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Escape strategy of Schreiber's green lizards (*Lacerta schreiberi*) is determined by environment but not season or sex

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Abstract

Antipredator escape behaviour shows great variation with well-established sources of variation being the physical environment and the ecological context. However, the relative roles of these sources are rarely assessed together. We measured the distance that Schreiber's green lizards, *Lacerta schreiberi* allowed a simulated predator to approach before fleeing (flight initiation distance; FID) to know which are the main determinants of escape decisions. The environment had direct effects on the lizards' escape strategy; FID showed strong positive relationship with distance to refuge on grassy, but not on rocky substrates. Furthermore, refuge distance and the escape angle had a complex, substrate-independent, interaction effect: either short refuge distances or large escape angles resulted in short FIDs. In contrast, neither season (reproductive *vs*. nonreproductive), nor sex affected FID. We suggest that the escape strategy of this lizard is determined mainly by the environmental settings, irrespective of the ecological context or sexual roles.

Keywords

green lizard, escape behaviour, flight initiation distance, distance to refuge

1. Introduction

Predation is one of the most important selection pressures that determines the morphology (Endler, 1991) and behaviour of animals (Lima, 1998). This is because avoiding or surviving predatory attacks is a key for increasing fitness (Lima & Dill, 1990). However, escape behaviour can be costly too, because by moving the prey may attract the predator, spend energy and lose resources and opportunities. Consequently, animals are supposed to escape when the fitness costs of staying exceed the costs of escaping (Ydenberg & Dill, 1986; Cooper & Frederick, 2007). For this reason, antipredator behaviour is very flexible given the variation in the actual costs-benefits relationships.

For instance, the effect of habitat structure on escape decisions is very important (Martín & López, 1995; Snell et al., 1988; Majláth & Majláthova, 2009). In dense vegetation, the flight initiation distance (FID; i.e. the distance between predator and prey when prey starts to flee) is generally shorter than in open habitat, because the prey can use cryptic behaviour in the former, while it is more conspicuous in the latter (Martín & López, 1995; Snell et al., 1988; Majláth & Majláthova, 2009; but see Smith, 1997). Another relevant environmental factor is the relative positions of the predator, the prey and the refuge. How close an animal allows a predator to approach is strongly dependent on the distance to the nearest available refuge and the angle between the prey-refuge and prey-predator routes. Usually, in most environments, the FID and the distance to the nearest refuge have a positive relationship (Dill & Houtman, 1989; Cooper, 1997a; Stankovich & Blumstein, 2005; but see Cooper & Wilson, 2007). If we take the escape angle into the model, the situation becomes more complex. The escape angle can depend on sensory performance constraints, acute changes in environmental factors, direct manipulation of sensory structures, availability and position of refuge(s) and obstacles, presence of conspecifics, etc. (Domenici et al., 2011a,b). If there is a refuge, the safest escape direction is directly towards the refuge or following a direction that maximize the distance from the predator while minimizing the time needed to reach the refuge (Domenici et al., 2011a,b). For example , when a predator approaches, *Uta stansburiana* lizards run nonrandomly directly toward the nearest refuge, but when the refuge is farther than 15 m, the escape behaviour of lizards changes to nondirectional running without hiding (Zani et al., 2009).

The FID increases with distance and angle to refuge in broad-headed skinks, *Eumeces laticeps* (Cooper, 1997a) and in eastern woodchucks, *Marmota monax* (Kramer & Bonenfant, 1997).

