

Short Notes

Run to shelter or bury into the sand? Factors affecting escape behaviour decisions in Argentinian sand dune lizards (*Liolaemus multimaculatus*)

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The goal of this study was to assess the main factors affecting escape strategies (escaping or sand burying) in sand dune lizards (*Liolaemus multimaculatus*). We recorded body size, substrate temperature, approach distance and shelter distance in the field, and performed an enclosure experiment to test whether mimicked predator types (aerial or terrestrial) affect escape behaviour. The frequency of sand-burying behaviour increased with distance to shelter (represented by patches of bunch grass; logistic regression, $P < 0.001$), which was the single significant predictor of the escape strategy chosen. However, in enclosure experiments the escape strategies adopted by lizards did not depend on predator type (contingency tables, $P = 0.62$).

Key words: burying, escape strategy, predator type

Vegetation structure and the availability of shelter are key factors that determine space use and microhabitat preference in lizards (Scott, 1976; Pianka, 1986; Huey, 1991; Lagos et al., 1995; Attum & Eason, 2006; Nemes et al., 2006). Small lizards are generally at high risk of predation, resulting in a trade-off between avoiding predators and competitors on the one hand, and the acquisition of food, mates and refuge sites under given microclimatic conditions on the other hand (McIvor & Odum, 1988; Rocha, 1995; Converse & Savidge, 2003; Attum & Eason, 2006). Taken together, the availability of shelters has profound implications for the ecology and survival of small lizards (Howard et al., 2003).

Research on predator–prey interactions and escape behaviour in lizards has received much recent attention. Iguanian lizards are often useful subjects for these kinds of studies, because they have high site fidelity, are often at high risk of predation and exhibit several escape strategies (Huey et al., 1983; Galdino et al., 2006), whose effectiveness depends on habitat structure and/or predator type (Schoener & Schoener, 1980).

The sand dune lizard, *Liolaemus multimaculatus* (Duméril & Bibrón, 1837), is a small diurnal sand-dwelling lizard endemic to the pampean coasts of the provinces of Buenos Aires and Río Negro in Argentina, and is categorized as vulnerable (Cei, 1993; Lavilla et al., 2000). Sand dune lizards are microhabitat specialists, preferring areas with low vegetation cover and bunch grasses as shelters (Kacoliris et al., 2006, 2008). They are, furthermore, sit-and-wait predators, but with a large prey spectrum (Vega, 1997, 2001). Males of sit-and-wait lizards are generally territorial, and for this reason differences in space use between sexes could exist (Cooper, 1994). With regards to escape behaviour in the presence of predators, two strategies exist: burying into the sand (Halloy et al., 1998) and/or escaping to shelters that consist of dense patches of bunch grass (*Spartina ciliata* and *Panicum racemosum*; Chebez & Kacoliris, 2008). Possible predators in the study area are raptors (*Caracara plancus* and *Milvago chimango*), gulls (*Larus dominicanus*, *Chroicocephalus maculipennis*), and terrestrial animals such as foxes (*Pseudalopex gymnocercus*), wild cats (*Oncifelis geoffroyi*) and snakes (*Philodryas patagoniensis* and *Clelia rustica*).

The goal of this work was to assess the main factors affecting escape strategies displayed by sand dune lizards. We tested the hypotheses that 1) the number of individuals that display sand-burying behaviour increases when the distance to shelter also increases; 2) adult lizards shows a greater frequency of sand-burying behaviour than juveniles; and 3) when aerial predators attack, the number of individuals that display sand-burying behaviour is greater than the number of individuals that display run-to-shelter behaviour.

The study site comprised a dune area located within Mar Chiquita Provincial Reserve (37°37'S, 57°16'W) in Buenos Aires Province, Argentina. Three different natural habitat types occur in the area. Ecotone grasslands are psammophytic on stable dune substrate, located between coastal dunes and pampas grasslands, with high and homogeneously spread vegetation cover. Sand grasslands are also psammophytic, but with low to medium vegetation cover dominated by plant species adapted to high salinity, a mobile substrate and low water availability. Interdunes are humid depressions with a mix of grasslands and hygrophytic plants. Sand grasslands and interdunes are distributed as patches in a matrix of active dunes with a lack of vegetation (Cabrera, 1976). Introduced trees (*Pinus* sp. and *Acacia* sp.) also occur within the study site.

