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Escape by juvenile Little Striped Whiptails (*Aspidoscelis inornatus*, Baird 1859) in response to predator approach speed (Lacertilia: Teiidae)

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Predation is an important ecological interaction that affects the survival of animals. To evade and survive predation, prey strategies vary based on the predator and on situational factors such as their reproductive condition and habitat structure (Osiejuk and Kuczynski, 2007; Heithaus et al., 2009; Morice et al., 2013; Piratelli et al., 2015). Organisms must decide both when and how to escape by rapidly assessing the risk they face during each predation interaction (Lima and Dill, 1990). The risk of predation is weighed against the benefits of other activities, such as foraging and reproduction (Bauwens and Thoen, 1981; Veasey et al., 2001; Cooper and Pérez-Mellado, 2004; Kraffe et al., 2008; Pérez-Cembranos et al., 2013). Animal escape behaviours are complex because decisions must be made quickly while allowing for efficient escape.

An economic model, the optimal escape theory, assesses costs and predicts when an animal will flee based on flight initiation distance (FID), the distance between animal and predator when escape begins. When the cost of continuing current activities meets or exceeds the cost of fleeing, then the animal should initiate escape (Ydenberg and Dill, 1986). According to tests of the model, escape responses can be adjusted based on the behaviour of the predator, such as speed and directness of approach (Burger et al., 1992; Hemmi, 2005; Cooper et al., 2009; Braun et al., 2010; Samia et al., 2016). In addition, environmental factors including habitat and temperature influence escape behaviours (Martín and López, 1995; Forsman, 1999; Özbilgin and Wardle, 2002; Stankowich and Coss, 2007).

The method of escape also could depend on situational factors (Caro, 2005; Nahin, 2007). Often speed is not sufficient: an evader simply might not be able to outrun its pursuer, making directional evasive manoeuvres potentially useful (Cresswell, 1993; Edut and Eilam, 2004; Caro, 2005). Many animals incorporate elements of directional manoeuvres into their escape strategies (Vannini, 1980; Djawdan and Garland, 1988; Caro et al., 2004; Lerner, 2011; Eifler and Eifler, 2014), and even a single manoeuvre can result in a decreased likelihood of capture (Humphries and Driver, 1967; Jones et al., 2011).

Across species of lizards, longer FIDs accompany faster predator approaches (Cooper 1997, 2006, 2011; Cooper et al., 2009). However, tenets of optimal escape theory have not been as well-studied among lizards that exhibit high levels of movement while foraging, such as whiptails (i.e., active foragers; Milstead, 1957; Samia et al., 2016). Our study aims to test predictions made by the optimal escape theory in active foragers. Because foraging mode influences aspects of lizard physiology, behaviour, and ecology (Samia et al., 2016), understanding its relationship to escape behaviour could provide insight into trade-offs between foraging and escape.

The Little Striped Whiptail (*Aspidoscelis inornatus* Baird, 1859, previously *Cnemidophorus inornatus*; Fig. 1) is a bisexual species that occurs in the Chihuahua Desert of North America, ranging from central Mexico near San Luis Potosí northward into western Texas, New Mexico, and Arizona in the southwestern USA (Duellman and Zweifel, 1962; Wright and Lowe, 1993; Hammerson et al., 2019). The species is fairly small, with a maximum snout–vent length (SVL) of ca. 70 mm, and it occupies mainly grassland but also desert shrubland and woodland habitats (Hammerson et al., 2019). The few known predators of *A. inornatus* include two snake species, the Coachwhip (*Masticophis flagellum*) and the Western Massasauga (*Sistrurus tergeminus edwardsii*), as well as two bird species, the Loggerhead Shrike (*Lanius ludovicianus*) and the Greater Roadrunner (*Geococcyx californianus*) (Graham and Kelehear,

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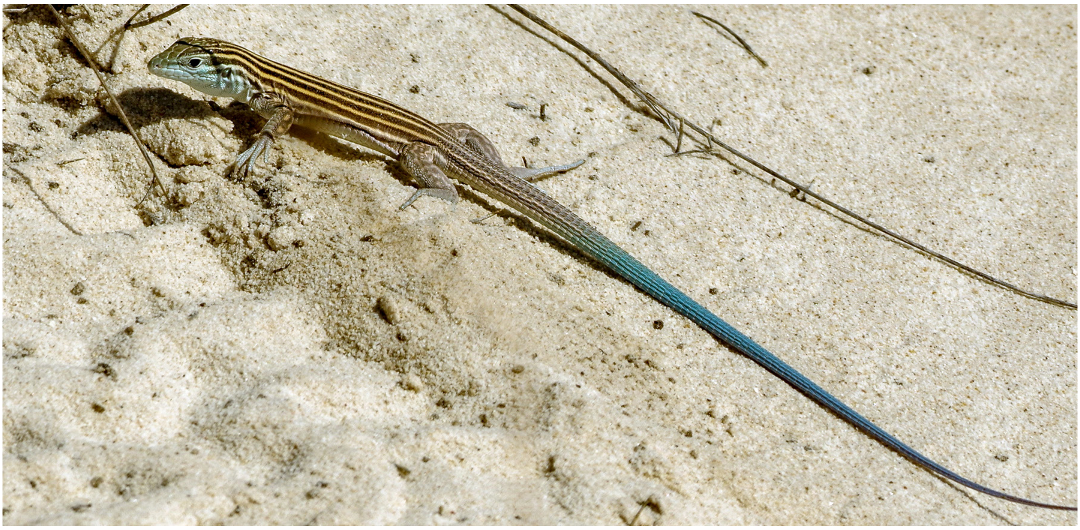

