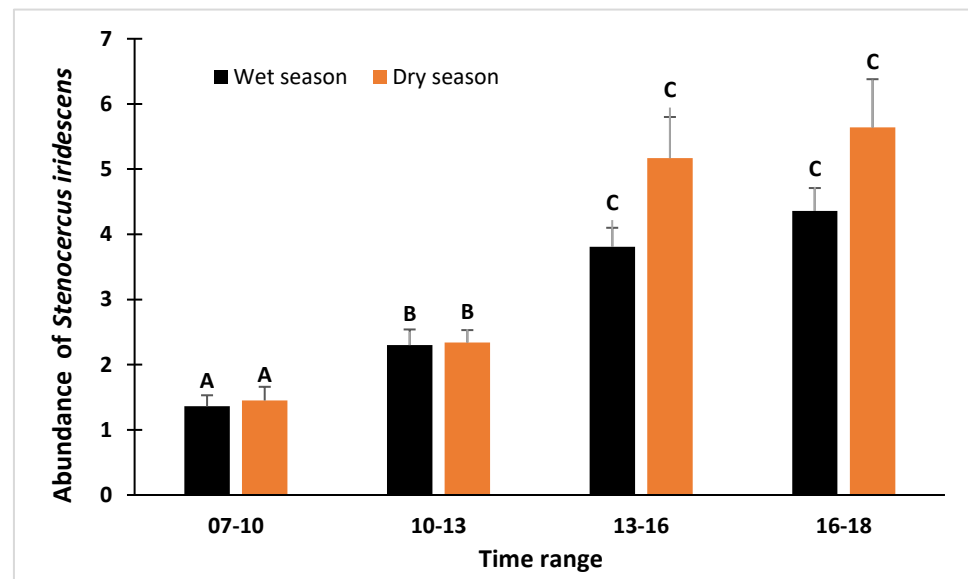| Variables	Estimate ($\pm$SE)	Z	*p*-Value
Dry Season			
Intercept	0.13 ($\pm$0.29)	0.46	0.646
Time range 10–13 h	0.78 ($\pm$0.27)	2.88	0.004
Time range 13–16 h	1.50 ($\pm$0.27)	5.63	<0.001
Time range 16–18 h	1.47 ($\pm$0.27)	5.52	<0.001
Heliophany	$-$0.17 ($\pm$0.07)	$-$2.31	0.021
Wet Season			
Intercept	0.31 ($\pm$0.18)	1.69	0.091
Time range 10–13 h	0.52 ($\pm$0.21)	2.46	0.014
Time range 13–16 h	1.03 ($\pm$0.20)	5.09	<0.001
Time range 16–18 h	1.16 ($\pm$0.20)	5.83	<0.001

Figure 2. Abundance of *Stenocercus iridescens* expressed as the number of individuals observed per transect during the four time ranges for the dry and wet season separately. Error bars represent the standard error. Different uppercase letters indicate significant differences among time ranges according to the post hoc tests (*p*-value < 0.05) for the wet and dry season separately.
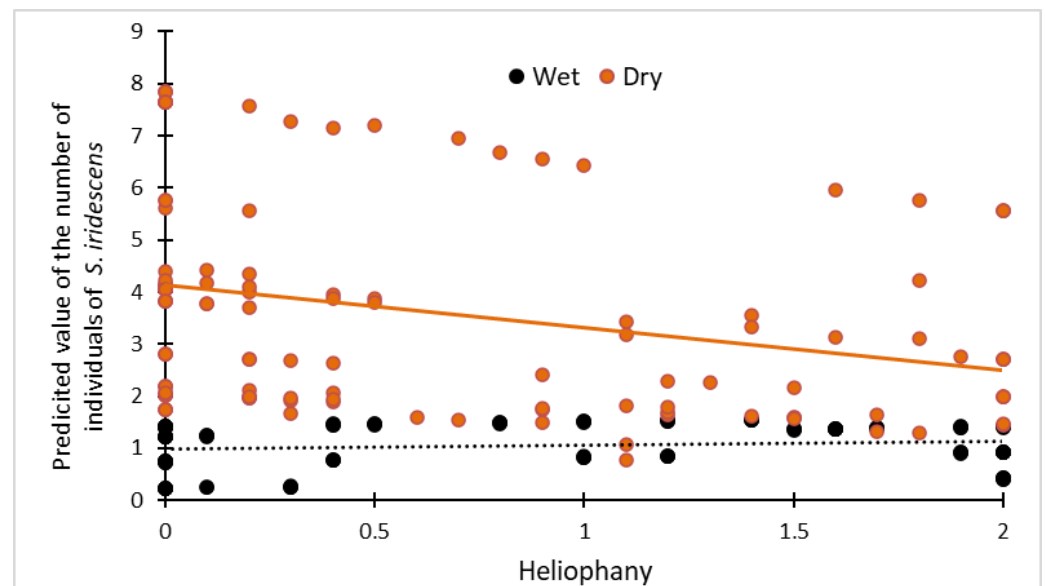

Figure 3. Scatterplot showing the relationship between the heliophany and the predicted number of individuals of *Stenocercus iridescens* in dry (orange spots) and wet (dark spots) seasons separately, obtained from the best candidate model.