The above discussed physical environmental factors are basic stanchions of antipredator escape behaviour. However, not every individual is expected to optimize its escape strategy in the same way, both individual state and ecological context might alter the cost-benefit ratio (Cooper & Frederick, 2007). For example, relative conspicuity to predators of different individuals may affect the risk of being detected and this should affect escape decisions. Some studies showed that visual conspicuousness of coloration correlates positively with shyness (Forsman & Appelqvist, 1998; Martín & López, 1999a; Cuadrado et al., 2001; Lindström et al., 2007; Cabido et al., 2009; Møller et al., 2011; but see Godin & Dugatkin, 1996); and in some lizards, FID vary among species, being inversely correlated with the degree of cryptic coloration (Heatwole, 1968; Johnson, 1970), or within a species as a function of the degree of conspicuousness in different microhabitats (Cooper, 1998a; Cuadrado et al., 2001). Also, in several cases, there are differences between the escape tactics of males and females. For example, in lizards with sexually dichromatic coloration, males, with more conspicuous colorations, have longer FIDs than females in some species (Lailvaux et al., 2003; Martín & López, 1999a) but not in others (Smith, 1996, 1997; Cooper & Wilson, 2007; Whiting, 2002). Male green lizards, *Lacerta viridis*, have longer FIDs than females before and after the mating season, but during the mating season the difference dissipates (Majláth & Majláthová, 2009).

In the present study, we examined the relative roles of microhabitat, position of the threat and refuge, ecological context, and sex in determining the escape strategy of adult Schreiber’s green lizards, *Lacerta schreiberi*. We considered two parts of the escape strategy: a preventive decision (distance to the nearest refuge before a potential attack) and an escape decision in an emergency situation (FID). We hypothesized that while the physical environment may have strong effects on escape strategy, differences in ecological context (i.e. being within or after the breeding season) and the sexual roles should have a modifying effect. We predicted that FID would increase with increasing refuge distance and escape angle, and that these effects would be less pronounced in exposed (i.e. open rocks) than in complex (grassy areas) microhabitats. Further, we expected males being shyer (i.e. having longer FIDs) than females, because they are more conspicuous due to their nuptial coloration (Martín & López, 2009), while both males and females should be more risk-taking in the reproductive than in the non-reproductive season to avoid losing reproductive opportunities. To test the above hypotheses and their predictions, we studied the escape behaviour of adult lizards of both sexes in different microhabitats and both within and outside of the reproductive season.

2. Matherials and methods

Data collection

The study was performed during the summer of 2008 and spring of 2009 at a large pine forest area (‘Valle de La Fuenfría’) in the Guadarrama mountains (40^{o}44’ N, 4^{o}02’ W; Madrid Province, Spain). The dominant vegetation consists of *Pinus sylvestris* forest, with shrubs such as *Juniperus communis* and *Cytisus scoparius*. In this area, Schreiber’s green lizards are active from March to September, mate in April–May, and produce a single clutch during June (Marco & Pérez-Mellado, 1990). Lizards occupy relatively moist well vegetated areas often close to streams (Salvador, 1988; Pérez-Mellado, 1998). In this area the most frequent predators of *L. schreiberi* are common kestrels (*Falco tinnunculus*), common buzzards (*Buteo buteo*), booted eagles (*Hieraaetus pennatus*), grass snakes (*Natrix natrix*), cats (*Felis catus*), dogs (*Canis familiaris*) and foxes (*Vulpes vulpes*).

We observed the escape behaviour of 31 adult females and 12 males in August 2008 and 36 males and 22 females in May 2009. The spring sample (May) coincided with the beginning of the breeding season, so females could only be in an early stadium of gravidity, while in summer (August) reproduction had finished and all females had already laid their eggs. We searched for lizards between 10.00 and 18.00h. The observations were carried out in sunny, warm and unwindy weather. We simulated a potential predator by an approaching human (RK) always wearing the same clothes. This is a conventional method in studies of lizard escape behaviour, because lizards identify humans as natural predators (e.g. Braña, 1993; Bulova, 1994; Martín & López, 1995, 1999a, 2000, 2003; Cooper 1997a,b,c, 1998a,b Amo et al., 2005).