Figure 1. Adult *Aspidoscelis inornatus* from Hudspeth County, Texas, USA. Photo by Drew Dittmer.

2016; Herr et al., 2017). No aspect of the escape behaviour of *A. inornatus* has been examined (Graham and Kelehear, 2016; Herr et al., 2017). We assessed the effect of predator approach speed on the escape response of juvenile *A. inornatus*, predicting that FID as well as flight distance (FD) would be greater with a fast rather than with a slow approach speed.

Materials and Methods

Study area. We collected data from 21–23 March 2018 at the Dalquest Desert Research Station, located in Presidio and Brewster Counties, Texas, USA (29.563°N, 103.806°W, datum = WGS84). Our 3.5 ha study site was characterized by open patches of sand and rock interspersed with vegetation, primarily creosote bush (Zygophyllaceae: *Larrea tridentata*), cactuses (Cactaceae: *Cylindropuntia leptocaulis* and *Echinocereus* sp.), monocot bushes (Asparagaceae: *Yucca* sp. and *Agave lechuguilla*), and ocotillo (Fouquieriaceae: *Fouquieria splendens*).

Trial setup. We measured escape behaviour from 10:30–16:30 h each day. The same person (SGS), wearing the same apparel, acted as the predator for all trials. A group of 4–5 people walked transects ca. 5–10 m apart to systematically search the study area for active *A. inornatus*. Once an *A. inornatus* individual was sighted, the predator positioned herself to allow for an approach unobstructed by vegetation and initiated the trial when the lizard was motionless for at least 2 s. Prior to each trial, we randomly determined the predator's approach speed (via coin toss; fast = ca. 1.6 ms^{-1}, slow = ca. 0.8 ms^{-1}). The predator walked directly towards the lizard at the designated speed, and immediately stopped when the lizard initiated flight.

Distance measurements. After each trial was completed, we placed four markers corresponding to the starting location of the predator, the starting location of the lizard, the location of the predator when the lizard began to move, and the first location at which the lizard stopped after fleeing. Based on the markers' locations, we measured (1) start distance (SD), the initial distance separating predator and lizard; (2) approach distance (AD), the distance travelled by the predator before the lizard initiated its flight response, where AD = SD – FID; (3) flight initiation distance (FID), the distance between predator and lizard when the lizard began fleeing; and (4) flight distance (FD), the distance the lizard travelled before stopping. In addition, we measured the angle between the predator's approach trajectory and the lizard's flight trajectory (i.e., escape angle). We flagged the start location of each observed lizard and did not observe another lizard within 10 m of that location to ensure that each lizard was observed only once. At the site of the lizard's initial position, we measured the ground temperature with an infrared temperature gun (Fluke 568 infrared thermometer, Fluke Corporation, Everett, Washington, USA).

Lizard data. To assess their size, we captured a subset of the focal lizards (n = 7; 24%) by noosing them. We measured their SVL, tail length, tail condition, and mass, then marked the lizards with non-toxic paint pens and released them at the site of capture within 2 h. None of the captured lizards were large enough to probe to determine their sex.

Data analysis. We used Minitab Statistical Software Version 18 (Minitab Inc., State College, Pennsylvania, USA) for statistical analyses. We assessed relationships between our measured escape variables using Pearson's Correlation and nonparametric tests to compare treatments for escape variables. Escape trajectories to the left and right were pooled so that escape angles ranged between 0° and 180°. Finally, we performed a regression analysis using a stepwise selection process (entry and exit = 0.1) to examine (1) the relationship between FID and AD, temperature, treatment, and AD*treatment, as well as (2) the relationship between FD and FID, AD, temperature, and AD*treatment.

