Living on the edge: Effects of body size, group density and microhabitat selection on escape behaviour of southern leopard frogs *Lithobates sphenocephalus*

Philip W. BATEMAN1*, Patricia A. FLEMING2

1 Department of Environment and Agriculture, Curtin University, Perth, Bentley WA 6845, Australia | 2 School of Veterinary and Life Sciences, Murdoch University, Perth, Murdoch WA 6150, Australia

Abstract Models of optimal escape strategy predict that animals should move away when the costs of fleeing (metabolic and opportunity costs) are outweighed by the costs of remaining. These theoretical models predict that more vulnerable individuals should be more reactive, moving away when an approaching threat is further away. We tested whether escape behaviour (including ‘escape calling’) of *Lithobates sphenocephalus* approached by a human was influenced by body size or the initial microhabitat that the individual was found in. Irrespective of their size, frogs in the open tended to remain immobile, enhancing their crypticity. Frogs in cover showed different responses according to their body size, but, contrary to our initial predictions, larger frogs showed greater responsiveness (longer flight initiation distance and distances fled) than small frogs. Small frogs tended to remain closer to water and escaped into water, while larger individuals were more likely to jump to terrestrial cover and call during escape. Density of frogs near the focal animal had no effect on escape behaviour.

This study indicates a range of escape responses in this species and points to the importance of divergent escape choices for organisms which live on the edge of different environments [Current Zoology 60 (6): 712–718, 2014].

Keywords Alarm call, Flight initiation distance (FID), Distance fled, Microhabitat selection, *Rana sphenocephala*

Organisms approached by predators have to make decisions about when to flee, in what direction, and how far to move away. Economic models have been developed to describe how organisms can vary their escape responses, balancing the perceived level of risk from the predator with the costs of fleeing (metabolic costs and opportunity costs) (Ydenberg and Dill, 1986). One of the important issues to consider is that individuals vary in their vulnerability to potential predation, and will, therefore, optimise both their habitat use and their escape responses accordingly (Cooper and Frederick, 2007).

The metabolic costs of transport increase exponentially for smaller animals, which reflects greater rate of muscle action to achieve the same distances moved, such that smaller animals may be more vulnerable to predation if they are slower or their costs of locomotion during escape are higher (Peters, 1986). When approached by a predator then, we might expect smaller individuals to have different escape and avoidance tactics from larger individuals. For example, Stankovich and Blumstein (2005) state that, across taxa, “there is some consistency in the effect of large animals having longer flight initiation distances than small animals (larger animals may be at greater risk due to increased visibility, higher quality as potential prey, or reduced escape speeds”). Smaller, juvenile *Psammodromus algirus* lizards are slower than larger adults and run for less time and for shorter distances than the adults; they also have shorter flight initiation distances (FID: the distance between an organism and an approaching predator or disturbance when the organism chooses to flee) (Martin and López, 1995). Juvenile *Sceloporus occidentalis* also show an increase in speed as they grow (Van Berkum et al., 1989). In the case of anurans, larger individuals tend to be capable of longer maximum jump lengths than smaller individuals (Emerson, 1978, Goater et al., 1993, John-Alder and Morin, 1990); and can also out-perform smaller individuals in terms of locomotor stamina, moving a greater absolute distance and demonstrating longer time to exhaustion, such is the case of *Bufo woodhouseii fowleri* and *B. bufo* (Goater et al., 1993; John-Alder and Morin, 1990). In some species, such as *Lithobates (Rana) pipiens* and *Pseudacris triseriata*, larger individuals are also capable of greater acceleration. However, this is not always the case, for example, smaller *Bufo americanus* are capable of great-

---

Received Feb. 10, 2014; accepted Apr. 10, 2014.

* Corresponding author. E-mail: Bill.Bateman@curtin.edu.au

© 2014 Current Zoology
er acceleration than larger individuals (Emerson, 1978). Smaller animals may also be vulnerable to a wider suite of predators, for example, in marine fish, smaller fish have greater predation risks than larger ones because many fish predators are gape-limited (Scharf et al., 2000) and survival amongst Trachemys scripta elegans turtle hatchlings increases with greater body size which appears to mitigate the depredations of diurnal avian predators (Janzen et al., 2000).

The risk of predation is also influenced by the density of conspecifics in the immediate vicinity of the focal animal (Ydenberg and Dill, 1986). Individuals may aggregate to decrease the risk to each individual through predator dilution (Hamilton, 1971) or because groups offer an advantage in terms of increased collective vigilance but reduced individual vigilance through the ‘many eyes’ effect (Krause and Ruxton, 2002).