Fieldwork was performed during January and February of 2008 and 2009. Each survey began at 1100, corresponding to the daily activity peak for this species (Vega et al., 2000), and finished at 1600. Three observers searched for lizards using visual encounter surveys that encompassed all microhabitat types (Crump & Scott, 1994). We simulated encounters with terrestrial predators in free-ranging sand dune lizards, and with terrestrial and aerial predators in an enclosure experiment.

Table 1. Main characteristics (mean \pm SE) of the parameters approach distance (AD, in cm), distance to the closest shelter (DCS, in cm), size of lizards (SVL, in mm) and substrate temperature (T, in degrees Celsius).

Variables	Mean \pm SE ($n=149$)	Range
AD	210.99 \pm 257.51	0–1427.00
DCS	1742.07 \pm 2020.26	0–5650.00
SVL	53.84 \pm 6.01	27.00–67.70
T	33.00 \pm 4.95	22.00–49.10

For free-ranging lizards, when an individual was found, the same observer (FK, wearing similar clothes) pursued the lizard, simulating a terrestrial predator. The following data were recorded: 1) approach distance, i.e. the distance between the observer and the lizard at which the escape behaviour was triggered (AD; to the nearest 1 cm); 2) the lizard's distance to the closest shelter (DCS; to the nearest 1 cm); 3) substrate temperature in the first location where the lizard was observed (T, to the nearest 1 °C); and 4) escape strategy displayed: taking refuge in a shelter (run-to-shelter), or burying into the sand (sand-bury). After the mimicked predator attack we captured the individual and recorded its sex (based on external features; Cei, 1993), snout–vent length (SVL, to the nearest 0.05 mm), and tail state (normal or autotomized/regenerated). Temperatures were recorded only during the 2008 season, whereas all the other independent variables were recorded only during the 2009 season.

For the experiment, we enclosed a 32 m² (8 m \times 4 m) sand field with plastic fences up to 1m high, placing a large bunch of grass that represented the preferred microhabitat for shelter (Kacolliris et al., in press) 6 m away from a starting point for the lizards. We captured adult lizards and kept them for one day in a terrarium for acclimatization. For data collection, lizards were put into the enclosure before simulating a terrestrial or an aerial predator attack. Terrestrial predators were simulated by the same observer (FK, wearing similar clothes) crawling in the lizard's direction, whereas aerial predators were simulated by a wooden bird model with a rope system that allowed the model to move in all directions above the enclosure. We again recorded the escape strategy displayed by each lizard (run-to-shelter or sand-bury).

Data are presented as means \pm SE. All tests were two-tailed, with a significance level of $\alpha=0.05$. Because escape strategy is a binary variable, its relation with other independent variables was assessed using logistic regression models. A simple logistic regression was performed to evaluate the relation between substrate temperature and the escape strategy, whereas a backward stepwise logistic regression was performed to test the relation between the independent variables (AD, DCS, SEX, SVL, TAIL) and escape strategy. For the enclosure experiments, we used contingency tables to assess whether the escape strategy depended on the type of predator.

A total of 149 free-ranging lizards (90 females and 59 males) were used for the experiment. While 88% ($n=130$) were normal-tailed, 12% ($n=19$) had autotomized/regener-

ated tails; tail condition had no influence on escape strategy. A total of 124 (84%) of the lizards ran to shelters in our presence, whereas 25 (16%) buried into the sand (Table 1). Substrate temperature and escape behaviour were uncorrelated with each other ($P=0.135$). Backward stepwise logistic regression modelling of escape strategy identified DCS ($-2 \log$ likelihood = 26.13, $P<0.001$) as its only predictor, while the other variables did not show significant correlations ($P=0.05$ in all cases; Table 2). As shown in Figure 1, the frequency of sand-burying behaviour increased with distance to the closest shelter.

We experimented with 68 lizards in the enclosure. Of the 42 lizards used in simulations of terrestrial predators, 22 (52%) displayed run-to-shelter behaviour, while 20 (48%) displayed sand-burying behaviour. In the case of aerial attacks (26 individuals tested), nine lizards (35%) displayed run-to-shelter, while 17 (65%) displayed sand-burying behaviour. The contingency table did not reveal significant differences between the predator types (chi-square = 1.84; $P=0.61$; $df=3$), rejecting our hypothesis that escape strategy depends on predator type.

