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Escape behaviour in the leopard lizard (*Gambelia wislizenii*): effects of starting distance and sex

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Abstract. Predation risk influences decision making, escape behaviour, and resource use. Risk assessment and behavioural responses to predation can depend on demographic and environmental factors. We studied the escape behaviour of the long-nosed leopard lizard (*Gambelia wislizenii*) when approached by a human predator (= "simulated predator"), analysing flight initiation distance (FID) and flight distance (FD) relative to demographic and environmental variables. Starting distance (SD) of the simulated predator and orientation of prey lizards relative to the simulated predator influenced FID, but body size of the prey lizard did not. Sex interacted with SD to affect FID. Females lengthened their FIDs as SD increased, while male FID was unrelated to SD. Flight distance increased with increasing SD. *Gambelia wislizenii*'s ecological role as an ambush predator may explain their escape behaviour; reproductive status potentially affected the interaction between sex and SD.

Keywords: antipredator behaviour, evasion, flight initiation distance, Great Basin Desert, Squamata.

Animal escape behaviour should reflect both the relative risk of predation and the cost of interrupting current activities to respond to predators (Ydenberg and Dill, 1986; Cooper and Frederick, 2007). Many factors can potentially affect predation risk including the speed and direction of predator approach (Cooper et al., 2003; Braun et al., 2010), type of predator (Kacoliris et al., 2009) and distance from refugia (Cooper, 1997). Costs that may factor into escape decisions may include loss of access to food (Cooper, 2009), loss of time to engage in social activities (Cooper, 2011) and loss of radiant heat when basking (Martin and Lopez, 2010). Demographic characteristics such as age, sex and reproductive status can contribute to intraspecific differences in evading predators (Stankowich and Blumstein, 2005; Cooper, 2011; Eifler and Eifler, 2014).

The way in which escape behaviour differs intraspecifically may be complex, with no current consensus on pivotal factors (Stankowich and Blumstein, 2005; Cooper, 2011). In lizards, traits such as age and sex have been shown to influence multiple stages of the escape sequence, sometimes in opposing directions (Cooper, 2011); detailed information about the effects of demographic status on escape behaviour is needed.

We investigated the effects of sex and body size on evasion decisions for the long-nosed leopard lizard *Gambelia wislizenii* (Crotaphytidae), a species that is somewhat unusual in that members are not territorial, and can show significant overlap between home ranges (Tollestrup, 1983). They are found throughout desert areas of the western United States, ranging from southeastern Oregon to portions of northern Mexico (Parker and Pianka, 1976; McGuire, 1996), and primarily occupying desert scrub ecosystems with varying levels of shrub cover (Tollestrup, 1983; Steffen and Anderson, 2006). Long-nosed leopard lizards spend a high percentage of their time stationary and tend to be ambush predators (McElroy et al., 2011). Not only do they exhibit sexual size dimorphism

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with females being larger than males, but, contrary to Bergmann's rule regarding latitudinal clines in body size, southern populations (Arizona and New Mexico) have a larger body size than those in northern populations (Great Basin Desert; Montanucci, 1967; Parker and Pianka, 1976; Lappin and Swinney, 1999). Habitat and diet preferences of *G. wislizenii* may explain their social organization (Tollestrup, 1983).

Our study was conducted from 21 June to 17 July 2015 in the desert scrub of the Alvord Basin Desert, located in the northern part of the Great Basin Desert in southeastern Oregon (42°18′N, 118°37′W, elevation 1295 m). The two most abundant plant species on the study plot were basin big sagebrush (*Artemisia tridentata*) and greasewood (*Sarcobatus vermiculatus*). The area is home to several lizard species, most commonly the long-nosed leopard lizard (*G. wislizenii*), the tiger whiptail (*Aspidoscelis tigris*), and the desert horned lizard (*Phrynosoma platyrhinos*).