Finally, animals far from cover are likely to perceive a higher risk from predators and alter their behaviour accordingly: e.g. black swans Cygnus atratus have a higher FID in response to humans when they are farther from refuge on water (Guay et al., 2013), and the FID of woodchucks Marmota monax in response to humans increased with distance from burrows (Bonenfant and Kramer, 1996). Concealment in vegetation can reduce FID, presumably because risk is perceived to be lower by a hiding individual (e.g. Camp et al., 2012).

In this study, we examine the effects of body size, group density, and initial microhabitat upon escape responses of southern leopard frogs Lithobates sphenocephalus around a large pond. We investigated whether variation in these variables influenced aspects of escape behaviour in L. sphenocephalus. We recorded FID, distance fled, number of hops made when escaping and whether animals moved to water or land post-disturbance: some species of frog preferentially flee to a safer area on land and others flee primarily back to water (Hayes, 1990, Licht, 1986, Martin et al., 2005, Martin et al., 2006). Once frogs have submerged, they are in a refuge from terrestrial predators, and can remain hidden under water or emerge in a different place (e.g. Cooper, 2011).

We also recorded whether frogs vocalised during escape. Frogs often produce a harsh, squeaking croak (‘escape call’) when fleeing from approaching disturbance such as a human observer, or when grasped (‘distress call’) (Williams et al., 2000; Wells, 2007). Lithobates sphenoecephalus produces a call similar to that described for its congener the American bull frog Lithobates catesbeianus (Cooper, 2011). Other taxa also produce fleeing vocalisations (e.g. hadeda ibises Bostrychia hagedash, Bateman and Fleming, 2011; Lio- laemus chiliensis lizards, Hoare and Labra, 2013) which have been proposed to function in various ways: to warn conspecifics of an approaching predator (alarm call); as a deimatic call (startle call) that aims to distract an approaching predator; or as honest signalling to inform the predator of the individual’s awareness of it and therefore the unprofitability of pursuing it.

This behaviour appears to be an important aspect of the species’ escape responses. If vocalisation is advantageous for successful escape, then predictions of the economic escape models should apply to this measure, as they do to other metrics. We made the following predictions on the escape responses of L. sphenocephalus:

Vegetation cover should provide greater protection for prey, and therefore we predict less reactivity for frogs in vegetation compared with open microhabitats.

Because we assume that smaller frogs have less efficient locomotion compared with larger conspecifics, we predict that small frogs should be less reactive than larger frogs, since the costs for them to move away when they did not need to are higher than those experienced by larger animals.

Due to the several hypothesised functions of escape vocalisations, we make non-directional predictions that the likelihood of an individual calling when fleeing will be influenced by frog size, density of frogs near the fleeing individual and microhabitat from which it flees.

1 Materials and Methods

We collected data over two days at a circular sink hole pond (circumference: 300 m) in central Florida, United States of America (27.1806° N, 81.3500° W), of which the shoreline, i.e., up to the water’s edge, was approximately 50% contiguous bare muddy sand and 50% contiguous long grass. At least two hundred frogs were estimated as present around the pond’s edge and in the grass banks further from the pond and in the pond itself, based on the numbers observed leaping away from the observer’s approach and from exploration of the area. We examined the escape behaviour of focal individuals approached by a human observer (PWB) at a set pace (1 m/s) who walked parallel to the shore line between 2 and 1.5 m from the water’s edge. We collected data between 10:00 and 11:00 am in May, on two sequential days when the weather was cloudless and hot (26°C). We collected data over two days as after one circuit of the pond most frogs around the pond had leapt to escape the observer. A second day’s data collected at the same time under the same weather conditions was
considered to be sufficiently temporally removed for the frogs to have returned to normal behaviour. Focal frogs were selected from individuals seen prior to their jump when approached or immediately upon their jump and within the direct line of sight of the observer. We recorded the initial microhabitat (in the open or in cover) where the frog was found, its initial distance from water, FID, and distance fled (measured with a metre pole) together with the number of jumps it took (higher number of jumps was considered to be an indication of increased risk perception): jumps tended to be in sets of immediately consecutive leaps (unless the frogs reached water) and so we recorded number of jumps until they stopped for at least five seconds, even if the frog jumped again. We also recorded whether the frog vocalised when fleeing, and what habitat it moved to (water or grass). The density of frogs in the immediate vicinity of the focal frog was recorded as the number of other frogs that moved away when the observer approached (i.e. number within a 1m radius). Focal frogs were categorised as ‘small’, ‘medium’ or ‘large’ frogs; although this categorisation was based on relatively brief sightings of frogs just prior to and during escape, we later caught several (n=31) frogs with a hand net and measured their SVL (cm), having already categorised them as ‘small’, ‘medium’ or ‘large’ and found that they reliably fell into different size classes (mean ± 1 SD: 3.4 ± 0.5, 5.5 ± 0.4, 7.6 ± 0.5, respectively; one-way ANOVA: $F_{2,19} = 145.66$, $P < 0.001$).

