



## Pursuit deterrence varies with predation risks affecting escape behaviour in the lizard *Callisaurus draconoides*

William E. Cooper, Jr

Department of Biology, Indiana University—Purdue University, Fort Wayne

### ARTICLE INFO

#### Article history:

Received 2 January 2010  
Initial acceptance 9 February 2010  
Final acceptance 9 April 2010  
Available online 8 June 2010  
MS. number: A10-00001R

#### Keywords:

animal communication  
approach speed  
distance fled  
escape behaviour  
flight  
initiation distance  
predation risk  
pursuit deterrence  
refuge distance  
Squamata

A growing body of evidence suggests that many prey attempt to prevent attack by signalling that they have detected a predator and are able to escape. Much of the evidence for pursuit deterrence is indirect in that signalling is not shown to reduce probability of attack. Indirect evidence is obtained by eliminating alternative hypotheses and demonstrating that signals are directed to predators. Other studies have shown that signalling is related to single predation risk factors. Because prey need not signal at low risk and should attempt to escape immediately when at high risk, pursuit–deterrent signals should occur most frequently at intermediate risk. Tests of escape theory have demonstrated that flight initiation distance (predator–prey distance when prey flees) increases as risk associated with various risk factors increases. I show that in the lizard *Callisaurus draconoides*, which signals by waving its tail, probability and timing of signalling are affected by degree of risk for several factors that strongly affect flight initiation distance, specifically distance to refuge, speed and directness of approach, and predator persistence. Flight initiation distance increased with risk for all factors, but for all but one factor, relationships to risk differed between signalling and escape, and differences were readily predicted from functional differences between these behaviours.

© 2010 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Some prey are believed to deter pursuit by signalling that they have detected a predator and are able to escape if attacked (Ruxton et al. 2004; Caro 2005). Signals may be given briefly before fleeing or repetitively to indicate escape ability relative to that of group members (FitzGibbon & Fanshawe 1988; Caro 2005). Caro (2005) recognized two categories of pursuit-deterrent signals, perception advertisement (awareness of the predator) and advertisement of relative escape ability, which correspond roughly to the dichotomy between brief signalling before fleeing and repetitive signalling. Signals of escape ability might benefit predators and prey having high escape ability because even if predators sometimes capture such prey, the probability of capture may be lower and the cost of capture may be greater than for individuals having lower escape ability. However, signals must also honestly communicate that the prey is able to escape or that capturing the prey will be too costly for withholding attack to be beneficial to the predator (Vega-Redondo & Hasson 1993; Bergstrom & Lachmann 2001). Here, I consider only signals from a solitary prey animal to a predator.

Thus, the signal indicates that the prey is aware of the predator and can escape if attacked. Such signals may be prolonged and presumably costly (e.g. dewlap displays by crested anoles, *Anolis cristatellus*, during approach by a model snake; Leal 1999) or brief and of low cost (e.g. arm waving by the Bonaire whiptail, *Cnemidophorus murinus*; Cooper et al. 2004; tail curling by the Cuban curly-tailed lizard, *Leiocephalus carinatus*; Cooper 2001).

Most evidence for pursuit deterrence is indirect (Ruxton et al. 2004; Caro 2005) because of the difficulty of demonstrating that signals deter attack, but in a few cases direct evidence shows that prey signals affect predator behaviour. For example, red foxes, *Vulpes vulpes*, do not attack brown hares, *Lepus europaeus*, that stand and face them (Holley 1993); the Puerto Rican racer, *Alsophis portiricensis*, does not attack anoles that perform displays (Leal & Rodriguez-Robles 1995); merlins, *Falco columbarius*, are less likely to capture skylarks, *Alauda alvensis*, that are stronger singers (Cresswell 1994), and stotting by Thomsons's gazelles, *Eudorcas thomsoni*, reduces probability of attack by cheetahs, *Acinonyx jubatus* (Caro 2005), and wild dogs, *Lycaon pictus* (FitzGibbon & Fanshawe 1988). Indirect evidence has been obtained by eliminating alternative functions such as social signalling, flash concealment and deflection (Woodland et al. 1980; Hasson et al. 1989; Cooper 2001; Ruxton et al. 2004; Murphy 2006) and by

Correspondence: W. E. Cooper, Jr, Department of Biology, Indiana University—Purdue University, Fort Wayne, IN 46835, U.S.A.

E-mail address: [cooperw@ipfw.edu](mailto:cooperw@ipfw.edu)

demonstrating that signals are directed to predators (Woodland et al. 1980; Caro et al. 1995; Cooper et al. 2004; Ruxton et al. 2004).

Relationships between predation risk and signalling have not been examined in light of escape theory. A prey should signal when risk of being attacked is appreciable, but it can escape. Caro (1986) found that Thomson's gazelles began stotting and successfully fleeing when cheetahs were about 40 m beyond the flight initiation distance (predator–prey distance when the prey flees) for chases ending in capture. If risk of being captured and opportunity costs of escaping are very low, prey need not signal, and escape theory predicts that they need not flee; if risk is too great, prey should flee immediately without signalling (Ydenberg & Dill 1986; Cooper & Frederick 2007). Blumstein (2003) and Stankowich & Coss (2006) recognized a zone of short predator–prey distances in which escape is immediate, an intermediate zone in which assessment occurs as specified by escape theory, and a zone of longer distances in which prey do not visibly react to predators. Given equal costs, pursuit-deterrent signals are predicted at intermediate predation risk in the intermediate zone, but not elsewhere.

