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Escape tactics in the lizard *Meroles cuneirostris*

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Abstract. Successful escape from predators may involve the use of multiple tactics. The wedge-snouted desert lizard (*Meroles cuneirostris*) flees from predators through a series of discrete moves with each move representing a specific manoeuvre type. By simulating the approach of a predator, we examined the role of sex and age (adult vs. juvenile) on the manoeuvre types used during escape, as well as the relationship between the number of moves needed to escape and the number of manoeuvre types employed. The eight defined manoeuvre types were used by all demographic groups, though there were differences among groups in the tendency to use certain manoeuvre types. In general, there was a strong difference in how adults and juveniles fled from predators. The number of manoeuvre types used by a lizard tended to increase with the number of moves required to escape and adults more readily added new manoeuvre types to an escape sequence. Demographic differences in escape behaviour might result from differing predation pressures incurred by juveniles and adults, and might also be related to the ontogeny of escape behaviour.

Keywords: antipredatory behaviour, behavioural ontogeny, Lacertidae, Namib Desert, predation risk.

Introduction

Predation is a multistep process and prey species can make a variety of decisions that influence their predation risk (Lima and Dill, 1990). Since decisions that reduce predation risk also impact other aspects of an animal's life (Lima and Dill, 1990), prey should be influenced by both the costs and benefits associated with a particular action (Ydenberg and Dill, 1986; Broom and Ruxton, 2005; Cooper and Frederick, 2007). Thus, escape behaviour can be influenced by a large number of variables that influence predation risk such as predator speed (Cooper, 2003; Martín and Lopez, 2003; Cooper and Whiting, 2007), type of predator (Cresswell, 1993; Pongrácz and Altbäcker, 2000; Stuart-Fox, Whiting and Moussalli, 2006), distance to predator (Blumstein, 2003) or refuge proximity (Bonenfant and Kramer, 1996; Cooper and Whiting, 2007). Prey characteristics such as age (Cooper, 2011), size (Roth and Johnson, 2004), and physiological state (Smith, 1997) may also influence predation risk and antipredatory decisions.

Decisions influenced by predation risk are pervasive, altering habitat choice and activity period (Kotler, Brown and Hasson, 1991; Eifler, Eifler and Harris, 2008) or foraging (Valone and Lima, 1987; Brown et al., 1988). Once an animal chooses to flee, actual evasion behaviour may involve multiple tactics (Nahin, 2007); characteristics of flight may be related to perceived risk (Cresswell, 1993). The availability of a variety of evasive tactics may allow for a graded response to threat (Magurran and Pitcher, 1987) and may promote evasion through confusion (Humphries and Driver, 1967, 1970). The deployment of different evasive tactics should reflect their cost and the threat level. Flight initiation distance has been used extensively to examine aspects of escape theory (Stankowich and Blumstein, 2005; Cooper and Frederick, 2007, 2010). However the specific manoeuvres used during flight have received far less attention, though they may be an important component of successful antipredator behaviour.

Meroles cuneirostris is a small, diurnal, sit-and-wait lacertid lizard found mainly along sparsely vegetated dune bases in the Namib Desert (Murray and Schramm, 1987), where it

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may be pursued by a suite of terrestrial predators including snakes (*Psammophis namibensis*), lizards (*Trachylepis occidentalis*) and several canids (*Canis mesomelas*, *Otocyon megalotis*, and *Vulpes chama*). *Meroles cuneirostris* does not use burrows, nor readily bury itself to avoid capture (pers. obs.). Rather, to successfully escape and no longer be detectable, it must put sufficient distance or cover between itself and a predator. We investigated escape behaviour for the lizard *Meroles cuneirostris*, documenting the diversity of escape manoeuvres and examining how prey characteristics (sex and age) and threat level (predator-prey encounter duration) influence their use.

