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Habitat degradation may affect niche segregation patterns in lizards

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A R T I C L E   I N F O

A B S T R A C T

Lizards partition resources in three main niche dimensions: time, space and food. Activity time and microhabitat use are strongly influenced by thermal environment, and may differ between species according to thermal requirements and tolerance. As thermal characteristics are influenced by habitat structure, microhabitat use and activity of lizards can change in disturbed habitats. We compared activity and microhabitat use of two abundant lizard species of the Semi-arid Chaco of Argentina between a restored and a highly degraded Chaco forest, to determine how habitat degradation affects lizard segregation in time and space, hypothesizing that as activity and microhabitat use of lizards are related to habitat structure, activity and microhabitat use of individual species can be altered in degraded habitats, thus changing segregation patterns between them. Activity changed from an overlapped pattern in a restored forest to a segregated pattern in a degraded forest. A similar trend was observed for microhabitat use, although to a less extent. No correlation was found between air temperature and lizard activity, but lizard activity varied along the day and among sites. Contrary to what was believed, activity patterns of neotropical diurnal lizards are not fixed, but affected by multiple factors related to habitat structure and possibly to interspecific interactions. Changes in activity patterns and microhabitat use in degraded forests may have important implications when analyzing the effects of climate change on lizard species, due to synergistic effects.

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1. Introduction

Resource partitioning among sympatric species has been proposed as the driving factor in species coexistence and diversity at the local level by reducing interspecific competition (Pianka, 1973; Schoener, 1974). Although any resource can be partitioned, animals partition resources in three main niche dimensions: time, space and food (Pianka, 1973; Schoener, 1974). Most of the studies on the subject have shown a clear partition on food (Vitt, 1991; Vitt and Carvalho, 1995) and space (Vitt, 1991; Vitt et al., 2000), whereas few works were made on temporal segregation of species (Pianka, 1973). In Neotropics temporal segregation seems to have a negligible influence in structuring lizard assemblages, with large overlap in diurnal activity periods (Vitt et al., 1999).

As lizard activity depends on thermal characteristics of the environment (Adolph, 1990; Adolph and Porter, 1993; Grant and Dunham, 1988) and the thermal quality of the environment varies along the day, lizards can only be active in some periods of the day, depending on their thermal requirements and constrains (Adolph and Porter, 1993; Grant and Dunham, 1988). Habitat structure is an important factor in regulating microclimate characteristics (Pringle et al., 2003), thus influencing the thermal quality along the day. Therefore, lizards in habitats with different structure should have different activity patterns. This seems to be true for sympatric *Cnemidophorus* (Dias and Rocha, 2004) and for *Ameiva ameiva* (Sartorius et al., 1999) in Brazil. Moreover, as different species may have different thermal requirements and habitat structure influences microclimatic characteristics, habitat disturbance can change patterns of niche overlap.

Herein we compare the daily activity and microhabitat use of two abundant lizard species of the Semiarid Chaco in a restored and a degraded Chaco forest, to determine how habitat degradation affects lizard segregation in time and space. We hypothesized that as activity and microhabitat use of lizards are related to habitat

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structure, activity and microhabitat use of individual species can be altered in degraded habitats, thus changing segregation patterns between them.

2. Materials and methods

2.1. Study site

The study was conducted in Salta province, northern Argentina, in the Semi-arid Chaco ecoregion (Secretaría de Desarrollo Sustentable y Política Ambiental and Ministerio de Desarrollo Social y Medio Ambiente, 1999). According to Köppen-Geiger's classification, the local climate type is Cwa (Peel et al., 2007). Mean temperature is 28.8 °C in January (warmest month) and 16.6 °C in July (coldest month). Annual rainfall averages 550 mm (summer rains, October–March) (Bianchi and Yáñez, 1992). Two forest fragments with contrasting vegetation conditions were selected (Fig. 1): 1) degraded forest (DF): Campo Grande cattle ranch (7500 ha) (24°43′S, 63°17′W), and 2) restored forest (RF): Los Colorados Biological Station (10,000 ha) (24°39′S, 63°17′W). Campo Grande is a cattle and goat ranch that has been highly degraded by overgrazing and deforestation. Vegetation is characterized by isolated clumps of trees and low, unpalatable shrubs intermingled with large, open areas of bare soil. Los Colorados preserves a typical Semi-arid Chaco woodland. *Schinopsis quebracho-colorado* and *Aspidosperma quebracho-blanco* (10–14 m high) are the dominant tree species. A dense shrub stratum (3–4 m high) is intermingled with grasses and cacti (Varela, 2001). The area was wire-fenced in

1976 and all domestic cattle removed. As a result, the present vegetation cover is very close to the primeval forest conditions (Varela, 2001). The main differences in vegetation between sites are detailed in Table 1.

