Brief communication

Influence of gaze and directness of approach on the escape responses of the Indian rock lizard, *Psammophilus dorsalis* (Gray, 1831)

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Animals often evaluate the degree of risk posed by a predator and respond accordingly. Since many predators orient their eyes towards prey while attacking, predator gaze and directness of approach could serve as conspicuous indicators of risk to prey. The ability to perceive these cues and discriminate between high and low predation risk should benefit prey species through both higher survival and decreased energy expenditure. We experimentally examined whether Indian rock lizards (*Psammophilus dorsalis*) can perceive these two indicators of predation risk by measuring the variation in their fleeing behaviour in response to type of gaze and approach by a human predator. Overall, we found that the gaze and approach of the predator influenced flight initiation distance, which also varied with attributes of the prey (i.e. size/sex and tail-raise behaviour). Flight initiation distance (FID) was 43% longer during direct approaches with direct gaze compared with tangential approaches with averted gaze. In further, exploratory, analyses, we found that FID was 23% shorter for adult male lizards than for female or young male (FYM) lizards. In addition, FYM lizards that showed a tail-raise display during approach had a 71% longer FID than those that did not. Our results suggest that multiple factors influence the decision to flee in animals. Further studies are needed to test the generality of these factors and to investigate the proximate mechanisms underlying flight decisions.

1. Introduction

Predator discrimination has evolved in prey species, in which the costs of failing to identify predation risk are high (Ydenberg and Dill 1986; Caro 2005; Adams *et al.* 2006). In some cases, it may be insufficient to simply detect the presence of a predator, since the mere presence of a predator does not necessarily indicate heightened threat (Carlile *et al.* 2006; Mathot *et al.* 2009). Rather, the behaviour of the predator (e.g. physical posture, direction of movement and gaze) may better indicate the degree of threat. For example, when cats stalk birds, they orient their eyes towards their prey (Leyhausen 1973).

Since anti-predator behaviour (e.g. fleeing and hiding) carries costs, assessing the degree of threat enables an appropriate response that balances benefits and costs to negotiate the trade-off between predation and starvation (Carter *et al.* 2008). Flight initiation distance (FID) is the distance between prey and the approaching predator at which escape is initiated. If prey behave optimally, one would expect FID to increase with predation risk (Cooper and Frederick 2007). Individuals that flee too late might be killed; while those that flee too early might increase their energy expenditure due to locomotion, and decrease their food intake and social activity (Kramer and Bonenfant 1997; Dawkins 2009). Hence, individuals should optimize their response by assessing the risk of predation and trading this off against the costs of flight.

A variety of features of the predator (e.g. size, approach speed, directness, gaze and physical condition), prey (e.g.

group size, morphology and experience) and environment (e.g. habitat openness) are likely to affect the perceived level of risk during a given encounter (Stankowich and Blumstein 2005; Stankowich 2008). For example, mobbing calls of group-living birds vary with the size and threat of the potential predator (Templeton *et al.* 2005; Griesser 2009). Similarly, a wading bird, the Red Knot (*Calidris canutus*), perceived gliding hawks as a higher risk (i.e., they had longer FIDs) than perching hawks (Mathot *et al.* 2009). Further, Black Iguanas (*Ctenosaura similis*), which are saxicolous herbivore lizards, showed longer FIDs in response to a human looking at them than to a human not looking at them (Burger *et al.* 1992). Hence, anti-predator behaviour appears to be risk-dependent, and this leads us to ask how different attributes of risk are integrated while making decisions about flight behaviour.

We tested the influence of gaze (coordinated orientation of the head and eyes, either directly towards or away) and directness of approach on escape behaviour of Indian rock lizards, *Psammophilus dorsalis* (Gray, 1831) (Squamata: Agamidae) by conducting simulated predator approach trials using a human 'predator' (see section 2.2, below, for a justification). We measured FID of Indian rock lizards for two crossed treatments: direct versus tangential approach; and direct versus averted gaze. We hypothesized that Indian rock lizards use gaze and approach (among other factors) as indicators of the risk posed by a predator and that they therefore vary their FID in response to these indicators. Specifically, we predicted that FID should be longest with direct approach and direct gaze. We also explored the possible influence of lizard sex, size and behaviour on FID.

