

Sand-diving as an escape tactic in the lizard *Meroles anchietae*



J. Sunny Evans^a, Douglas A. Eifler^b, Maria A. Eifler^{b,*}

^a Department of Entomology and Plant Pathology, Oklahoma State University, Stillwater, OK, 74078, USA

^b Erell Institute, 2808 Meadow Drive, Lawrence, KS, 66047, USA

ARTICLE INFO

Article history:

Received 9 May 2016

Received in revised form

13 October 2016

Accepted 9 January 2017

Keywords:

Antipredatory behavior

Lacertidae

Namib desert

Predation risk

ABSTRACT

Risk assessment and behavioral responses to predation can depend on demographic and environmental factors. We studied the escape behavior of the sand-diving lizard *Meroles anchietae* in the Namib Desert, using simulated predator approaches and measuring latency to burying in sand. Lizards showed a clear preference for burying on a slipface. Flight initiation distance was largely influenced by the starting distance separating the lizard and pursuer, and whether the animal was initially sighted on or off a slipface. In general, longer starting distances were associated with longer flight initiation distances. The total flight distance covered by lizards before burying was inversely related to body size, and positively related to initial distance from a slipface crest. Distance from a slipface crest was associated with increased total flight distance, most dramatically for those initially sighted on a dune slipface. Even when shelter is ubiquitous, sand-dive patterns depend on location on a dune and body condition.

© 2017 Elsevier Ltd. All rights reserved.

1. Introduction

An animal's escape behavior should reflect both the cost of interrupting current activities to respond to predators and the relative risk of predation (Ydenberg and Dill, 1986; Cooper and Federick, 2007). Costs that may factor into escape decisions include loss of access to food (Cooper, 2009), loss of time and energy to engage in social activities (Martín and López, 1999; Cooper, 2011) and loss of radiant heat when basking (Martín and López, 2010). Predation risk can be affected by many factors, including speed and direction of predator approach (Cooper et al., 2003; Braun et al., 2010) or type of predator (Kacolisiris et al., 2009). In addition, distance from a refuge as well as position of a refuge relative to the direction of predator approach can influence perceived risk (Grant and Noakes, 1987; Dill and Houtman, 1989; Bonenfant and Kramer, 1996; Cooper, 1997); demographic characteristics such as age, sex and reproductive status all can play a role in the costs and perceived risks associated with escape behavior as well (Stankowich and Blumstein, 2005; Cooper, 2011; Eifler and Eifler, 2014).

Access to refuges can be an important influence on an animal's habitat selection or activity (Blázquez and Rodríguez-Estrella, 1997; Eifler and Fogarty, 2006); refuges can be selected based on

characteristics influencing predation risk such as location (Cooper et al., 1999; Kerr et al., 2003; Martín and López, 2003). Decisions about when to enter a refuge may depend on proximity (Martín and López, 1995, 2000; Cooper, 1997; Eifler, 2001; Cooper et al., 2003) as well as other indices of predation risk such as predator speed and persistence (Stapley, 2003; Amo et al., 2004; Martín and López, 2005). Some lizards escape predators by rapidly burying themselves in sand (Darwin, 1962; Arnold, 1995; Attum et al., 2007; Kacolisiris et al., 2010), in which case potential refuges might literally be "at their feet". However, no studies have assessed escape patterns of lizards using habitats where refuges are ubiquitous. For a sand-diving lizard, perhaps the typical notion of predation risk needs to be altered (Attum et al., 2007).

The shovel-snouted sand lizard of the Namib Desert *Meroles anchietae* (= *Aporosaura anchietae*) is a small lacertid that inhabits the large shifting aeolian sand dunes along a fog belt in the Namib Desert in south-western Africa (Louw and Holm, 1972). *Meroles anchietae* has many morphological adaptations to aid survival in hyper-arid environments including fringed toes that allow running across sand at speed and a shoveled snout for both penetrating into sand dunes and moving within sand when buried (Louw and Holm, 1972; Arnold, 1995). The ability for *M. anchietae* to dive into and move within the sand to evade predators and extreme microclimate variations is a behavior that has allowed them to exploit dune tops and slipfaces, which are normally devoid of vegetation (Louw and Holm, 1972). Their locomotion has become so specialized that they have difficulty moving effectively on other substrates, as

* Corresponding author.

