



Escape distance and escape latency following simulated rapid bird attacks in an Andean lizard, *Phymaturus williamsi*

Gustavo A. Fava^{a,b,*} and Juan C. Acosta^a

^a Gabinete de Diversidad y Biología de Vertebrados del Árido y Semiárido (DIBIOVA), Departamento de biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, Provincia de San Juan, Argentina

^b Centro de Investigaciones de la Geósfera y la Biósfera (CIGEOBIO, CONICET-UNSJ), Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, Provincia de San Juan, Argentina

*Corresponding author's e-mail address: gustavo.fava21@gmail.com

Received 31 July 2017; initial decision 6 September 2017; revised 1 August 2018; accepted 4 August 2018; published online 4 September 2018

Abstract

Predatory birds represent the greatest risk for many lizard species. However, little is known about the functional relationship between the escape distance and escape latency of lizards during a rapid bird attack. We hypothesised that escape latency and distance in the Andean lizard species *Phymaturus williamsi* would increase proportionally, but vary according to the means of escape. Over a three-year period we observed seven types of antipredatory behaviour in 98% *P. williamsi* lizards on simulated predatory bird attacks. Escape distance and latency were positively correlated. 65% of lizards emerged from their refuge within 2 min of an attack. All of these behaviours were positively correlated with escape latency and distance, although we found the former to be more precise. This study contributes to a better understanding of the general antipredatory behaviour in this species of Andean lizard, and will assist in future decisions concerning its conservation.

Keywords

ecology, predator–prey interaction, antipredatory behaviour, hiding behaviour, direct attack, predatory birds.

1. Introduction

Most animals, with rare exceptions, are either predators or potential prey (Desfilis & Font, 2002). Potential prey animals have a wide variety of an-

tipredatory strategies to reduce the possibility of their being converted into actual prey (Edmunds, 1974; Blumstein & Daniel, 2005; Blumstein, 2006; Shepard, 2007). An antipredatory behaviour only endures if the benefits of that behaviour outweigh its costs, as any non-beneficial activity will be eliminated through natural selection (Blumstein & Daniel, 2005; Pafilis et al., 2009). The selection of antipredatory behaviours, therefore, appears to be related to the particular environment in which the predation takes place (Reynolds & Bruno, 2013).

Reptiles, particularly Sauria, face great pressure from predators (McKinney & Ballinger, 1966; Ávila & Morando, 2002; López et al., 2003; Shepard, 2007). From the perspective of lizards as prey, flight is energetically costly (Ydenberg & Dill, 1986; Pérez-Cembranos et al., 2013) and has a negative impact on opportunities for vital activities such as feeding or mating (Ydenberg & Dill, 1986; Cooper & Frederick, 2007).

Among all of their possible predators, certain bird species are considered to be lizards' principal threat (Jaksic et al., 1982; Poulin et al., 2001; Lopes et al., 2005; Carlile et al., 2006). When these birds attack in flight, they do so quickly, directly and from a great distance, rarely generating a shadow recognisable to their prey (Curio, 1976; Labra & Leonard, 1999; Cooper, 2009; Cooper & Blumstein, 2015; Ventura et al., 2016; Cabezas-Cartes et al., 2018). The prey's behaviour to avoid capture from this type of predation, therefore, is based principally on swift escape (Brock et al., 2015).

In order to study the predation risk posed to various lizard taxa, humans have commonly simulated predators due to the various advantages that this confers (Cooper et al., 2009; Cooper, 2011). The initial escape distance (between the predator and the prey when escape is initiated), and the escape latency (time between initial awareness and initiation of escape behaviour) (Cooper & Blumstein, 2015) and distance (from the initial position to the closest refuge) are the most utilised indicators of predation risk in lizards (Martín, 2002; Diego-Rasilla, 2003; Cooper, 2009, 2011). Cooper & Martín (2016) established a relationship between these variables in a slow predatory attack. Few studies, however, have focused on the behavioural responses to natural predators such as birds (Labra & Leonard, 1999; Halloy et al., 2007; Cooper, 2009; Kacoliris et al., 2009; Ventura et al., 2016; Cabezas-Cartes et al., 2018).

The distance between predator and prey (Cooper, 2011) is usually more difficult to measure than the latency period and the distance between a

lizard's initial and final positions, especially during a predatory bird attack that is fast and direct. In such attacks, the relationship between predation risk variables is unknown. The use of alternative antipredatory behaviours to predict predation risk in lizards has also not been thoroughly studied.

Within the family Iguanidae, the genus *Phymaturus* is ideal for the ecological study of antipredatory behaviours due to its exceptional diversity, limited distribution (Lobo et al., 2010, 2013) and vulnerable conservation status (Abdala et al., 2012). The species *Phymaturus williamsi* (Lobo et al., 2013) is endemic to the Andes mountain range, in the province of San Juan, Argentina. Although there are not many previous studies concerning the behaviour of this species, escape responses to the shadows of predatory birds (*Geranoaetus melanoleucus*, *Agriornis montanus*, *Turdus chiguanco* and *Cinclodes atacamensis*) have been observed in the study area (Fava et al., 2018). When approached slowly by a human aiming to capture them using a lasso, however, these lizards remain docile, allowing approach to within less than three metres (García-Muñoz & Sillero, 2010). The adverse effects of climate change in these delicate environments could also threaten *P. williamsi* population growth, especially since juveniles of this species have a low thermoregulation tolerance (Gordillo, Victorica, Acosta & Villavicencio, pers. comm.). It is therefore extremely important to have a better understanding of this species' population dynamic to take correct conservation decisions.

The main objective of this work was to examine the relationship between the escape distance and escape latency of *P. williamsi* when faced with a potential predatory bird. Particular interest was paid to the influence of these variables on the frequency and latency of other available antipredatory behaviours used during flight. These variables were analysed to test the null hypothesis that there are no differences between variables that indicate predation risk for *P. williamsi*. The frequency and latency of individuals remaining hidden after the simulated attack was also measured, to see if escape distance and latency changed according to whether or not a lizard sought shelter or the period for which they remained hidden.

It is thought that adverse effects from climate change in these delicate environments could threaten the *P. williamsi* population, especially since juveniles of this species have a low thermoregulation tolerance (Gordillo, Victorica, Acosta & Villavicencio, pers. comm.). It is therefore extremely important to gain a better understanding of the behaviour of this species in order to make appropriate conservation decisions.