2.2. Lizard sampling

Sampling was carried out in the summer (January and February) of 1992 and 1993, and in spring (September) of 1993. Diurnal visual encounter surveys were conducted by two observers in 235 1 km-long transects (159 transects in RF and 76 transects in DF) along internal paths and at different hours of the day in both sites. Lizards observed along each transect were identified, registering the microhabitat used (bare ground, grass/herbs and shrubs). This data was used in a previous article to study the effect of forest degradation on abundance and microhabitat selection in Chaco lizards (see Pelegrin et al., 2009), and will not presented here. All registered lizards were assigned to the time interval of the corresponding transect, and grouped in seven intervals of two hours each. At the moment of samplings, daylight was available for about 14 h, from 07:45 (sunrise) to 21:15 (sunset). Transects between 07:00 and 13:00 hs (99 transects) were "morning transects", while transects between 13 and 21:00 (136 transects) where "afternoon transects". Since survey time differed among transects, lizard abundance was represented in (lizards (transect hour)$^{-1}$).

Air temperature (°C) was taken at the beginning and at the end of each transect by using a 0–100 °C thermometer. The mean of these two temperature measures was assigned to the corresponding
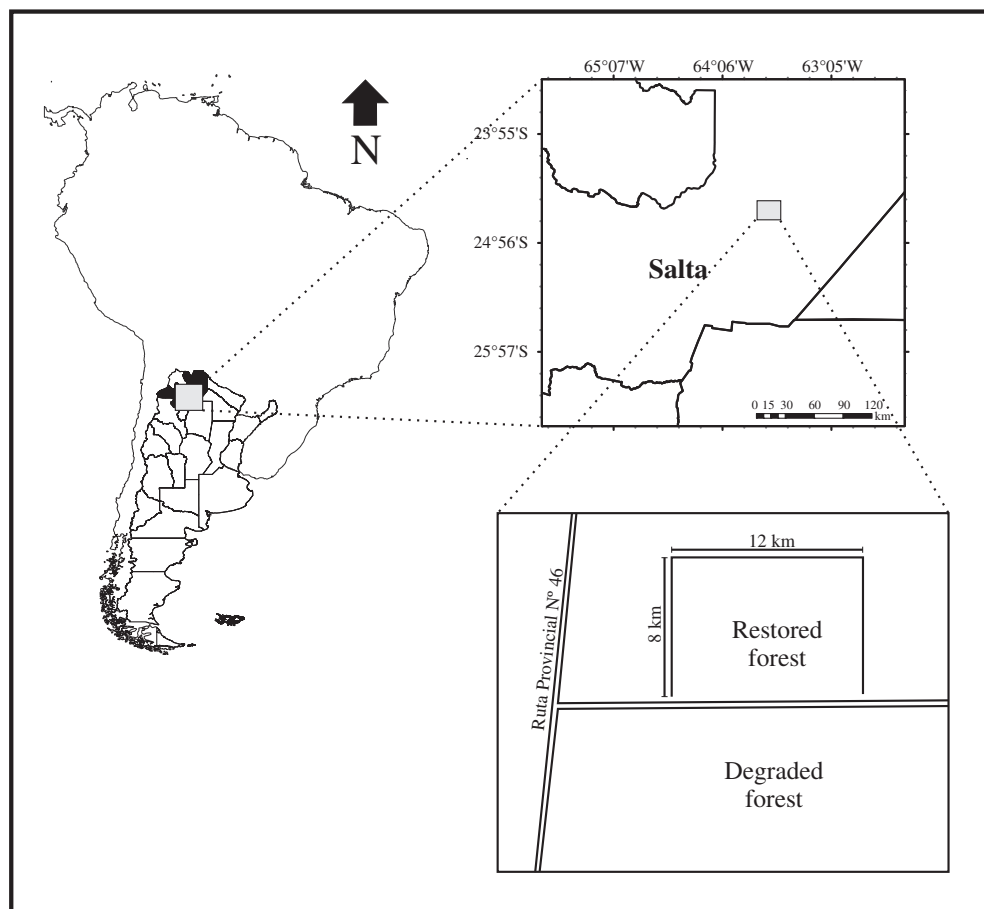

Fig. 1. Location of the study sites.