2. Materials and methods

2.1 *Study area and species*

The experiment was conducted in Rishi Valley, which is located among mid-elevated hills of Chittoor District, Andhra Pradesh, India (13.63 N, 78.45 E; c. 750 m elevation). The hill slopes are largely covered with thick scrub vegetation, interspersed with granite boulders and sheet rock. Fieldwork was carried out from November 2009 to January 2010 (the non-breeding season) when the maximum temperature was 25–30°C.

Indian rock lizards are found in the drier parts of most of peninsular India (Daniel 2002), reaching their highest densities where there are flat rocks or boulders, interspersed with scrub (Radder *et al.* 2005). They are territorial and show sexual dimorphism in size and coloration (Radder *et al.* 2006a). In the post-breeding season, adult males are yellow to dull orange in colour dorsally and black ventrally. In the breeding season, they are bright orange or red dorsally and black ventrally. Adult females, sub-adult males, sub-adult females and juveniles are usually mottled brown and grey dorsally and cream ventrally, such that they are cryptic in their rocky environment (Radder *et al.* 2005).

This species is a habitat specialist: at our study site, individuals were found mostly on sheet-rocks and large boulders.

2.2 *Experimental design*

We simulated predator approach by walking towards individual lizards, as human disturbance stimuli are analogous to predation risk (Frid and Dill 2002; Martín *et al.* 2004; Blumstein 2010), and previous field studies have suggested that a human's orientation and approach are conspicuous cues of predatory risk (Burger and Gochfeld 1990; Cooper 1997a; Watve *et al.* 2002).

To experimentally examine the effect of approach angle and gaze on FID of lizards, subject lizards were first found and observed from a distance (c. 40 m) using binoculars. Only basking lizards (i.e. lizards that remained stationary on the upper surface of a rock) were selected, as vigilance levels in basking and foraging lizards may vary (Devereux *et al.* 2006). Each trial involved walking towards the subject lizard either directly or tangentially (at an angle of c. 5–8° towards the right, ie clockwise, direction from the subject). This was crossed with a second treatment, with gaze (head and eyes in coordination) oriented either directly towards the subject or averted (turned 90° to the right). All trials were conducted between 0900 and 1100 hours. Experimental treatments for each trial were selected at random by flipping a coin twice, and the approach was always in a straight line, from a direction such that no vegetation or rocks prevented the observer and the lizard from seeing each other. All lizards were approached by the same person (RS) wearing the same clothes and walking at c. 1.6 m/s (Fernandez-Juricic *et al.* 2002). Any given lizard was used only once (i.e. was subjected to only one combination of approach and gaze), and because Indian rock lizards are territorial (Radder *et al.* 2006a), we shifted sites (*n*=19 sites, >500m apart, but with similar habitat) after testing 3–7 individuals at each site so that we did not inadvertently test the same individual more than once. To prevent possible information transfer from one lizard to another at the same site, we made sure that successive lizards were out of sight of each other.

Each trial was carried out in the following manner. The 'predator' (RS) walked towards the lizard from a starting point 20 m away. None of the lizards fled before the predator reached the 20 m start point. An observer with 8×42 binoculars stood >40m from the subject lizard and noted the location of the predator when the subject fled. The FID was then measured using a measuring tape. Before each trial, we divided the subject lizards into two categories according to their size and colour. To estimate size, we took photographs of each lizard before the trial and subsequently estimated snout-vent length (SVL), using as a scale various small features (eg, depressions, lichen blotches) on the rock on which the lizard was perched. Estimated SVL and colour

were then used to divide subjects into adult males (AM; SVL >90mm; dorsally yellow; n=31) and females/young males (FYM; SVL 50–85mm; dorsally mottled brown; n=66). We did not test juveniles (SVL < 50mm). We combined females and young males into the size–sex category FYM because is it very difficult to separate these two classes (Radder *et al.* 2006b).

2.3 *Data analyses*

We separated our analyses into confirmatory and exploratory parts (Harrell 2001). In confirmatory analyses, we investigated differences or relationships that had been specified *a priori* as being the target of our experiment. For these, we used a linear regression model to investigate the effect of approach type and gaze (and their interaction) on the FID of lizards. We $\log_e$ transformed the response variable (FID) so that model assumptions were better met (residuals from an analysis with untransformed FID showed substantial skew).