2. Material and methods

2.1. Study area

Sampling was conducted at Quebrada Vallecito, along the slopes of Río Mantantiales (31°11.0–31°11.5' S; 69°41.8–69°43.5' W; WGS84), which corresponds to Cordón de Las Burras, located between 2700 and 3200 m above sea level in the Andean Frontal Cordillera, Department of Calingasta, San Juan Province, Argentina. The region has a desert climate based on the Köppen climate classification (Poblete & Minetti, 1999). The mean annual temperature is 16°C, with large annual fluctuations (absolute minimum temperatures of –8°C and absolute maximum temperatures above 27°C). The region has winter precipitation, with an annual mean precipitation of 70.8 mm. Phytogeographically the study area is typical of the province of Puna, comprising mainly shrubs, such as *Adesmia pinifolia*, *Ephedra breana* and *Lycium tenuispinosum*; cacti, such as *Maihueniopsis glomerata* and *Lobivia formosa*, and isolated grasslands of *Stipa ichu* and *Aristida mendocina* (Márquez et al., 2015).

2.2. Sampling design

Nine field surveys were conducted between 2013 and 2015, with a total of 279 lizards sampled. In each survey, the sampling was done randomly using a transect that was 3.6 km long, with a fixed width of 60 m, ascending without doubling back across landscape features, to ensure that each lizard was considered as an independent sample. The exhaustive search was conducted by two researchers simultaneously, using binoculars with a dioptré of 10 × 50, positioned on two opposing slopes bordering the sampling area. The transect surveys were performed during months when this lizard species was known to be most active, in autumn (April), spring (September) and summer (December), and between the hours of 11:00 and 18:00 (Victorica and Acosta, pers. com.). Surveys were performed with a minimum of 45 days between them to ensure the seasonal independence of the samples.

2.3. Field experiment protocol

In order to simulate the potential attack of a bird of prey, a methodology was adopted (Figure 1) similar to that used in other experiments that simulate this type of lizard predation (Ventura et al., 2016). Models of predators were created to mimic the silhouette of birds previously recorded in the study area

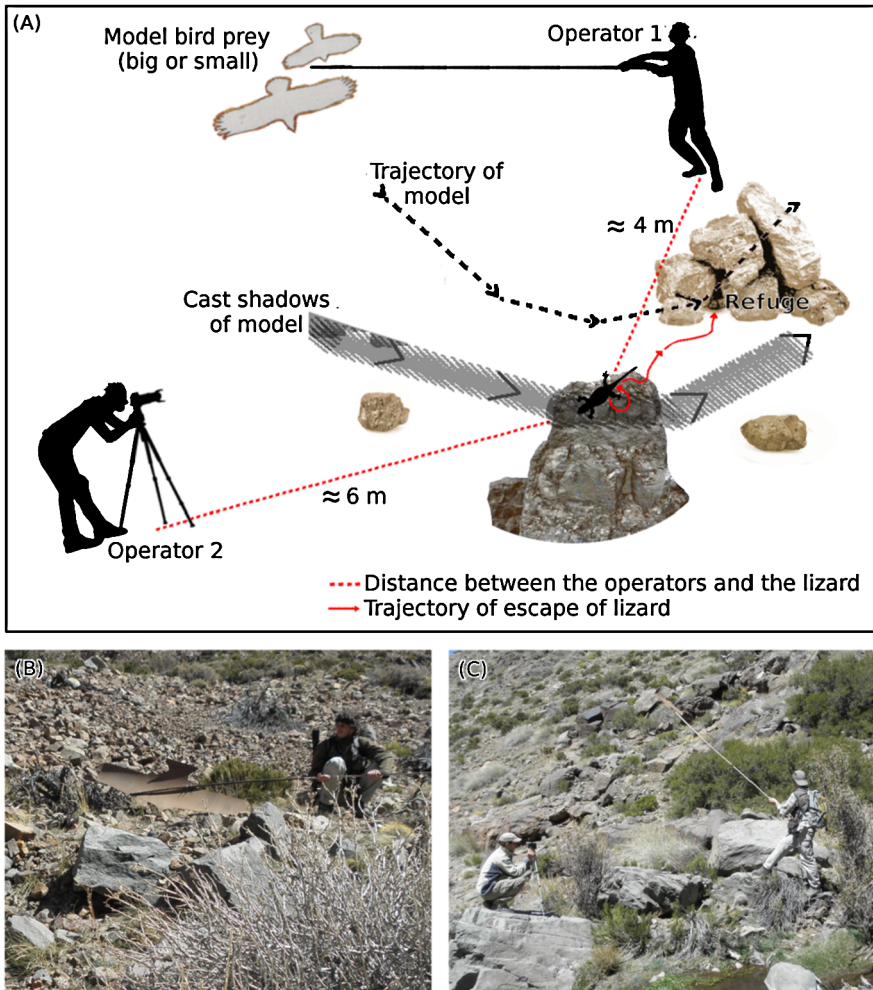


Figure 1. Methodology of field experiment. (A) Protocol illustrated; (B) position of first operator, pre-stimulus, using the model bird of prey; (C) protocol applied by the operators. Andes Mountain Range, Calingasta, Province of San Juan, Argentina.

(Fava et al., 2012), and whose diets included lizards. Specifically, these were: *Geranoaetus melanoleucus* (Jiménez & Jaksic, 1990; Trejo et al., 2006), *G. polyosoma* (Jiménez, 1995; De Lucca, 2001; Pérez et al., 2013), *Falco sparverius* (Mella Ávila, 2002; Sarasola et al., 2003) and, less commonly recorded, *Phalcooenus megalopterus* (Di Stefano & Donadio, 2009), as

well as some passerine species such as *Agriornis montanus* and members of the genus *Turdus* (Lopes et al., 2005).

In order to design the model bird silhouette, averages of estimated wingspan (length in cm from tip to tip with open wings) and body length (measured from the rectrices to the head) of potential predators were used. Two models resulted from this process, the first measuring 35×59 cm and the second 94×137 cm. The model predators were made using a light wood, and simulated the form of a bird with wings and tail feathers open. There was slight colouring on the underside, similar to that of most of the selected bird of prey species, which would be visible to a lizard (Ferguson-Lees & Christie, 2001; Lovette & Fitzpatrick, 2016). Both models were used equally during the simulations. During the sampling process the first operator, using the model bird of prey mounted on the end of a 3.5 m aluminium rod, simulated an attack in which either the silhouette model or its projected shadow suddenly approached the lizard at a velocity of approximately 2.5 m/s (Figure 1). The second operator, positioned at a horizontal distance of 6 m from the lizard, recorded the experiment (Figure 1A, C) using a video recorder a $60\times$ zoom and a frame capture rate of 25 frames per second. To reduce possible confounding factors affecting the lizards' risk perception (Burger & Gochfeld, 1993), the same operator, wearing the same clothes, sampled all lizards of a similar way (Figure 1B), while the other operator recorded the lizards' behaviours (Figure 1C). In order to avoid potential stressful effects caused by a human presence, observers moved cautiously, without making any threatening movements and, once in position, gave the animals ten minutes to become accustomed to their presence. Tests were considered invalid whenever a lizard demonstrated behaviour changes before the onset of the simulation.