Table 1
Proportion (%) of bare ground, litter/grass/herb and shrub cover in restored and degraded forest (taken from Leynaud and Bucher (2005)).

Cover type	Restored forest	Degraded forest
Bare ground	7	46
Litter/grass/herbs	93	54
Shrubs	34	7
Tree canopy	80	76

transect, while all measures (470 measures) were used to describe the thermal profile of each site. The lizard fauna in the study area includes 13 species (Lavilla et al., 1995; Leynaud and Bucher, 2005), from which *Teius teyou* and *Liolaemus chacoensis* are among the more common species. *T. teyou* (Teiidae) is a heliothermic, middle sized lizard (144 mm SVL) distributed from southern Bolivia and Brazil to Monte Desert, in southern Argentina (Cei, 1986b). The species is very abundant, preferring open microhabitats (Pelegrin et al., 2009; Videla and Puig, 1994). *L. chacoensis* (Liolaemidae) is a small (50 mm SVL) Chaco endemic species (Cei, 1986a), very common in both disturbed and well preserved Arid and Semi-Arid Chaco forest (Pelegrin and Bucher, 2012; Pelegrin et al., 2009).

As with other lizard sampling methods, the possibility that the visual encounter technique might be influenced by differences in detectability related with the surrounding environment cannot be discarded. However, we assume that if differences existed, the possible error introduced would be small and similar in both sites, therefore not influencing comparisons between them.

2.3. Data analysis

Niche breadth was calculated for time (activity) and space (microhabitat) using the normalized Levins' index (Colwell and Futuyma, 1971). We also calculated Pianka's standardized Niche Overlap Index (Winemiller and Pianka, 1990) for time and microhabitat. The distribution of lizards observed along the day was compared among species and between each species and a hypothetical homogeneous distribution through a Kolmogorov–Smirnov test. The mean number of lizards registered in morning and afternoon transects were compared with a *t*-test at each site. The

influence of site, hour, air temperature and abundance of a sympatric species (*L. chacoensis* or *T. teyou*) on the abundance of each of the studied species was analyzed by using Generalized Linear Models (GLM).

We tested the correlation between lizard abundances (lizards (transect hour)$^{-1}$) and transect mean temperature by using both Spearman's linear correlation model, and polynomial regression (Zar, 1996). Mean temperature was compared among sites through a Wilcoxon test. All tests were made in R (R Core Team, 2012), with an alpha level of 0.05.

3. Results

3.1. Activity – time niche

Activity of *T. teyou* differed among sites (Kolmogorov–Smirnov test, $D = 0.4227$, $P = 0.013$). In RF, the activity of *T. teyou* was not homogeneous (Kolmogorov–Smirnov test, $D = 0.5833$, $P < 0.0001$). The distribution of *T. teyou* along the day in RF showed no differences with that of *L. chacoensis* (Kolmogorov–Smirnov test, $D = 0.1444$, $P = 0.6782$) (Fig. 2). The number of *T. teyou* was not different between morning and afternoon (Table 2).

In DF, the activity of *T. teyou* was not homogeneous (Kolmogorov–Smirnov test, $D = 0.5652$, $P = 0.0013$). The distribution of *T. teyou* along the day in DF differed from that of *L. chacoensis* (Kolmogorov–Smirnov test, $D = 0.4408$, $P = 0.0019$) (Fig. 2). The number of *T. teyou* observed in the morning was significantly different from that observed in the afternoon (Table 2).

The activity of *L. chacoensis* was not different among sites (Kolmogorov–Smirnov test, $D = 0.1431$, $P = 0.5974$). In RF the activity pattern of *L. chacoensis* was not homogeneous (Kolmogorov–Smirnov test, $D = 0.6375$, $P < 0.0001$) (Fig. 2). The number of *L. chacoensis* was not different between morning and afternoon (Table 2).