Data were collected from 07:30 to 13:30 h and from 15:00 to 18:00 h, during periods of highest activity (pers. obs.; Steffen and Anderson, 2016). Tests were conducted in areas unobstructed by vegetation so that the animal could be seen clearly and an approach would be unimpeded. To elicit a flight response, a standardized approach method was used; prey lizards were approached at a steady walking pace (about 2 m/s), by the same researcher (FEJ), wearing the same apparel, a common method for studying escape behaviour (Cooper and Wilson, 2007; Cooper, 2008a). The simulated predator (= person making the approach) walked directly at the animal until an escape attempt was made. Four specific places were marked during the approach: (1) the starting location of the simulated predator and (2) the prey lizard, (3) the location of the simulated predator when the lizard began to move and (4) the ending location of the lizard's movement. Three measurements were taken: the distance initially separating the simulated predator and lizard before the approach began (starting distance = SD), the distance separating the simulated predator and the lizard when lizard began moving (flight initiation distance = FID), and the distance moved by the lizard during its initial flight (flight distance = FD). We also recorded the lizard's orientation to the simulated predator's trajectory at the beginning of the approach: lizard facing towards, away from or lateral to the simulated predator. Lizards used were individually marked as part of another study. To avoid pseudoreplication, our animals were sampled only once.

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 lizard characteristics (sex, size and orientation) and SD, FID and FD.

Gambelia wislizenii typically initiated flight when the simulated predator was within about 2 m (FID; table 1). Flight initiation distance (FID) was not directly related to body size (table 2), but was significantly related to SD and the interaction between SD and sex (table 2). When analysed separately, female FID was significantly related to SD ($F_{1,21} = 16.11$, $P = 0.001$, $R^2 = 0.434$; fig. 1) while the relationship was not significant for males ($F_{1,19} = 0.88$, $P = 0.359$, $R^2 = 0.044$). Orientation also influenced FID; lizards facing the simulated predator tended to have shorter FIDs than those facing away or laterally (table 2). The flight distance (FD) of *G. wislizenii* was relatively short, with individuals typically fleeing about 0.5 m on their initial move (table 1). Flight distance was greater for larger SD, but was otherwise unrelated to our measures (table 2).

Sex was related to escape behaviour in *G. wislizenii*, with FID influenced by SD for females but not for males. In this regard, our results contrast with many other studies of lizards; in a review of 30 studies on lizard escape behaviour, 23 species did not exhibit sex differences in FID (Cooper, 2011). However, the role of starting distance is a relatively understudied aspect of escape (Blumstein, 2003, 2010; Cooper, 2005). Among birds, mammals, and lizards, the vast majority showed a significant positive relationship between SD and FID; the additional monitoring cost associated with a

Table 1. Summary statistics (mean ± SE) for *Gambelia wislizenii* body measurements and escape variables. SVL: snout-vent length; FID: flight initiation distance; FD: flight distance.

	SVL (mm)	Mass (g)	FID (m)	FD (m)
All lizards ($n = 43$)	100.2 ± 1.0	26.9 ± 1.0	1.99 ± 0.16	0.50 ± 0.05
Females ($n = 23$)	103.4 ± 1.3	29.1 ± 1.6	2.13 ± 0.24	0.46 ± 0.09
Males ($n = 21$)	96.9 ± 1.2	24.56 ± 1.0	1.83 ± 0.21	0.54 ± 0.07

Table 2. General linear model results testing the effect of lizard size and starting conditions on flight initiation distance (FID) and flight distance (FD). Degrees of freedom for all tests were the same (1, 34) except for orientation (2, 34). Significant terms are highlighted in bold. Model $R^2 = 0.4639$ for FID and 0.3221 for FD.

	FID		FD	
	Coefficient (*SE*)	*F* (*P*)	Coefficient (*SE*)	*F* (*P*)
Starting distance	**0.102 (0.042)**	**5.72 (0.022)**	**0.059 (0.016)**	**12.77 (0.001)**
Body size	0.028 (0.025)	1.33 (0.256)	0.0026 (0.0097)	0.07 (0.786)
Sex	0.494 (0.263)	3.52 (0.069)	0.136 (0.103)	1.76 (0.194)
Orientation	**0.076 (0.217) & 0.482 (0.242)**	**3.79 (0.033)**	−0.150 (0.084) & 0.101 (0.094)	1.57 (0.222)
Starting distance × Sex	**−0.093 (0.037)**	**6.10 (0.019)**	−0.024 (0.014)	2.73 (0.108)

