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SHORT COMMUNICATION

The effects of seasonality on the foraging behavior of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata: Tropiduridae) living in sympatry in the Caatinga of northeastern Brazil

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ABSTRACT. In this study, we performed field observations of 38 and 84 specimens of the lizards *Tropidurus hispidus* (Spix, 1825) and *Tropidurus semitaeniatus* (Spix, 1825), respectively, inhabiting a Caatinga in the state of Rio Grande do Norte, northeastern Brazil, in order to describe the foraging behavior, measure the foraging intensity (number of movements, time spent stationary, distance traveled and number of attacks on preys) and investigate the effects of seasonality on the foraging strategies of these two species of lizards. During the dry season, both species showed no significant differences in foraging intensity. In the wet season, on the other hand, only the distance traveled was similar for both species. *Tropidurus semitaeniatus* displayed a larger mean number of movements (9.8 ± 1.2) and attacks on preys (1.7 ± 0.3) when compared to *T. hispidus* (3.0 ± 0.8 moves; 0.3 ± 0.1 attacks). Additionally, mean time spent stationary was significantly longer for *T. hispidus* (596.6 ± 1.0 seconds) than for *T. semitaeniatus* (587 ± 2.1 seconds). Results suggest that the low number of movements and short distance traveled (maximum of 1000 cm during 10-minute intervals) are consistent with the categorization of *T. hispidus* and *T. semitaeniatus* as sit-and-wait foragers. Given our results, we conclude that both species co-exist under limiting conditions during the dry season, with similar foraging behavior and similar rates of foraging intensity, segregating with respect to these variables in the wet season.

KEY WORDS. Foraging mode; lizards; sympatric species.

Species of *Tropidurus* (Wied, 1820) are abundant diurnal lizards that occur from open formations to forested habitats (Frost 1992, Harvey & Gutberlet 2000, Frost *et al*. 2001). In Brazil, the genus is widely distributed, with species living in the Amazon and the Atlantic forests (including "Restingas": coastal sand dunes habitats), the Caatingas and the Cerrados (Araújo 1987, 1991, Rodrigues 1987, Rocha & Bergallo 1990, Vitt 1993, 1995, Vitt & Caldwell 1993, Vitt *et al*. 1996, Ribeiro *et al*. 2008).

In South America, sympatry is common among co-generic species of lizards, and the genus *Tropidurus* is no exception (*e.g*. Vitt 1991, 1995, Colli *et al*. 1992, Colli *et al*. 2002, Faria & Araújo 2004, Van Sluys *et al*. 2004). On rock outcrops within the Caatingas of northeastern Brazil, two species of *Tropidurus* occur sympatrically and syntopically: *Tropidurus hispidus* (Spix, 1825) and *Tropidurus semitaeniatus* (Spix, 1825). The former species is widely distributed, ranging from central-eastern and northeastern Brazil to Venezuela, whereas the latter is endemic to the Caatingas (Vanzolini *et al*. 1980).

Previous studies have investigated the diets of both *T. hispidus* and *T. semitaeniatus* in a Caatinga in the state of Pernambuco (Vitt 1995), and the diet of *T. hispidus* populations in the Amazon Forest (Vitt *et al*. 1996) and the rocky meadows ("campos rupestres") of the state of Minas Gerais (Van Sluys *et al*. 2004). Additionally, Ribeiro & Freire (2009a) reported a hylid frog *Scinax x-signatus* previously unrecorded as prey for *T. hispidus*, in a Caatinga habitat in the state of Rio Grande do Norte. In contrast, information on the foraging behavior for the two *Tropidurus* species is scarce, particularly for the Caatingas. In fact, the only study mentioning the foraging behavior of *T. hispidus* was conducted in the Amazon region of Brazil (Vitt *et al*. 1996). In addition, the role of *T. semitaeniatus* as a seed disperser (Ribeiro *et al*. 2008) in the Caatinga (state of Rio Grande do Norte) and the drinking behavior of this species (Ribeiro & Freire 2009b) were described.