In the exploratory part of our analysis, we examined the effects of variables that we did not set out to test *a priori*, but instead decided to examine during and after data collection. Since the results of these analyses are meant to be indicative rather than confirmatory, we allowed ourselves more flexibility in model specification and selection. Significant effects are thus meant to suggest further lines of research rather than to represent formal tests of hypotheses. All analyses were conducted in the programming and statistical language R 2.11.1 (R Development Core team 2012). The full dataset as well as scripts used in analyses and visualisation are available from the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.1h551).

3. Results

In our confirmatory analyses, we modelled the natural logarithm of FID as a function of approach (direct or tangential), gaze (direct or averted) and the interaction between the two. We found no significant interaction ($F_{1,93}=0.39$, $P=0.53$), and subsequently dropped this term in the model. Both main effects were significant (approach: $F_{1,94}=4.44$, $P=0.037$; and gaze: $F_{1,94}=5.84$, $P=0.017$). A direct approach (model coefficient±SE: 0.183±0.087) and direct gaze (0.209±0.086) increased FID relative to their putatively less threatening alternatives. These estimates correspond to a c. 20% increase in FID for a direct versus tangential approach and an additional c. 23% increase in FID when gaze was direct versus when it was averted. Thus, the shortest FIDs occurred when approaches were made tangentially with gaze averted, and the longest FIDs were seen with a direct approach and direct gaze (figure 1).

In further exploratory analyses, we examined the potential relationship between lizard size–sex categories and FID. To investigate the effect of size–sex category (AM versus FYM) on FID, we began with a model that included approach, gaze

and size-sex category as predictors, together with all interactions. No interactions were close to significant (all $P>0.09$) and so we based our inferences on a purely additive model (as before, on the $\log_e$ scale of the response variable, FID). FID was significantly related to size–sex category ($F_{1,93}=8.76$, $P=0.004$), with AM lizards fleeing at distances c. 23% closer than did FYM lizards (model coefficient: −0.264±0.089).

While conducting the experiment, we noticed that some individuals showed distinct tail-raise behaviour 2–4 s before fleeing, presumably in response to the approach. This behaviour involved lizards raising their bodies and tails above the ground in an alert position, with the effect of making them more visible to the observer. On continued approach, they lowered their tail before fleeing. This was seen relatively frequently in FYM lizards (35% of 66), but almost never in AM lizards (3% of 31). Among FYM lizards alone, the incidence of this tail-raise display was somewhat elevated with direct compared with averted gaze (47% of 34 versus 22% of 32, Fisher test $P=0.04$), but it did not appear to be related to the direction of approach (direct: 33% of 39, tangential: 37% of 27, Fisher test $P=0.80$). To assess whether the tail-raise display allows better prediction of FID we modelled the natural logarithm of FID (of FYM lizards only, for reasons of sample size) as a function of additive effects of approach, gaze, and whether or not the tail-raise display was observed. FYM lizards that showed this display fled at considerably greater distances (c. 71% greater) than those that did not ($F_{1,62} = 37.02$, $P<0.001$; model coefficient: 0.540±0.089).
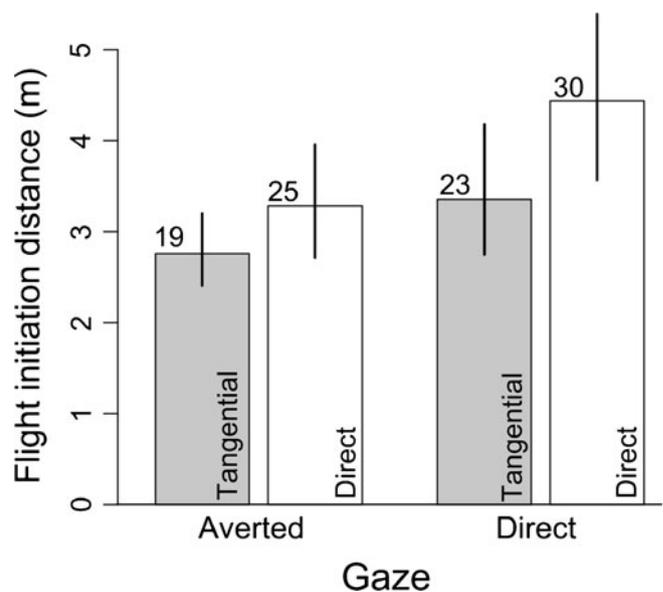

Figure 1. Flight initiation distance of the Indian rock lizard (*Psammophilus dorsalis*) in relation to approach (tangential and direct) and gaze (averted and direct). Bar heights show means; error bars represent 95% confidence intervals of the means, generated by 10,000 bootstrap resamples (because flight initiation distances showed skewed distributions). Numbers above the bars are sample sizes (number of trials).

