



RESEARCH PAPER

Predation Risk and Opportunity Cost of Fleeing While Foraging on Plants Influence Escape Decisions of an Insular Lizard

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Abstract

Cost-benefit models of escape behaviour predict how close a prey allows a predator to approach [flight initiation distance (FID)] based on cost of not fleeing (predation risk) and cost of fleeing (loss of opportunities). Models for FID have been used with some success to predict distance fled (DF). We studied effects of foraging opportunity cost of fleeing and examined differences between age-sex groups in the omnivorous Balearic Lizard, *Podarcis lilfordi*. Balearic lizards forage on the ground for invertebrate prey and climb the thistle *Carlina corymbosa* to forage on its inflorescences. We studied escape behaviour in three experimental groups, with human beings as simulated predators: lizard foraging above ground on *C. corymbosa*, foraging on the ground away from thistles and on the ground with cut inflorescences. Flight initiation distance was shorter for lizards with cut inflorescences than for (1) lizards above ground due to the greater risk above ground due to conspicuousness of black lizards on yellow flowers; and (2) lizards on ground away from flowers due to the cost of leaving while feeding. The only age-sex difference was slightly greater FID for adult males than subadults, presumably because larger adult males are more likely to be attacked by predators. Other potential factors affecting this difference are discussed. Experimental group and age-sex group did not interact for FID or DF. Because lizards foraging on inflorescences above ground fled to the base of the plants to refuge provided by spiny thistle leaves, their DF was shorter than in the other groups, which fled across the ground, usually without entering refuge. DF did not differ between groups on the ground or among age-sex groups. The predicted shorter DF for lizards with cut inflorescences than on ground without inflorescences did not occur. We hypothesize that the opportunity cost was small due to the abundance of blooming thistles and that DF may be less sensitive to opportunity cost than FID.

Introduction

When a prey detects an approaching predator, it must decide whether, when and how far to flee. Economic models have been very successful in predicting when prey start to flee and to a lesser extent how far they flee based on costs and benefits associated with fleeing and not fleeing (Stankowich & Blumstein 2005; Cooper 2010). Prey are assumed to assess and continuously update the risk of predation and cost of fleeing to

inform decision about their behavioural options for antipredatory defence (Lima & Dill 1990). Two explicit models predict flight initiation distance (FID), the distance between the prey and approaching predator when the prey begins to flee. In both models, a prey monitors a predator continuously as it approaches. As the predator draws nearer, predation risk (cost of not fleeing) increases, but cost of fleeing decreases because the prey may obtain some of the potential benefits of its current activity while the predator approaches.

A model by Ydenberg & Dill (1986) predicts that prey initiate escape at the distance where cost of not fleeing and cost of fleeing are equal. In contrast, the model of Cooper & Frederick (2007, 2010) predicts that escape begins at the FID for which the prey's fitness at the conclusion of the encounter is maximized. The optimal FID is based on predation risk, cost of fleeing and a third factor, the prey's initial fitness (residual reproductive value). Inclusion of the prey's initial fitness is important because prey that have higher fitness are predicted by [Clark's \(1994\) asset protection principle](#). Calculations and examples in which fitness can be enhanced even if the prey dies indicate that prey can achieve higher fitness if they make an optimal decision regarding FID than by escaping when costs of fleeing and not fleeing are equal. In the Ydenberg & Dill model (1986), the best that a prey can do is break even, that is, not lose fitness ([Cooper & Frederick 2007](#)).

Despite the conceptual differences between models, they can be used interchangeably to test qualitative predictions at the ordinal about relative magnitudes of FID under greater and lesser risk and cost for a wide range of factors that affect risk and cost. This is because (1) precise FID values predicted by the break even and optimality models cannot be calculated because exact fitness costs and benefits are unknown; and (2) initial fitness of prey frequently does not differ between experimental groups when effects of other factors are being tested. In both cases, FID is longer when cost of not fleeing is greater and shorter when cost of fleeing is greater.