Values for FID were squareroot-transformed while the distance from water and distance fled were log-transformed to meet the requirements of parametric statistic tests. The effect of body size on distance to water was tested by one-way ANOVA with Tukey’s HSD post hoc test. We tested whether there were differences in initial (open or cover) or post-disturbance (water or grass) habitat selection between the three size classes by Pearson’s $\chi^2$ analysis with expected values calculated assuming an equal proportion of animals were using open or cover habitat across each size class.

The effects of body size and initial habitat selection (categorical variables), as well as the density of frogs and distance from water (continuous variables) were tested for their effect on FID, distance fled, number of jumps, whether the frog landed in cover (grass) or water and whether or not the frog vocalised during escape as five separate dependent factors using ANCOVA. The analysis of FID used a gamma distribution function, number of jumps a Poisson distribution, and a binomial function was used for analysis of whether or not the frogs vocalised during escape or landed in grass or water.

### Results

The behaviour of a total of 74 focal frogs was recorded: $n=20$ small, $n=31$ medium-sized, and $n=23$ large frogs. About half of all frogs were initially located in cover (grass): 40% of small, 61% of medium-sized and 65% of large frogs. The number of frogs in the immediate vicinity of each focal frog averaged 2.82 ± 1.50 (range 1–6) individuals. We estimated a population of over 200 frogs around the pond and so feel confident that pseudo replication of individuals was minimal or non-existent.

Although there was no statistically significant difference between size classes in whether they were initially using cover (grass) or were in the open (on sand) ($\chi^2 = 3.22$, $P = 0.200$), there was a significant difference in how distant frogs of different sizes were located in relation to the water ($F_{2,71} = 18.12$, $P < 0.001$)–smaller frogs were initially located closer to water, while larger frogs were located further away from water. Consequently, when they moved away from the observer, 90% of small frogs jumped into water, compared with 68% of medium-sized and 43% of large frogs ($\chi^2 = 10.41$, $P = 0.005$). Distance fled was correlated with the animal’s initial distance from water (Fig. 1), simply reflecting those animals that jumped as far as they needed to jump to reach water.

There was no significant effect of density of other frogs in the immediate vicinity of the focal frog on its FID or the distance fled (Table 1).

![Fig. 1 Relationship between distance fled and the distance to water for Lithobates sphenocephalus](image)

Each dot represents an individual but there are multiple overlapping points.
Table 1 Summary of ANCOVA on the influence of five variables on escape behaviour of *Lithobates sphenoecephalus*

<table>
<thead>
<tr>
<th>Variable</th>
<th>df</th>
<th>FID (m)</th>
<th>Distance fled (m)</th>
<th>No. jumps</th>
<th>Moved to water?</th>
<th>Alarm called?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance from water (m; log-transformed)</td>
<td>1</td>
<td>0.02</td>
<td>31.40 ***</td>
<td>1.75</td>
<td>0.31</td>
<td>0.18</td>
</tr>
<tr>
<td>Density (number of frogs within 1m radius of focal individual)</td>
<td>1</td>
<td>0.00</td>
<td>0.32</td>
<td>0.51</td>
<td>0.83</td>
<td>0.11</td>
</tr>
<tr>
<td>Size category (small, medium, large)</td>
<td>2</td>
<td>60.44 ***</td>
<td>15.36 ***</td>
<td>0.79</td>
<td>3.34</td>
<td>7.19 *</td>
</tr>
<tr>
<td>Microhabitat frog was hiding in (0=open, 1=grass)</td>
<td>1</td>
<td>6.19 **</td>
<td>9.55 ***</td>
<td>0.56</td>
<td>6.08 *</td>
<td>0.00</td>
</tr>
<tr>
<td>Size x Microhabitat</td>
<td>2</td>
<td>43.17 ***</td>
<td>6.88 *</td>
<td>1.99</td>
<td>3.99</td>
<td>1.79</td>
</tr>
</tbody>
</table>

Values shown are the Wald coefficients. Bold values indicate statistical significance at *P*<0.05, **P**<0.01, or ***P***<0.001.

