Playing dead to stay alive: death-feigning in *Liolaemus occipitalis* (Squamata: Liolaemidae)

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Abstract: Predation is the major selective force that drives the development of a series of defense mechanisms by the species. These mechanisms are efficient in that it limits the ability of predators to detect, recognize and subdue their prey. In lizards for example, the tail loss and locomotor escape are the most common defensive behavior reported on the literature. Additionally, in response to external stimuli, some lizards exhibit a peculiar defensive behavior: death-feigning or thanatosis. Here we describe the first record of death-feigning in a population of *Liolaemus occipitalis* in a coastal sand dune habitat in Southernmost Brazil. A total of 86 individuals were tested. During handling 75.6% of lizards feigned death. The duration of this behavior was longer when the observer remained closer to the lizards, suggesting the ability of *L. occipitalis* to evaluate the predation risk.
Keywords: *thanatosis, behavior, sand-dune lizard, pampa, restinga.*

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Resumo: A pressão exercida pela predação é a principal força seletiva que direciona o estabelecimento de uma série de mecanismos de defesa por parte das espécies. Esses mecanismos são eficientes na medida em que limitam a capacidade dos predadores em detectar, reconhecer ou subjugar suas presas. Em lagartos, por exemplo, os comportamentos defensivos mais frequentemente citados na literatura são a autotomia caudal e a fuga. Além disso, em resposta a estímulos externos, alguns lagartos podem exibir um comportamento peculiar: fingem-se de mortos (tanatose). Neste estudo descrevemos o primeiro registro de tanatose em uma população de *Liolaemus occipitalis* em área de dunas costeiras no extremo Sul do Brasil. Um total de 86 indivíduos foram testados. Durante o manuseio, 75,6% dos lagartos exibiram o comportamento de tanatose. A duração deste comportamento foi maior quando o observador permanecia a distâncias mais curtas dos lagartos, sugerindo uma capacidade de *L. occipitalis* em avaliar o risco de predação.
Palavras-chave: *tanatose, comportamento, lagartixa-das-dunas, pampa, restinga.*