Escape theory predicts flight initiation distance from a prey's fitness, cost of escaping, and loss of fitness expected due to predation risk (Ydenberg & Dill 1986; Stankowich & Coss 2006, 2007; Cooper & Frederick 2007, 2010). In some cases escape theory may be used to predict probability of fleeing and distance fled (Cooper 2009a). As predation risk increases, probability of fleeing, flight initiation distance and distance fled (if no refuge is used) increase (Cooper 2009a). Therefore, probability of performing pursuit-deterrent displays and these escape behaviours should bear similar relationships to degree of various risk factors over some range from zero to intermediate risk. However, at higher risk levels, the escape variables continue to increase, but the probability of signalling is expected to decrease.

I tested effects of risk factors (distance to refuge, speed and directness of approach by a predator, and predator persistence) on signalling by zebra-tailed lizards, *Callisaurus draconoides*. This species putatively signals by elevating and waving its tail, exposing bold black and white ventral coloration (Dial 1986). Hasson et al. (1989) showed that tail waving was most likely at intermediate distances to refuge, but they did not study effects of the most prominent risk factors for escape (Stankowich & Blumstein 2005).

By simulating an approaching predator, I reexamined the effect of distance to refuge on signalling and tested new hypotheses about effects of predator approach speed, directness of approach and predator persistence on pursuit-deterrent signalling and escape behaviour. I predicted that (1) lizards at intermediate distances from refuge would signal more frequently before fleeing than lizards closer to refuge (at lower risk) or further from refuge (at higher risk); (2) flight initiation distance and distance fled would increase as distance to refuge increased because of the corresponding increase in risk; (3) for the greater of two predator approach speeds, the probability of signalling before fleeing would be lower and both flight initiation distance and distance fled would be longer; (4) probability of signalling before fleeing, probability of fleeing and flight initiation distance would decrease as approach by a predator became less direct because of decreasing risk; (5) probability of signalling would be lower and flight initiation distance would be longer during the second of two successive approaches by a predator because a persistent predator poses a stronger threat than one that gives up quickly.

## METHODS

### *Study Site and Animals*

I conducted the study in June and July of 2009 at Rillito River Park in Tucson, Arizona, U.S.A. The park is situated along each side

of the Rillito River for approximately 10 km. On the north side of the Rillito River, some portions of a paved path pass through areas of sandy soil planted with desert vegetation and maintained by the city government. Major plants on the site are saguaro cactus (*Carnegiea gigantea*), yucca (*Yucca* spp.), mesquite trees (*Prosopis* spp.) and palo verdes (*Parkinsonia* (formerly *Cercidium*) spp.). These plants provide shade and refuges from predators: *C. draconoides* do not enter discrete refuges, such as holes or crevices, but they sometimes hide beneath branches of trees or bushes at the end of escape runs or hide on the far sides of yuccas.

Rillito River Park was an excellent study site for two reasons. First, the abundance of *C. draconoides* is exceptionally high there. Second, the lizards are well habituated to the presence of humans on the path because of the frequent use of the path by people walking, running, biking and skating. Lizards on or very close to the path flee from humans, but lizards off the path usually do not flee when people stay on the path while passing them. Their habituation is specific (Hemmi & Merkle 2009) to people on the path because lizards flee when people deviate from the path to approach them. The specific habituation permitted me to approach closely enough to facilitate observations. This is an important advantage because zebra-tailed lizards are difficult to observe because they are very wary in many areas where they are not frequently exposed to people.

Little is known regarding natural predators of *C. draconoides*, but they are eaten by snakes, larger lizards, birds, including the road-runner *Geococcyx californianus*, and presumably mammals (Tanner & Krogh 1975; Vitt & Ohmart 1977). At Rillito River Park, several raptor species and other birds large enough to eat the lizards are common. Snakes, including rattlesnakes (*Crotalus* spp.) known to eat lizards, occur in the river bed. Although coyotes, *Canis latrans*, and other mammals eat lizards, domestic cats are the most likely mammalian predators at the study site.

### *Data Collection*

Use of a human investigator to simulate an approaching predator by walking towards prey is a standard method of studying both escape behaviour and pursuit deterrence (reviewed in Caro 2005; Stankowich & Blumstein 2005). This method has the great advantages of permitting large numbers of observations and efficiency of approaching prey in specified manners across natural terrain. One possible disadvantage is that some prey species show predator-specific differences in escape responses (Stuart-Fox et al. 2006). Examination of this issue for a confamilial of *C. draconoides* revealed no differences in types of responses to a researcher, a model snake and a stuffed raptor (Cooper 2008). Another possibility is that some prey may be more likely to use pursuit-deterrent signalling before fleeing for some predators than for others. Even if this were the case for *C. draconoides*, frequent signalling when approached by people permits quantification of signalling behaviour.

I searched for lizards while walking very slowly along a path or on the ground adjacent to it. When I detected a lizard, I approached by walking towards it using a preselected combination of approach speed and directness until the lizard waved its tail or fled. When starting distance (the distance between predator and prey when approach begins) was measured, I moved to the desired distance, oriented towards the lizard, stopped for 5 s, and then began to approach. Approach speeds (slow:  $0.56 \pm 0.01$  m/s; fast:  $2.31 \pm 0.03$  m/s;  $N = 10$  each; estimates of variability here and throughout are SE) were practised to ensure consistency, and they are reported below for each data set. I stopped moving immediately when the lizard fled, observed its escape, and recorded the occurrence of tail waving, flight initiation distance, distance fled and distance to the nearest refuge as required for a particular

Download English Version:

<https://daneshyari.com/en/article/2417143>

Download Persian Version:

<https://daneshyari.com/article/2417143>

[Daneshyari.com](https://daneshyari.com)