4. Discussion

Our results confirm that approach direction and gaze affect FID in Indian rock lizards, suggesting that these lizards modulate their fleeing behaviour by assessing relative risk. FID was independently and additively increased by about 20% by each of the more threatening predator behaviours (direct approach and direct gaze) over their less threatening alternatives. In addition, we found that the FID of female/young male (FYM) lizards was substantially greater (c. 30%) than that of adult male (AM) lizards. We can think of several possible reasons for this difference: FYM lizards might be at greater risk (perhaps because of a predator preference for smaller lizards, or because they are slower than larger lizards) or they might pay lower energetic costs of locomotion due to their smaller size; or perhaps AM lizards are more reluctant to abandon their vantage posts. Similar effects on FID by approach type and gaze have been observed in other reptile species (Burger *et al.* 1992; Larimer *et al.* 2006; Braun *et al.* 2010; Cooper and Pérez-Mellado 2011). There is mixed evidence from other species for an effect of size-sex classes on FID (Rivas and Burghardt 2001; Gotanda *et al.* 2009).

Tail-raise behaviour was displayed largely by FYM lizards. The act of tail-raising in lizards has been speculated to be a sign for communicating sex-specific social information (Martins 1993; Radder *et al.* 2006b). This is consistent with our observation that >95% of tail-raises we observed were by FYM individuals. Additionally, our results suggest that tail-raise behaviour might be a signal used by FYM lizards to communicate their alertness to potential predators. FID of FYM lizards that displayed tail raise behaviour was substantially greater (c. 71%) than that of FYM individuals that did not display. Theoretical models of the evolution of pursuit-deterrent signals predict that both predator and prey would benefit if the prey communicates its likelihood of escape to the predator. For example, stotting in impalas (*Aepyceros melampus*) is an honest signal of the performer's physical condition and its alertness (Caro 1994). Similarly, Puerto Rican crested anoles (*Anolis cristatellus*) perform push-up displays and northern curly-tailed lizards (*Leiocephalus carinatus*) curl their tails to communicate their alertness to predators (Leal 1999; Cooper 2001). Thus, honest signalling can avoid a costly encounter (Hasson 1991; Yachi 1995).

Several questions about the anti-predator behaviour of the Indian rock lizard remain. Our study was carried out in the non-breeding season when female lizards are not carrying eggs and males are not holding territories. How selection for increased parental investment and mate acquisition will affect escape responses on male and female lizards respectively needs further investigation.

Apart from how the internal state of lizards affects their responses, questions also remain about the precise cues they use. It is relatively easy to imagine how directness of approach

can immediately affect escape responses, since a head-on approach will (for a given speed) result in the largest rate of change of distance with time and also the largest rate of change of the perceived size of the predator with time. But what specific cue is it that lizards actually use as the basis for their escape decisions? Angle of approach, rate of change of distance or rate of change of size? Separating these will require careful investigation (Cooper 2006). Although lizards may be evaluating simple physical quantities and rates to respond appropriately to approach, such simplicity is less obvious for their response to gaze. Distinguishing between a predator with a direct gaze and one with a tangential gaze requires some inference, or at least a thumb rule, about the position of the predator's eyes with respect to the rest of its head. What aspect of the eyes or face is used by lizards? Is the ability to distinguish between facial angles innate or learnt (Burger *et al.* 1991, 1992; Cooper 1997a)? Again, exciting experiments remain to be carried out.

In addition to gaze and directness of approach, several other aspects of a predator's movement are likely to be relevant to risk, including speed and acceleration of approach, and type of predator (Cooper 1997b; Templeton et al. 2005; Griesser 2009). Studying how lizards integrate multiple aspects of risk into their anti-predator decision making is a considerable challenge for the future.

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