The observer walked (approx. 1 $m \cdot s^{-1}$) until an adult lizard was located. After this, the observer simulated a predator attack by approaching the lizard directly at a slow speed (approx. 0.6 $m \cdot s^{-1}$) until the lizard fled. We recorded the sex of animals (sexual dichromatism was easily discerned by sight) and the following escape behaviour variables: (i) ‘flight initiation distance’ (FID): distance between the lizard and the simulated predator that elicited escaping, (ii) ‘refuge distance’: distance between the lizard and the refuge used to hide, (iii) ‘escape angle’: the angle formed by the line between the lizard and the predator and the line between the lizard and the first stopping point after escaping. An escape angle of 0° indicated the direction of escaping directly away from the predator, while 180° was the direction of escaping towards the predator (Martín & López, 1996). We also noted the microhabitat in which the lizard was initially (grass *vs*. open rocks). The observations were made in different parts of a large field area, and density of lizards was high, so we assumed that the chance of repeated observations of the same individuals was low, hence, we considered the data as independent (Bulova, 1994; Martín & López, 1995; Cooper, 1997b).

Statistical analyses

We ran two General Linear Models (GLMs). The first GLM was built with refuge distance as the dependent variable, and sex, microhabitat type and season as fixed factors to reveal patterns related to general risk-taking. Second, we ran a GLM with FID as the dependent variable, sex, microhabitat type and season as fixed factors and refuge distance and escape angle as covariates to reveal patterns of escape strategy. The original models included all single effects and two-way interactions. We applied backward stepwise model selection based on the $P < 0.05$ criterion. There are several model selection approaches available, but this one is generally considered as a conservative choice (Murtaugh, 2009). We first removed the nonsignificant interactions in the order of decreasing P value and then did the same with the single effects. We never removed single effects that were part of significant interactions. All analyses were done by using the SPSS 17.0.1 (SPSS, Chicago, IL, USA) statistical software.

3. Results

Refuge distance was not significantly related to any of the analysed potential predictors (Table 1). However, FID was significantly affected by microhabitat, refuge distance and the microhabitat × refuge distance and refuge distance × escape angle interactions, but not by sex, season or any of their interactions (Table 2). Backward stepwise selection produced similar results to the original model including all effects. FID was strongly positively related to refuge distance in the grass microhabitat ($R^2 = 0.23$, $p < 0.001$; Fig 1a) but not in the rocky microhabitat ($R^2 = 0.06$, $p = 0.22$; Fig. 1b). With respect to the refuge distance × escape angle interaction (Fig. 2.), we found that 1) if a lizard was close to the refuge, it allowed the predator to approach closer independently of escape angle, 2) if the escape angle was small, the lizard increased FID when the refuge distance increased, but 3) if the escape angle was large, the lizard allowed the predator to approach closer independently of refuge distance.

4. Discussion

Our results were not entirely consistent with our predictions. While our data revealed strong and complex environmental influence on lizard escape behaviour (FID), we did not find any effect of sex or ecological context. None of the analysed environmental variables affected refuge distance. This is, however, interesting because the detectability of lizards and predator attack success should be higher on open rocky substrate than in dense vegetation and thus we expected different preventive strategies (e.g. different distances to potential refuges). In contrast, the environment had several effects on escape decisions in an emergency situation (represented by FID). In several lizard species, individuals have longer FID in areas with low cover, because they are more conspicuous in that environment (Martín & López, 1995; Snell et al., 1988; Majláth & Majláthova, 2009). Depending on the microhabitat, *L. schreiberi* lizards showed two different escape tactics; in grassy substrates offering vegetation cover, FID strongly depended on the refuge distance, but not in rocky substrates without cover. In a meta-analysis with 17 lizard species, a positive correlation between refuge distance and FID was found, and this relationship was stronger when the variability of refuge distance was higher (Cooper, in press). This suggests variation in the flexibility of escape strategies: there may be either low flexibility with individuals choosing similar refuge distances and, thus, reacting to predators similarly, or high flexibility with variable refuge distances and the subsequent refuge-distance-dependent FID. The habitat-dependent escape strategies in our study might be explained by similar grounds if the variability of distances to available refuges was lower in rocky than in grass substrates. Alternatively, differences might result from the above-mentioned detectability and predator attack success differences in different microhabitats. Also, thermal differences between exposed and refuge locations in different microhabitats, and their associated thermal costs, may be important (Martín & López, 1999b, 2010). Thus, in sunny exposed rocky microhabitats the substrate temperature can be very high whereas refuge temperature inside crevices is cold, while in microhabitats covered by vegetation, external and refuge temperatures are more balanced, which could result in a more predictable escape behaviour.