Materials and methods

During 9-14 May 2010, we conducted predator approach trials along the base of Station Dune near the Gobabeb Research and Training Centre, Namib-Naukluft National Park, Namibia (23.561667S, 15.040833E). The portion of the dune used for the study was removed from areas of interest to Centre visitors and our study animals would have had minimal previous exposure to humans. To minimize the influence of environmental conditions, we restricted trials to 9:00-11:00 on clear calm mornings. We simulated predator approaches, using a human “predator” to examine the escape behaviour of *M. cuneirostris*. Observers walked along the base of the dune until a lizard was detected. Upon detection, the lizard’s initial location was noted relative to vegetation: ‘open’ (>50 cm from the nearest vegetation), ‘edge’ (0-50 cm from vegetation canopy), or ‘cover’ (under the canopy of vegetation), as well as the lizard’s sex and age. We did not determine the initial distance between observer and lizard. Juveniles (∼40 mm SVL and 2 g) were identified by size and the presence of clear brightly coloured tails, a trait lost in adults (∼60 mm SVL and 7-8 g), who are sexually dimorphic in body markings (Branch, 1998). The few encountered individuals with transitional fading tail colours were not pursued or included in the study. A single observer approached the lizard at a constant pace with the observer changing trajectory as the lizard moved. The observer always tried to walk directly at the lizard (= pure pursuit; Nahin, 2007), with occasional side steps to avoid obstacles. As the lizard was approached, it typically performed a series of discrete moves. Each move was logged while the observer continued to approach the lizard until the lizard performed a move that resulted in the animal not being visible to the observer. At that point, the lizard was regarded as having “escaped” and the trial ended. Typically, “escaped” lizards went around a corner, to the other side of an elevated area, or into vegetation, where with some effort contact might have been re-established, but which, for the sake of the study, we considered the end point. We avoided repeat sampling of individuals by conducting each session on a different section of the dune.

Each move was classified by manoeuvre type. We recognized eight manoeuvre types: 1) ran TOWARD the nearest vegetation, 2) ran AWAY from the nearest vegetation, 3) ran INTO vegetation (or deeper into vegetation), 4) ran OUT of vegetation, 5) SKIRTED around vegetation, 6) ran PAST vegetation, where a single move brought the lizard first closer and then further from vegetation, 7) ran LONG distance (>2 m, relatively straight), 8) ran in a ZIG-ZAG path. In instances where a long or zig-zag movement occurred, this characterization took precedence over other categories that might also apply. The vast majority of observed moves were less than 1 m in distance.

We used Minitab version 15 (Minitab Inc., State College, Pennsylvania, USA) for data analysis, with significance generally being assigned to $\alpha \leqslant 0.05$. To compare the prevalence of different manoeuvre types under different conditions, we pooled the counts for all individuals within a demographic class. For some comparisons, we characterized each individual by whether a specific manoeuvre type was used (e.g., what was start manoeuvre? did the individual ever skirt?). We used Chi-square tests to identify differences among demographic classes in the use of manoeuvre types and log-linear tests to examine relationships between multiple factors, their interactions and the use of manoeuvre types. For specific contingency analyses, we only included those manoeuvre types where more than 80% of the values were $\geqslant 5$. General linear models (GLM) were used to examine the relationship between the level of manoeuvre use, escape sequence duration, and demographic status. We used a stepwise model identification process for GLM and present final models with factors significant at $\alpha \leqslant 0.10$. The diversity of escape behaviour (D) was calculated for comparison purposes using the Simpson index (Schall and Pianka, 1980): $D = 1/\sum_{i=1}^{n} p_i^2$, where p_i is the proportion of the ith manoeuvre type.

Results

Observations were made on 108 lizards, with 899 separate moves recorded. Initial sightings of lizards occurred 68.5% in open areas, 25% on edges and 6.5% under cover. There were no significant differences in use of space between sexes (log-linear test: $G_2^2 = 0.40$, $P = 0.81$), age classes ($G_2^2 = 0.86$, $P = 0.64$) or associated with the interaction of sex and age ($G_3^2 = 3.81$, $P = 0.14$).

The number of moves required to escape ranged from a single move to 49; the average number of moves (mean ± SE = 8.33 ± 0.87) did not differ between the sexes (GLM:

Table 1. Number of initial escape manoeuvres for *Meroles cuneirostris* by demographic group.

	Juvenile female	Juvenile male	Adult female	Adult male	Total
Toward	20	13	10	15	58
Away	0	2	0	1	3
Into	2	0	1	3	6
Out	0	2	0	2	4
Skirt	10	5	4	1	20
Past	0	0	0	0	0
Long	4	3	1	7	15
Zig-zag	0	0	0	1	2
TOTAL	36	25	17	30	108

Table 2. Number of initial escape manoeuvres for *Meroles cuneirostris* by location.

	Cover	Edge	Open	Total
Toward	0	14	44	58
Away	0	3	3	6
Into	6	0	0	6
Out	1	0	0	1
Skirt	0	8	12	20
Past	0	0	0	0
Long	0	1	14	15
Zig-zag	0	1	1	2
TOTAL	7	27	74	108