In this study, we conducted seasonal and quantitative field observations on the foraging movements of *T. hispidus* and *T. semitaeniatus* in the Caatinga of northeastern Brazil. Because *Tropidurus* lizards are traditionally considered "sit-and-wait" foragers (Schoener 1971, Rocha 1994), our initial prediction was that little variation would be observed between the

foraging behaviors of these two species. We chose the Ecological Station of the Seridó (ESEC Seridó, Serra Negra do Norte, State of Rio Grande do Norte, 06º34'S, 37º15'W) to conduct our field work. This region is part of the Morphoclimatic Domain of the Caatingas (*sensu* Ab'Sáber 1974), more precisely the Northern Sertaneja Depression ecoregion, and contains two different areas with climatic extremes that give rise to lower vegetation characterizing the Seridó and the Cariri (Velloso *et al*. 2002). The climate is hot dry semi-arid (Ab'Sáber 1974), with a short irregular wet season between March and May, and rainfall varying from 500 and 700 mm/year. Mean annual temperatures range between 28ºC and 30ºC year-round, with maximum temperatures of more than 40ºC and minimum temperatures between 17ºC and 20ºC. Vegetation is hyperxerophillic shrubby-arboreal, with herbaceous undergrowth only in the wet season (Varela-Freire 2002). The various rocky outcrops found within this vegetation are partly shady during the wet season, but become fully exposed to the sun during the dry season, as a result of deciduous seasonality.

We randomly selected five rocky outcrops surrounded by vegetation to observe the foraging behavior of *T. hispidus* and *T. semitaeniatus*. In order to account for seasonal differences, our observations took place both in the dry season, characterized by whitish vegetation, deciduous seasonality and increased sunlight exposure, and in the wet season, characterized by renewed foliage, reinvigorated vegetation and partial shade.

Foraging intensity is the measure of a predator's physiological and behavioral activity while searching for prey and while preying (Rocha *et al*. 2000). Since foraging intensity is expressed mainly in terms of movement, we have applied the following indices to assess the foraging intensity of *T. hispidus* and *T. semitaeniatus*: number of moves (NM), time spent stationary (TS in seconds), distance traveled (DT in cm; a measure inferred from the distance between the initial location of the lizard up to the furthest point traveled to), and number of attacks on preys (NAP). Observations took place twice a day (7-10 h and 14-17 h) over two consecutive days every month in the dry (October to December 2006) and wet (April to June 2007) (Nimer 1972) seasons. The time intervals above were selected based on our preliminary observations and published data (Vitt 1995) indicating that they correspond to highest lizard activity. Samples were recorded using the Focal Animal method (Altmann 1974) for 10 minutes, alternating between observers whenever possible. All observations were carried out using a voice recorder and a digital regressive chronometer. In order to minimize observer's interference, we waited five minutes after the subject had been located to start recording. Whenever a lizard seemed to react to the presence of an observer, or when it disappeared from sight, the observation was disregarded, following Vitt *et al*. (1996). The foraging indices (NM, TS, DT, NAP) were recorded and calculated for each lizard using the arithmetic mean by species and by seasonality. This methodology was adapted from that described in Strüssman *et al*. (1984), Magnusson *et al*. (1985) and Gasnier *et al*. (1994). The Mann-Whitney U test (Zar 1999) was used to determine whether *T. hispidus* and *T. semitaeniatus* exhibit different foraging behaviors, according to the indices applied, and to assess the existence of seasonal variations in foraging intensity between the species. Data were analyzed using SPSS version 13.0. The significance level adopted for obtaining critical values on the tests was 0.05, and descriptive statistics are represented in the text as mean ± 1 standard error.