Besides microhabitat type, the relationship between escape angle and refuge distance also have a strong effect on FID. We found that if a lizard was very close to its refuge, it allowed the predator to approach closer, irrespective of escape angle. Also, if the escape angle was large, the lizard allowed the predator to approach closer, irrespective of the refuge distance. Only if the escape angle was small, the FID was dependent on refuge distance. These results were expected because if the lizards are close to the refuge, they can delay escape as they can run to and reach the refuge quickly irrespective of the predator’s position. If the escape angle is small, meaning that the refuge is not blocked by the predator, lizards should adjust their FID depending on refuge distance (or time needed to reach it) (Cooper, 1997a; Stankovich & Blumstein, 2005). However, if the escape angle is large, meaning that the predator is blocking the lizard’s way to its refuge, lizards may face a conflict and, then, a better option might be to let the predator to approach closer while relying on crypsis as long as possible. This is because most individual lizards will finally run directly to the known refuge even if the predator is in that direction, which can still be safer than escaping to an unkown refuge where lizards may face dangerous encounters with another type of predator (e.g. saurophagous snakes) or an agressive conspecific (Amo et al., 2005). In the case of the lizard *Holbrookia propinqua* similar results were observed, with the predator being situated between the refuge and the lizard (Cooper, 1999a). In contrast, when the refuge is between the predator and prey, the FID increases with distance and angle to refuge; as shown both in the skink *Eumeces laticeps* (Cooper, 1997a) and the marmot *Marmota monax* (Kramer & Bonenfant, 1997).

In contrary to our expectations, we did not find any effect of gender or breeding season on the escape strategy of *L. schreiberi*. Conspicuous animals often suffer higher predation risk (Stuart-Fox et al., 2003; Husak et al., 2006), but this depends on the abilities of detection of potential predators too. Most research on predation risk suffered by lizards involves raptors as predators (Olsson, 1993; Stuart-Fox et al., 2003), while snakes (Husak et al., 2006) and mammals (Whiting, 2002) are less often considered. However, different types of predator can use totally different predatory behaviour and it is likely that the escape behaviour against them is not comparable. For example, raptors have very good tetrachromatic colour vision and they are very sensitive to slow or little movement (Honkavaara et al., 2002; Jones et al., 2007; Lind et al., 2013). This may expalin that males of the Western green lizard (*L. bilineata)*, a closely related species, suffer higher predation by common kestrels, *Falco tinnunculus*, than females (Constantini et al., 2007). Nevertheless, this sex bias could be caused either because males really do not compensate for the higher predation risk of having more conspicuous coloration or simply by the higher activity of males in the mating season. The latter was suggested by an experiment using painted epoxy-lizard models of Sand lizards (*Lacerta agilis)*, which avoid the effect of different activity levels, and did not find differences between sexes in predation rate (Olsson, 1993). In contrast, mammals have just dichromatic colour vision (Loop et al., 1987; Neitz et al., 1989; Hunt et al., 2011). Hence, the breeding coloration of male *L. schreiberi*, which include a strong UV component (Martín & López, 2009), may not be so conspicuous for mammal predators, and male lizards might not need to compensate against a mammalian (i.e. human) predator.

