

Observations on the escape behaviour in *Teius oculatus* and *T. teyou* (Reptilia: Squamata: Teiidae)

Pier CACCIALI^{1,2,3,*}, Gunther KÖHLER¹ and Raúl MANEYRO⁴

1. Senckenberg Forschungsinstitut und Naturmuseum, Senckenberganlage 25, 60325, Frankfurt a.M., Germany.

2. Guyra Paraguay, Av. Cnel. Carlos Bóveda, Parque Asunción Verde, Viñas Cué, Paraguay.

3. Instituto de Investigación Biológica del Paraguay, Del Escudo 1607, Asunción, Paraguay.

4. Laboratorio de Sistemática e Historia Natural de Vertebrados, Facultad de Ciencias,
Universidad de la República, Iguá 4225, Montevideo, Uruguay.

*Corresponding author, P. Cacciali, E-Mail: pcacciali@senckenberg.de

Received: 10. March 2015 / Accepted: 26. August 2015 / Available online: 29. May 2016 / Printed: June 2016

Abstract. Lizards exhibit a variety of anti-predator strategies, but the most commonly used is escape. In the case of the lizard genus *Teius* they use mimesis with vegetation as a first strategy and escape as the second tactic. These lizards are fast runners and can run even using only the hind legs. Here we present data on the escape behaviour on *Teius oculatus* and *Teius teyou* in different environments. A total of 30 days of field work were carried out in different areas of Paraguay during 2013 and 2014. We analysed a total of 103 records of *Teius teyou* and 35 of *T. oculatus*. All individuals of *T. oculatus* kept a close distance to vegetation/shelters, while *T. teyou* were more exposed to sight. Differences in foraging distances from the shelters between *T. teyou* and *T. oculatus* are statistically significant ($K=0.2952$, $p=0.9609$). Approach distance was similar between these two species ($U=1687.5$, $Z=5.28$, $p\leq 0.01$), but usually *T. oculatus* allowed a closer approach distance. After the first sprint (once a lizard was detected) *T. oculatus* almost always remained under the vegetation, while *T. teyou* showed more diverse patterns of behaviour; there was a significant difference between the species ($\chi^2=51.069$, $df=3$, $p<0.0001$). These are the first records of escape behaviour in lizards of the genus *Teius*. Knowledge of behaviour and habitat use can help addressing conservation actions in places with anthropogenic alterations. In this case, *T. teyou* is a species adapted to forage near human dwellings and can be even present in gardens. On the other hand, *T. oculatus* seems to be shyer, but is able to inhabit small vegetation patches. Despite being two species living close to humans, the preservation of different kinds of shelters may be required to maintain the suitability of the habitat.

Key words: approach distance, anti-predator strategy, lizards, shelter use, Paraguay.

Introduction

The most common anti-predator strategies used by lizards are mimesis and escape (Cloudsley-Thompson 1994). Nevertheless, there are complex mechanisms involved in these tactics that depend on whether the predator detects the prey and if the prey is caught or not (Martins 1996). These mechanisms are important because they represent co-evolutionary interactions between predator and prey where natural selection plays a central role (Schall & Pianka 1980). Because the costs of fleeing could be high, sprints in lizards are observed only when predators represent a serious threat (Burger & Gochfeld 1990, Cooper 1997, Kramer & Bonenfant 1997, Martín & López 1999). A high rate of harassment by predators can lead to a higher shyness and wariness by lizards (Stone et al. 1994).

Furthermore, environmental features like vegetation can influence the escape behaviour in lizards and therefore the interactions between predator and prey (Bulova 1994, Downes & Shine 1998). The vegetation can provide a better shelter

when it is dense and lizards flee from threats earlier when vegetation is sparse (Martín & López 1995). In some cases the lizard's sprint performance depends on temperature (Waldschmidt & Tracy 1983), improving with the increase in temperature (up to a point). Reproductive state and body size also seem to affect flee behaviour in lizards (Bauwens & Thoen 1981, Martín & López 2003). In conclusion, the escape behaviour in lizards can vary depending on several factors.

