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ORIGINAL PAPER

Prey-predator interactions between two intraguild predators modulate their behavioral decisions

Welton Dionisio-da-Silva[1,2] · André Felipe de Araujo Lira[3] · Cleide Maria Ribeiro de Albuquerque[2]

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Abstract

Intraguild predators can have behavioral mechanisms to maximize foraging and/or avoid predation. However, there is a lack of information about the influence of such prey-predator interactions on the daily activity of the species involved. Therefore, we investigated the daily activity of two intraguild predators, *Tityus pusillus* Pocock, 1893 and *Ananteris mauryi* Lourenço, 1982, in the presence and absence of each other. Animals were observed in three experimental conditions, containing individuals of *T. pusillus* (control 1), *A. mauryi* (control 2), and both species (treatment). In addition, we evaluated the correlation between the number of active individuals with air temperature and humidity. Our results showed that *T. pusillus* and *A. mauryi* have similar daily activity between 18:00 and 05:00 h. However, *T. pusillus* was more active and shifted from a sit-and-wait hunting mode to actively hunting when in the presence of *A. mauryi*. In contrast, under predation risk, *A. mauryi* did not change its level of activity but became more vigilant by reducing the frequency of rest, hydration, and mating attempts. Activity of *A. mauryi* was positively correlated with air humidity whereas activity of *T. pusillus* was negatively correlated. This work highlights the influence of intraguild predators in the behavioral decisions during daily activities of each other, indicating adaptive behaviors in both prey and predator.

Keywords Adaptive behavior · Adaptive foraging · Antipredator behavior · Daily activity · Intraguild predation · Scorpions

Introduction

Prey-predator relationships have been a central issue in many behavioral studies focusing on how species may modify their behavioral decisions in order to increase their survival. Traditionally, many studies have focused on how animals can change their behavior and habitat exploitation activities to avoid predation, as well as to optimize prey encounter during foraging (e.g., Snyder and Wise 2000; Okuyama 2002; Schmidt et al. 2012, 2014; Wilkinson et al. 2015; Belgrad and Griffen 2016; Nisani et al. 2018). In many ecological systems, such interactions involve species acting as both predator and competitor for similar food resources, a phenomenon termed intraguild predation (IGP) (Holt and Polis 1997; Polis et al. 1989). The relationship between intraguild predators is particularly important because of the potential of IGP to affect community structure and diversity, regulate trophic cascades in food webs, and influence ecosystem productivity and population dynamics (Polis and McCormick 1986, 1987; Holt and Polis 1997; Kondoh 2008; Stouffer and Bascompte 2010; Ryan and Cantrell 2015). Furthermore, behavioral decisions to avoid predation between intraguild predators play a key role in the persistence of species in complex food webs (Okuyama 2002; Kondoh 2003, 2007; Urbani and Ramos-Jiliberto 2010). For instance, Okuyama (2002) found that the jumping spider *Phidippus octopunctatus* (Peckham & Peckham, 1883) reduced its foraging activity in the presence of its predator, *Phidippus audax* (Hentz, 1845), to avoid predation and consequently they reduced their predation rate on a shared prey, *Drosophila melanogaster* (Meigen, 1830).

✉ Welton Dionisio-da-Silva
weltonxdc@gmail.com

1 Programa de Pós-Graduação em Ciências Biológicas, Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, João Pessoa, PB CEP 58051-090, Brazil

2 Programa de Pós-graduação em Biologia Animal, Departamento de Zoologia, Centro de Biociências, Universidade Federal de Pernambuco, Recife, PE CEP 50670-420, Brazil

3 Programa de Pós-Graduação em Ciência Animal Tropical, Departamento de Morfologia e Fisiologia Animal, Universidade Federal Rural de Pernambuco, Recife, PE CEP 52171-900, Brazil

As IGP generally occurs when small species are preyed upon by larger ones (Polis et al. 1981; Polis and McCormick 1987; Moreno-González and Hazzi 2012; Lira et al. 2017a, b), it is expected that the smaller species have behavioral mechanisms to coexist with their intraguild predators (Urbani and Ramos-Jiliberto 2010). For instance, smaller scorpions avoid the period of higher activity of larger scorpions (Polis and McCormick 1987) in addition to changing foraging sites to avoid predation risk (Sánchez-Piñero and Urbano-Tenorio 2016). Furthermore, the surface activity of arthropods can be influenced by microclimate variations; these animals can increase their activity at optimal values of air temperature and humidity to avoid desiccation risk (Cloudsley-Thompson 1962) or even to maximize their locomotor performance, such as other ectothermic animals (Carlson and Rowe 2009; Nime et al. 2013; Webber et al. 2015).