There was a significant effect of body size and an effect of initial microhabitat on both FID and distance fled (Table 1). Large frogs had longer FID (Fig. 2A, B) and fled a greater distance (Fig. 2C, D) compared with small frogs. There was also an effect of microhabitat selection on these data, since animals located in cover (grass) showed longer FID (Fig. 2A) and also fled a greater distance (Fig. 2C) than animals located in the open (bare sand) (Fig. 2B, D). The significant body size x microhabitat interaction reflects differences in effect of body size on the responses of animals in cover vs. in the open: in cover, larger animals were likely to show greater responsiveness (longer FID and distances fled) compared with smaller individuals, but for frogs in the open, irrespective of their size, all animals tended to sit-and-wait until the observer was very close to them before moving.

Although the number of hops was correlated with the distance fled measures (Fig. 3), the ordinal data for number of hops is likely to have reduced the level of discrimination for these data (contrasting with the continuous data for distance fled). None of the factors tested significantly influenced the number of escape jumps performed (Table 1).

There was a significant effect of size category and initial microhabitat on whether frogs moved to water (or cover) (Table 1). All the animals that were initially in the open jumped to water. 40% of frogs that were initially in vegetation when first sighted jumped to water, but 60% jumped to another clump of vegetation. The interaction between size and initial microhabitat reflects that only two of the small frogs moved to cover (the rest moved to water) while a greater proportion of the animals that were initially located in vegetation were the larger individuals.

There was an effect of body size on whether a frog vocalised during escape (Table 1). 70% of large frogs, 58% of medium-sized, but only 20% of small frogs vocalised when disturbed. None of the other factors tested influenced whether or not a frog vocalised during escape.

3 Discussion

We found effects of body size and initial microhabitat on escape measures, but no effect of density of frogs in the area immediately around the focal frog. Frogs in the open tended to sit-and-wait until the observer was very close before moving, irrespective of their size. Only when frogs were in cover did we record differences between the frog size categories: larger individuals were likely to show greater responsiveness (longer FID and distances fled) compared with smaller individuals.
Fig. 3  Relationship between total distance fled and the number of hops recorded for each focal Lithobates sphencephalus

Each data point representing an individual small, medium-sized or large frog.

In terms of escape vocalisation, the only effect we recorded was that of body size: there was an increased likelihood for frogs to vocalise during escape with increasing size. We discuss these findings in terms of our predictions.

Contrary to our first prediction, L. sphencephalus in the open were less reactive than animals in cover; however, this reflects similar findings for Iberian green frogs Rana perezi (Martin et al., 2006). If moving increases the level of risk that animals are exposed to, i.e. increases the costs of moving, then it is predicted that animals will be less likely to flee Ydenberg and Dill (1986). For many frog species, immobility is crucial to maintain crypsis and it is a major component of behavioural defence against predation (Cooper et al., 2008b). Lithobates sphencephalus in the open, without the benefit of vegetation cover, appear to be relying on crypsis, the efficacy of which would be lost if the animal moved, as has been observed in Craugastor frog species that usually kept entirely still when approached by humans (Cooper et al., 2008b) and only fled when perceived risk (angle of approach or simulated attack) was high (Cooper et al., 2008b). This may explain the differences in responsiveness for animals in the open or in vegetation.

Supporting our second prediction, we found that smaller L. sphencephalus were less reactive compared with larger frogs. This could be due to larger individuals having lower costs of locomotion compared with smaller conspecifics (Peters, 1986). Larger animals can therefore afford to move away earlier whereas smaller individuals may rely on crypsis for longer to reduce their chances of making a costly move that was unwarranted. Small frogs also tended to remain closer to water and were more likely to escape to water, while large frogs were initially further from water and when they moved away, were likely to also move towards grass clumps. Smaller frogs were more likely to be in the open: this may reflect differences in foraging strategies, intraspecific competition or predation, and should be considered in future research.