Escape behaviour by sand dune lizards depends on shelter availability and proximity. When close to a shelter (at distances less than 3 m), lizards prefer to run to the refuge rather than bury into the sand. As distances to the closest shelter increase, the number of individuals that use sand-burying behaviour also rises. Overall, running to shelters is the most common escape strategy displayed, whereas sand burying is only used when shelters are unavailable or out of reach. Overall, running to shelters seems the preferred strategy over sand burying when facing predators.

When sand-buried, lizards are only positioned a few millimetres below the surface, and may be unearthed if a predator is able to determine their location. On the other hand, shelters such as bunches of grass provide a dense barrier against large animals, but small lizards can enter them easily, virtually disappearing from predators' sight and reach. It is also common that lizards bury when inside the bunch grass.

Our results show that lizards do not modify their escape behaviour depending on temperature, which might, however, modify their levels of activity. Further studies should include the body temperature of individuals as

Table 2. Scores ($-2 \log$ likelihood) and P values of the logistic regression between escape behaviour used by lizards and explicative variables: ED (escape distance), DCS (distance to closer shelter), SVL (snout–vent length), TAIL (tail status) and SEX.

Variables	Scores	P values
ED	0.261	0.610
DCS	26.134	0.000
SVL	0.804	0.370
TAIL	0.002	0.968
SEX	0.053	0.819

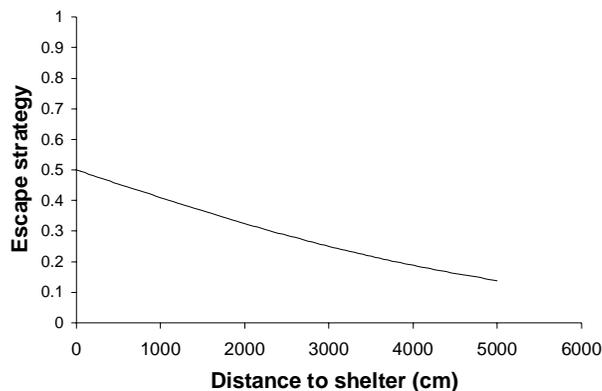


Fig. 1. Logistic regression showing the relation between the distance to the closest shelter and the escape strategy displayed by lizards. Zero represents sand-burying behaviour, and 1 represents run-to-shelter behaviour.

well as temporal variables of predator escape (delay until lizards display behaviours and the behaviours' durations). The lack of correlation between size and sex and escape behaviour conforms with previous autoecological studies that also failed to find differences in microhabitat use between these categories (Kacoliris et al., 2009).

Our data do not support the idea that differential escape strategies are used depending on whether a predator is aerial or terrestrial. We initially assumed that sand burying was a more effective strategy against aerial predators. Terrestrial predators are more likely able to dig up a buried lizard, which would be out of reach during an aerial pursuit. On the other hand, sand burying could be a parsimonious behaviour for lizards because individuals do not need to move away from their original positions. However, 65% of attacks with the aerial predator replica resulted in sand-burying behaviour, and further experiments are required in order to accurately assess whether an actual difference in lizard escape strategies exists between terrestrial and aerial predators.

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REFERENCES

Attum, O.A. & Eason, P.K. (2006). Effects of vegetation loss on a sand dune lizard. *Journal of Wildlife Management* 70, 27–30.

Cabrera, A.L. (1976). *Regiones Fitogeográficas Argentinas*. Buenos Aires: Editorial ACME.

Cei, J.M. (1993). *Reptiles del Noroeste, Nordeste y Este de la Argentina. Herpetofauna de las Selvas Subtropicales, Puna y Pampas*. Torino: Museo Regionali di Scienze Naturali (Monografie 14).

Chebez, J.C. & Kacoliris, F. (2008). Lagartija de las dunas. In *Los que se Van. Fauna Argentina Amenazada, Tomo 1*, 274–276. Chebez, J.C. (ed.). Buenos Aires: Albatros.

Converse, S.J. & Savidge, J.A. (2003). Ambient temperature, activity, and microhabitat use by ornate box turtles (*Terrapene ornata ornata*). *Journal of Herpetology* 37, 665–670.

Cooper, W.E. (1994). Prey chemical discrimination, foraging mode, and phylogeny. In *Lizard Ecology*, 95–116. Vitt, L.J. & Pianka, E.R. (eds). New Jersey: Princeton University Press.

Crump, M.L. & Scott Jr, N.J. (1994). Standard techniques for inventory and monitoring. Visual encounter surveys. In *Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians*, 84–92. Heyer, W.R., Donnelly, M.A., McDiarmid, M.W., Hayek, L.C. & Foster, M.S. (eds). Washington and London: Smithsonian Institution Press.