E-mail address: maria.eifler@gmail.com (M.A. Eifler).

predicted for animals with highly specialized locomotory abilities (Louw and Holm, 1972; Attum et al., 2007).

Sand-diving is a specialized behavior that is possible because the aeolian dunes are well aerated, providing an adequate supply of oxygen and loosely packed on their slipface, making them easy to enter. Within the genus *Meroles*, diurnal predator evasion is likely to be the impetus for the evolution of a sand-diving escape strategy (Arnold, 1995). Although subsurface refugia are seemingly ubiquitous, *Meroles* lizards frequently choose to attempt to outrun approaching animals perceived as a threat, either quickly submerging within the sand or fleeing in bursts of extreme speed, appearing to fly over the surface of the dune before either burying, or stopping while still on top of the sand to watch the threat (pers. obs.). Since the lizards are always located where they can bury, the factors triggering burying are not readily apparent.

The objective of our study was to assess factors influencing escape patterns of the shovel-snouted sand lizard. We hypothesized that sand-diving during an escape event is non-random, and predicted that lizard's location previous to an escape and body condition were relevant to sand-diving.

2. Materials and methods

We collected data on an aeolian sand dune system at the Gobabeb Training and Research Station in Namibia, during 4–14 January 2012. The wind that forms the sand dunes packs them to varying degrees of firmness on the windward side, while the leeward side is made of loosely compressed and well oxygenated sand known as slipfaces. The extremely sparse vegetation on the dunes consists of only a few species of plants that are concentrated towards the base of the dune slopes. We collected data on escape activity of individual lizards in the morning from the time of their first emergence until activity had noticeably halted (pers. obs.; 0830–1130 h), and in the late afternoon from the time lizard activity resumed until they had ceased activity for the night (1600–1900 h).

Lizards were initially located and observed from a distance through binoculars, to minimize interaction before the simulated predator maneuvered into the desired position for approach. To minimize variability, the same person acted as the predator in all trials (DAE = simulated predator), wore the same clothing and walked all trials at same speed because some species are known to alter their escape tactics based on predator approach speed (Cooper et al., 2003; Cooper, 2009). The simulated predator approached the lizard at a constant pace, changing trajectory as the lizard moved, trying always to walk directly at the lizard (=pure pursuit, Nahin, 2007). If the lizard crested a dune and was temporarily out of sight, the simulated predator continued to move to the cresting point and adjusted his trajectory upon resighting the lizard. All lizards were pursued to the point at which they buried themselves in the sand, at which point they were captured.

For each trial, we recorded the lizard's initial position on a dune (on-slipface or off-slipface), and simulated predator's initial position relative to the lizard (above, below, or level). To determine the total flight distance (TFD) of the lizard, a meter tape was laid along the flight path using the actual tracks of the focal animal. For 49 of our 51 trials, we measured the distances initially separating the simulated predator and lizard before the approach began (starting distance = SD), and the distance separating them when the lizard began moving (flight initiation distance = FID). We also measured approach distance (AD), defined as the distance covered by the simulated predator during a trial before the lizard began moving, and calculated as $AD = SD - FID$. For each trial, we also measured the distances from the lizard's initial position to the nearest slipface, slipface crest and slipface bottom. For lizards that buried on-

slipface, we also determined the burying position relative to the length (crest-to-bottom) of the slipface. Upon capture, we weighed, measured (snout-to-vent length = SVL) and sexed the lizards. Each animal was color marked with a unique code of colored beads sewn into the base of the tail before release; we only conducted trials once per lizard.