Results

We conducted simulated predator escape trials on 29 juveniles with a mean (range) SVL of 41.8 mm (40–44) and mass 2.1 g (1.8–2.3). We found no difference in escape response between the slow (n = 14) and fast (n = 15) treatments for any of our distance-based variables (Table 1). Both AD and FD were negatively correlated with FID (Pearson's Correlation; $r = -0.598$; $P = 0.001$ and $r = -0.383$, $P = 0.040$, respectively). In addition, SD and FD were positively correlated with AD ($r = 0.836$, $P < 0.001$ and $r = 0.412$, $P = 0.026$, respectively). However, SD was not significantly correlated with either FID or FD ($r = -0.059$, $P = 0.760$ and $r = 0.251$, $P = 0.189$, respectively). The regression analysis yielded models with AD as the sole significant variable for FID ($F_{1,27} = 15.01$, $P = 0.001$, $R^2 = 35.7\%$) and FD ($F_{1,27} = 5.54$, $P = 0.026$, $R^2 = 17.0\%$). Escape angle varied with approach speed. Focal lizards that were approached quickly fled at larger escape angles than lizards that were approached slowly (Table 1). The distribution of escape angles differed with approach speed ($\chi^2 = 8.9$, $df = 3$, $P = 0.030$; Fig. 2).

Discussion

Our results indicate that juvenile *A. inornatus* adjust both the timing and nature of escape responses based on predator approach speed. Foraging lizards start fleeing when a predator is perceived as a great enough threat (Cooper and Frederick, 2007). In *A. inornatus*, we found a negative correlation between AD and FID, indicating that the distance over which a predator makes a direct approach can influence their escape response. The longer FD associated with longer AD might occur because lizards may perceive a more persistently approaching predator as a greater threat and flee farther (producing a longer FD; Cooper, 2003; Cooper and Blumstein, 2015).

In our study, approach speed had little effect on flight timing even though increasing predator approach speed has been linked to FID for some lizards (Cooper, 2003; Cooper and Blumstein, 2015). However, predator approach speed did affect escape angles. To maximize the distance from the predator, lizards approached during our trials should flee in a direct line away from the predator (in a 0° escape angle; Nahin, 2007). However, our results demonstrated marked deviation from 0° escape angles in both the slow and fast treatments, with fast approaches generally provoking larger escape angles (Fig. 2). Variability in escape angle has been documented for multiple taxa, including fish, insects, and crustaceans (Domenici et al., 2008, 2011). Deviating from an expected path of escape decreases the ability of predators to anticipate where prey will be and thereby increases chances of successful escape (Domenici et al., 2008). Larger escape angles reflect changes in direction

Table 1. Escape variables for fast (n = 15) and slow (n = 14) approaches in juvenile *Aspidoscelis inornatus* escape trials, listing median values and ranges. Wilcoxon Signed-Rank tests values (W) and their respective P-values indicated that only escape angle varied significantly with approach speed.

Characteristic	Slow	Fast	*W* (*P*)
Start distance (cm)	338 (176–530)	358 (189–449)	214 (0.88)
Approach distance (cm)	215 (59–492)	202 (112–396)	199 (0.66)
Flight initiation distance (cm)	117 (38–314)	130 (30–117)	213 (0.91)
Flight distance (cm)	39 (17–94)	47 (13–147)	186 (0.31)
Escape angle (°)	27 (6–88)	49 (0–136)	161 (0.03)

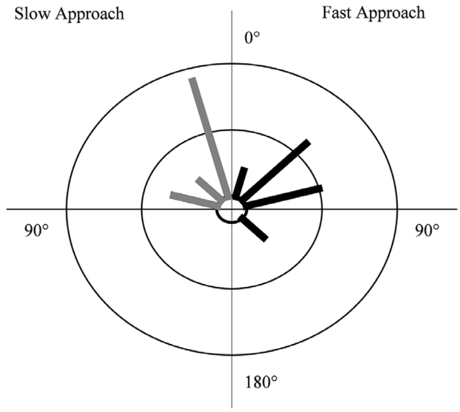

Figure 2. Radial histogram of escape angle frequency relative to approach speed for *Aspidoscelis inornatus*. Escape angles in response to a slow approach speed are on the left (grey bars) and to a fast approach speed on the right (black bars). 0° = an escape angle directly away from the approaching threat and 180° = flight directly toward the threat. Responses are binned into 30° increments and graphed at the mid-interval angle. Concentric circles represent frequency increments of five lizards.

while fleeing, which likely improves evasion of a pursuer (Cooper and Sherbrooke, 2016). Further, smaller animals are comparatively more flexible around their centre of mass, resulting in more manoeuvrability than their larger-bodied predators (Howland, 1974; Domenici and Blake, 1993). When pursuing manoeuvrable prey, predators need to turn at an angle that can compromise their speed, as has been documented for birds and fish (Domenici and Blake, 1993; Lind et al., 2002). Juvenile *A. inornatus* were considerably smaller than the approaching predator. Perhaps they fled at escape angles > 0° because their manoeuvrability allowed them to effectively escape from a perceived threat that they could not outrun. With faster approaching threats, a larger escape angle increases the potential for a small animal to outmanoeuvre a larger pursuer. Future experimental studies are needed to tease apart the relative importance of lizard body size and age class on escape trajectories and their characteristics.

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