Records of predators of *Teius* are scarce, but include *Speotyto cunicularia* (Burrowing Owl), *Mivago chimango* (Chimango), *Oxyrhopus rhombifer* (False Coral Snake), *Philodryas aestiva* (Common Green Racer), *P. mattogrossensis* (Miranda Green Racer), *P. patagoniensis* (Patagonian Racer), *Erythrolamprus miliaris* (South American Water Snake), and *E. poecilogyrus* (Wied's Groundsnake) (Bruch 1925, Gallardo 1977, Carreira Vidal 2002, Tejerina et al. 2005, Cabrera 2009, Weiler & Núñez 2015). Nevertheless, probably several birds and mammals use *Teius* as a potential dietary source.

With respect to the three species in the genus

Teius no information is available on their defensive behaviour. These diurnal lizards are exceptional runners and can often be observed basking in the sun or searching actively for prey (mainly arthropods) (Cappellari et al. 2007, Carreira & Maneyro 2013). *Teius* were described as opportunistic feeders of any available invertebrate and occasionally small vertebrates, carrion, and even fruits (Hutchins et al. 2003).

The brown and green colouration of *Teius* could be used for mimesis with the vegetation; nevertheless, the lizard is vulnerable and easily detected on vegetation-free grounds. Cei (1993) stated that *T. teyou* is a good runner, running from one shrub to another (occasionally in bipedal manner) during the hottest hours of the day. Nevertheless, Cacciali & Köhler (2014) reported that the activity of this species decreases during hottest hours (12:00–15:00) in the summer months (December–February); however, these authors also observed crepuscular activity in *T. teyou* (i.e. in the short twilight period after sunset and before darkness)

There are some references about other Teiinae's escape behaviours such as *Ameiva ameiva* stating that this species always runs away when a potential predator approaches close, but frequently stops and continues slowly if the person (or any other threat) remains motionless (Avila-Pires 1995). Additionally, *A. ameiva* is very noisy when moving through vegetation and its presence can be inferred easily without looking directly at the animal (Avila-Pires 1995).

Here we provide the first systematic field observation data on escape behaviour of *Teius oculatus* and *T. teyou* from different localities of Paraguay.

Materials and methods

Data collection

We carried observations on *Teius oculatus* and *T. teyou*, two of the three species that compose the genus.

Thirty days of field work were conducted in five different areas of Paraguay during 2013 and 2014 (Table 1). In each area we actively searched for *Teius* along roads (when available), trails, or paths, and also randomly through the vegetation. Usually observations started around 8:00 h when we performed an active search of lizards at intervals of 1.5 to 2 hours. Daily observations finished around 20:00 h, depending on the climatic conditions.

When individual *Teius* were detected they were discriminated into categories depending on how far they were from the closest bush. Categories were: ≤ 5 cm, 6–20cm, 21–50cm, and ≥ 51 cm (Fig. 1). Their burrows might not be necessarily in the closest bush, but shrubs and tall grasses provide the first shelter for the lizards. Individuals observed crossing roads were not included in the category ≥ 51 cm, because roads were not always available at the sites. Thus, only animals basking and foraging were included.

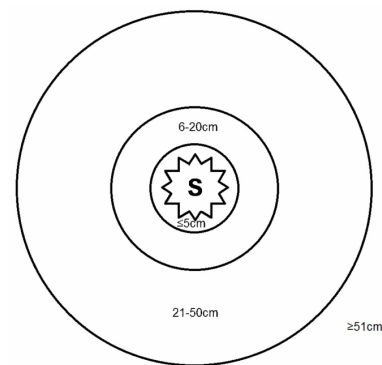


Figure 1. Schematic representation of categories or intervals of distance from the lizards to the shelter (S).

Sometimes the lizards started to run before they were seen, and thus it was not possible to assess the exact approach distance (distance at which lizards started to run from the observer *sensu* Martín & López 2000).

Based on preliminary observations we defined four categories of activity once the lizard started to run:

1. Enter a shelter. The lizard runs straight into a refuge. It is important to note that “enter a shelter” does not necessarily imply entry of a burrow. Here, cover vegetation (usually the closest) is considered a first shelter, although usually the burrow was in the closest shelter.

Table 1. Localities and dates of surveying and species studied in each area.