$F_{1,104} = 0.19$, $P = 0.67$), age classes (GLM: $F_{1,104} = 0.37$, $P = 0.55$), or with the interaction between sex and age (GLM: $F_{1,104} = 0.57$, $P = 0.45$). Individuals used 1-7 manoeuvre types before escaping. The most common initial manoeuvres were toward and skirting (tables 1 and 2). Initial manoeuvres used by a lizard did not vary between sexes (log-linear test: $G_2^2 = 1.656$, $P = 0.43$) but was related to age class ($G_2^2 = 8.56$, $P = 0.01$) and to the interaction between sex and age ($G_2^2 = 7.14$, $P = 0.03$; table 1). Low counts precluded statistical testing, but inspection of our data suggests that initial manoeuvres may be related to location; individuals already under cover tended to stay there and long moves were initiated primarily by lizards in the open (table 2). The final move before escaping was one of four manoeuvre types, but predominately involved either skirting or moving into vegetation (>95% of all trials, table 2); the prevalence of these two ending moves depended on age (log-linear test: $G_1^2 = 12.06$, $P = 0.005$), but there was no significant difference between the sexes ($G_1^2 = 0.57$, $P = 0.44$) nor associated with the interaction of sex and age ($G_1^2 = 0.28$, $P = 0.59$). Skirting was more commonly used by juveniles and moves into vegetation occurred more commonly among adults (table 3).

Each of the eight manoeuvre types was used by each demographic class; some types were more common for certain demographic classes and some types were more common in general (table 4). The most common manoeuvres among all demographic classes were toward and skirting (table 4). The proportional contribution of each manoeuvre type to escape repertoires did not depend on sex (log-linear test: $G_7^2 = 12.667$, $P = 0.08$), but did depend on age ($G_7^2 = 47.820$, $P = 0.0001$) and the interaction of sex and age ($G_7^2 = 32.762$, $P = 0.0001$); the diversity of escape behaviour was slightly greater for adults than juveniles (table 4). For example, skirting use differed among demographic groups, with juveniles showing the greatest use of skirting and adult females

Table 3. Number of final escape manoeuvres for *Meroles cuneirostris* by demographic group; the other 4 manoeuvre types never occurred during the final move.

	Juvenile female	Juvenile male	Adult female	Adult male	Total
Toward	1	0	1	0	2
Into	9	4	9	15	37
Skirt	26	21	7	13	67
Long	0	0	0	2	2
TOTAL	36	25	17	30	108

Table 4. Escape manoeuvres used by demographic classes of *Meroles cuneirostris*. Manoeuvre type values represent the proportion of moves performed by a demographic group. (χ^2 tests were used with original counts to identify variation among demographic classes in the use of individual manoeuvre types: $^*P \leqslant 0.05$, $^{**}P \leqslant 0.01$, $^{***}P \leqslant 0.001$).

	Juvenile female	Juvenile male	Adult female	Adult male
n (lizards)	36	25	17	30
n (moves)	322	209	109	259
Toward	0.193	0.335	0.440	0.254
Away	0.047	0.043	0.055	0.039
Into*	0.049	0.029	0.119	0.077
Out**	0.037	0.024	0.038	0.054
Skirt***	0.624	0.521	0.248	0.429
Past	0.003	0.014	0.018	0.027
Long***	0.025	0.029	0.018	0.085
Zig-zag*	0.022	0.005	0.064	0.035
Simpson index (D)	2.30	2.54	3.59	3.73

Table 5. General linear models for the number of manoeuvre types and frequency of specific manoeuvre types used during an escape sequence. Models were identified with a stepwise procedure using $\alpha \leqslant 0.1$ for entry and removal. Factors for the final model are presented as $F(P)$; "–" = factors not in the final model.

	Moves before escape	Sex	Age	Sex × Age interaction	R^2
Manoeuvre types	83.77 (0.001)	–	4.59 (0.03)	–	0.452
Toward	99.36 (0.001)	–	–	6.94 (0.01)	0.502
Away	62.7 (0.001)	–	–	–	0.371
Into	–	–	4.36 (0.04)	–	0.039
Out	32.6 (0.001)	–	–	–	0.235
Skirt	257.5 (0.001)	–	6.54 (0.01)	–	0.718
Past	19.96 (0.001)	–	3.87 (0.05)	–	0.180
Long	12.54 (0.001)	3.88 (0.05)	–	3.01 (0.09)	0.187
Zig-zag	19.34 (0.001)	–	2.79 (0.1)	–	0.169

using this manoeuvre much less than any other group (table 4). Long moves were most prevalent in adult males, while zig-zagging occurred with adults more than juveniles (table 4). The two age classes varied in whether they ever used certain manoeuvre types, with individual juveniles more likely to skirt at least once, while adults were more likely to move into vegetation at least once (skirt: Chi-square test: $\chi^2_3 = 13.677$, $P = 0.003$; into: $\chi^2_3 = 9.251$, $P = 0.03$).