Furthermore, in a meta-analysis, it was found that in two-thirds of lizard species there are no differences between males and females in escape strategy (Cooper, in press) and some of these lizard species have sexual dichromatism like in our study species. In *Platysaurus broadley*, there was no difference on predation risk between males and females, which could explain the lack of differences between sexes on FID and RD (Whiting, 2002). The lack of sexual differences in *L. schreiberi* might be also explained if the more conspicuous males could escape faster than the more cryptic females, as it occurs in many other species (Cullum, 1998; Lailvaux et al., 2005). However, in the agamid lizard *Phrynocephalus vlangalii,* a species without sexual dimorphism, FID do not differ between the sexes and is unrelated to individual escape performance capacity, although males flee farther than females (Qi et al., 2014). But the reason could be more complex if opposite constraints affect escape decisions of *L. schreiberi*. In the case of females, cryptic coloration do not change seasonally, so females can always use the same effective mimicry (i.e. short FID) and would not need to change their escape strategy between seasons. In the case of males, during the breeding season coloration is more conspicuous, which should initially require a shyer behaviour (i.e. long FID), but conflicting reproductive requirements (i.e. mate searching, territorial defense, etc) may force males to be more active and risk more (i.e. short FID) (Magnhagen, 1991; Cooper, 1997b, 1999b; Cooper & Wilson, 2007). After breeding, male coloration change to less conspicuous and there are no reproductive constraints, which may allow males to be more confident (i.e. short FID).

In conclusion, we have found that the escape behaviour of *L. schreiberi* is based on environmental factors, being fine-tuned in one, but not in another microhabitat type. The relative positions of the predator, the prey and the refuge had the expected effects on escape decisions. However, contrary to our expectations, gender and ecological context did not modify escape decisions dictated by the environment. Likely, this statement could change if the animals have other constraints, such as nearby presence of food or conspecifics, which can result in lost opportunities after escaping (Cooper, 1997b, 1999b, 2000; Cooper & Wilson, 2007). Future studies are needed to see whether the conspicuous nuptial coloration of male *L. schreiberi* did not increase their exposure to predation, or whether males just accepted the costs of their ornaments due to conflicting reproductive requirements. Similarly, understanding the cost-benefit relations in gravid *vs*. postpartum female escape decisions would be an important step forward in revealing how different sources of selection shape escape behaviour.

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Table 1. Results of a General Linear Model for the effects of different environmental factors and ecological context on refuge distance of *L. schreiberi* lizards. Nonsignificant effects are shown as seen after a one-by-one back-substitution to the final model.

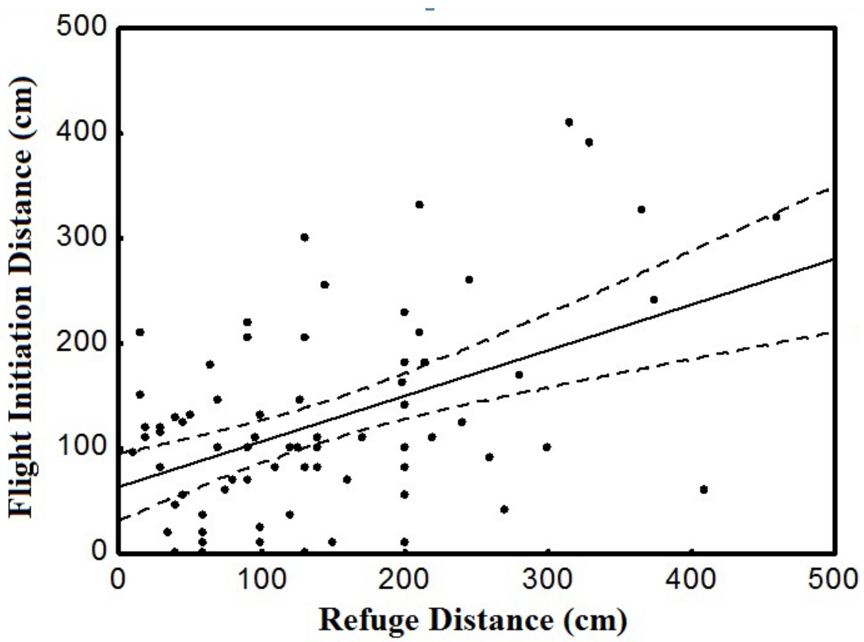
variable/factor	**df**	***F***	***p***
microhabitat	1,94	1.887	0.173
season	1,94	1.405	0.239
sex	1,94	0.203	0.653
microhabitat *season	1,94	0.632	0.429
microhabitat *sex	1,94	0.450	0.833
season *sex	1,94	0.193	0.662