Locality	Dates	Location	Coordinates	Target species
Itakyry 1	11-15.11.2013	District of Itakyry, Alto Paraná	25°01'53"S, 54°59'33"W	<i>Teius oculatus</i>
Itakyry 2	26-30.12.2013	District of Itakyry, Alto Paraná	24°58'26"S, 55°03'42"W	<i>Teius oculatus</i>
San Rafael	27-31.01.2014	Distrito Alto Verá, Itapúa	26°30'42"S, 55°47'20"W	<i>Teius oculatus</i>
Solito	16-20.12.2013	Near General Brugez, Presidente Hayes	24°17'27"S, 58°50'14"W	<i>Teius teyou</i>
Kumaré	17-21.12.2014	Near Asentamiento San Fernando, Concepción	22°53'51"S, 57°24'05"W	<i>Teius teyou</i>
Laguna Blanca	02-06.01.2014	Near Santa Bárbara, San Pedro	23°46'52"S, 56°17'29"W	<i>Teius teyou</i>

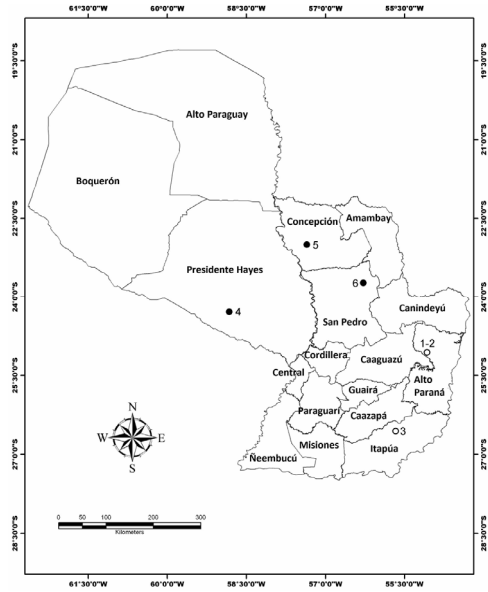


Figure 2. Localities sampled in this work. 1 and 2- Itakyry, 3- San Rafael, 4- Solito, 5- Kumaré, and 6- Laguna Blanca. White circles represent localities for *T. oculatus*, and filled circles localities for *T. teyou*.

2. Remain motionless. The lizard stops running in an open area and remains there for some seconds before it moves again.

3. Keep moving slowly. The lizard keeps moving to a close shelter. This is a common strategy in runner lizards (as described by Avila-Pires 1995, for *Ameiva ameiva*), where the lizard continues to move away slowly.

4. Run again. The lizard sprints again after a short stop, regardless if it changes the direction compared to the first run.

Study areas

This study was performed in five different places (Table 1). Observations on *Teius oculatus* were performed in study areas in southern and eastern Paraguay, whereas data on *T. teyou* were collected in Chaco regions in northern and north-western Paraguay (Fig. 2).

Below we present a description of each study area (satellite images were obtained from Google Earth 7.1 accessed on 10-Sep-2014):

1. Itakyry: Cerrado vegetation dominated by dwarf palms and shrubs of no more than 1.5 m of height and medium sized patches (up to 3 m) of forests (Fig. 3a-b) developed over ferruginous (reddish) soils. The small patches of native vegetation were mixed with abundant parcels of culture fields (Fig 4a-b). In this area, two populations of *Teius oculatus* were analysed (Table 1).