Statistical analyses were performed using Minitab 17 (College Park, Pennsylvania), with a significance level of 0.05. We used general linear models (GLM) to examine the influence of individual characteristics and local conditions on FID, TFD and burial location. We applied the stepwise variable selection procedure to identify the final models. Using the residuals resulting from the regression of log SVL and log mass, we characterized body condition; larger values were associated with lizard that were heavy for their body length.

3. Results

Escape behavior was recorded for 51 individuals. Lizards exhibited a preference for burying on a slipface when evading predators ($\chi^2 = 19.966$, $df = 1$, $P < 0.001$); every animal initially sighted on a slipface eventually buried on a slipface and 35% of lizards initially sighted off-slipface areas also buried on a slipface ($n = 9$ of 26). There was no size difference between lizards that started on-vs off-slipface (t -test: SVL, $t = 1.68$, $df = 40$, $P = 0.101$; body condition, $t = 0.87$, $df = 40$, $P = 0.392$). For animals starting off-slipface, there were neither size differences, nor differences in initial distance to a slipface between those that eventually buried on a slipface and those that did not (t -test: SVL, $t = 0.15$, $df = 15$, $P = 0.881$; body condition, $t = 0.99$, $df = 12$, $P = 0.340$; initial distance to slipface, $t = 0.62$, $df = 6$, $P = 0.560$). Lizards burying on-slipface tended to bury in the upper reaches of a slipface; the mean burying location was 62% up slope from the base of a slipface and significantly greater than the 50% up that would be expected if burying location was random (1-sample t -test: $t = 2.43$, $n = 29$, $P = 0.022$).

Flight initiation distance was strongly related to both SD and the interaction between SD and starting location (Table 1). Longer SDs were significantly associated with longer FIDs; the slope of the relationship was greater for lizards that were initially off-slipface (Table 2, Fig. 1). Approach distance was related to both SD and lizard condition (Table 2). Longer SDs and less-robust body condition were significantly associated with longer ADs (Table 2).

Total flight distance was highly variable (range = 0–167 m, mean = 37 m) but was significantly related to lizard body size and initial location on the dune (Table 2). Smaller lizards tended to have longer TFD (Table 1, Fig. 2). In addition, initial distance from a slipface crest was positively related to TFD and was significantly related to the interaction between initial distance from a slipface crest and whether the lizards started on- or off-slipface (Table 1, Fig. 3). For animals starting off-slipface, the TFD did not differ between animals burying on- or off-slipface (t -test: $t = 0.77$, $df = 19$, $P = 0.452$).

4. Discussion

4.1. Habitat preference

Although lizards can and did sometimes bury off-slipface, fleeing *M. anchietae* showed a clear preference for burying on slipfaces when evading predators, despite there being more off-slipface dune surface in our study area. Several factors may contribute to their preference. Slipfaces may be preferred over other areas for ease of entry and aeration of the sand. The harder packed sand requires more energy to enter (Arnold, 1990) and is

Table 1

Pearson's Correlation coefficients (r (P)) between lizard size (snout-to-vent length (SVL)), body condition, escape variables and proximity to slipfaces. Significant values are in bold.

	SVL	Body condition	TFD	FID	SD	Distance to slipface
Body Condition	-0.005 (0.974)					
TFD	-0.435 (0.002)	-0.167 (0.246)				
FID	0.248 (0.086)	0.237 (0.102)	-0.154 (0.296)			
SD	0.283 (0.048)	0.077 (0.597)	-0.098 (0.507)	0.798 (<0.001)		
Distance to Slipface	0.004 (0.979)	-0.171 (0.249)	0.373 (0.011)	-0.089 (0.557)	-0.078 (0.607)	
Distance to Slipface Crest	0.108 (0.485)	-0.178 (0.247)	0.302 (0.046)	-0.015 (0.923)	-0.015 (0.922)	0.809 (<0.001)

Escape variables: TFD = total flight distance, FID = flight initiation distance, SD = starting distance.

Table 2

General linear model analyses for escape variables.