Many studies of single species have verified predictions of the models of FID for diverse risk and cost of fleeing factors (Lima & Dill 1990; Stankowich & Blumstein 2005; Cooper 2011a). Some factors for which higher risk is associated with longer FID include distance to refuge, directness of the predator's approach, predator approach speed, presence or absence of predator eye contact and degree of plant cover (reviewed by Stankowich & Blumstein 2005; Cooper 2010, 2011a). Some factors for which higher cost of fleeing is associated with shorter FID include the presence of food and of potential mates or sexual rivals (Cooper & Pérez-Mellado 2004; Stankowich & Blumstein 2005; [Cooper et al. 2006](#)). Some of these factors depend on aspects of the predator, including its behaviour. Others are intrinsic for each prey species, individual and setting. The latter features include crypsis, body armour, body condition, body size, loss of body parts by autotomy and experience with predators (reviewed by Stankowich & Blumstein 2005; Cooper & Wilson 2008; Cooper 2011b).

Most of the research about antipredator behaviour measured FID as an estimator of risk perception by prey. However, the cost-benefit logic escape models conceived for FID have been applied with mixed success to distance fled (DF) by a prey before stopping. Distance fled is expected to be shorter when predation risk is lower, and fleeing farther increases potential loss of benefits, especially by loss of reproduction or feeding opportunities (Martín & López 1998; Cooper & Vitt 2002; Cooper & Pérez-Mellado 2004; Cooper et al. 2006; Cooper 2009). When food is present, DF by the prey is predicted to be shorter to avoid costs of losing the food item and of searching for another one. Furthermore, prey often maintain distances to refuge according to risk and expected benefits. Thus, the number of available refuges and distance to them could also affect DF (Martín & López 2000).

Although predation risk and cost of fleeing factors may interactively or independently affect escape decisions, very few studies have examined the effects of simultaneous risk and cost factors (Cooper et al. 2003; Cooper 2011a). Researchers usually test effects of two or more risk levels by modifying the threat posed by the predator by varying factors such as approach speed, directness of attack or eye contact (Cooper 2003, 2011b; Cooper et al. 2003, 2009b, 2010, 2012; Stankowich & Blumstein 2005). In other studies, differences in escape behaviour are examined in relation to features of the prey, predation intensity to which their population is exposed or habitats characteristics related with risk level, such as cover, visibility or distance to refuges (Martín & López 2000; Cooper et al. 2009c; Cooper & Pérez-Mellado 2012). In our study, the prey are exposed to similar predators, but the risk level and expected foraging benefits varied between microhabitats occupied by lizard prey. Risk was higher on the plant, where flowers were present as a food resource, than on the ground, where food was absent. We created a third situation in which the food was present in the microhabitat with lower risk.

We studied the escape behaviour of the Balearic lizard, *Podarcis lilfordi* (Squamata, Lacertidae), which is omnivorous, frequently consuming plant material such as flowers and nectar (Pérez-Mellado & Corti 1993). From late June to early August, *P. lilfordi* frequently climb to inflorescences of the thistle *Carlina corymbosa* and eat its flowers (own data). While a lizard is foraging on an inflorescence, risk of predation is presumably higher than when it is on the ground. That is mainly due to the greater conspicuousness of a melanistic lizard on a background of yellow flowers. Also, we have to take into account the instability or shakiness of the plant, as well as the difficulty to move

over plants and the uncovered situation. We predicted that FID would be greater due to this risk, but the presence of flowers as food is expected to lead to shorter FID. Because lizards on the ground did not forage on flowers, their FID would be expected to be longer than above ground on flowers due to lower cost of fleeing in the absence of flowers as food, but shorter due to the lower risk conferred by being less conspicuous. In the absence of information about the relative magnitudes of these factors, we could not predict the relative magnitudes of FID on inflorescences above ground and on the ground.

To separate the effects of the risks and costs, we studied escape in the two natural situation just described and in an artificial situation in which we cut blooming inflorescences from *C. corymbosa* and placed them on the ground. For this group, risk of being on the ground was equal to that of lizards foraging on the ground away from flowers. Due to very strong effects of presence of food on escape (Cooper 2000; Cooper et al. 2003, 2006), we predicted that FID would be longer at ground level for lizards away from flowers than lizards on flowers. For the two groups with flowers, we predicted longer FID for those that had climbed above ground because they had equal costs of leaving the food, but greater conspicuousness.