2. San Rafael: This is one of the biggest patches of

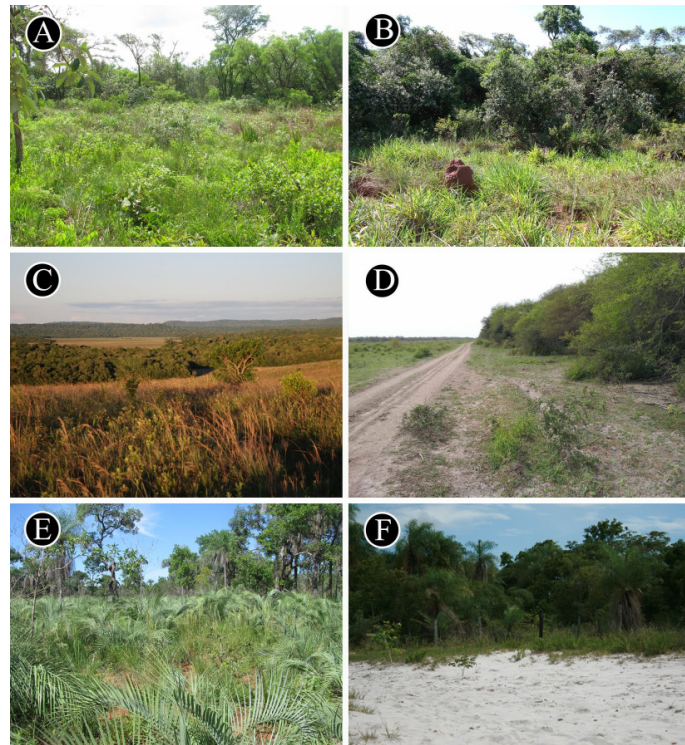


Figure 3. Vegetation structure in each study area: A- Itakyry 1, B- Itakyry 2, C- San Rafael, D- Solito, E- Kumaré, and F- Laguna Blanca.



Figure 4. Landscape configuration in each study area. A- Itakyry 1, B- Itakyry 2, C- San Rafael, D- Solito, E- Kumaré showing main headquarter in the upper right corner (red bar 100 m), and F- Laguna Blanca. Yellow bars represent 500 m.

Alto Paraná Atlantic Forest in Paraguay, having different types of vegetation. *Teius* are present in an area of Southern Mesopotamian Grasslands, a formation of natural grasslands mixed with tall forests (30 m), with the presence of many streams and flooding fields (Fig. 3c, 4c). Forests were mainly stretched across reddish sandstones.

3. Solito: A typical Chaco environment with xerophytic and thorny forests with abundance of cactus and bromeliads, and reduced herbaceous stratum (Fig. 3d). Exotic grasses (for cattle farming) were also present (Fig. 4d). Soil consisted of poorly drained white clays.

4. Kumaré: Very variable vegetation, which was rooted over reddish sandy soils or white clays (Fig. 4e). In this case we observed populations in the farm's headquarter, a very modified environment with human dwellings and gardens (Fig. 4e), and in a pasture area with patches of native vegetation constituted by dwarf palms and some small shrubs (Fig. 3e). A small headquarter (consisting of a small wooden ranch) was also present here.

5. Laguna Blanca: This particular environment was a confluence of Cerrado, Humid Chaco, and Alto Paraná

Atlantic Forest, and possessed the only "true" lake in Paraguay. Vegetation was diverse (patches of tall forests mixed with shrubs and Cerrado flora) set over white sand (Fig. 3f, 4f).

Data analyses

We generated a histogram of frequencies using the data of the categories shown in Figure 1 ($\leq 5\text{cm}$, 6-20cm, 21-50cm, and $\geq 51\text{cm}$), based on animals basking and foraging. To estimate relationships among number of individuals and distance from the shelter, we performed a non-parametric Kruskal-Wallis test, using individuals as replicates and distance categories as group datasets.

We considered approach distance (Martín & López 2000) as the shortest distance between the lizards and the observer, before the lizards flee. We recorded the distance between observer and the individual, and from the sample we recorded minimum and maximum approach distances for each species in each locality, and we generated a box plot. We assessed normality in data and differences in approach distances between both species with a Mann-Whitney test in the Mann-Whitney U-Test Calculator of

Table 2. Number of individuals of *T. oculatus* and *T. teyou* found in each locality, with number of individuals in each category of distance to the shelter or the nearest bush. Additionally, minimum and maximum approach distances (AD, in m) are given for each species in each locality.

Species	Locality	N	Distance from shelter				AD
			≤5cm	6-20cm	21-50cm	51cm≤	
<i>Teius oculatus</i>	1 Itakyry 1	5	5	-	-	-	1.5 – 3
	2 Itakyry 2	9	7	2	-	0	1.5 – 3
	3 San Rafael	22	18	4	-	0	2 – 5
<i>Teius teyou</i>	4 Solito	53	3	9	17	24	3 – 7
	5 Kumaré	18	2	3	6	7	2 – 7
	6 Laguna Blanca	32	-	7	6	19	3 – 6

the website Social Science Statistics (<http://www.socscistatistics.com>).

We took absolute and relative number of lizards in each category after the first run (see Data obtaining). Here we made a χ^2 test, with Yate's correction to assess differences between both species with the software Past 3.05 (Hammer et al. 2001).