This methodology assumed that the observed specimen responded primarily to the visual stimulus of the approaching model predator. The latter was always made to approach head first, eliminating variation in form relative to the direction of movement. Trials in which the model bird did not cast a shadow towards or across a lizard's body required repositioning according to the position of the lizard relative to the sun. After observing a lizard's behaviour (seeking shelter or pausing for at least ten seconds), recording continued for an additional two minutes to capture the lizard's post-stimulus behaviour.

In the laboratory, the video records of the antipredatory behaviours were transcribed to a matrix for statistical analysis. Escape distance was defined as the distance between a subject's initial position upon stimulation and the point of pausing for at least ten seconds or in a shelter where at least half its body was hidden. This measurement was made using a metal tape measure. The escape latency and the latency for all other behaviours was measured from the moment a change in behaviour was recorded until it ceased, and was measured in frames per second.

2.4. Categories of behaviours

Each of the video recordings was analysed in order to obtain a better understanding of the antipredatory behaviours of *Phymaturus williamsi*. Each behaviour was identified based on ethograms obtained from the literature (Carpenter & Ferguson, 1977; Cabezas-Cartes et al., 2018) and by using a dictionary of animal behaviour, ecology and evolution (Barrows, 2011), as detailed in Table 1.

2.5. Statistical analysis

Analysis of variance (ANOVA) was used to analyse the variation in frequency and latency of the behaviours manifested by *Phymaturus williamsi* during each experiment. Prior to the analysis, the normality and uniformity of the variances were verified using the Kolmogorov–Smirnov D and Levene's tests, respectively. The Tukey test was applied to detect differences between groups.

General linear models with binomial negative distributions were used to analyse variances within the escape distances and latencies, and in the functions of the frequencies and latencies of each behaviour as response variables. These models were analysed using the `glm.nb` function with the log link function from the "MASS" package of the R software environment (Venables & Ripley, 2002; R Core Team, 2016). Graphical diagnoses (`qqnorm`) were used to confirm that the models fulfilled the criteria for Pearson's residual distribution and variance uniformity. The models were simplified by progressively eliminating any non-significant variables and by comparison of the maximum plausibility (`logLik`). The model selection was based on the Akaike information criterion (Zuur et al., 2009).

Table 1.

Description, measurement type, sampling rules and records of behaviour variables found in *Phymaturus williamsi* as a prey animal.

Antipredatory behaviour	Description	Measurement type, sampling rules and record
Cowering	The lizard crouches in reaction to the stimulus, without any other displacement from its initial position (Hinde, 1970 in Barrows, 2011).	Event. Prey focused sampling and continuous recording of the antipredatory response. The data records were expressed as latency in frames per second recorded to each specific antipredatory behaviour.
Head bobbing	The lizard moves its extended head or the front part of its body in a rhythmic pattern, first downward and then upward in a rhythmic pattern, without any other displacement from its initial position (Carpenter & Ferguson, 1977).	
Forelimb waving	The lizard moves the forelimbs rapidly up and down in a rhythmic pattern (Halloy & Castillo, 2002).	
Displacement	The lizard moves using its feet, changing its body position at less than 90° angle to the direction of escape (Tinbergen & Van Iersel, 1947; Barrows, 2011).	
Body turning	The lizard redirection its body between 90° and 180° angle to the direction of escape on the initial position (Cooper, 2008).	State. Prey focused sampling and continuous recording of the antipredatory response. The data records were whether the antipredatory behaviour occurred.
Vigilance	The lizard explores, directs and moves its head towards the direction of the attack, without body moving (Cooper, 2008).	
Jumping	The lizard pushes its feet against the ground and propelling its body upward into the air, changing its initial position (Emerson, 1985 in Losos & Sinervo, 1989).	
Hiding	The lizard conceals its entire body beneath an object, always entering its headfirst towards the tail (Martín & López, 1999b).	

Table 1.
(Continued.)

Antipredatory behaviour	Description	Measurement type, sampling rules and record
Emerging from refuge	The lizard begins to come out from its refuge, starting headfirst and revealing at least half of its body from under the refuge (Martín & López, 1999b).	Event. Prey focused sampling on the selected refuge and continuous recording for two minutes. The gathered data was expressed as the seconds of latency during which the hidden behaviour persisted.

3. Results

3.1. Behaviour frequency and latency

Seven antipredatory behaviours were recorded for *Phymaturus williamsi* individuals exposed to a bird of prey attack stimulus. Six individuals did not display any behaviours at all, while the rest (97.85%) demonstrated an average of two behaviours (SD = 0.75), an average escape distance of 30.08 cm (SD = 24.75; range = 0–149 cm) and an average latency of 0.65 s (SD = 0.41, range = 0–4.12 s) for each behaviour (Figure 2). The most frequent antipredatory behaviour seen was a body turn (Figure 2A,B), with this behaviour employed first by 64% of sampled individuals. The next most frequent behaviour was displacement (Figure 2C,F), which was seen as the first or second behaviour in 54% of cases. Vigilance behaviour was recorded in 43% of cases (Figure 2D), followed by displacement in 57% of cases (Figure 2E) between the first and fourth behaviour employed (Figure 2A–F). The remaining behaviours were observed occasionally.

The frequency of each antipredatory behaviour was significantly different in comparison with the others ($F = 314.8$; $p < 0.0001$). Body turning behaviour did not show a statistical difference with displacement behaviour ($z = 2.43$, $p = 0.07$) but was significantly higher than vigilance behaviour ($z = 12.66$; $p < 0.001$). Head bobbing, jumping, and cowering behaviours were not significantly different (in all cases $p > 0.15$) and were significantly less frequent than vigilance behaviour (in all cases $z > 30$ and $p < 0.001$; Figure 3).

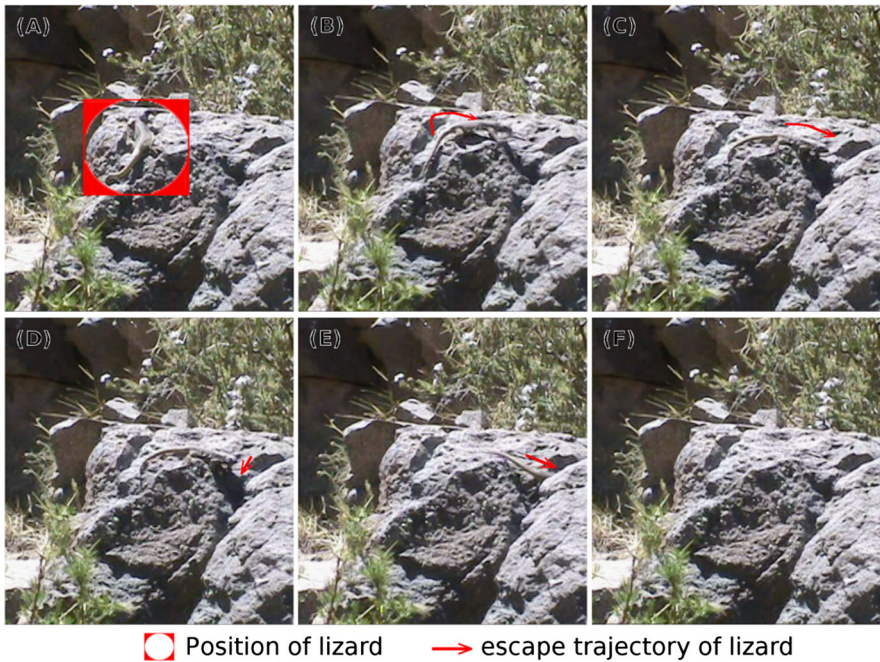


Figure 2. Records of antipredatory behaviour in *Phymaturus williamsi* (FPS). (A) Initial position of lizard basking; (B) trajectory of body turning behaviour; (C) trajectory of displacement behaviour; (D) vigilance behaviour; (E) trajectory of displacement behaviour and lizard with half its body under cover and (F) lizard concealed in a refuge. Andes Mountain Range, Calingasta, Province of San Juan, Argentina.