The number of manoeuvres used by a lizard was positively related to the number of moves required to escape and to age (table 5), with adults more readily adding new manoeuvres to an escape sequence. When individual manoeuvre types were examined, some patterns emerged related to escape, age, or the interaction between sex and age. Long move frequency increased with the total number of moves, but is related to sex and the interaction of sex and age (table 5), with adult males using long moves more than other groups (table 4). Moving into vegetation was the only manoeuvre type whose frequency was not related to number of moves, but was related to age (table 5), with adults more likely to move into vegetation than juveniles. Skirting vegetation frequency was related to number of moves, as well as lizard age (table 5), with juveniles increasing the use of skirting more readily than adults (table 4). Finally, all manoeuvre types except into were more prevalent with longer escape sequences (table 5).

Discussion

The flight behaviour of *M. cunerostris* depends on 1) the amount of effort required to escape and 2) demographic status. Animal escape behaviour should reflect the level of predation risk; the time required to escape can be viewed as an indicator of predation risk. The level of escape manoeuvre diversity exhibited by populations of whiptail lizards (*Cnemidophorus tigris*) increases with indices of predation pressure (Schall and Pianka, 1980), bank voles (*Clethrionomys glareolus*) use a greater number of antipredator responses when encountering the scent of predators who specialize more strongly on hunting voles (Jędrzejewski, Rychlik and Jędrzejewska, 1993), and shoals of minnows (*Phoxinus phoxinus*) make use of more dramatic and less predictable evasive tactics as the intensity of predator attacks increases (Magurran and Pitcher, 1987). For *M. cunerostris*, longer escapes mean a greater opportunity for factors such as chance or fatigue to work against the lizard. As the escape sequence lengthens, perceived risk may also increase and lizards may use more dramatic manoeuvres in an effort to achieve escape. The positive correlation between the number of manoeuvre types used and the number of moves required to escape may depend on risk in several ways. Leaving the proximity of cover, making long moves, or engaging in zig-zig moves involve greater effort and exposure, possibly occurring when more simple manoeuvres such as skirting do not result in escape. In addition, the mere addition of more manoeuvre types may be of benefit. Many animals exhibit variability in their behaviours that decrease the likelihood that a predator can anticipate their actions (Roeder, 1967; Driver and Humphries, 1988). A single manoeuvre type such as a zig-zag can result in a decreased likelihood of capture (Humphries and Driver, 1970; Jones, Jackson and Ruxton, 2011), as when escaping gazelle run circuitously to open distance from pursuing cheetahs (FitzGibbon, 1990). An unpredictable or non-systematic sequence of behaviours may confer an advantage, but requires a large repertoire of movements (Chance and Russell, 1959).

There are a number of reasons to expect adult and juvenile behaviour to differ: they may differ in the risk posed by different predators (Blomberg and Shine, 2000), in the ability to successfully employ certain tactics (Medill, Renard and Larivière, 2011), or in acquired experience with predators (Seyfarth and Cheney, 1986). Factors such as speed and endurance in lizards can be influenced by size (Miles, Snell and Snell, 2001; Brãna, 2003) and such a relationship could lead to certain size classes favouring certain manoeuvres. Skirting was more likely to occur among juveniles and to result in escape, while moving into vegetation was more likely to be used by adults and to be their final move. Size-related differences in thermal requirements may contribute to the willingness of juveniles and adults to enter vegetation (Sinervo and Adolph, 1989; Maia-Carneiro and Rocha, 2013). These age-related differences in escape behaviour may reflect age-related differences in predation risk. Likewise, habitat use may be influenced by predation risk (Kotler, Brown and Hasson, 1991; Eifler, Eifler and Harris, 2008). At our study site, predators such as venomous snakes (e.g., *Bitis caudalis*) may represent a greater threat to juveniles and are most commonly seen near vegetation, and the lizard *Trachylepis occidentalis* has been observed ambushing and eating *M. cunerostris* as they enter vegetation (pers. obs.). Further, adult *M. cunerostris* can cannibalize juveniles darting into vegetation (Childers and Eifler, 2013). Juvenile chameleons use different habitats than adults due to the risk of cannibalism (Keren-Rotem, Bouskila and Geffen, 2006). Thus, juvenile *M. cunerostris* may have good reason to be reluctant to enter vegetation, even when approached by a potential predator.

Our results also indicate that sex as well as its interaction with age account for variation in escape behaviour and need to be more carefully examined. The social system of *M. cuneirostris* is not well understood, but social status and reproductive condition have the potential to influence antipredator behaviour. Male and female *M. cuneirostris* have distinct colour patterns, which could influence conspicuousness and ultimately the effectiveness of different manoeuvre types. Exploring the factors influencing the initiation of escape behaviour has proven a productive investigative path; careful examination of the diversity of evasive tactics employed by lizards will likely provide another fruitful approach to understanding antipredator decisions.

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