Introduction

In general, animals show a series of traits and defensive mechanisms to avoid predation and stay alive. Organisms reduce the probability of being predated by using many adaptations or behavioral strategies, which may present specific behaviors (displays) that can discourage a predator's attack (Greene 1988). Predation pressure is a fundamental selective force for the development of a series of traits that increase prey survival, by limiting the predator ability to detect, recognize, approach, subjugate or consume the prey (Endler 1986, Greene 1988, Lima & Dill 1990). In general, antipredator mechanisms are an important factor in the evolutionary processes of many animals (e.g., Vermeij 1982, Lima & Dill 1990). Vertebrates, in particular the Squamata, exhibit extremely diverse antipredator tactics (e.g., Pough et al. 2004, Rocha 1993), making this group an interesting model to examine evolutionary mechanisms to avoid predation (e.g., Greene 1988). In snakes, many defensive displays have been characterized including various ways of intimidating or avoiding aggressors (Greene 1988, Tozetti et al. 2009). Unfortunately, much less information is available on the defensive behavior of lizards compared to snakes. The most reported defensive behavior of lizards in the literature is tail loss (autotomy) and locomotor escape (Greene 1988, Roberts et al. 1998, Rocha-Barbosa et al. 2008). Additionally, some lizards exhibit a peculiar defensive behavior: death-feigning. Death-feigning (thanatosis) is a state of immobility assumed by many animals in response to external stimuli. This behavior has been considered a defense mechanism against predators and is shared by mammals (e.g., Francq 1969), birds (e.g., Sargeant & Eberhardt 1975), fishes (e.g., Howe 1991), amphibians (e.g., Gargaglioni et al. 2001, Bertoluci et al. 2007), reptiles (e.g., Greene 1988), and insects (e.g., Acheampong & Mitchell 1997). Death feigning is also known as catalepsy, or tonic immobility. In most cases, animals that exhibit this behavior "play dead" by maintaining a rigid posture or by simulating fully relaxed muscles (e.g. fainting; Greene 1988). Apparently thanatosis is a behavior that rarely occurs spontaneously (Greene 1988). Immobility might discourage sequential attacks, allowing escape, as demonstrated in experiments using invertebrates (Miyatake et al. 2004). While efficiency in this defensive behavior have been poorly tested, its occurrence in several vertebrate groups suggests a favorable evolutionary pressure toward its maintenance (Miyatake et al. 2004). In frogs, for example, the thanatosis was pointed out as an important secondary defense mechanism in *Phillomedusa* (Sazima 1974). In lizards, death-feigning has been reported for several different families, such as Anelytropsidae (Torres-Cervantes et al. 2004), Crotaphytidae (Gluesing 1983), and Scincidae (Langkilde et al. 2003). Among tropidurid lizards, this behavior has been observed in *Eurolophosaurus nanuzae* Rodrigues, 1981 (Galdino & Pereira 2002), *E. divaricatus* Rodrigues, 1984 (Gomes et al. 2004, Kohlsdorf et al. 2004) previously *Tropidurus nanuzae* and *T. divaricatus* (Frost et al. 2001), *T. torquatus* Wied, 1820 and *T. hispidus* Spix, 1825 (Bertoluci et al. 2006). Bertoluci et al. (2006) has also reported anecdotal records for several other species in the tropidurid family. Among Liolaemidae, this behavior has been reported only in *Liolaemus lutzae* Mertens, 1938 (Rocha 1993). This family consists of 229 species (including subspecies) belonging to the genera *Ctenoblepharys*, *Phymaturus,* and *Liolaemus*. The latter comprises most of the species of the family, with 200 species (Pincheira-Donoso et al. 2008a). Considering the great diversity in ecological specializations and morphology, *Liolaemus* is an important group to study adaptive radiations (Pincheira-Donoso et al. 2008b). The South American *Liolaemus* lizards occurs in Argentina, Bolivia, Brazil, Chile, Paraguay, Peru, and Uruguay, which represents the widest range of environments occupied by a single lizard genus. The *Liolaemus occipitalis* Boulenguer, 1885 is a small sand-dune-lizard associated to coastal habitats and its geographic distribution restricted to Rio Grande do Sul and Santa Catarina States, southern Brazil (Bujes & Verrastro 2008), and Uruguay (Verrastro et al. 2006). It is primarily an insectivorous reptile that reproduces between September and March (Verrastro & Krause 1994). Despite being a threatened species (Marques et al. 2002), available data on its natural history and behavior obtained in the field are scarce. In addition, the impact that sand dune habitats have been enduring highlight the importance of ecological studies on species associated to this environment (Seeliger 2003). Here we report observations of the defensive behavior of *L. occipitalis* in nature and the first record of death-feigning in this species.

Methods

The data presented in this study was collected between November 2009 and January 2010 in the municipality of Rio Grande, RS, in an area known as Balneário Cassino, southernmost Brazil (32º 07' 54.65'' - 32º 17' 35.07'' S and 52º 06' 38.80'' - 52º 20' 53.36'' W) located at sea level. The area consists of well preserved wet habitats formed by meadows with a mosaic of dunes, sand dune vegetation and temporary lagoons. The climate is classified as subtemperate (Maluf 2000), with an average annual maximum temperature of 23.3 °C and average annual minimum temperature of 12.7 ºC. The seasons are well defined, with rainfall homogeneously distributed along the year and averaging 1252 mm between 1931and1990 (INMET 2010). During field surveys of the regional herpetofauna, we captured 86 individuals of *Liolaemus occipitalis* using pitfall traps with drift fences (Brasileiro et al. 2005). The lizards remained a maximum of eight hours in buckets containing water and shelter to protect them against the sunlight, minimizing the stress on captured animals. All lizards were handled carefully during measurements (body size and mass), sex determination, and assessment of the reproductive condition of females by palpation (Fitch 1987). While being held, some individuals feigned death (Figure 1). The animals that exhibited this behavior were immediately placed on the ground and observed from two distances, 1 and 7 m, whose order was set at random. In one of the distances, individuals were observed until recovery. The animal was then captured by hand and if death-feigning was observed again, the observation was repeated from a second distance from the lizard. The duration of the behavior was recorded in each observation. Only animals that exhibited this behavior from the two distances from the observers (treatments) were considered. Because this species exhibit intraspecific agonistic interactions (M.B. Santos, personal observation), we only tested individuals that were alone in the traps. This measure was taken to reduce the stress level of lizards prior to manipulation. Each observation was considered a sample. Comparisons between the durations of the behavior from different distances were conducted with a paired Wilcoxon test (Zar 1999). After recording the behavior, lizards were toe-clipped (Waichman 1992) before being released five meters from traps. Recaptured animals were not included in the behavior assessment.