Thus, considering the potential of interactions between intraguild predators to influence the stability of food webs and population dynamics, we investigated the behavior of two intraguild predators in the presence of each other (a prey-predator system), the scorpions *Tityus pusillus* Pocock, 1893 and *Ananteris mauryi* Lourenço, 1982. Furthermore, we evaluated whether variation of air temperature and humidity along the nocturnal period would influence their surface activity. *Tityus pusillus* and *A. mauryi* are two sympatric scorpions co-occurring on leaf litter (Lira et al. 2018). However, *A. mauryi* are smaller scorpions (adult size, 13.6–24.1 mm compared with 24.1–34.9 mm of *T. pusillus*; Lira et al. 2018) which can be harmed in antagonistic interactions with *T. pusillus* (Lira et al. 2017a). *Tityus pusillus* is a sedentary scorpion hunting in upper layers of leaf litter and waiting for prey in ambush posture (Lira et al. 2013, 2018). Conversely, *A. mauryi* are more active spending time wandering and actively hunting their prey, moving around mainly through the bottom layers of leaf litter in the interstitial spaces between leaves (Lira et al. 2013, 2018). In such microhabitat, *A. mauryi* can find small arthropods to feed on and greater complexity of habitat that allows avoidance of predation (Schmidt and Rypstra 2010; Kalinkat et al. 2013). Therefore, we predict that *A. mauryi* will reduce their activity in the period of greater activity of *T. pusillus*. In addition, we predict that *A. mauryi* will change its behavioral acts to enhance the predator avoidance, whereas *T. pusillus* will perform more acts that optimize the predation. We think that *T. pusillus* will be more active at high air temperature and low humidity, whereas, in contrast, *A. mauryi* will be more active at low temperature and high humidity.

Methods

Sample collection and maintenance

Tityus pusillus and *A. mauryi* individuals were collected from Campo de Instrução Marechal Newton Cavalcante (07° 50′ 32.7″ S, 035° 06′ 33.2″ W), a semi-deciduous second-growth fragment of Atlantic Forest, northeast Brazil. Field collections were carried out by four researchers between April 2018 and June 2018 at 19:00 and 22:00 h using UV flashlights. Scorpions were identified by species, following procedure of Lourenço (2002), and separated by age (immature or adult) and sex. No juveniles or pregnant females were used in this experiment. The animals were kept individually in plastic terraria (9.5 cm of diameter and 7.5 cm of depth) containing shelter (cardboard), water supply, and fed weekly with cockroach nymphs, *Nauphoeta cinerea* (Olivier, 1789). Before the experiments, scorpions were kept under observation for a period of 30 days to assure that the individuals were healthy; they were then left without food for a week to stimulate foraging during the trials.

Experimental trials

Experiments were performed using rectangular arenas (47 × 31.5 × 15.5 cm) containing a 3-cm layer of sifted leaf litter (previously dried at 50 °C for 24 h) and ten leaves of Fabaceae (~ 12 cm in length) to serve as shelter. Two water-soaked cotton balls were available in the arena as an ad libitum water source. Immediately before the experiments, scorpions were marked with non-toxic paint on the dorsal surface of the mesosoma to facilitate identification during the behavioral observations. All experimental trials were conducted with arenas placed outdoors to have a gradual switch between light and dark periods.

We first determined the daily activity and behaviors of the scorpions so as to classify their behavioral acts. *Tityus pusillus* and *A. mauryi* ($n = 12$ per trial; sex ratio 1:1 each) were placed in different arenas and instantaneous scan samplings (Altmann 1974) were performed for 15 min every hour over a consecutive 48 h (12:12 light:dark period) with three replicates. Prior to experiments, animals were left in the arenas for 24 h to allow chemical cue dissemination, as these arachnids can be orientated by chemical stimuli (Abushama 1964; Brownell and Farley 1979; Nisani et al. 2018). Scorpions were considered active if they were not hiding below the leaves or cotton balls and could be seen by the observers performing any behavioral act except rest.