Podarcis lilfordi sometimes hide into a refuge when escape, but other times just run for some centimetres before stopping, without entering a refuge (own data). We observed that lizards over plants in Aire, such as *C. corymbosa*, *Crithmum maritimum* or *Euphorbia paralias*, usually flee jumping to the ground and remaining hidden on the base of the same plant where they were foraging. When applied to DF, the models for FID predicted shorter DF for lizards on flowers due to cost of leaving but greater DF for lizards above ground due to greater conspicuousness or for lizards further away from an available refuge. Thus, we predicted longer DF by lizards on flowers when above ground than on the ground because of the greater risk, but shorter because of the closer distance to refuge. The final result will depend on the balance between risks and benefits of each situation. Because lizards feeding on flowers on the ground were not on the flowers, they were not as conspicuous as lizards foraging on inflorescences above ground. Cost of leaving the food predicts shorter DF when flowers were present than absent on the ground.

Escape behaviour often differs among ages and between sexes (Stankowich & Blumstein 2005; Cooper 2011b). Differences between adult and juvenile individuals might be attributable to differences in size, reliance on crypsis or smaller size by juveniles or

previous experiences with predators. In some studies, males and females have different FID or DF, due to sexual dimorphic characteristic, such as a greater conspicuousness or size of males or the reproductive state of the female (Cooper 2011b). Therefore, we also examined differences between age-sex groups. It is difficult to make predictions about effects of sex and age on escape behaviour, because the complexity of factors that affect it and the lack of consensus on previous studies. Thus, we expected shorter FID for subadult than adult lizards, in a similar way that it is reported in most of the previous studies (Martín & López 2003; Whiting et al. 2003; Cooper 2011b). Nevertheless, we did not expect any difference between sexes, considering that males and females of *P. lilfordi* have the same colour pattern, and in July most of females are not pregnant.

Methods

Study Species and Site

We conducted the study on Aire, an islet off the coast of Menorca (Balearic Islands, Spain; 39°48'N, 4°17'E, 15 m.a.s.l.) during July and early August 2008 and July 2010, on sunny days from 07:00 to 11:00 hour GMT, when lizards were actively foraging. The vegetation in the study area was sparse, with some low plants and bushes that provide food and refuge for the lizards. Holes in stone fences and rocks provide additional refuges. The main flowering plant at the study site during summer is *C. corymbosa* (Asteraceae), a thistle 10–70 cm high with bright yellow flowers (Meusel & Kästner 1990).

Podarcis lilfordi (Squamata, Lacertidae) is a medium-sized lacertid lizard (average SVL 68 mm in males, 63 in females and 58 in subadults, own data). It reaches very high population densities in Aire island (Pérez-Mellado et al. 2008), facilitating data collection. Balearic lizards are mainly insectivorous, but they also consume parts of a wide variety of plant species, as well as nectar (Pérez-Mellado & Corti 1993). Although active and ambush foraging modes strictly apply to insectivores, it could be applied to *P. lilfordi*, which was ancestrally insectivorous. The Balearic lizard appears to have retained the typical proportion of time spent moving of active foraging while foraging for animal prey and to have added substantial time for consumption of plant material (own data).

No mammalian or ophidian predators of lizards are present on Aire (Pérez-Mellado 1989), where birds are the main predators. Kestrels (*Falco tinnunculus*) do not breed on Aire, but visit the islet frequently and

are the major predators of *P. lilfordi*; a breeding colony of two gull species (*Larus cachinnans* and *Larus audouinii*) is present on Aire, which very occasionally capture lizards (V. Pérez-Mellado, pers. obs.; and see also Martín & López 1990; Martínez-Abraín et al. 2003; Matias & Catry 2010).

Experimental Procedure

Human experimenters served as simulated predators (Frid & Dill 2002). Although human beings are not natural predators of lizards, they have been very useful as simulated predators in escape experiments with different taxa (reviewed by Stankowich & Blumstein 2005). We have conducted several previous studies in this population with similar methods and lizards reacted to experimenters as it was to be expected in response to natural predators (Cooper & Pérez-Mellado 2004; Cooper et al. 2006, 2009b). Although it is possible that antipredatory responses specific to other predators might not be observed, the lizard *Sceloporus virgatus* exhibited similar escape responses to a human being and models of a raptorial bird and a snake (Cooper 2008).