The recorded latencies for the different aforementioned behaviours for *P. williamsi* did not show significant differences between themselves (in all cases $p > 0.64$).

3.2. Escape latency and distance

The escape latency of lizards was positively correlated with the escape distance ($z = 3.433$; $SE = 0.0016$; $p = 0.0006$; Figure 4) when a direct attack by a bird of prey was simulated.

The escape distance for *Phymaturus williamsi* was significantly greater in individuals that also demonstrated greater latency in the behaviours of displacement (Negative Binomial GLM; $z = 3.80$, $SE = 0.01$, $p > 0.0001$; Figure 5A) and body turning (Negative Binomial GLM; $z = 2.42$, $SE = 0.02$, $p = 0.016$; Figure 5B). Conversely, individuals who did not hide demonstrated a significantly lower escape distance (Negative Binomial GLM;

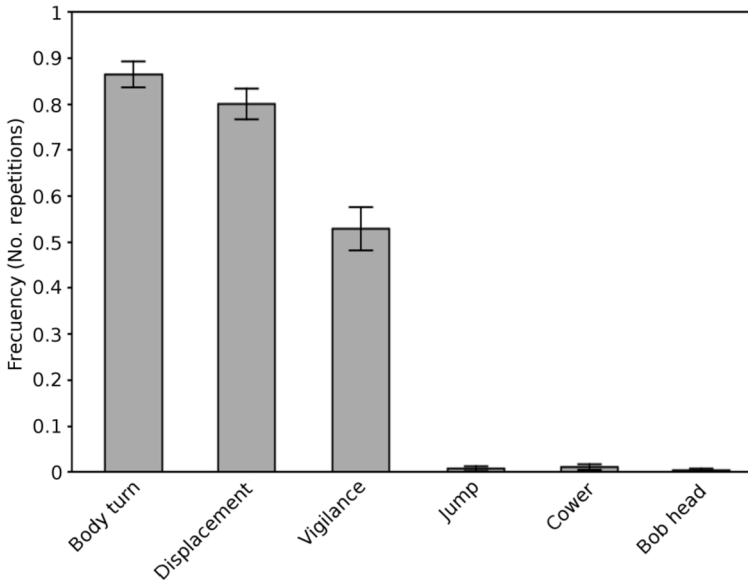


Figure 3. The frequency of repetition of antipredatory behaviours observed in *Phymaturus williamsi* per experiment.

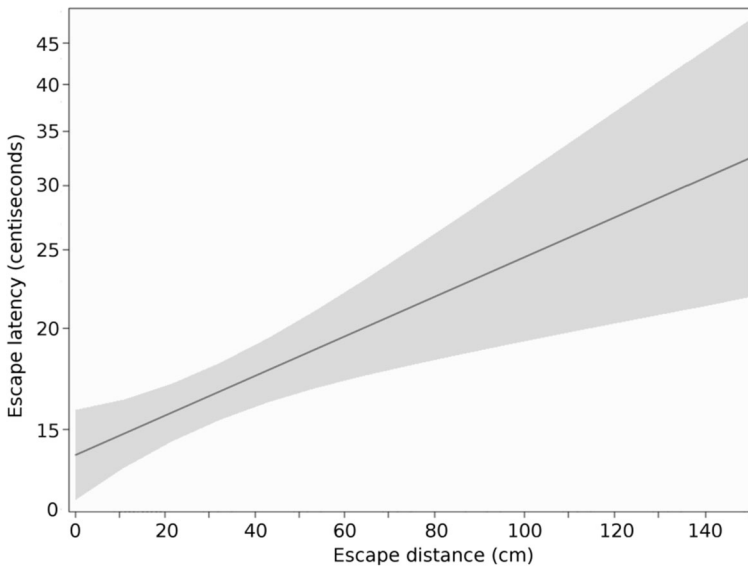


Figure 4. The relationship between escape distance and escape latency for *Phymaturus williamsi* when attacked by a simulated predatory bird.

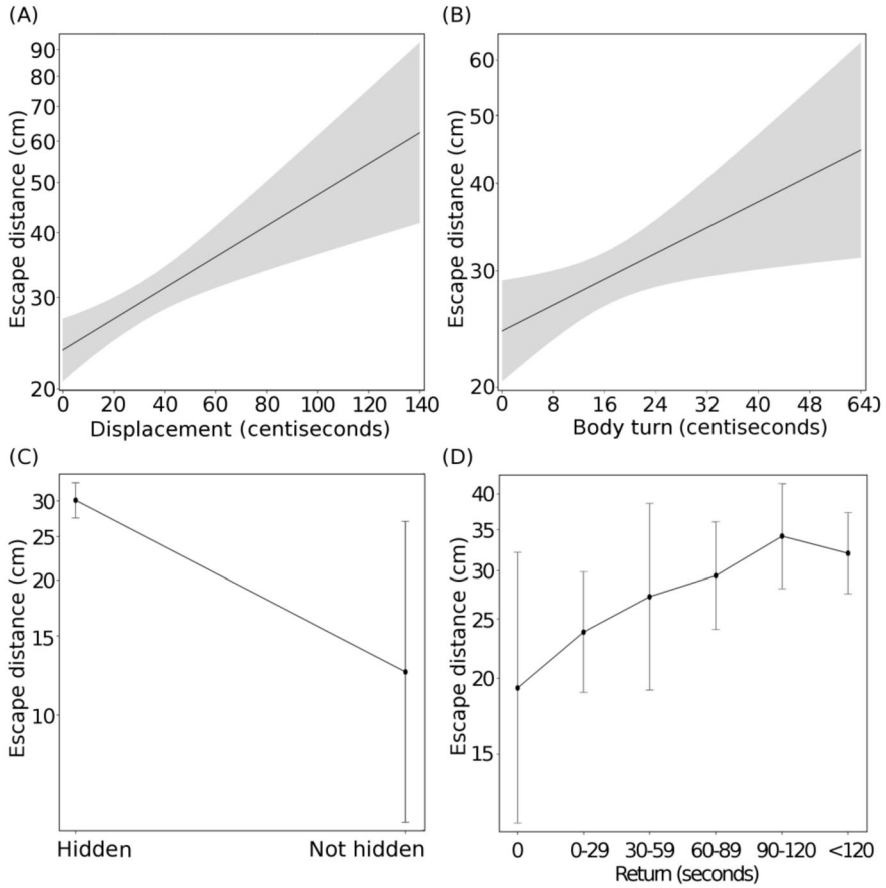


Figure 5. Variability in the escape distance for *Phymaturus williamsi* in the functions of (A) the latency for displacement; (B) body turning; (C) hiding and (D) emerging from a refuge.