After characterization of the daily activity and scorpion behavioral acts, we evaluated the behavioral acts of the species in the absence and presence of each other. Trials consisted of conspecifics of *T. pusillus* (control 1), conspecifics of *A. mauryi* (control 2), and heterospecific pairs (treatment) to record behavioral changes under predation pressure; all trials had a sample size of 12 animals with a 1:1 sex ratio and were replicated six times. Treatment trials have 1:1 species ratio and 1:1 sex ratio and individuals of *A. mauryi* were initially placed for 24 h to expose their chemical cues on the substrate and then removed. After this period, *T. pusillus* were placed in the arena to allow for their chemical cue exposure for 24 h. Then, *A. mauryi* were reintroduced in the arena.

Observations started 1 h after acclimation. During acclimation, the animals only search and took shelter. In these experiments, scan samplings of 15 min every hour (Altmann 1974) were performed during the dark period (18:00–5:00 h) by two experienced observers (Dionisio-da-Silva W and Lira AFA) using a red-light lamp (Machan 1968). Frequency of behavioral acts were quantified during all observation period in the three experimental conditions. Temperature and relative humidity during the active period were only recorded for conspecific trials to avoid interference of heterospecific interactions in the number of active individuals rather than response to microclimatic conditions, using a digital thermohygrometer (Incoterm–7663.02.0.00).

Data analysis

Data normality was evaluated through of Jarque-Bera tests. Welch's *t* test was used to detect the effect of the heterospecific treatment on the proportion of active scorpions (*T. pusillus* and *A. mauryi*). Mann-Whitney's tests and Welch's *t* tests were performed to assess the differences in relative frequency of each behavioral act of *T. pusillus* and *A. mauryi* between treatments. Finally, Spearman's correlations were used to evaluate the relationship between the variables (air temperature and humidity) and avoid covariance; and also, to correlate the number of active scorpions with the corresponding values of air temperature and humidity for every hour (we used the data of the control arenas to avoid effect of the scorpions' competition). All analyses were carried out using normtest and Hmisc packages (Gavrilov and Pusev 2014; Harrell Jr. 2019) in R Studio v. 1.1.463 (RStudio Team 2019).

Results

Similar daily activities and variability levels of overall activity were observed when comparing the daily activity pattern of *T. pusillus* and *A. mauryi*. Based on a 48-h observation, the active period was determined as 18:00–05:00 h where 30–50% of *T. pusillus* and 30–80% of *A. mauryi* were active per hour. Only one *A. mauryi* and two *T. pusillus* remained active up to 06:00 h and 07:00 h, respectively (Fig. 1). During the light period, all *T. pusillus* individuals rested below the leaves while *A. mauryi* rest below the wet cotton balls. All behavioral acts observed were classified into five categories, of which immobility and exploration were further subdivided into two (Table 1). Both species differed in the hunting mode, with *T. pusillus* mostly in the alert behavior (73.3%), while *A. mauryi* was in the foraging behavior (56.84%).

During the experiment period, humidity and temperature varied between 70 and 86% and 25.5 and 28.4 °C, respectively. We used only air humidity in posterior analysis because of its covariance with air temperature (Spearman rank correlation, $r_s = -0.52$; $P = 0.0095$). Nocturnal activity of both scorpion species exhibited a distinct relationship with air humidity. The number of active *T. pusillus* was negatively correlated with air humidity ($r_s = -0.34$, $P = 0.0032$). In contrast, *A. mauryi* was positively correlated with air humidity ($r_s = 0.33$, $P = 0.0047$).

During the heterospecific trials, in contrast to the conspecific trials, *T. pusillus* was stimulated to increase their predation, and significantly increase their number of active individuals (72.7% of individuals were active; Welch's *t* test, $T_{14.84} = -11.09$; $P < 0.0001$) and their foraging activities on the substrate ($T_{9.23} = -2.37$, $P = 0.0498$). Individuals spent 6.75 ± 2.73 h (mean ± SD) feeding on one *A. mauryi*. They usually eat the entire individual, excluding the pincers and telson. In contrast, the number of active *A. mauryi* was similar on the presence or absence of *T. pusillus* (Welch's *t* test, $T_{20.32} = -1.37$; $P = 0.1862$). However, *A. mauryi* modified their behavior in the presence of the predator, reducing rest ($T_{8.06} = 3.44$, $P = 0.0086$), hydration (Wilcoxon-Mann-Whitney test, $W = 36$; $P = 0.0036$) and mating attempts ($W = 30$, $P = 0.0284$; Table 1).