A total of 122 focal samplings were conducted: 84 for *T. semitaeniatus* (43 in the dry season and 41 in the wet season,) and 38 for *T. hispidus* (22 in the dry season, and 16 in the wet season). Even though search and observation efforts were equivalent for both species, *T. semitaeniatus* was more abundant and was consequently encountered more often than *T. hispidus*. The analysis of foraging intensity, regardless of seasonality, showed that number of moves was significantly higher for *T. semitaeniatus* (11.2 ± 0.9 moves; range 0-41 moves) than for *T. hispidus* (7.1 ± 1.0 moves; range 0-28 moves; Mann-Whitney U test, z = -2,669, p = 0,008). Furthermore, time spent stationary was shorter for *T. semitaeniatus* (583.4 ± 2.0 seconds; range 497-600 seconds) than for *T. hispidus* (590.2 ± 1.9 seconds; range 541-600 seconds; Mann-Whitney U test, z = -2.289, p = 0.022). Lizards of both species traveled equivalent distances (*T. semitaeniatus*: 199.2 ± 16.3 cm; range 0-805 cm; *T. hispidus*: 206.9 ± 34.5 cm; range 0-1,000 cm; Mann-Whitney U test, z = -0.625, p = 0.532) and performed close numbers of attacks on preys (*T. semitaeniatus*: 1.5 ± 0.2 attacks; range 0-9 attacks; *T. hispidus*: 1.2 ± 0.2 attacks; range 0-8 attacks; Mann-Whitney U test, z = -1.050, p = 0.294). Seasonal comparisons of foraging intensity between the two species showed no significant differences in the dry season (Tab. I). On the other hand, during the wet season only the distance traveled was similar for both species (Tab. I). Indices for both number of moves and number of attacks on preys were significantly higher for *T. semitaeniatus*, while time spent stationary was comparatively longer for *T. hispidus* (Tab. I).

During the dry season, the vegetation of the Caatinga becomes completely dry reducing the foraging sites of *T. hispidus* and *T. semitaeniatus* to rocky formations that serve as observation points (waiting sites) which are visited alternately during displacements. From these sites, the lizards wait with their heads pointing down, and quickly jump on to potential preys spotted moving through the leaf litter accumulated in the rock crevices or around the rocks. During the wet season, on the other hand, the vegetation of the Caatinga becomes invigorated and produces many flowers. The flowers attract insects such as bees, beetles and butterflies, acting as insect baits for the lizards that stay motionless near them. When an insect is spotted landing on a nearby flower, the lizard quickly jumps onto it. Furthermore, when foraging during the wet season, *T. hispidus*, a habitat generalist, benefits from including the flowers on the trees above the rocky surfaces for foraging. In contrast, *T. semitaeniatus*,

typically saxicolous, does not climb to the highest parts of the trees and limits itself to capturing preys in the flowers of plants at the level of the rock surfaces (Figs 1 and 2).

Figures 1-2. *Tropidurus hispidus* on tree branch (1) and *T. semitaeniatus* on the rocky outcrop (2), where both the lizards waiting for preys near an inflorescence, during the wet season at the Estação Ecológica do Seridó, Brazil.

Foraging mode has been considered of fundamental importance in interpreting ecological and behavioral characteristics of lizards, as well as the natural history of a species (Huey *et al*. 1983, Pianka 1986, Vitt 1990, Vitt *et al*. 1996). Lizards are traditionally classified into two categories according to foraging mode: active foragers or sit-and-wait foragers (Vitt & Congdon 1978, Huey & Pianka 1981). Foraging in *Tropidurus* reflects a history of sit-and-wait foraging involving a set of associated characters in the family Tropiduridae and most of the Iguania (Cooper 1994). The foraging behavior described here and the indices of foraging intensity, such as low number of movements and short distances traveled (Huey & Pianka 1981) are consistent with the categorization of *T. hispidus* and *T. semitaeniatus* as sit-and-wait foragers, similar all other tropidurids studied (e.g. Howland *et al*. 1990, Rocha & Bergallo 1990, Vitt 1991, Colli *et al*. 1992, Vitt & Carvalho 1995, Vitt *et al*. 1996). Even though phylogeny is believed to play an important role in the foraging mode of lizards (Cooper 1995), the two foraging strategies mentioned above must be considered as extreme points of a variation gradient. Species can modulate their hunting strategies according to pressures imposed by the environment, such as seasonality (Huey & Pianka 1981, Rocha 1994).