$z = 1.82$, $SE = 0.28$, $p = 0.049$; Figure 5C). This variable was significantly higher in individuals who delayed the resumption of their activity for between 1.31 and 2 minutes after seeking shelter (Negative Binomial GLM; $z = 1.99$, $SE = 0.29$, $p = 0.046$; Figure 5C) and for those that remained hidden for more than two minutes (Negative Binomial GLM; $z = 1.82$, $SE = 0.28$, $p = 0.049$; Figure 5D). The latency of vigilance, cowering, jumping, and head bobbing behaviours in prey lizards did not display significant variation in relation to the function of the escape distance.

The escape latency for *P. williamsi* rose significantly for vigilance (Negative Binomial GLM; $z = 28.44$, $SE = 0.001$, $p > 0.0001$, Figure 6A), dis-

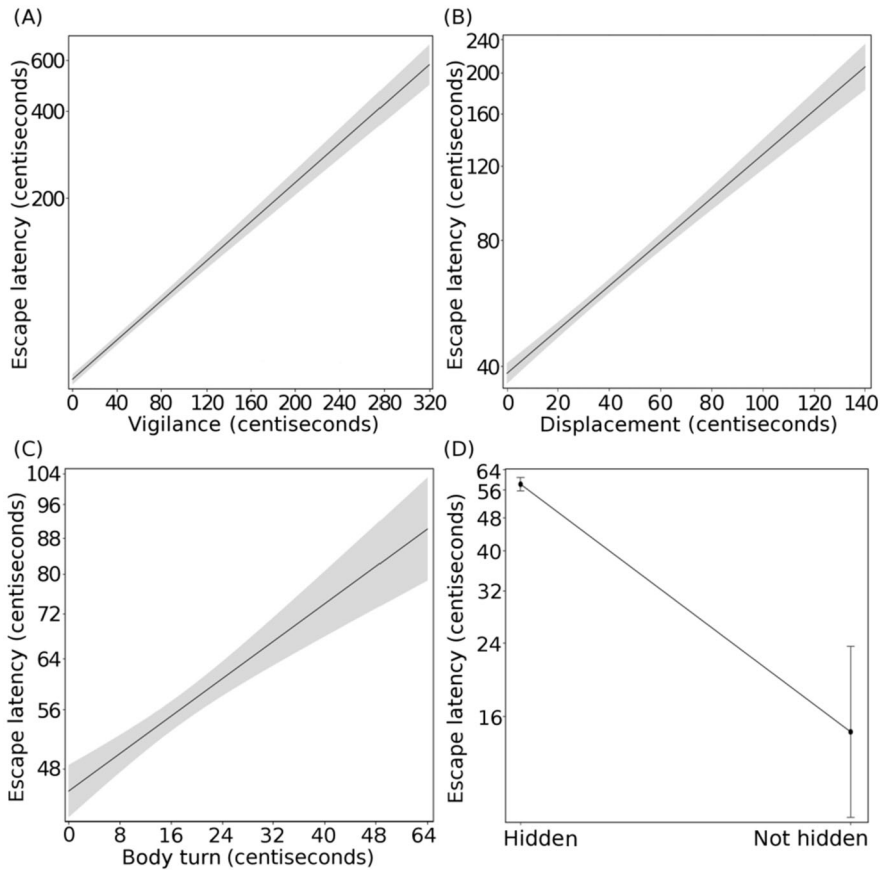


Figure 6. Variability in the escape latency for *Phymaturus williamsi* in the functions of (A) the latency for vigilance; (B) displacement; (C) body turning and (D) hiding.

placement (Negative Binomial GLM; $z = 20.42$, $SE = 0.002$, $p > 0.0001$, Figure 6B) and body turning behaviours (Negative Binomial GLM; $z = 7.26$, $SE = 0.002$, $p > 0.0001$, Figure 6C). Conversely, this variable decreased significantly for individuals who did not hide (Negative Binomial GLM; $z = -5.66$, $SE = 0.24$, $p = 0.023$; Figure 6D). The escape latency did not vary significantly for covering, jumping, or the resumption of activity after seeking shelter ($p > 0.05$).

3.3. Frequency of seeking shelter and time to resumption of activity

A total of 264 lizards (94.62% of the population sampled) hid when faced with a simulated bird of prey attack. Of these, 43 individuals (16.29%)

emerged from their refuges in less than 30 s, 19 individuals (7.19%) emerged between 30 s and 1 min, 53 (20.08%) emerged between 1 min and 1 min 30 s, 55 individuals (20.83%) emerged between 1 min 30 s and 2 min, and the remaining 94 individuals (35.61%) were still hidden after more than 2 min.

4. Discussion

4.1. Antipredatory behaviours of prey lizards

Observing the reactions of *Phymaturus williamsi* to a sudden attack by a simulated bird of prey was a simple and effective method to quantify predation risk variables, and to make comparisons with other studies (Labra & Leonard, 1999; Ventura et al., 2016; Cabezas-Cartes et al., 2018).

The responses utilised by the prey lizards to quickly escape from predators could be quantifiably differentiated from other behaviours in their repertoire based on their latency. The most employed antipredatory behaviours were body turning, displacement, vigilance and hiding behaviours, similar to other vertebrate prey animals (Ydenberg & Dill, 1986; Martín, 2002). These behaviours allow lizards to gauge the danger of an attack in relation to the safety offered by the closest shelter and weigh this information before deciding whether to flee and hide (Martín & López, 1999a, b, 2001; Cooper, 1998, 2009).

As in other studies, a lizard's position, the direction of the attack, the escape velocity, the distance to the selected shelter, and the elapsed time spent hidden were determining factors for the choice of antipredatory behaviours (Martín, 2002; Amo et al., 2007); the distance between predator and prey when flight began was not considered (Martín & López, 1999a, b, 2001; Cooper, 1998, 2009, 2011; Cooper & Martín, 2016). When *P. williamsi* emerge from their shelters seeking resources (mainly for thermoregulation), they tend to position themselves so that their head is at a 180° angle to selected refuges, such as cracks or openings between rocks, on the steepest slopes. From this position, a lizard has the best field of view to maintain vigilance about its surroundings and to detect a possible predator, providing safety during thermoregulatory activities and balancing the time necessary to escape (Martín, 2002). The escape angle of *P. williamsi* was seen to be highly variable, between 90° and 180°, making their flight path less predictable than other species which always orient in the direction of escape (Ydenberg & Dill, 1986; Cooper & Frederick, 2007). The ability to flee quickly and turn

their body during flight enables these lizards to escape predators more effectively as they can change their direction of escape (Eilam, 2007; Bulbert et al., 2015; Cooper & Sherbrooke, 2016). Also, escaping using a body turn may move the anterior end of the lizard away from a predator, increasing the probability that the predator will contact the tail, which may be autotomised (Smith, 1996; Cooper & Wilson, 2007; Cooper, 2008).