Results

We analysed a total of 103 records of *Teius teyou* and 35 records of *T. oculatus*. All individuals of *T. oculatus* kept a close distance from vegetation/shelters, and they were never more than 20 cm from it (Table 2). In contrast, *T. teyou* foraged in bigger areas on vegetation-free ground and at a greater distance to the shelters (Table 2). At Laguna Blanca lizards of this species were seen up to 13 m from vegetation, and sometimes close to tourists. The evident difference related to the distance from the shelter in both species is clear because *T. oculatus* has a negative correlation trend, whereas *T. teyou* has a positive trend (Fig. 5). The differences in foraging distances from the shelters were statistically significant between *T. teyou* and *T. oculatus* ($K=0.2952, p=0.9609$).

The approach distance was more similar between the two species than the distance to the shelters. Nevertheless, the difference in the latter is significant ($U=1687.5, Z=5.28, p\leq 0.01$). Usually, *T. oculatus* allowed a minimum approach distance of 1.5 m. *T. teyou* started to run earlier when they were further away from the shelter (Fig. 6). The values are overlapping between 2 and 5 m.

After the first sprint *T. oculatus* almost always remained under the vegetation (Table 3). The six individuals that remained motionless were close to some bushes. *Teius teyou* showed more diverse patterns of escape behaviour. Most of them (53%) ran to hide under vegetation cover (similar to *T. oculatus*), although many lizards kept moving

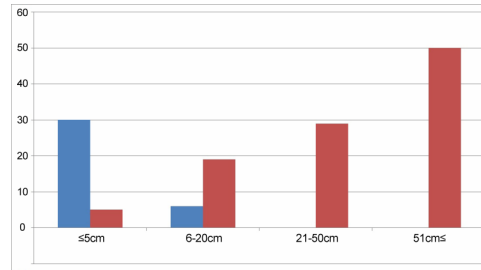


Figure 5. Frequencies of individuals in each category of distance from shelter. Blue bars represent *T. oculatus* and red *T. teyou*.

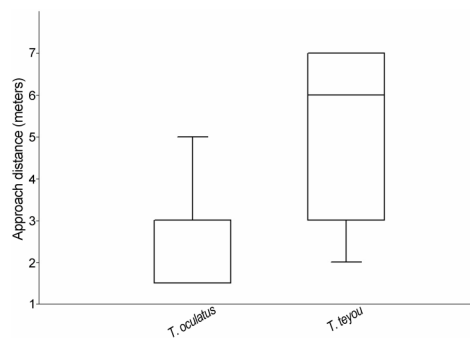


Figure 6. Box plot of minimum and maximum approach distances (in m) for *T. oculatus* and *T. teyou*.

Table 3. Behaviour showed by lizards after the first run: 1- enter a shelter, 2- remain motionless, 3- keep moving slowly, 4- run again. A: number of individuals, B: relative rate.

	<i>T. oculatus</i>				<i>T. teyou</i>			
	1	2	3	4	1	2	3	4
A	29	6	-	-	55	7	36	5
B	82	18	-	-	53	7	35	5
	%	%			%	%	%	%

slowly away (35%), often looking behind, and usually reaching some cover, and a few individu-

als stopped running and remained at uncovered places or restarted running (Table 3). Statistically there were significant differences between both species in the behaviour shown after the first run ($\chi^2=51.069$, $df=3$, $p<0.0001$).

In Laguna Blanca and Kumaré lizards that were far away from any available shelter, remained motionless after the first run. Individuals from Solito mostly showed the other three types of escape behaviour (enter a shelter, keep moving slowly, and run again). It is important to notice that in Laguna Blanca many tourists are present during the warm season that matches with the activity period for *Teius*, and the lizards therefore could be more habituated to anthropic activities. Also, individuals from the surroundings of Kumaré were found in gardens or harvest fields of human dwellings, and lizards were sharing their habitat with poultry, cats, and dogs.