In DF, the activity of *L. chacoensis* was not homogeneous (Kolmogorov–Smirnov test, $D = 0.675$, $P < 0.0001$) (Fig. 2). The activity of the species was not different between morning and afternoon (Table 2). Seventy three percent (15.4 out of 21 lizards. (transect.hour)$^{-1}$) of the *L. chacoensis* found in this site were active when *T. teyou* was almost absent, between 13:00 and 21:00 hs (Fig. 2).
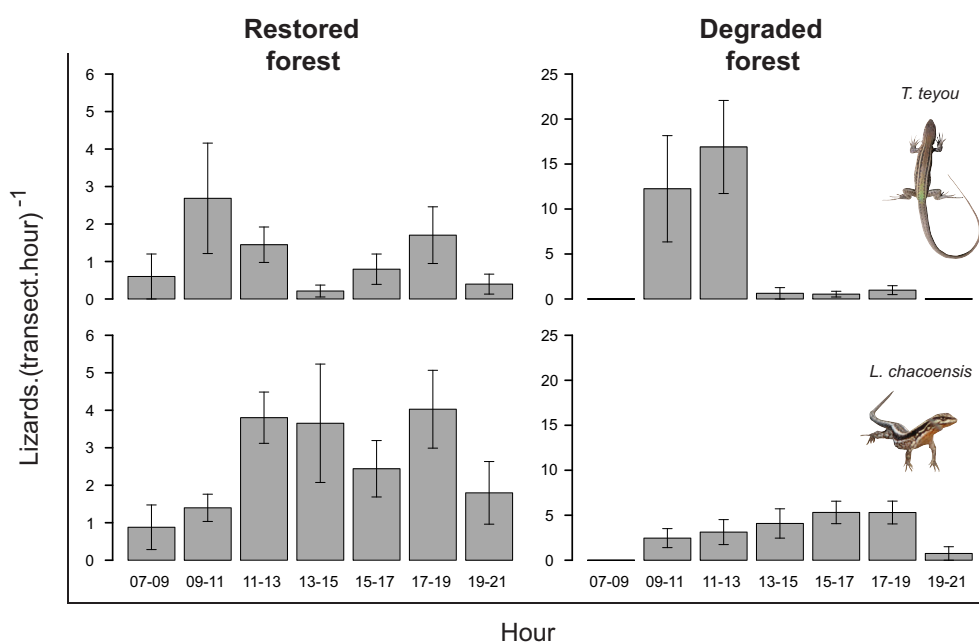
Fig. 2. Relative abundance (lizards (transect hour)$^{-1}$) of *Teius teyou* and *Liolaemus chacoensis* in two-hour intervals in restored and degraded forest. Standard error bars are shown.

Table 2

Comparison of abundance (mean lizards (transect hour)$^{-1}$ ± se) of *L. chacoensis* and *T. teyou* between morning and afternoon at restored and degraded forest (*t*- test, $P \leq 0.05$).

Site/species	Morning	Afternoon	*t*	*df*	*P*
	Mean ± se	Mean ± se			
Restored forest					
N° transects	73	86			
L. chacoensis	3.57 ± 0.42	3.19 ± 0.55	−0.7863	151.453	0.4329
T. teyou	1.88 ± 0.63	0.98 ± 0.32	1.2572	107.419	0.2114
Degraded forest					
N° transects	50	26			
L. chacoensis	2.75 ± 0.89	4.69 ± 0.76	−1.6643	58.833	0.1014
T. teyou	14.46 ± 3.74	0.73 ± 0.28	3.6585	25.275	0.001169

Activity of *L. chacoensis* was explained by site and presence of *T. teyou* (GLM; 78.8% of total deviance explained, ANOVA, $\chi^2_{[NA]} = -502.63$, $P < 0.001$) while activity of *T. teyou* was explained by site, hour, and presence of *L. chacoensis* (GLM; 64.7% of total deviance explained, ANOVA, $\chi^2_{[NA]} = -5425.6$, $P < 0.0001$).

L. chacoensis time niche breadth was larger than that of *T. teyou* both in restored (*L. chacoensis* = 0.798; *T. teyou* = 0.598), and degraded forest (*L. chacoensis* = 0.658; *T. teyou* = 0.207), with a reduction of 17.5% for *L. chacoensis* and 63.8% for *T. teyou* in degraded forest. Niche overlap (Pianka index) had a 35% decrease, from 0.73 in the restored forest to 0.47 in degraded forest.