	F	df	P	R^2
Flight initiation distance				0.872
Distance to slipface crest	3.58	1,31	0.068	
Starting distance	118.40	1,31	<0.001	
Initial location	3.14	1,31	0.086	
Initial location * Starting distance	22.14	1,31	<0.001	
Approach distance				0.531
Body condition	6.32	1,39	0.016	
Starting distance	41.82	1,39	<0.001	
Total flight distance				0.497
SVL	8.20	1,32	0.007	
Distance to slipface crest	12.95	1,32	0.001	
Initial location	2.29	1,32	0.140	
Initial location * Distance to slipface crest	8.92	1,32	0.005	

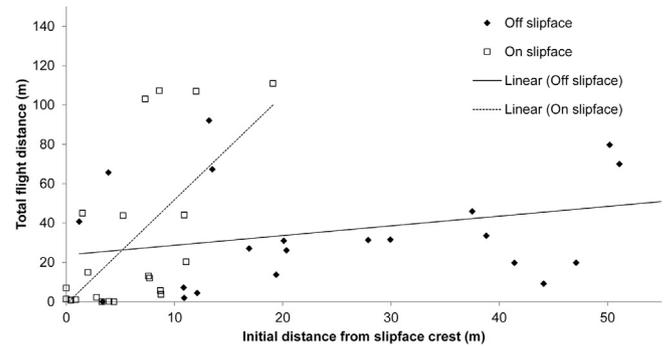


Fig. 3. Relationship between initial distance from a slipface crest and total flight distance for *M. anchietae*. Solid regression line depicts the trend for lizards starting off-slipface (TFD = 0.49*Initial distance + 23.75). Dashed regression line depicts the trend for lizards starting on-slipface (TFD = 5.30*Initial distance - 1.21).

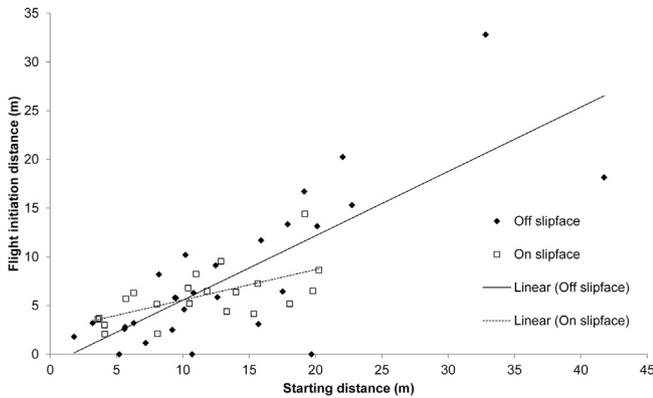


Fig. 1. Relationship between starting distance and flight initiation distance for *M. anchietae*. Solid regression line depicts the trend for lizards starting off-slipface (FID = 0.66*SD - 1.04). Dashed regression line depicts the trend for lizards starting on-slipface (FID = 0.31*SD + 2.42).

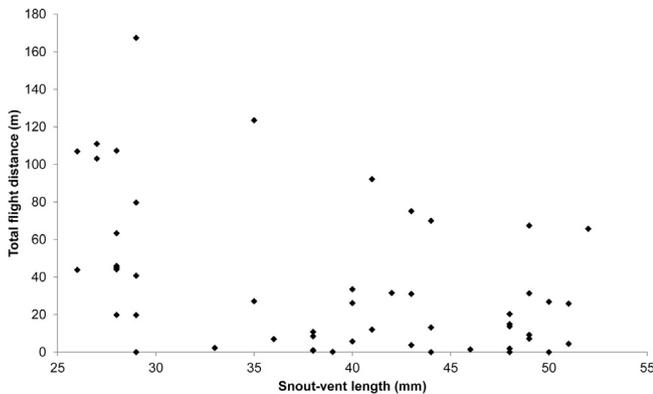


Fig. 2. Relationship between body size (SVL) and total flight distance for *M. anchietae*.