Discussion

Probably due to differences in vegetation preferences *Teius oculatus* was more difficult to detect than *T. teyou*, which inhabits places with little herbaceous stratum. In addition, *T. teyou* is more exposed to sight as this species is found in more open areas as compared to *T. oculatus*, and probably the constant presence of tourists in Laguna Blanca made this population less shy than others. Schulte II et al. (2004) found no relation between morphology or vegetation shape and escape behaviour of *Liolaemus* lizards. They concluded that species in exposed habitats, far from available refuges, will rely more on crypsis than on speed (Schulte II et al. 2004). However, both *T. oculatus* and *T. teyou* have similar brown and green colour patterns that are rather conspicuous when outside the vegetation cover. Thus, lizards of the genus *Teius* are more likely to use speed as the main strategy against predation than crypsis.

Approach distance in the escape behaviour in lizards is mostly conditioned by the presence of predators (Cooper 2003, Diego-Rasilla 2003). However, Cooper (2009) also found intraspecific variation in the escape behaviour of the lizard *Sceloporus virgatus*, arguing that should be due to dietary differences. On the other hand, Ydenberg & Dill (1986) showed that the approach distance increases with the distance to the refuges. In this study we did not observe predators, thus vegetation (or any available shelter) could be the only

factor affecting approach distance in the different populations of *Teius*. The effect of vegetation on approach distance was also documented for lizards of the genera *Anolis* (Regalado 1998, Cooper 2006), *Lophognathus* (Blamires 1999), and *Aspidoscelis* (Punzo 2007). In our study we found differences in approach distance between *T. oculatus* and *T. teyou* with overlapping ranges between 2 and 5 m. As was stated above, *T. oculatus* inhabits areas with denser vegetation than *T. teyou*, and it was never observed farther than 20 cm from shelter. Thus, in this case the vegetation plays an important role when considering approach distance, and therefore escape behaviour. Lizards in more exposed areas avoid a close approach distance. Regalado (1998) found even intraindividual variation in approach distance since lizards can be adapted to the presence of observers. This was the case for the population in Laguna Blanca, where individuals of *T. teyou* were found foraging close to tourists. Recently Lattanzio (2014) evidenced that adults of *Ameiva festiva* allow closer approach distances than juveniles. We made no discrimination among age ranges, so we cannot confirm if this is also the case for *Teius*.

After the first run, Avila-Pires (1995) stated that *Ameiva ameiva* keeps moving slowly if the observer remains motionless. We observed this for some individuals of *T. teyou*; but the most common for *Teius* lizards is running to a shelter

Escape behaviour could have implications of evolution (Fernández et al. 2011). These authors found that the southernmost sympatric lizards *Liolaemus magellanicus* and *L. sarmientoi* exhibit similar patterns in temperature dependence, but with a lower performance in *L. magellanicus*, which suggest a recent colonisation for this species, while *L. sarmientoi* is more adapted to that environment (Fernández et al. 2011). In the case of *Teius*, both species are mainly distributed in allopatry, with sympatric zones in only some areas of their distributions (Avila 2002). A better understanding of the evolutionary history and biogeography of *Teius* is needed to know if great differences in exposure (distance from shelter while foraging) and approach distance between *T. oculatus* and *T. teyou* reflect adaptations to environmental factors. With the available data, it is difficult to infer the colonisation process in the genus *Teius*.

Understanding behaviour and habitat use also has implications for conservation strategies. The habitat alteration by humans has consequences on the ecology of the lizards, and improved knowl-

edge allows us to assess possible conservation measures (Smith & Ballinger 2001). In this case, *T. teyou* is adapted to forage near human dwellings and can be even present in gardens. This might be a good strategy to survive natural habitat loss. On the other hand, *T. oculatus* seems to be more cautious and avoids moving far from vegetation. Nevertheless, the species is able to inhabit small patches as observed in Itakyry 2 where a population of *T. oculatus* was recorded in an area of ca. 462 km² (Fig. 4b). These facts provide evidence that despite these two species coexisting with humans the preservation of different kinds of shelters is required for their long-term survival.