In common with other studies (Ydenberg & Dill, 1986; Cooper & Frederick, 2007), we found that lizards exposed to a rapid and direct predatory attack had little opportunity to adjust their behaviours to maximize the cost/benefit ratio. Body turning and displacement behaviours have energy costs, but allow the prey to distance itself from its predator, while vigilance allows prey to detect predators with little or no unnecessary energy expenditure, even though it implies a higher possibility of capture (Martín, 2002). If a lizard is close to shelter, it can opt to flee quickly as the flight cost is low, and once hidden they can further evaluate any potential risk. However, if a lizard needs to move over a longer distance to escape a predator's reach, they may adjust their antipredatory response. In other words, lizards can opt for less costly behaviours that increase the probability of capture only when the predator is still far away (Cooper, 1998; Martín, 2002; Cooper & Blumstein, 2015; Cooper & Martín, 2016). Vigilance behaviour in lizards is essential if they are to evaluate the probability of a real threat and avoid the high cost of fleeing a predator that is not stalking them. On the other hand, less frequent behaviours such as cowering, jumping and head bobbing can be interpreted as failed decisions in this case (simulating a direct bird attack), as they indicate movement without moving away from the predator; these behaviours increase the escape latency and diminish the possibilities of future fitness contributions (Martín, 2002).

The variations in antipredatory behaviour mechanisms exhibited by *P. williamsi* demonstrated a positive relationship between the functions of the required escape distance and latency. The variance in escape latency, however, presented a greater residual adjustment than escape distance. It can be said therefore that escape latency is a more precise indicator of predation risk, as it not only indicated the distance of the escape trajectory, but also the incidence of other, different behaviours, as seen for other lizards when a predator approached them slowly (Cooper & Martín, 2016).

Head bobbing and forelimb waving were not important antipredatory responses for *Phymaturus williamsi* (Font et al., 2010, Halloy et al., 2013)

when confronted with a direct and fast attack. In this study, head bobbing was a casual response to the simulated bird of prey, and differed from preliminary studies using a lasso for capture (Acosta, pers. comm.). Similarly, forelimb waving behaviour was not observed in this study, although it has been reported for other species when threatened by a slowly approaching predator (Halloy et al., 2013). It is likely that prey animals use these behaviours to warn or demonstrate their escape ability when the threat risk is lower, if the predator is, for example, farther away or attacking slowly (Martín, 2002; Blumstein & Daniel, 2005; Pafilis et al., 2009; Cooper & Martín, 2016).

4.2. Hiding behaviour and time taken to emerge from refuges

The majority of *Phymaturus williamsi* sampled sought shelter and remained hidden for a prudent amount of time after detecting a direct attack. These responses proved to have a positive relationship with the escape distance of prey lizards and could be explained as the necessary recovery time. Similarly, the decision to stay hidden and out of reach of any potential predator is crucial if a lizard is to obtain information about the predatory behaviour and reduce to a minimum the risk of another attack that could prove fatal (Cooper, 1998; Martin, 2001, 2002; Polo et al., 2011; Cooper & Blumstein, 2015). Very few lizards did not respond at all to the simulated predator, although crypsis is an alternative passive defence to gain time when seeking shelter has a high cost, for example in those lizards with low body temperatures that needed to bask (Martin, 2002).

4.3. Conclusion

The simulated direct attack of a bird of prey on a basking lizard allowed us to record seven antipredatory behaviours, the most prominent of which were body turning, displacement, vigilance and hiding behaviours. The latency of the chosen behaviours allowed us to easily quantify a positive relationship between the escape distance and latency, while the latter variables displayed a positive relationship proving them to be reliable predation indicators for lizards. That being said, the variance of the escape latency in relation to the antipredatory behaviours was less than the escape distance, making the first a more precise measure of predation risk in lizards. The methodology applied here could be useful for testing other antipredatory variables in lizards not addressed in this work (for example, differences in age groups, seasonal variation, environmental differences, predator size, type of shelter selected,

and distance to the nearest refuge). The information obtained for *Phymaturus williamsi* in this study gives us a deeper understanding of this species and enables us to further evaluate its conservation status in relation to other herpetofauna in these underexplored environments.

Acknowledgements

We wish to thank R. A. Nievas, M. Olmedo, R. Acosta, R. Gómez Alés, T. Martínez, M. Rodríguez, R. Fernández, F. Valdez and A. Victorica for their assistance in recording the field experiments. We are especially grateful to A. Labra, L. Avila, C. Robles, C. Abdala, F. Kacoliris and to our anonymous reviewers for their suggestions. This study was supported by a doctoral fellowship (GAF) of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET (National Scientific and Technical Research Council), Argentina). Financial support was received by a project fellowship CIC-ITCA (JCA).

References

- Abdala, C.S., Acosta, J.L., Acosta, J.C., Álvarez, B.B., Arias, F., Ávila, L.J., Blanco, M.G., Bonino, M.B., Jorgelina, M., Brancatelli, G., Breitman, M.F., Cabrera, M.R., Cairo, S., Corbalán, V., Hernando, A., Ibargüengoytía, N.R., Kacoliris, F., Laspiur, A., Montero, R., Morando, M., Pelegrin, N., Pérez, C.H.F., Quinteros, A.S., Semhan, R.V., Tedesco, M.E., Vega, L.A. & Zalba, S.M. (2012). Categorización del estado de conservación de las lagartijas y anfisbenas de la República Argentina. — Cuad. Herpetol. 26: 215-248.
- Amo, L., López, P. & Martín, J. (2007). Refuge use: a conflict between avoiding predation and losing mass in lizards. — Physiol. Behav. 90: 334-343.
- Ávila, L.J. & Morando, M. (2002). *Liolaemus petrophilus* (NCN). Saurophagy. — Herpetol. Rev. 33: 52.
- Barrows, E. (2011). Animal behavior desk reference, a dictionary of animal behavior, ecology, and evolution. — CRC Press, Boca Raton, FL.
- Blumstein, D. & Daniel, J. (2005). The loss of antipredator behavior following isolation on islands. — Proc. Roy. Soc. Lond. B: Biol. Sci. 272: 1663-1668.
- Blumstein, D. (2006). The multipredator hypothesis and the evolutionary persistence of antipredator behavior. — Ethology 112: 209-217.
- Brock, K.M., Bednekoff, P.A., Pafilis, P. & Foufloupoulos, J. (2015). Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): the sum of all fears? — Evolution 69: 216-231.
- Bulbert, M.W., Pae, R.A. & Bernal, X.E. (2015). Danger comes from all fronts: predator-dependent escape tactics of Tungara frogs. — PLoS ONE 10: e0120546.

