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

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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.

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 Frederick, 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 (Kacoliris 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 Rodrígues-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; Kacoliris 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

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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