Acknowledgments. PC thanks Nelson Silva, Pastor Pérez, Martha Motte, Enrique Bragayrac, Jorge A. Céspedes, María E. Tedesco, Víctor Zaracho, Gloria Céspedes, Irene Gauto, Celeste Gauto, Pamela Marchi, and Hugo Cabral for help during field work and Nelson Pérez, Daniel Espínola, Rosario Gabaglio, Ana María Macedo, and Karina Atkinson, Jean-Paul Brouard for their hospitality. We thank the following institutions for assistance: Asociación Etnobotánica Paraguaya, Guyra Paraguaya, Para La Tierra, Red Paraguaya de Conservación en Tierras Privadas. Photographs of Figure 3C and 3D by Irene Gauto and Miguel Yegros, respectively. PC received financial support from Consejo Nacional de Ciencia y Tecnología, through the program PRONII (Paraguay) for fieldwork.

References

- Avila, L.J. (2002): Geographic distribution of lizards of the genus *Teius* (Squamata: Teiidae: Teiinae) in Southern South America. *Biogeographica* 78: 15–33.
- Avila-Pires, T. (1995): Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zoologische Verhandelingen* 299: 1–706.
- Bauwens, D., Thoen, C. (1981): Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *Journal of Animal Ecology* 50: 733–743.
- Blamires, S.J. (1999): Factors influencing the escape response of an arboreal agamid lizard of tropical Australia (*Lophognathus temporalis*) in an urban environment. *Canadian Journal of Zoology* 77: 1998–2003.
- Bruch, C. (1925): Comunicaciones herpetológicas. *Physis* 82: 97–98.
- Bulova, S.J. (1994): Ecological correlates of population and individual variation in antipredator behaviour of two species of desert lizards. *Copeia* 1994: 980–992.
- Burger, J., Gochfeld, M. (1990): Risk discrimination of direct versus tangential approach by basking black iguanas (*Ctenosaura similis*): variation as a function of human exposure. *Journal of Comparative Psychology* 104: 388–394.
- Cabrera, M.R. (2009): *Lagartos del Centro de la Argentina*. Fundación de Historia Natural Félix de Azara, Córdoba.
- Cacciali, P., Köhler, G. (2014): Notes on daily activity patterns in *Teius teyou* (Squamata: Teiidae) in the Dry Chaco. *Herpetological Bulletin* 129: 24–25.
- Cappellari, L.H., de Lema, T., Prates Jr., P., da Rocha, C.F.D. (2007): Diet of *Teius oculatus* (Sauria, Teiidae) in southern Brazil (Dom Feliciano, Rio Grande do Sul). *Iheringia Série Zoologia* 97: 31–35.
- Carreira Vidal, S. (2002): Alimentación de los ofidios de Uruguay. Monografía de Herpetología (6). Asociación Herpetológica Española, Barcelona.
- Carreira, S., Maneyro, R. (2013): Guía de Reptiles del Uruguay. Ediciones de la Fuga, Montevideo.
- Cei, J.M. (1993): Reptiles del noroeste, nordeste y este de la Argentina. Monografía XIV, Museo Regionale di Scienze Naturali, Torino.
- Cloudsley-Thompson, J.L. (1994): Predation and defence amongst reptiles. R & A Publishing Limited, Somerset, England.
- Cooper, W.E. (1997): Threat factors affecting antipredator behavior in the broad-headed skink (*Eumeces laticeps*): repeated approach, change in predator path, and predator's field of view. *Copeia* 1997: 613–619.
- Cooper, W.E. (2003): Risk factors affecting escape behavior by the desert iguana, *Dipsosaurus dorsalis*: speed and directness of predator approach, degree of cover, direction of turning by a predator, and temperature. *Canadian Journal of Zoology* 81: 979–984.
- Cooper, W.E. (2006): Risk factors affecting escape behaviour by Puerto Rican *Anolis* lizards. *Canadian Journal of Zoology* 84: 495–504.
- Cooper, W.E. (2009): Variation in escape behavior among individuals of the Striped Plateau Lizards *Sceloporus virgatus* may reflect differences in boldness. *Journal of Herpetology* 43: 495–502.
- Diego-Rasilla, F.J. (2003): Influence of predation pressure on escape behaviour of *Podarcis muralis* lizards. *Behavioural Processes* 63: 1–7.
- Downes, S., Shine, R. (1998): Safety or solitude? Using habitat selection experiments to identify a lizard's priorities. *Animal Behavior* 55: 1387–1396.
- Fernández, J.B., Smith Jr., J., Sclaro, A., Ibarguengotyía, N.R. (2011): Performance and thermal sensitivity of the southernmost lizards in the world, *Liolaemus sarmientoi* and *Liolaemus magellanicus*. *Journal of Arid Environments* 36:15–22.
- Gallardo, J.M. (1977): Reptiles de los alrededores de Buenos Aires. EUDEBA/ Lectores, Buenos Aires.
- Hammer, Ø., Happer, D.A.T., Ryan, P.D. (2001): PAST: Paleontological Statistics software package for education and data analysis. *Paleontologica Electronica* 4: art.9.
- Hutchins, M., Murphy, J.B., Schlager, N. (2003): Grzimek's Animal Life Encyclopedia, 2nd edition. Volume 7, Reptiles. Farmington Hills, Gale Group, Canada.
- Kramer, D.L., Bonenfant, M. (1997): Direction of predator approach and the decision to flee to a refuge. *Animal Behaviour* 54: 289–295.
- Lattanzio, M.S. (2014): Temporal and ontogenetic variation in the escape response of *Ameiva festiva* (Squamata: Teiidae). *Phyllomedusa* 13: 17–27.
- Lema, T., Araujo de, M.L., Azevedo, A.C.P. (1983): Contribuição ao conhecimento da alimentação e do modo alimentar de serpentes do Brasil. Comunicações do Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Série Zoologia 26: 41–121.
- Martín, J., López, P. (1995): Influence of habitat structure on the escape tactics of the lizard *Psammotromus algirus*. *Canadian Journal of Zoology* 73: 129–132.
- Martín, J., López, P. (1999): An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. *Oikos* 65: 328–333.
- Martín, J., López, P. (2000): Fleeing to unsafe refuges: effects of conspicuousness and refuge safety on the escape decisions of the lizard *Psammotromus algirus*. *Canadian Journal of Zoology* 78: 265–270.
- Martín, J., López, P. (2003): Ontogenetic variation in antipredator behavior of Iberian rock lizards (*Lacerta monticola*): effects of