- Burger, J. & Gochfeld, M. (1993). The importance of the human face in risk perception by Black Iguanas, *Ctenosaura similis*. — J. Herpetol. 27: 426-430.
- Cabezas-Cartes, F., Boretto, J.M., Acosta, J.C., Jahn Blanco, G., Laspiur, A. & Ibagüengoytía, N. (2010). Reproductive biology of *Phymaturus cf. palluma*: a vulnerable lizard from the highlands of the Andes, San Juan, Argentina. — Herpetol. Conserv. Biol. 5: 430-440.
- Cabezas-Cartes, F., Boretto, J.M., Halloy, M., Krenz, J.D. & Ibagüengoytía, N.R. (2018). Maternal behaviour in response to predation threats in a vulnerable lizard from Patagonia, Argentina. — J. Zool. 304: 175-181.
- Carlile, P.A., Peters, R.A. & Evans, C.S. (2006). Detection of a looming stimulus by the Jacky dragon: selective sensitivity to characteristics of an aerial predator. — Anim. Behav. 72: 553-562.
- Carpenter, C.C. & Ferguson, G.W. (1977). Variation and evolution of stereotyped behavior in Reptiles. — In: Biology of the Reptilia, ecology and behavior (Gans, C.G.A. & Tinkle, D.W., eds). Academic Press, New York, p. 335-554.
- Cooper, W.E. & Blumstein, D.T. (2015). Escaping from predators: an integrative view of escape decisions and refuge use. — Cambridge University Press, Cambridge.
- Cooper Jr., W.E. & Frederick, W.G. (2007). Optimal flight initiation distance. — J. Theor. Biol. 244: 59-67.
- Cooper Jr., W.E. & Martín, J. (2016). Predator-prey distance and latency to flee from an immobile predator: functional relationship and importance. — Curr. Zool. 62: 117-122.
- Cooper Jr., W.E. & Sherbrooke, W.C. (2016). Strategic escape direction: orientation, turning, and escape trajectories of Zebra-Tailed Lizards (*Callisaurus draconoides*). — Ethology 122: 542-551.
- Cooper Jr., W.E. & Wilson, D.S. (2007). Beyond optimal escape theory: microhabitats as well as predation risk affect escape and refuge use by the Phrynosomatid Lizard *Sceloporus virgatus*. — Behaviour 144: 1235-1254.
- Cooper Jr., W.E., Hawlena, D. & Pérez-Mellado, V. (2009). Effects of predation risk factors on escape behavior by Balearic lizards (*Podarcis lilfordi*) in relation to optimal escape theory. — Amphibia-Reptilia 30: 99-110.
- Cooper Jr., W.E. (2011). Age, sex and escape behaviour in the Striped Plateau Lizard (*Sceloporus virgatus*) and the Mountain Spiny Lizard (*S. jarrovi*), with a review of age and sex effects on escape by lizards. — Behaviour 148: 1215-1238.
- Cooper Jr., W.E. (1998). Effects of refuge and conspicuousness on escape behaviour by the Broad-Headed Skink (*Eumeces laticeps*). — Amphibia-Reptilia 19: 103-108.
- Cooper Jr., W.E. (2008). Visual monitoring of predators: occurrence, cost and benefit for escape. — Anim. Behav. 76: 1365-1372.
- Cooper Jr., W.E. (2009). Rapid covering by shadow as a cue to predation risk in three lizard species. — Behaviour 146: 1217-1234.
- Curio, E. (1976). The ethology of predation. — Springer, New York.
- De Lucca, E.R. (2011). Observaciones del Aguilucho Común (*Buteo polyosoma*) en el centro y sur de la Argentina. — Not. Faun. 77: 1-15.

- Desfilis, E. & Font, E. (2002). Efectos de la experiencia sobre el comportamiento depredador de los reptiles. — Rev. Esp. Herpetol. 16: 79-94.
- Di Stefano, S. & Donadio, E. (2009). Monitoreo de indicadores de diversidad en la Reserva de Biosfera San Guillermo: paisaje, ecosistemas, comunidades, poblaciones e individuos. — Plan de monitoreo de la Biodiversidad de San Guillermo, San Juan.
- Diego-Rasilla, F.J. (2003). Influence of predation pressure on the escape behaviour of *Podarcis muralis* lizards. — Behav. Process. 63: 1-7.
- Edmunds, M. (1974). Defence in animals: a survey of anti-predator defences. — Longman, Burnt Mill, UK.
- Eilam, I.A. (2007). Wait before running for your life: defensive tactics of spiny mice (*Acomys cahaerinus*) in evading barn owl (*Tyto alba*) attack. — Behav. Ecol. Sociobiol. 62: 923-933.
- Emerson, S.B. (1985). Jumping and leaping. — In: Functional vertebrate morphology (Hildebrand, M., Bramble, D.M., Liem, K.F. & Wake, D.B., eds). Belknap Press, Cambridge, MA, p. 58-72.
- Fava, G., Acosta, J.C., Laspiur, A. & Moreno, M.V. (2012). Avifauna del Valle de Calingasta y sus alrededores, Provincia de San Juan, Argentina. — Acta Zool. Lilloana 56: 66-81.
- Fava, G., Acosta, J.C., Victorica, A.E., Martínez, T. & Rodríguez, M. (2018). *Phymaturus williamsi* (Williams' Andean Lizard). Predator-prey interaction. — Herpetol. Rev. 49: 332-333.
- Ferguson-Lees, J. & Christie, D.A. (2001). Raptors of the world. — Houghton Mifflin, Boston, MA.
- Font, E., Carazo, P., Pérez I de Lanuza, G. & Barbosa, D. (2010). Comportamiento y comunicación animal: ¿Qué nos enseñan los lagartos?. — Acta Zool. Lilloana 54: 12-35.
- García-Muñoz, E. & Sillero, N. (2010). Two new types of noose for capturing herps. — Acta Herpetol. 5: 259-263.
- Halloy, M. & Castillo, M. (2002). Forelimb wave displays in lizard species of *Liolaemus* (Sauria: Liolaemidae). — Herpetol. Nat. Hist. 9: 127-133.
- Halloy, M., Robles, C., Salica, M.J., Semhan, R., Juárez Heredia, V. & Vicente, N. (2013). Estudios de comportamiento y ecología de lagartijas de los géneros *Liolaemus* y *Phymaturus* (Iguania: Liolaemini). — Cuad. Herpetol. 27: 15-26.
- Halloy, M., Boretto, J.M. & Ibarguengoytía, N.R. (2007). Signs of parental behavior in *Liolaemus elongatus* (Sauria: Liolaemidae) of Neuquén, Argentina. — S. Am. J. Herpetol. 2: 141-147.
- Jaksic, E.M., Greene, H.W., Schwenk, K. & Seib, L. (1982). Predation upon reptiles in Mediterranean habitats of Chile, Spain, and California: a comparative analysis. — Oecologia 53: 321-324.
- Jiménez, J.E. (1995). Historia natural del Aguilucho *Buteo polyosoma*: una revisión. — Hornero 14: 1-8.
- Jiménez, J.E. & Jaksic, F.M. (1990). Historia natural del águila *Geranoaetus melanoleucus*: una revisión. — Hornero 13: 97-110.