Mean air temperature of degraded forest (mean ± SE: 31.63 ± 0.32; *n* = 150) was higher than that of restored forest (28.92 ± 0.25; *n* = 318) (Wilcoxon test, V = 50721, $P < 0.0001$). At hourly intervals there were differences between sites at 1000–1100, 1100–1200, 1500–1600, 1600–1700, and 1800–1900 hs (Fig. 3). No correlation was found between lizard activity and mean temperature of the transects in either of the sites or for either of the studied species under the linear correlation model of Spearman (Restored forest: *T. teyou* Rho = −0.26, $P = 0.26$, *L. chacoensis* Rho = 0.16, $P = 0.35$; Degraded forest: *T. teyou* Rho = −0.19, $P = 0.42$, *L. chacoensis* Rho = 0.38, $P = 0.27$) or the polynomial regression model (Restored forest: *T. teyou* Adjusted $R^2 = -0.02$, $F_{2,18} = 0.79$, $P = 0.47$, *L. chacoensis* Adjusted $R^2 = -0.009$, $F_{2,33} = 0.84$, $P = 0.44$; Degraded forest: *T. teyou* Adjusted $R^2 = -0.04$, $F_{2,17} = 0.63$, $P = 0.54$, *L. chacoensis* Adjusted $R^2 = -0.003$, $F_{2,7} = 0.99$, $P = 0.42$).
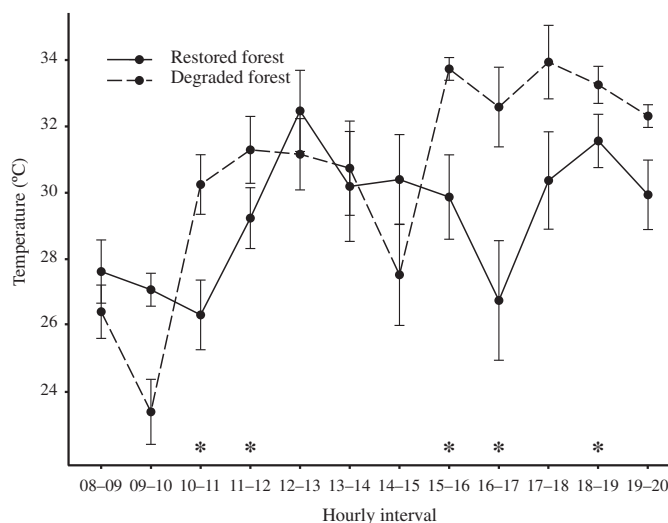
Fig. 3. Mean air temperature (°C) ± se at hourly intervals in degraded forest and restored forest. Asterisks indicate significant differences in temperature between sites (Wilcoxon test, $P < 0.05$).

3.2. Microhabitat use − space niche

L. chacoensis spatial niche breadth was narrower than that of *T. teyou* in restored forest (*L. chacoensis* = 0.24; *T. teyou* = 0.69). In degraded forest, *L. chacoensis* niche breadth was wider than that of *T. teyou* (*L. chacoensis* = 0.59; *T. teyou* = 0.24). Spatial niche breadth in degraded forest had a 59% increase for *L. chacoensis* and a 65% decrease for *T. teyou*. Niche overlap (Pianka index) had a 28% decrease, from 0.898 in the restored forest to 0.644 in degraded forest.

4. Discussion

The opener habitat of degraded forest probably led to a higher air temperature, when compared to the more vegetated restored forest. Although we found no significant correlation between temperature and lizard activity, lizard activities were not homogenous along the day. At early morning, degraded forest tended to be colder than restored forest, which may explain the low lizard activity in the first hours of the day.

When compared between sites, lizard activity showed evident variations: In degraded forest *T. teyou* restricted its activity to morning and midday, being almost absent in the afternoon, whereas in the restored forest it was active throughout the day, although in low abundances. Activity of *L. chacoensis* was similar among sites. However, the almost homogeneous activity observed in the restored forest turned into a midday–afternoon activity in degraded forest, mainly in moments when *T. teyou* was almost inactive.

Microhabitat selection by *T. teyou* and *L. chacoensis* was studied by Pelegrin et al. (2009) among a degraded and a restored Chaco forest showing that modifications in habitat characteristics leaded to changes in abundance and microhabitat selection in these lizard species. In this study we show that use of microhabitat categories also changed between sites and differently among species.

The observed changes in activity and microhabitat use among time and sites, determined a decrease in niche breath and niche overlap in the degraded forest. Thus, lizard activity went from overlapped in the restored forest to segregated in degraded forest. Similarly, the use of microhabitats was less overlapped in degraded than in restored forest. As shown in a previous study (Pelegrin et al., 2009), *T. teyou* used significantly less bare ground and more shrubs in degraded forest than in restored forest, while *L. chacoensis* did not change microhabitat use among sites. Moreover, both species selected shrubs in degraded forest (Pelegrin et al., 2009).