- body-size-dependent thermal-exchange rates and costs of refuge use. *Canadian Journal of Zoology* 81: 1131-1137.
- Martins, M. (1996): Defensive tactics in lizards and snakes: the potential contribution of the Neotropical fauna. *Anais de Etologia* 14: 185-199.
- Punzo, F. (2007): Sprint speed and degree of wariness in two populations of whiptail lizards (*Aspidoscelis tessellata*) (Squamata Teiidae). *Ethology Ecology & Evolution* 19: 159-169.
- Regalado, R. (1998): Approach Distance and Escape Behavior of Three Species of Cuban *Anolis* (Squamata, Polychrotidae). *Caribbean Journal of Science* 34: 211-217.
- Schall, J., Pianka, E. (1980): Evolution of escape behavior diversity. *The American Naturalist* 115: 551-566.
- Schulte, J.A. II, Losos, J.B., Cruz, F.B., Núñez, H. (2004): The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropiduridae: Liolaemini). *Journal of Evolutionary Biology* 17: 408-420.
- Smith, G., Ballinger, R. (2001): The ecological consequences of habitat and microhabitat use in lizards: a review. *Contemporary Herpetology* 3: 1-37.
- Stone, P.A., Snell, H.L., Snell, H.M. (1994): Behavioral diversity as biological diversity: introduced cats and lava lizard wariness. *Conservation Biology* 8: 569-573.
- Tejerina, P., Tallade, P., Tiranti, S. (2005): El análisis de egagrópilas como metodología complementaria del plan de relevamiento de vertebrados de las áreas protegidas de la provincia de La Pampa, Argentina. Pp: 166. Libro de Resúmenes de la XI Reunión Argentina de Ornitología, Buenos Aires, Argentina.
- Waldschmidt, S., Tracy, C. (1983): Interactions between a lizard and its thermal environment: implication for sprint performance and space utilization in the lizard *Uta stansburiana*. *Ecology* 64: 476-484.
- Weiler, A., Núñez, K. (2015): Powerful venom evidence in *Philodryas mattogrossensis* (Serpentes: Dipsadidae) feeding on a *Teius teyou* (Sauria: Teiidae). *Herpetology Notes* 8: 545-547.
- Ydenberg, R.C., Dill, L.M. (1986): The economics of fleeing from predators. *Advanced Studies on Behavior* 16: 229-249.
-