Results and Discussion

Eighty-six lizards (47 males, 31 females, and 8 juveniles) were captured. The average size of animals was 47.5 ± 9.3 mm SVL (range - females: 37.0 – 66.0 mm; males: 40.0 – 63.0 mm; juveniles: 22.0 – 30.0 mm) and the average body mass was 3.60 ± 1.6 g (range - females: 1.3 – 5.3 g; males: 1.8 – 7.8 g; juvenile: 0.3 – 0.8 g). During handling, 65 lizards (75.6%) feigned death, 35 were males, 23 were females and seven were juveniles (Figure 2). This represents 74.5% of males, 74.2% of females, and 87.5% of juveniles.

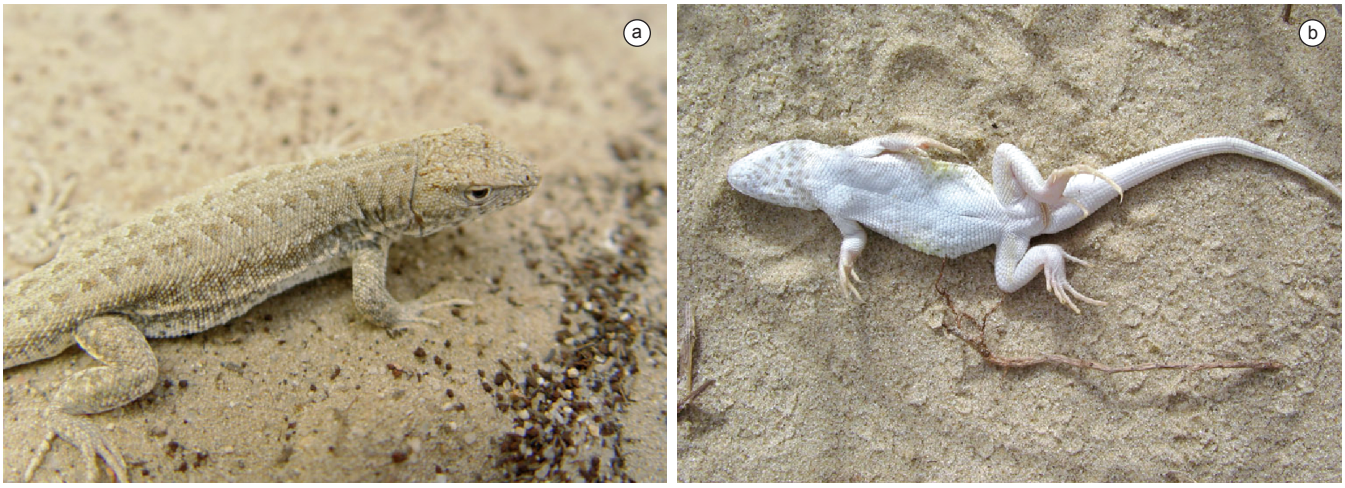

Figure 1. a) general aspect of an individual of *Liolaemus occipitalis* Boulenguer, 1885; and b) an individual feigning death.