only habitable at shallower depths based on lower oxygen diffusion rates. Animals may choose to avoid microhabitats that impair physical performance (Pough, 1970; Irschick and Losos, 1999). The locomotor abilities of *Meroles* spp. are particularly well-suited for movement in loose sands (Arnold, 1990) and the skin structure of *M. anchietae* indicates that they may have lost the capability to use densely packed sand (Arnold, 1995). Some of our lizards seemed reluctant to bury off-slipface, running themselves nearly to the point of exhaustion before awkwardly burying themselves off-slipface. The reluctance to bury off-slipface by *M. anchietae* may be due to these habitats being more dangerous; the more densely packed sand results in lizards being buried closer to the surface and presumably relatively easy to catch by any predator that digs. Further, burying on-slipface leaves a less obvious sign to predators of a lizard's position beneath the sand. Slipfaces should be preferable for masking an escaped lizard's location because small disturbances of the surface have the obscuring effect of causing sand to slide down. Also, lizards burying on-slipface tend to swim farther below the surface before stopping than do lizards burying off-slipface (pers. obs.).

Some species may be facultative in their use of escape strategies. For *Liolaemus multimaculatus* on coastal dunes of Argentina, distance to shelter (vegetation) influences the likelihood of fleeing vs burying (Kacolis et al., 2009). Other lizards capable of sand-diving do not necessarily show the same preferences. In a comparative study of three sympatric skink species living in sand dune habitat in the desert of North Sinai, Egypt, the two species with the most dramatic morphological specializations preferred sand burial to the use of vegetation as refugia from predators (Attum et al., 2007). The sand-burying species were also more likely to be found on looser sand than less specialized species. In our study area, the sympatric congener *M. cuneirostris* lacks the sand-diving specializations of *M. anchietae*, infrequently visits slipfaces, and rarely buries to escape (Eifler and Eifler, 2014).

4.2. Taking flight

The decision to initiate flight from a predator can be influenced by a variety of factors associated with risk, many of which are directly tied to an ability to effectively reach safety, such as distance from a refuge or predator speed. In our study the two factors most closely linked to FID were SD and its interaction with starting location being on- or off-slipface. The role of SD is a relatively understudied aspect of escape (Blumstein, 2003; Cooper, 2005). In a study of 68 bird species, the vast majority showed a significant positive relationship between SD and FID; the additional monitoring cost associated with a predator approaching from afar may alter the cost-benefit relationship to favor longer FIDs (Blumstein, 2003). For such animals, monitoring costs may not be strongly influenced by SD, but the effect of SD on FID may more likely represent variation in perceived risk (Cooper, 2005). Possibly, SD could also influence perceived risk by influencing the time prey have to avoid detection or to evaluate predator persistence (Cooper, 2005). If being on-slipface is the preferred location for burying, then being off-slipface represents a less desirable location from which to detect an approaching threat.

Approach distance represents an alternative perspective on how animals might evaluate the level of risk associated with predator approach. For a given SD, increasing FID is also a decrease in AD. But the two measures both might contribute to assessing predation risk. Whereas proximity in the form of FID measures distance a predator still must cover to reach prey, AD is the complement, the distance already covered by the predator, which represents an aspect of predator behavior that the prey can observe and assess. Perhaps not surprisingly, AD is related to SD; predators starting farther out cover more distance before they become a threat. But body condition is important in a prey's assessment as less robust individuals waited longer before deciding to move. We are unaware of other studies that have focused on AD, but risk assessment may rely on alternatives to FID or on multiple factors (Cooper, 2005).

4.3. Total flight distance

The distance lizards fled before burying was highly variable. Some lizards simply buried as soon as the approach started, while others covered more than 100 m before burying. This could be, in part, related to the penetrability of the sand surface and predation risks associated with potential burying sites. While initial location played some role—distance from slipface crest was correlated with TFD ($r^2 = 0.3$; Table 1)—initial location did not explain all the variation in TFD. The longest TFDs were actually performed by animals initially located on-slipface (Fig. 3). Lizards tended to bury in the upper reaches of slipfaces, indicating not only a preference for slipfaces but also position on them; the relationship is especially strong for animals initially located on-slipface.