Table 2. Results of a General Linear Model for the effects of different environmental factors and ecological context on flight initiation distance (FID) of *L. schreiberi* lizards. Nonsignificant effects are shown as seen after a one-by-one back-substitution to the final model.

variable/factor	**df**	***F***	***p***
microhabitat	1,85	23.976	**<0.0001**
refuge distance	1,85	5.034	**0.027**
escape angle	1,85	0.979	0.325
season	1,85	1.074	0.303
sex	1,85	0.999	0.320
microhabitat*refuge distance	1,85	20.278	**<0.0001**
microhabitat*escape angle	1,85	0.170	0.681
microhabitat *season	1,85	0.005	0.946
microhabitat *sex	1,85	2.299	0.133
refuge distance *escape angle	1,85	6.810	**0.011**
refuge distance *season	1,85	0.134	0.716
refuge distance *sex	1,85	2.893	0.092
escape angle *season	1,85	0.001	0.975
escape angle *sex	1,85	1.571	0.213
season *sex	1,85	1.489	0.225

Figure 1. The effect of refuge distance on flight initiation distance (FID) of *L. schreiberi* lizards in a) grassy substrates or b) in rocky microhabitat types.

a)



b)

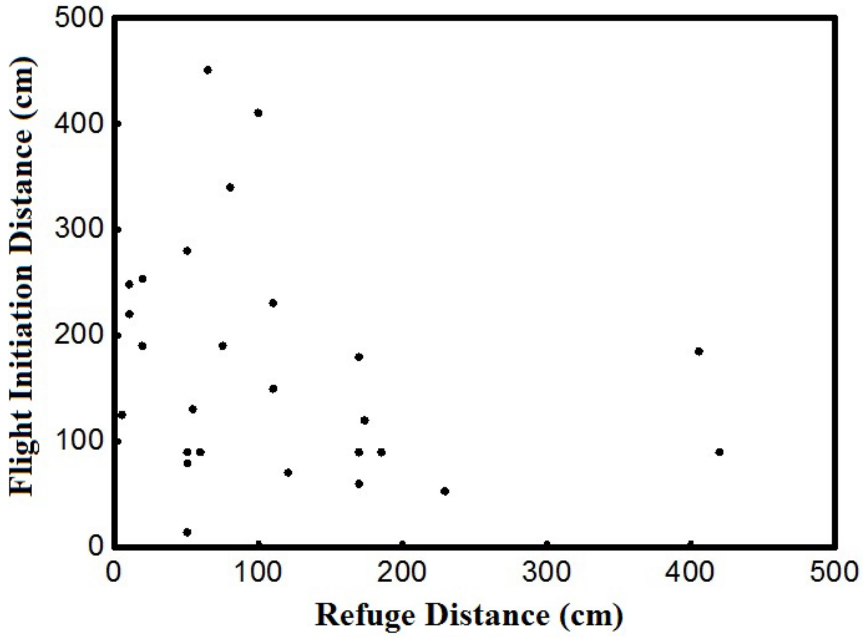


Figure 2. The effects of refuge distance, and escape angle on flight initiation distance (FID) of *L. schreiberi* lizards (shown in the z axis with a colour code at 50 cm intervals). The colour code of FID was: 1: 0-50cm, 2: 50-100cm, 3: 100-150cm, 4: 150-200cm, 5: 200-250cm, 6: 250-300cm, 7: 300-350cm, 8: 350-400cm. The equation of the relationship was: FID= 0.744*refuge distance + 0.352*escape angle – 0.006*refuge distance*escape angle.