When the predators (*T. pusillus*) contacted the prey (*A. mauryi*) the latter immediately tried to walk away to avoid predation. Despite this, 55.56% of the *A. mauryi* individuals

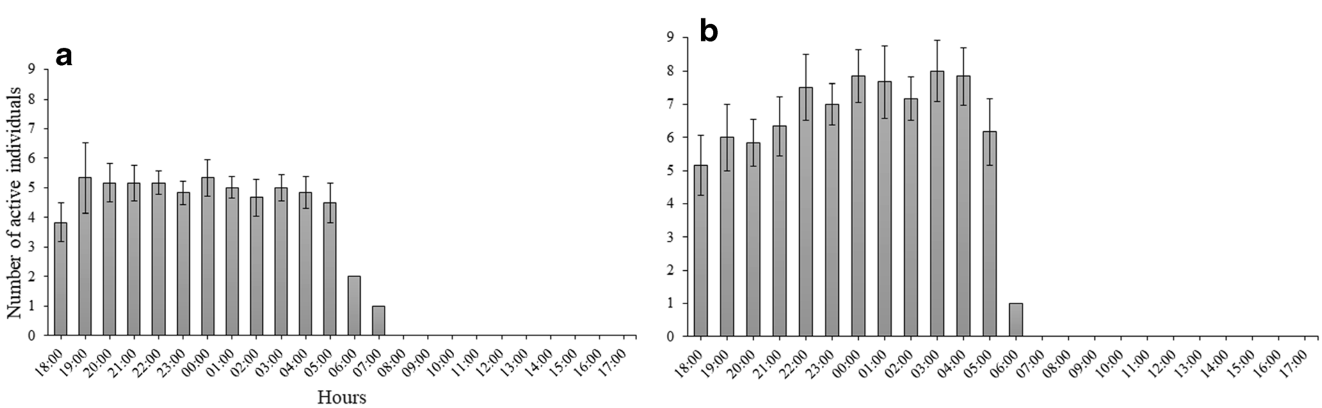

Fig. 1 Period of activity of **a** *Tityus pusillus* Pocock, 1893 and **b** *Ananteris mauryi* Lourenço, 1982 during a 24-h period (mean ± SE). The dark period (night and dawn) was between 18:00 and 5:00 h

Table 1 Behavioral acts performed by *Tityus pusillus* Pocock, 1893 and *Ananteris mauryi* Lourenço, 1982 and the relative frequency of the behavioral acts in conspecific (control) and heterospecific (treatment) arenas

Behavioral act	Description	*Tityus pusillus*		*Ananteris mauryi*	
		Control	Treatment	Control	Treatment
1. Immobility					
1.1 Rest	Individuals are motionless with closed pincers.	1.63	2.1	*7.16*	*0.52*
1.2 Alert	Individuals are motionless with open pincers.	73.3	62.5	17.6	20
2. Exploration					
2.1 Foraging	Individuals walking slowly or fast around the arena with open pincers.	*14.52*	*27.07*	56.84	70.52
2.2 Climbing	Individuals trying to climb the arena	5.4	6.25	2.6	5.8
3. Cleaning	Individuals rubbing their pincers in the exude from their oral appendages.	2.34	1.56	1.62	1.07
4. Hydration	Individuals keeping on the water supply.	1.87	0	*12.38*	*1.57*
5. Mating attempt	Male trying to mate with females by grasping them with open pincers.	0.94	0.52	*1.8*	*0.52*

Frequencies in italics indicate statistically significant differences between control and treatment in each species

were captured by *T. pusillus*. Of those captured, 4.71% used metasoma autotomy by shedding their "tail" to escape from predation.

Discussion

Our results showed that, despite *T. pusillus* and *A. mauryi* scorpions cohabiting in the leaf litter, they clearly differ in their habits, in their relationship with air humidity, and in the frequency of behavioral acts when in the presence of heterospecifics. Overall, *T. pusillus* spent more time in the alert behavior with a sit-and-wait posture. However, in response to the presence of *A. mauryi*, this species increased their surface activity and the frequency of foraging (actively hunting). In contrast, when perceiving the presence of its predator, *A. mauryi* did not change their surface activity but changed behavioral acts that would reduce their predation risk; for example, they became more vigilant by reducing rest, hydration, and mating attempts.