Galdino, C.A.B., Pereira, E.G., Fontes, A.F. & Van Sluys, M. (2006). Defense behaviour and tail loss in the endemic lizard *Eurolophosaurus nanuzae* (Squamata, Tropicuridae) from southeastern Brazil. *Phyllomedusa* 5, 25–30.

Halloy, M., Etheridge, R. & Burghardt, G.M. (1998). To bury in sand: phylogenetic relationships among lizard species of the *boulengeri* group, *Liolaemus* (Reptilia: Squamata: Tropicuridae), based on behavioural characters. *Herpetological Monographs* 12, 1–37.

Howard, R., Williamson, I. & Mather, P. (2003). Structural aspects of microhabitat selection by the skink *Lampropholis delicata*. *Journal of Herpetology* 37, 613–617.

Huey, R.B. (1991). Physiological consequences of habitat selection. *American Naturalist* 137, 91–115.

Huey, R.B., Pianka, E.R. & Shoener, T.W. (1983). *Lizard Ecology. Studies of a Model Organism*. Cambridge, Massachusetts: Harvard University Press.

Kacoliris, F.P., Celsi, C.E. & Monserrat, A.L. (2009). Microhabitat use by the sand dune lizard *Liolaemus multimaculatus* in a pampean coastal area in Argentina. *Herpetological Journal* 19, 61–67.

Kacoliris, F.P., Horlent, N. & Williams, J. (2006). Herpetofauna, coastal dunes, Buenos Aires Province, Argentina. *Check List* 2, 15–21.

Kacoliris, F.P., Williams, J.D. & Molinari, A. (in press). Selection of vegetation key features and escape behavior in sand dune lizards (*Liolaemus multimaculatus*). *Animal Biology*.

Kacoliris, F.P., Williams, J., Sánchez Véliz, G. & Rafael, A. (2008). Observaciones sobre el uso de cavidades en la arena por parte de la lagartija de los médanos (*Liolaemus multimaculatus*). *Cuadernos de Herpetología* 22, 87–89.

Lagos, V.O., Contreras, L.C., Meserve, P.L., Gutiérrez, J.R. & Jaksic, F.M. (1995). Effects of predation risk on space use by small mammals: a field experiment with a neotropical rodent. *Oikos* 74, 259–264.

Lavilla, E., Richard, E. & Scrocchi, G. (2000).

- Categorización de los Anfibios y Reptiles de la República Argentina*. San Miguel de Tucumán: Asociación Herpetológica Argentina.
- McIvor, C.C. & Odum, W.E. (1988). Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* 69, 1341–1351.
- Nemes, S., Vogrin, M., Hartel, T. & Olleler, K. (2006). Habitat selection by the sand lizard (*Lacerta agilis*): ontogenetic shifts. *North-Western Journal of Zoology* 2, 17–26.
- Pianka, E.R. (1986). *Ecology and Natural History of Desert Lizards*. New Jersey: Princeton University Press.
- Rocha, C.F. (1995). Ecología termal de *Liolaemus lutzae* (Sauria: Tropiduridae) em uma área de restinga do sudeste do Brazil. *Revista Brasileira de Biologia* 55, 481–489.
- Schoener, T.W. & Schoener, A. (1980). Ecological and demographic correlates of injury rates in some Bahamian *Anolis* lizards. *Copeia* 1980, 839–850.
- Scott, N.J. (1976). The choice of perch dimensions by lizards of the genus *Anolis* (Reptilia, Lacertilia, Iguanidae). *Journal of Herpetology* 10, 75–84.
- Vega, L.E. (1997). Reproductive activity and sexual dimorphism of *Liolaemus multimaculatus* (Sauria: Tropiduridae). *Herpetological Journal* 7, 49–53.
- Vega, L.E. (2001). Herpetofauna: diversidad, ecología e historia natural. In *Reserva de Biosfera Mar Chiquita: Características Físicas, Biológicas y Ecológicas*, 213–226. Iribarne, E.O. (ed.). Mar del Plata: Editorial Martin.
- Vega, L.E., Bellagamba, P.J. & Fitzgerald, L.A. (2000). Long-term effects of anthropogenic habitat disturbance on a lizard assemblage inhabiting coastal dunes in Argentina. *Canadian Journal of Zoology* 78, 1653–1660.

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