Proximity to a dune crest when initially positioned on-slipface influences how far a lizard will flee before diving; positions nearer to the crest were preferred, possibly because they provide a good vantage point to watch for predators. During our study, we did observe lizards perched at crest tops several times. Animals positioned on a crest are able to watch for predators approaching from all directions, while being very close to optimal burial sites. A lizard could spot an approaching predator from a greater distance, and bury themselves quickly. Several of the lizards we followed crossed the crest multiple times while fleeing, so that they left our line of sight when they moved onto the opposite side, a tactic that would not be effective for aerial predators, but is conceivably a successful way to avoid terrestrial attackers. Body size (and age) can play important roles in how a threat is assessed. Smaller animals may be less experienced, slower or the target of a different suite of

predators than larger individuals (Caro, 2005). In the sympatric *Meroles cuneirostris*, juveniles employ escape maneuvers differently than adults and display a different microhabitat preference for effecting escape (Eifler and Eifler, 2014). A more detailed study incorporating different types of predators (terrestrial vs aerial), and more knowledge of interspecific social behavior might better elucidate the factors that prompt a lizard to dive or flee.

Acknowledgements

We would like to thank those at the Gobabeb Research and Training Centre for operational and logistical support; L. White, R. Marchard, K. Malela and L. Nguluka provided invaluable assistance in the field. Our work was supported by the National Science Foundation (grant number 1065532) through the International Research Experience for Students (IRES) program. Lizards were captured and handled in accordance with the Animal Behavior Society's and the Herpetological Animal Care and Use Committee of the American Society of Ichthyologists and Herpetologists guidelines for the ethical treatment of animals under the approval of Erell Institute's Animal Care and Use Committee (IACUC proposal no. 2011–01).

References

- Amo, L., López, P., Martín, J., 2004. Trade-offs in the choice of refuges by common wall lizards: do thermal costs affect preferences for predator-free refuges? *Can. J. Zool.* 82, 897–901.
- Arnold, E.N., 1990. Why do morphological phylogenies vary in quality - an investigation based on the comparative history of lizard clades. *P. Roy. Soc. Lond B Biol.* 240, 135–172.
- Arnold, E.N., 1995. Identifying the effects of history on adaptation - origins of different sand-diving techniques in lizards. *J. Zool.* 235, 351–388.
- Attum, O., Eason, P., Cobbs, G., 2007. Morphology, niche segregation, and escape tactics in a sand dune lizard community. *J. Arid. Environ.* 68, 564–573.
- Blázquez, M.C., Rodríguez-Estrella, R., 1997. Factors influencing the selection of basking perches on carbon cacti by spiny-tailed iguanas (*Ctenosaura hemilopha*). *Biotropica* 29, 344–348.
- Blumstein, D.T., 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manage.* 67, 852–857.
- Bonenfant, M., Kramer, D.L., 1996. The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. *Behav. Ecol.* 7, 299–303.
- Braun, C.A., Baird, T.A., LeBeau, J.K., 2010. Influence of substrate temperature and directness of approach on the escape responses of juvenile collared lizards. *Herpetologica* 66, 418–424.
- Caro, T., 2005. *Antipredator Defenses in Birds and Mammals*. University of Chicago Press, Chicago, IL.
- Cooper Jr., W.E., 1997. Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Can. J. Zool.* 75, 943–947.
- Cooper Jr., W.E., 2005. When and how do predator starting distances affect flight initiation distances? *Can. J. Zool.* 83, 1045–1050.
- Cooper Jr., W.E., 2009. Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). *Behav. Ecol. Sociobiol.* 63, 1765–1771.
- 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., Frederick, W.G., 2007. Optimal flight initiation distance. *J. Theor. Biol.* 244, 59–67.
- Cooper Jr., W.E., Pérez-Mellado, V., Baird, T., Baird, T.A., Caldwell, J.P., Vitt, L.J., 2003. Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizards, *Cnemidophorus murinus*. *Behav. Ecol.* 14, 288–293.
- Cooper Jr., W.E., VanWyk, J.H., Mouton, P, Le, F.N., 1999. Incompletely protective refuges: selection and associated defenses by a lizard, *Cordylus cordylus* (Squamata: Cordylidae). *Ethology* 105, 687–700.
- Darwin, C., 1962. *The Voyage of the Beagle*. Doubleday and Co, Garden City, NY.
- Dill, L.M., Houtman, R., 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinensis*). *Can. J. Zool.* 67, 233–235.
- Eifler, D., 2001. *Egernia cunninghami* (Cunningham's skink): escape behavior. *Herpetol. Rev.* 32, 40.
- Eifler, D.A., Eifler, M.A., 2014. Escape tactics in the lizard *Meroles cuneirostris*. *Amphibia-Reptilia* 35, 383–389.
- Eifler, D.A., Fogarty, S., 2006. Perch selection by post-breeding female collared lizards (*Crotaphytus collaris*). *Amphibia-Reptilia* 27, 461–463.
- Grant, J.W.A., Noakes, D.L.G., 1987. Escape behaviour and use of cover by young-of-the-year brook trout, *Salvelinus fontinalis*. *Can. J. Fish. Aquat. Sci.* 44, 1390–1396.
- Irschick, D.J., Losos, J.B., 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural

- habitat use in Caribbean anoles. *Am. Nat.* 154, 293–305.
- 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.
- Kacoliris, F., Williams, J., Molinari, A., 2010. Selection of key features of vegetation and escape behavior in the sand dune lizard (*Liolaemus multimaculatus*). *Anim. Biol.* 60, 157–167.
- Kerr, G., Bull, M.C., Burzacott, D., 2003. Refuge sites used by the scincid lizard *Tiliqua rugosa*. *Austral Ecol.* 28, 152–160.
- Louw, G.N., Holm, E., 1972. Physiological, morphological and behavioral adaptations of the ultrapsammophilus, Namib Desert lizard, *Aporosaura anchietae* (Bocage). *Madoqua* 1, 54–62.
- Martín, J., López, P., 1995. Influence of habitat structure on the escape tactics of the lizard *Psammodromus algirus*. *Can. J. Zool.* 73, 129–132.
- Martín, J., López, P., 1999. Nuptial coloration and mate guarding affect escape decisions of male lizards *Psammodromus algirus*. *Ethology* 105, 439–447.
- Martín, J., López, P., 2000. Costs of refuge use affect escape decisions of Iberian rock lizards *Lacerta monticola*. *Ethology* 106, 483–492.
- Martín, J., López, P., 2003. Changes in the escape responses of the lizard *Acanthodactylus erythrurus* under persistent predatory attacks. *Copeia* 2003, 408–413.
- Martín, J., López, P., 2005. Wall lizards modulate refuge use through continuous assessment of predation risk level. *Ethology* 111, 207–219.
- Martín, J., López, P., 2010. Thermal constraints of refuge use by Schreiber's green lizards, *Lacerta schreiberi*. *Behaviour* 147, 275–284.
- Nahin, P.J., 2007. Chases and escapes: the mathematics of pursuit and evasion. Princeton University Press, Princeton.
- Pough, F.H., 1970. The burrowing ecology of the sand lizard, *Uma notata*. *Copeia* 1970, 145–157.
- Stankowich, T., Blumstein, D.T., 2005. Fear in animals: a meta-analysis and review of risk assessment. *P Roy. Soc. Lond B Biol.* 272, 2627–2634.
- Stapley, J., 2003. Differential avoidance of snake odours by a lizard: evidence for prioritized avoidance based on risk. *Ethology* 109, 785–796.
- Ydenberg, R.C., Dill, L.M., 1986. The economics of fleeing from predators. *Adv. Stud. Behav.* 16, 229–249.