In the experimental trials, the conspecific and heterospecific arenas had equal density of scorpions, which are visually weak animals (Hjelle 1990). Therefore, differences in the behavior are likely to result from response to chemical cues. Arthropods, including some scorpions, can use airborne and substrate chemical cues to detect conspecifics, competitors, and prey to optimize foraging or avoid predation and competition (e.g., Miller and Formanowicz 2011; Hettyey et al. 2015; Binz et al. 2016; Nisani et al. 2018; Pears et al. 2018). In the presence of *A. mauryi*, *T. pusillus* were much more active and increased the frequency of foraging (active hunting) rather than the alert behavior (sit-and-wait posture). The sit-and-wait hunting mode is efficient when prey are scarce because it has a low energy cost and increases the encounter rate when the predator cannot move faster than prey. However, when prey are abundant, have a clumped distribution, or there is interspecific competition, it is more efficient for the predator to shift to actively hunting (Huey and Pianka 1981; Fausch et al. 1997; Fulton and Bellwood 2002; Scharf et al. 2006). Furthermore, Santos et al. (2018) showed that *A. mauryi* populations have a clumped distribution. Therefore, *T. pusillus* could have increased their activity and foraging to increase the efficiency in predation of *A. mauryi*.

Because sit-and-wait predators are sedentary, they have a narrow extent of movement and their chemical cues on the substrate indicate a strong predation risk for their prey, which can then alter the level of activity or microhabitat use to avoid predation (Persons et al. 2001; Preisser et al. 2007; Schmitz 2008). However, *A. mauryi* did not change their level of activity in the presence or absence of *T. pusillus*, suggesting a distinct strategy of this species. *Ananteris mauryi* avoided behavioral acts that would increase their predation risk such as rest, hydration, and mating attempts. However, it is not clear whether *A. mauryi* can perceive *T. pusillus* presence through its airborne and substrate chemical cues or just touching him with pedipalps, which have resulted in fast avoidance of *A. mauryi* in our observations.

Interestingly, *A. mauryi* was more vigilant as indicated by decreasing rest but did not reduce foraging under predation risk by *T. pusillus*. To avoid predation in environments with high risk, animals can stay more vigilant by reducing their rest rather than their foraging (Sharpe and Van Horne 1998; Tchabovsky et al. 2001). In a motionless state, *A. mauryi* would be more vulnerable to capture by *T. pusillus* that forage more to find it. However, rest deprivation can be harmful to scorpions because it results in decreased alert behaviors and increased rest behaviors as a compensation, on the subsequent night (Tobler and Stalder 1988). Furthermore, *A. mauryi* also reduced hydration behaviors in the presence of the predator.

Although scorpions withstand a greater dehydration level (ca. 40% of their body mass) when compared with other arthropods (Cloudsley-Thompson 1962; Hadley 1974; Riddle et al. 1976), *Ananteris* are humiculous scorpions that have preference for moist environments and are more vulnerable to desiccation risk than other species (Lourenço 2015; Dionisio-da-Silva et al. 2018). Because hydration and rest behaviors are performed when the animal is immobile and vulnerable to attacks from enemies, the avoidance of these behaviors can reduce the predation risk but will increase desiccation risk.

Although it has potential to cause chronic physiological stress as well as known for other arthropods (e.g., Persons et al. 2002; Stoks et al. 2006; Dievel et al. 2016), for instance, Persons et al. (2002) observed that wolf spider *Pardosa milvina* (Hentz, 1844) had a negative physiological effect of being under constant predation risk. These spiders when exposed to chemical cues of their predator, *Hogna helluo* (Walckenaer, 1837), ate fewer prey to avoid predation risk, and, consequently, lost weight more quickly and produced lighter egg sacs with fewer eggs. Yet, as predator avoidance, the *P. milvina* climbed the walls of the experimental containers significantly more when silk and excreta of *H. helluo* were on the substrate. Climbing behavior is often reported to avoid predation by ground-dwelling arthropods (Brown and O'Connell 2000; Persons et al. 2002; Sánchez-Piñero and Urbano-Tenorio 2016). In contrast, *A. mauryi* does not have difference in the frequency of climbing in the presence of *T. pusillus*. *Ananteris mauryi* are more active in the bottom layers of the leaf litter, where there is greater complexity of habitat that improves predator avoidance, whereas *T. pusillus* are more active in the upper layers (Schmidt and Rypstra 2010; Kalinkat et al. 2013; Lira et al. 2013, 2018). Therefore, when *A. mauryi* were under predation risk of *T. pusillus*, they may have two escape responses: (1) avoid climbing as a natural avoidance of the upper layers of the leaf litter that are inhabited by *T. pusillus* and other large predators, or (2) climb the vegetation to avoid predation such as other arthropods do.