We found no support for our third prediction. Flight responses of L. sphencephalus were not influenced by the density of animals in the immediate vicinity of our focal individual. Similarly, FID was not influenced by density of frogs nearby in R. perezi (Martin et al., 2006), although Hayes (1990) reported a positive correlation between FID and density for American green frogs R. clamitans and northern leopard frogs R. pipiens. The advantages of group membership vary with many factors, e.g. group size, food density, predator behaviour, and, therefore, according to the predictions of the economic escape model, prey responses are similarly likely to vary according to the species under consideration, as well as the particular environment, e.g. animals may be less willing to leave high quality foraging patches (Ydenberg and Dill, 1986).

Body size was the only factor that appeared to affect whether or not frogs vocalised during escape. The lizard Liolaemus chiliensis produces ‘distress calls’ when captured; nearby conspecifics seem to react to these calls by becoming immobile for a period (Hoare and Labra, 2013). If frogs call as a warning to conspecifics, it might be predicted that there would be an increased likelihood of escape vocalisation as the number of conspecifics nearby increased, but we found no effect of frog density. If frogs call to startle predators, there might be more escape vocalisation when the predator is close to them when they flee, i.e. a short FID; however, we found a greater likelihood of larger frogs calling and the larger frogs showed longer FID. Finally, if frogs call as a form of honest signalling, they might be more likely to vocalise when they are close to cover (in case it does not succeed in deterring the predator); however, there was no effect of initial microhabitat on escape vocalisation.

Is there a simple biological explanation for increased likelihood of calling in larger animals? Lesser short-toed larks Calandrella rufescens of better nutritional and immunological status produced harsher calls (a call
with more energetic investment) when near a predator than did individuals in poorer conditions (Laioło et al., 2004), implying that such calls may be energetically expensive: larger individuals may have the resources to invest in such calls. Alternatively, relatively simple croaks may not be expensive to produce but may simply be a non-adaptive side effect of escape behaviour: Capranica (1968) called the short, loud grunt given by _L. catesbeianus_ escaping into water a ‘warning call’, but suggests that, on the basis of this call being produced in contexts other than escape, such sounds may simply be a deflation of the lungs influencing the buoyancy of the animal. This may be a possible interpretation, but the observation that the _L. sphenopechalus_ in this study were more likely to call when escaping to grass, rather than water implies that it is not necessarily to do with adjusting buoyancy. Viewandt (1969) also notes that an abrupt, forceful vocalization in _L. catesbeianus_ characterised by a sudden expulsion of air from the lungs and calls were often emitted during ‘much jumping and splashing’ during intraspecific fighting. Cooper (2011) observed that when _L. catesbeianus_ called during escape, nearby frogs were more likely also to escape: it is possible that even if such calls have an origin in a physiological component of escape, they have become accepted as indicators of fleeing conspecifics to nearby individuals.

Escape behaviour of organisms that inhabit an ecotone at the interface between two very different habitat types (e.g. shorelines or river banks and pond edges) where they can escape to either habitat, have to choose between these habitats. This can be particularly important where there are divergent costs and benefits of these habitats, e.g. thermal costs and different types of predators. Such organisms are likely to be useful in elucidating the economics of escape decisions because they face such different choices. This is particularly interesting for organisms where their choices change ontogenetically, or as they change body size. Differences in escape behaviour may either reflect differences in evolutionary history, such as sympatric _Rana pretiosa_ and _R. aurora_ preferring to escape to water or to escape to land respectively (Licht, 1986), or dynamic decision making, such as black swans, _Cygnus atratus_ demonstrating a higher FID when they are farther from refuge on water (Guay et al., 2013). In addition to frogs and waterbirds, semi-aquatic taxa such as snakes, e.g. _Nerodia_ sp. (Burger, 2001; Cooper et al., 2008a; Weatherhead and Robertson, 1992); mammals, e.g. water voles _Arvicola amphibia_ _lis_ (terrestris) (Barreto and Macdonald, 1999) and invertebrates, e.g. grasshoppers _Paroxya atlantica_ (Bateman and Fleming, 2011a) are all likely to be fruitful model groups in studying this context.

In conclusion, escape behaviour in _L. sphenopechalus_ varies with body size and microhabitat. Both factors therefore need to be considered simultaneously in assessing their escape behaviour. These animals use a variety of antipredator behaviour, including crypsis, fleeing to either water or land, and altering their escape decision according to the initial microhabitat in which they are initially found. The calling behaviour is intriguing, but did not conform to any of our predictions; further work should explore the escape calling in frogs, in particular potential differences between the sexes: most female anurans are bigger than males and larger animals were more likely to call when escaping than were smaller ones.

References