4. Discussion

Most studies on daily activity patterns have been carried out in temperate regions where environmental conditions strongly change between seasons and where a strong daily temperature variation also occurs with a maximum during midday when the activity peak of reptiles occurs [29,30]. However, there are not many studies on Neotropical lizards' activity patterns and habitat selection [29,31,32]. Most of the studies have been carried out in high latitudes, where the environmental temperature range is radically different during the year. In the tropics, the temperature is very stable during the day and year. Studies in tropical zones seems to show that tropical lizards have unimodal or bimodal activity patterns. Those with a unimodal activity pattern are active around noon, whereas those

lizards with bimodal activity patterns are more active during the morning and afternoon, avoiding the hours with the highest solar radiation [33].

Here, we found that the variable with the highest relative importance predictor (ωp) was the time range in which the transects were performed. In our study, the activity pattern of *Stenocercus iridescens* was higher in the range from 13:00 h to 16:00 h and even higher from 16:00 h to 18:00 h (Figure 2). This could be explained as at least some Neotropical lizards avoid the hours of highest radiation (noon) to thermoregulate [15]. The independent role played by heliophany and seasonality in the activity pattern of *Stenocercus iridescens* is not clear. However, the interaction between heliophany and seasonality seems to have an impact (Figure 3, Table 2). Our results suggest that heliophany (sunshine) has a different influence during the dry or wet season (Figure 3). The relationship between the heliophany and the number of individuals of *Stenocercus iridescens* counted in dry and wet seasons separately showed that the predicted value is not affected by heliophany during the wet season. Interestingly, during the dry season, the heliophany showed a negative relationship with observed individuals and *Stenocercus iridescens* avoided the maximum heliophany periods (Figure 3). The lack of the effect of the air temperature and the effect of the heliophany on activity patterns could be due to the high solar radiation in Ecuador owing to the perpendicularity of the sun rays, whereas the daily thermal variation is low. Thus, heliophany is more important than temperature.

Recently, ref. [34] pointed out the trade-off between water and thermal regulation in terrestrial ectotherms, suggesting that they should be considered as two integrated systems. Our finding on the negative effect of heliophany during the dry season might be explained by the water-specific heat capacity and its relationship with ectotherm vertebrates [35]. It is possible that *Stenocercus iridescens* found refuge in small puddles (rainy season), when water could help individuals to lose heat, or even air saturation during the wet season might keep a more stable environmental temperature range [36], and therefore, the activity pattern does not depend on the heliophany. Environmental characteristics in Palearctic regions exert little influence on thermal preference with the exception that females from habitats with permanent access to water had lower thermal preferences [34. However, sexual dimorphism was not considered in the analysis of our data.

During the dry season, *Stenocercus iridescens* would need behavioral strategies (similar to what many lizards do in high latitudes) to face a quick loss or earn corporal heat because of a lack of water or environmental humidity [35,36]. Likewise, [37] suggested that lizards exposed to dehydration thermoregulate less precisely than hydrated lizards, and if dehydrated lizards are less active, they can change the daily activity pattern according to their thermal preference. Dehydration negatively affected thermoregulation and dehydrated lizards reduced their preferred body temperature and showed a species-specific pattern of hourly change in thermal preference. Furthermore, they more frequently used the colder parts of the gradients and spent more time hidden [36,38]. Something similar could explain *Stenocercus iridescens'* low records when heliophany was higher (noon) during the dry season (Figure 3). Additionally, since our study was performed in a disturbed area with low tree coverage, the heliophany could have a more marked effect owing to the lack of shadow, making the thermoregulation of lizard species particularly difficult [19].

5. Conclusions

In conclusion, the activity pattern of *Stenocercus iridescens* could be influenced by heliophany and not by air temperature as other studies suggest for Neotropical lizards with different ecological preferences [31,36]. Heliophany could also explain the change in *Stenocercus iridescens'* daily activity patterns between the rainy and dry season. Therefore, we suggest further studies of reptiles to perform a brief pilot survey in order to check the peak activity patterns in the study area at that moment. Deforestation opens the canopy, increasing the solar radiation penetration, reducing the humidity, and increasing wind speed, and thus affecting the ectotherms' sensitivity to desiccation [39]. Moreover,

ecological studies on Neotropical lizard activity patterns are scarce, and further studies are needed in the face of climate change.

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