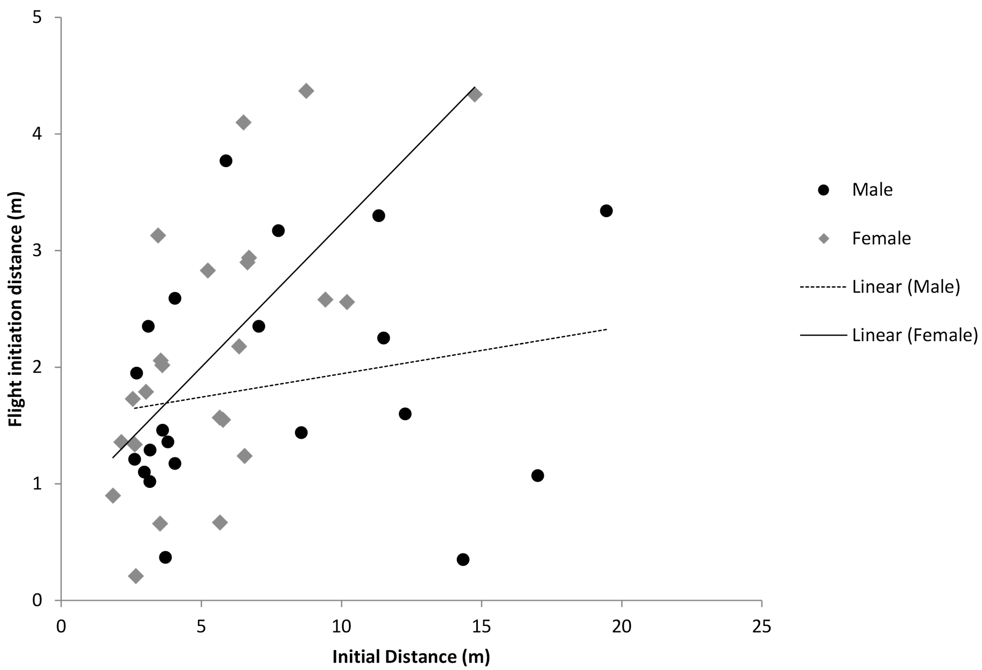

Figure 1. Relationship between SD and FID for *Gambelia wislizenii*.

predator approaching from afar may alter the cost-benefit relationship to favour longer FIDs (Blumstein, 2003; Samia et al., 2013). *Gambelia wislizenii* is an ambush predator that spends much of its time motionless, surveying its surroundings (McElroy et al., 2011). 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, 2008a; Cooper and Sherbrooke, 2013).

In a study of museum specimens, female *G. wislizenii* in the Great Basin were proposed to be more vulnerable to predation than males, although reasons presented were largely speculative (Lappin and Swinney, 1999). However, reproductive status can influence escape tactics in lizards (Bauwens and Thoen, 1981; Stapley and Keogh, 2004; Husak, 2006; Cooper and Wilson, 2007). During the time of our study, the population included females that were either gravid or had recently laid eggs, as well as non-reproductive individuals. We could not definitively assign reproductive status at the time of our FID trials because some lizards were captured and marked for another study prior to our trials; reproductive status may have changed in the interim, but reproductive female *G. wislizenii* are more brightly coloured (McGuire, 1996) and so are potentially more conspicuous to predators. In addition, running speeds may be slower and energetic costs higher in reproductive female lizards, all of which may make them more vulnerable to predation. The effect of reproductive status on perceptions of predatory risk in *G. wislizenii* merits further study.

If SD influences predation risk, then SD could also influence escape decisions by prey such as FD in addition to when to initiate flight (FID), but we know of no other research demonstrating a relationship between starting distance and flight distance (table 2). Variables indicative of increased predation risk such as predator approach speed and direction can influence FD as well as the decision to enter a refuge (Cooper, 1997; Cooper et al., 2003; Cooper and Wilson, 2007). Although some Crotaphytid lizards flee to refuges when threatened (e.g., Eifler and Fogarty, 2006), our study population of *G. wislizenii* did not employ a strategy of retreating to refuges (pers. obs.). Rather, our lizards responded to increased starting distance as if greater predation risk was presented by making longer moves in response to a predator's approach (i.e., had longer FDs).

Possibly, SD could also influence perceived risk by influencing the time prey have to avoid detection or to evaluate predator persistence (Cooper, 2005; Cooper and Blumstein, 2014). The orientation of a lizard relative to a predator may represent a gauge of the lizard's ability to assess risk (Cooper, 2008b). If so, our results were counter to expectations based on previous research regarding predator approach and FID since orientation did not seem to influence our prey lizard's ability to detect the approaching researcher; our lizards that were facing away from or were lateral to the predator had the longest FIDs, which means that prey lizards began their escape when the predator was farther away compared to those facing towards the predator. More focused research is needed to address how prey orientation might influence risk assessment.

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