Figura 1. a) aspecto geral de um indivíduo de *Liolaemus occipitalis* Boulenguer, 1885; e b) indivíduo exibindo o comportamento de tanatose.

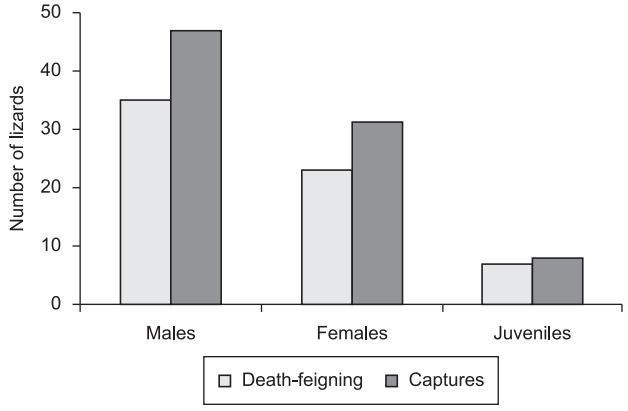

Figure 2. Absolute number of *Liolaemus occipitalis* lizards captured by pitfall traps with drift fence and number of lizards that feigned death during handling.

Figura 2. Número absoluto de indivíduos de *Liolaemus occipitalis* capturados em armadilha de interceptação e queda e que apresentaram o comportamento de tanatose durante a manipulação.

The death-feigning behavior observed in our study was similar to that described in *Tropidurus* species by Bertoluci et al. (2006). During handling, *L. occipitalis* lizards exhibited very relaxed muscles, remained immobile in the observer's hand, and maintained this posture when placed on the ground (Figure 1). During death-feigning, simultaneous slow and lateral tail movements and intermittent movements of opening and closing the eyes were observed. Some studies show that habitat characteristics confer different probabilities of predation of lizards (Shepard 2007). Although *L. occipitalis* is associated with open environments like sand dunes, the presence of shrubs, even sparse ones, provides shelter and protection against predators (Bujes & Verrastro 1998). In addition, the cryptic coloration and the ability of digging burrows are probably its main strategies against predation. Also, *L. occipitalis* is an ambush forager (M.B. Santos, personal observation), which might decrease the time of exposure to visually-oriented predators. Apparently, when a predator is detected, the main active defense strategy of *L. occipitalis* is to escape and the capacity of burying (Bujes & Verrastro 1998). However, the capacity of escape, especially the speed, depends on body temperature as well as reproductive conditions (Shine 1980, Plummer 1997, Miles et al. 2000). As a result of these constraints, a diversification in defense strategies might increase the probability of survival of individuals. Because thanatosis only occurs if stimulated (e.g. handling), this could indicate that this strategy represents an extreme measure used after a first attack by the predator. Thus, escape and cryptic behavior combined represents ways to avoid perception or capture, while death-feigning might be a strategy used when the lizard has been already captured by the predator. It should be pointed out that the duration of thanatosis was significantly longer ($T = 0.0$; $P = 0.028$; $n = 12$) when the observed remained near (average duration = 10.2 $\pm$ 1.99 minutes; range = 7.2 - 12.7 minutes) than when the observed was farther away from lizards (average duration = 2.0 $\pm$ 1.14 minutes; range = 0.5 - 3.83 minutes), suggesting that the animals are capable of evaluating the threat level.

It should be pointed out that during previous studies conducted with other populations of *L. occipitalis,* death-feigning was rarely observed (M.B. Santos, personal observation). The high frequency of records of this behavior in the population of the present study might be associated with a selective process toward this defensive mechanism. Studies on experimental handling demonstrated that the duration of death feigning observed in insects was a result of different selection pressures caused by predation (Prohammer & Wade 1981). However, in our study, this hypothesis still needs to be further investigated with experimental studies in which the actual predation pressure is quantified, as well as the efficacy of death-feigning to avoid the action of predators.

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