- Kacoliris, F.P., Guerrero, E., Molinari, A., Moyano, B. & Rafael, A. (2009). Run to shelter or bury into the sand? Factors affecting escape behaviour decisions in Argentinian sand dune lizards (*Liolaemus multimaculatus*). — *Herpetol. J.* 19: 213-216.
- Labra, A. & Leonard, R. (1999). Intraspecific variation in antipredator responses of three species of lizards (*Liolaemus*): possible effects of human presence. — *J. Herpetol.* 33: 441-448.
- Lobo, F., Laspiur, A. & Acosta, J.C. (2013). Description of new Andean species of the genus *Phymaturus* (Iguania: Liolaemidae) from northwestern Argentina. — *Zootaxa* 3683: 117-132.
- Lobo, F., Espinoza, R.E. & Quinteros, S. (2010). A critical review and systematic discussion of recent classification proposals for liolaemid lizards. — *Zootaxa* 2549: 1-30.
- López, P., Juke-Lorena, J.J. & Martín, J. (2003). *Lacerta monticola* (Iberian rock lizard). Predation. — *Herpetol. Rev.* 34: 245.
- Lopes, L.E., Fernandes, A.M. & Marini, M.Â. (2005). Predation on vertebrates by Neotropical passerine birds. — *Lundiana* 6: 57-66.
- Losos, J.B. & Sinervo, B. (1989). The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. — *J. Exp. Biol.* 145: 23-30.
- Lovette, I.J. & Fitzpatrick, J.W. (2016). *Handbook of bird biology*. — Wiley & Sons, Chichester.
- Márquez, J., Ripoll, Y., Dalmaso, A., Ariza, M. & Jordan, M. (2015). Árboles Nativos de la Provincia de San Juan. — Universidad Nacional de San Juan, San Juan.
- Martín, J. & López, P. (1999a). An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. — *Oikos* 84: 499-505.
- Martín, J. & López, P. (1999b). When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. — *Behav. Ecol.* 10: 487-492.
- Martín, J. & López, P. (2001). Repeated predatory attacks and multiple decisions to come out from a refuge in an alpine lizard. — *Behav. Ecol.* 12: 386-389.
- Martín, J. (2002). Comportamiento bajo riesgo de depredación: optimización de las decisiones de escape en lacértidos. — *Rev. Esp. Herpetol. Spec. Vol.*: 71-78.
- Mckinney, C.O. & Ballinger, R.E. (1966). Snake predators of lizards in western Texas. — *Southwest. Nat.* 11: 410-412.
- Mella Avila, J.E. (2002). Dieta del Cernícalo (*Falco sparverius*) y del Tucúquere (*Bubo magellanicus*) en un ambiente cordillerano de Chile central. *Unión de Ornitólogos de Chile*. — *Bol. Chil. Ornitol.* 9: 34-37.
- Pafilis, P., Foufopoulos, J., Poulakakis, N., Lymberakis, P. & Valakos, E.D. (2009). Tail shedding in island lizards (Lacertidae, Reptilia): decline of antipredator defenses in relaxed predation environments. — *Evolution* 63: 1262-1278.
- Pérez-Cembranos, A., Pérez-Mellado, V. & Cooper, W.E. (2013). Predation risk and opportunity cost of fleeing while foraging on plants influence escape decisions of an insular lizard. — *Ethology* 119: 522-530.
- Pérez, M.A., Borghi, E.C. & Beninato, V.A. (2013). *Phymaturus extrilidus*. Predation. — *Herpetol. Rev.* 44: 679.

- Poblete, A.G. & Minetti, J.L. (1999). Configuración espacial del clima de San Juan. — Acta síntesis del cuaternario de la Provincia de San Juan, INGENIO, Universidad Nacional de San Juan, San Juan.
- Polo, V., López, P. & Martín, J. (2011). Uncertainty about future predation risk modulates monitoring behavior from refuges in lizards. — *Behav. Ecol.* 22: 218-223.
- Poulin, B., Lefebvre, G., Ibáñez, R., Jaramillo, C., Hernández, C. & Rand, A.S. (2001). Avian predation upon lizards and frogs in a Neotropical forest understorey. — *J. Trop. Ecol.* 17: 21-40.
- R Core Team (2016). R: a language and environment for statistical computing. — R Foundation for statistical computing, Vienna, available online at <https://www.R-project.org/>.
- Reynolds, P. & Bruno, J. (2013). Multiple predator species alter prey behavior, population growth, and a trophic cascade in a model estuarine food web. — *Ecol. Monogr.* 83: 119-132.
- Sarasola, J.H., Santillan, M.A. & Galmes, M.A. (2003). Food habits and foraging ecology of American Kestrels in the semiarid forests of central Argentina. — *J. Raptor Res.* 37: 236-243.
- Shepard, D. (2007). Habitat but not body affects predator attack frequency on lizard models in Brazilian Cerrado. — *Herpetology* 63: 193-202.
- Smith, G.R. (1996). Correlates of approach distance in the striped plateau lizard (*Sceloporus virgatus*). — *Herpetol. J.* 6: 56-58.
- Tinbergen, N. & Van Iersel, J.J.A. (1947). Displacement reactions in the three-spined stickleback. — *Behaviour* 1: 56-68.
- Trejo, A., Kun, M. & Seijas, S. (2006). Dieta del Águila Mora (*Geranoaetus melanoleucus*) en una transecta oeste-este en el ecotono norpatagónico. — *Hornero* 21: 31-36.
- Venables, W.N. & Ripley, B.D. (2002). *Modern applied statistics with S*. Fourth. — Springer, New York, NY.
- Ventura, S.P., Passos, D.C., Machado, L.L., Horta, G. & Galdino, C.A. (2016). Escape tactics by a Neotropical montane lizard: a comparison of flight responses against natural and nonnatural predators. — *Acta Ethol.* 20: 9-15.
- Ydenberg, R.C. & Dill, L.M. (1986). The economics of fleeing from predators. — *Adv. Stud. Behav.* 16: 229-249.
- Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2009). A protocol for data exploration to avoid common statistical problems. — *Methods Ecol. Evol.* 1: 3-14.