The foraging intensity indices for both number of moves and number of attacks on preys obtained for *T. hispidus* in the Caatinga are similar to those reported for the same species in the Amazon region (Vitt *et al*. 1996), particularly during the wet season. On the other hand, our observations using the Focal Animal method, especially in the wet season, revealed differences in the foraging intensity of *T. hispidus* and *T. semitaeniatus* in regards to most indices evaluated (e.g. number of moves, time spent stationary, and number of attacks on preys), indicating that *T. semitaeniatus* is more active than *T. hispidus* (Tab. I). These differences support the idea that foraging intensity may vary between species even when they exhibit the same foraging strategy (Gasnier *et al*. 1994). Additionally, the number of moves and distance traveled for both *T. hispidus* and *T. semitaeniatus* were larger than those recorded for the polychrotid lizard *Anolis auratus*, also a sit-and-wait forager (Magnusson *et al*. 1985), being smaller than those recorded for active foragers such as the teiid lizards *Ameiva ameiva*, *Cnemidophorus lemniscatus* and

Table I. Seasonal comparisons for measures of foraging intensity during ten-minute focal animal observations of *T. hispidus* (Th) and *T. semitaeniatus* (Ts) at the Ecological Station of the Seridó, Brazil. (NM) Number of moves, (TS) time spent stationary (seconds), (DT) distance traveled (cm), (NAP) number of attacks on preys. Data are represented as mean ± 1 SE (range) and p values are based on the Mann-Whitney U test. Significant differences are highlighted with an asterisk.

Index	Dry season			Wet season		
	Th (n = 22)	Ts (n = 43)	p	Th (n = 16)	Ts (n = 41)	p
NM	10.1 ± 1.4 (3-28)	12.5 ± 1.4 (0-41)	0.374	3.0 ± 0.8 (0-11)	9.8 ± 1.2 (1-38)	0.0001*
TS	585.5 ± 2.9 (541-598)	580 ± 3.4 (497-600)	0.528	596.6 ± 1.0 (585-600)	587 ± 2.1 (549-599)	0.0001*
DT	252.5 ± 48.1 (10-1000)	212.7 ± 23.9 (0-805)	0.792	144.3 ± 45.6 (0-620)	185.0 ± 22.1 (12-650)	0.0820
NAP	1.8 ± 0.4 (0-8)	1.3 ± 0.2 (0-6)	0.245	0.3 ± 0.1 (0-2)	1.7 ± 0.3 (0-9)	0.0030*

Kentropyx calcarata. These differences fit the hypothesis that sit-and-wait foraging and active foraging are extremes of a continuum of foraging strategies that has various intermediate degrees (Schoener 1971, Magnusson *et al*. 1985).

Our results show that the foraging behavior strategies of *T. hispidus* and *T. semitaeniatus* are affected by the marked seasonality of the Caatinga. During the harsher conditions imposed by the dry season (e.g. scarce food sources) the two species are constrained to coexist under limiting resources, a finding supported by the observed similarities in their foraging behavior and intensity. In the wet season, on the other hand, the different characteristics of the vegetation allow these two species to segregate from each other through different hunting strategies: whereas *T. hispidus* spends more time stationary near a single flower (or inflorescence), resulting in a lower number of attacks on preys, *T. semitaeniatus* moves more from flower to flower (or among inflorescences) performing a larger number of attacks. Finally, we conclude that the foraging behavior and intensity of *T. hispidus* and *T. semitaeniatus* living sympatrically on rocky outcrops in this area of the Caatinga has allowed their coexistence under limiting conditions in the dry season, acting as segregating factors that contribute to their coexistence in the wet season.

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