The presence of *T. pusillus* was also determinant for the decline of mating attempts of *A. mauryi*. Mating is dangerous to perform under predation risk because the courtship of scorpions may last a long time (several minutes) (Stockmann 2015; Olivero et al. 2017). Although information about courtship of *Ananteris* is scarce (Mattoni et al. 2015), Dionisio-da-Silva et al. (2018) found that *A. mauryi* presents a non-overlapping reproductive period with *T. pusillus*, reproducing in the dry season, whereas *A. mauryi* reproduces in the rainy season. These authors speculate that such strategy may be a combination of predation avoidance by *A. mauryi* and the distinct moisture requirements of these species (*A. mauryi*: high humidity; *T. pusillus*: low humidity). Our findings support this assumption as *A. mauryi* reduced its mating behavior in the presence of *T. pusillus* and they also have a greater number of active individuals during high humidity, contrary to *T. pusillus.*

Small invertebrates avoid temperature and humidity conditions that cause water loss because desiccation is a major physiological risk for them (Cloudsley-Thompson 1962). Furthermore, the resistance to desiccation depends on their abundance of cuticular lipids and body surface area in proportion to their mass (Cloudsley-Thompson 1962; Toolson and Hadley 1977; Polis 1990; Lourenço 2012). Thus, small-sized animals are more susceptible to water loss, such as *A. mauryi* that have preference for moist environments and inhabits the humid bottom layers of the leaf litter (Cloudsley-Thompson 1962; Sampaio et al. 1993; Lourenço 2012; Lira et al. 2018). Therefore, under high air humidity, *A. mauryi* increased their activity in order to avoid water loss. Moreover, they also had a preference for resting in humid places (under the wet cotton) during the period of inactivity (light period). In contrast, for *T. pusillus*, there were a greater number of active scorpions when air humidity was low what suggests that they are more resistant to water loss than *A. mauryi*. It was probable that *T. pusillus* used the air humidity as an indicator of ecological condition rather than a physiological requirement. *Tityus pusillus* could avoid higher relative humidity to avoid surface activity during rainfall periods. Strong negative effects of diurnal rainfall were observed on the surface activity of the wandering spider *Phoneutria reidyi* (FO Pickard-Cambridge, 1897) (Queiroz and Gasnier 2017). Because the rainfall washes chemical cues of prey and predators, it makes difficult to perceive prey and risk of predation. Therefore, decreased activity in a humid environment would be beneficial to optimize foraging (Queiroz and Gasnier 2017).

Overall, our predictions were partially corroborated. *Tityus pusillus* and *A. mauryi* had a similar period of activity during the night; however, *T. pusillus* were more active in periods of low air humidity, whereas *A. mauryi*, which are more vulnerable to desiccation, have a preference for high humidity. Furthermore, both species had adaptive behavior in the presence of each other, but just *T. pusillus* increase the number of active individuals. *Tityus pusillus* optimize their foraging by increasing their activity and shifting from the sit-and-wait hunting mode to actively hunting. While *A. mauryi* did not change their activity level, they showed a strong antipredator behavior due to their several changes in their behavioral decisions to enhance their survival in the presence of a predator.

This work highlights the influence of an intraguild predator in the behavioral decisions during daily activity of an intraguild prey as well as the inverse. Yet, it elucidates how combination of response to microclimatic variation and adaptive behavior between prey and predator could be associated with non-overlapping reproductive periods and spatial partitioning of these animals recorded in previous studies.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article did not contain any studies with human participants and also did not involve endangered or protected species. It was approved by Sistema de Autorização e Informação em Biodiversidade/Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO/ICMBIO no. 36336-1) and complied with Brazilian law. All procedures of this work were determined to assure the animals' welfare. Animal collection and handling was conducted with the use of tweezers without harming the animals. The experiments were conducted with only healthy animals. Water supply and shelters were made available for the animals during the experimental trials, and food was also made available during their rearing. Application of non-toxic paint markings on the individuals during the experiments is a minimally invasive technique. The animals were returned to the wild after the study.

Informed consent This article did not contain any studies with human participants.

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