Although we found no significant correlations between air temperature and lizard activity in either of the study sites, the influence of temperature on lizard activity cannot be discarded. Other studies have shown that temperature influences not only activity, but also habitat selection in reptiles (Adolph and Porter, 1993; Sartorius et al., 1999). Lack of temperature records at the moment of sightings may be obscuring this relation in our data.

Bimodal activity patterns were reported in summer, changing into unimodal patterns at the beginning and at the end of the favorable season, both for Iguanian and Teiid lizard species (Belver et al., 2010; Videla and Puig, 1994; Villavicencio et al., 2002). In the restored Chaco forest, activity of both species followed the expected pattern for the season, a bimodal distribution; whereas in degraded forest activity turned into a unimodal pattern. The reduced availability of refugees and the higher temperatures may have narrowed the interval of usable hours for the lizards. In fact, time niche breadth was reduced for both species.

Body temperature of *L. chacoensis* seems to be correlated to substrate temperature (Laspiur et al., 2007), which would be an indicator of thigmothermy. However, other *Liolaemus* species showed

the ability to alternate between heliothermy and tigmothermy (Martori et al., 2002), depending on the thermal characteristics of the habitat. In Chile, saxicolous *Liolaemus* choose among microhabitats with higher thermal inertia, thus extending their activity period (Mella, 2007). Probably thermoregulatory behaviors and a more intense use of shrubs may have allowed *L. chacoensis* to be active in the hottest hours of the day. Conversely, *T. teyou* restricted its activity to morning-midday, thus avoiding overheating.

Interspecific interactions may also influence activity patterns in sympatric species. The presence of aggressive species has already been reported as an important factor at structuring lizard assemblages. Bigger and aggressive species would displace smaller ones by predation and competition (Langkilde and Shine, 2004; Langkilde et al., 2005), as reported in Amazonia with the teiid *Ameiva ameiva* (Sartorius et al., 1999). *Teius teyou* has been observed chasing *L. chacoensis* in captivity (N. Pelegrin, pers. obs.), but predation has not been confirmed by gut content studies of *Teius* species in the field (Acosta et al., 1991; Alvarez et al., 1992; Cappellari et al., 2007; D'Agostini et al., 1997; Varela and Bucher, 2002). The reduced availability of refuges in degraded forest could have led *L. chacoensis* to avoid being active in the same period as *T. teyou*, since they have similar microhabitat preferences (Pelegrin et al., 2009). Predator avoidance has been reported to be a factor even more important than thermoregulation in the process of microhabitat selection in lizards (Downes and Shine, 1998).

Changes in activity patterns of *T. teyou* and *L. chacoensis* observed between sites seems to indicate that daily activity patterns of Chaco lizards are not fixed, but influenced by habitat degradation through changes in habitat structure, and regulated by both internal and external factors, and possibly including interspecific interactions. This contrasts with the generalization that neotropical diurnal lizards have overlapped activities, and time niche is unimportant in structuring lizard assemblages (Vitt et al., 1999). According to our results and supporting our hypothesis, some Chaco lizard species modified their activity periods at certain circumstances, which leaded to new segregation patterns.

Here we discussed how activity patterns and microhabitat use in common Chaco lizard species are affected by habitat degradation through a combination of factors including thermal quality of the environment, availability of microhabitats, thermoregulatory strategies of the species and maybe interspecific intractions. Understanding how habitat degradation affects ecological traits of lizard species could be an important factor to be included when analyzing the impact of climate change on these animals. Under the model of Adolph and Porter (1993), activity and energy allocation for reproduction are directly related. Thus, a reduction in hours of activity will reduce the amount of energy available for reproduction. The reduction of lizard activity induced by climate change could cause the extinction of about 20% of lizard species by 2080 (Sinervo et al., 2010). According to the present work, lizards of degraded areas would be even more susceptible to extinction than that of areas in good condition, as an increase in temperatures and the lack of refugees could leave lizards with no options to thermoregulate. Habitat degradation and climate change may have synergistic effects, affecting lizards of threatened areas (like Chaco ecorregion) even faster.

5. Conclusions

Our results show that activity patterns of neotropical diurnal lizards are not fixed, being instead affected by habitat structure. Differences in habitat structure result in species-specific changes in activity and microhabitat use, which may lead to shifts in niche segregation patterns. These habitat-mediated changes may become more significant under the context of climate change, by reducing potential activity time and availability of microhabitats for thermoregulation.

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