We tested lizards in three different situations: (1) active lizards foraging on the ground; (2) lizards foraging above the ground on *C. corymbosa* inflorescences; and (3) lizards eating *C. corymbosa* cut inflorescences and offered to lizards on the ground. Situation (3) was performed by cutting blooming fresh inflorescences of *C. corymbosa* and tying six of them to a piece of fine cardboard to prevent lizards from escaping with the whole inflorescences.

Before trials in situations (1) or (2), the investigator slowly walked through the area searching for an active lizard. After detecting one of them, he moved to a location that afforded the lizard a clear view of him and at a starting distance of 5–10 m. Before each trial in situation (3), we placed the cardboard with attached inflorescences on the ground in an open area in the zone where *C. corymbosa* occurs naturally, withdrew 10 m and remained still. We conducted a trial after a lizard had approached and started to feed on the florets.

In all trials, the same experimenter approached directly towards the lizard at a practiced speed of 80 m/min. At this speed, starting distance has no effect on FID in *P. lilfordi* (Cooper et al. 2009a). As soon as the lizard fled, the investigator stopped and recorded FID and DF by the lizard before stopping for at least 1 s. Distances were measured with a metric rule to the nearest 0.01 m. We also noted the age and sex of the individual (adult male, adult female or

subadult) and the GMT hour. When we finished the trial for one individual, another individual was usually in sight, which we could distinguish from the previous one. Trials in the two natural situations were conducted in blocks of 2–3 trials in one situation alternating with blocks 2–3 trials in the other situation in 2008. Trials with cut inflorescences were conducted in 2010. Ideally, the sequence of testing would have been counterbalanced. Nevertheless, we believe that sequential bias was minimal because approach protocols were identical in the 2 yr, weather very similar, and blooming *C. corymbosa* was similarly abundant in the 2 yr, and the trials with cut inflorescences were conducted at the site where lizards were simultaneously feeding on intact *C. corymbosa*. To avoid pseudoreplication, we moved through an area only once. Moreover, density of lizards was high enough to do repetition of the same individual unlikely.

We tested 11 males, 19 females and 15 subadults on *C. corymbosa*; 20 males, 9 females and 5 subadults on the ground; and 8 males, 9 females and 8 subadults with cut *C. corymbosa* inflorescences on the ground. In two trials, we were unable to record DF.

Statistical Analysis

Data were analysed with separate 3×3 factorial ANOVAs for FID and DF, with all factors and levels being independent groups (Sokal & Rohlf 1995). We tested homogeneity of variances using the Fligner–Killeen test and normality using the Shapiro–Wilk test (Crawley 2009). Although some distributions were not normal, their variances were homogeneous, so we applied an ANOVA test, which is robust when data depart only slightly from normality (Sokal & Rohlf 1995). When we detected significant main effects, we applied Tukey's HSD test to examine differences between pairs. We analysed data using R 2.15.1 (R Core Team 2012). Data are presented as mean \pm 1.0 SE. All tests were two-tailed, with $\alpha = 0.05$. Effect sizes are reported as classical η^2 , which is given by the sum of squares for a particular effect divided by the total sum of square, varies from 0 to 1 and may be interpreted similarly to R^2 (Cohen 1973).

Results

Flight Initiation Distance

FID for all data pooled was 112 ± 6 cm, but FID differed significantly between the foraging situations (ANOVA, $F_{2,95} = 8.25$, $p < 0.001$; Fig. 1) and age-sex classes ($F_{2,95} = 3.32$, $p = 0.04$). The interaction

between foraging situations and sex and age classes was not significant ($F_{4,95} = 0.48, p = 0.75$). FID was significantly shorter when lizards foraged on *C. corymbosa* inflorescences on the ground (71 ± 6 cm) than both above ground on the plant (125 ± 10 cm; Tukey's HSD test, $p < 0.001$) and when foraging on the ground without *C. corymbosa* (124 ± 11 cm; $p = 0.002$). FID did not differ significantly between lizards foraging above ground level on *C. corymbosa* and lizards on the ground without *C. corymbosa* ($p = 1.00$). Although the main effect of foraging situation was significant, the effect size was small ($\eta^2 = 0.13$).

FID was 129 ± 12 cm for adult males, 111 ± 9 for adult females and 90 ± 8 for subadults. FID was significantly greater for adult males than for subadults (Tukey's HSD test, $p = 0.04$). The other differences in FID were not significant (adult males vs. adult females, $p = 0.43$; adult females vs. subadults, $p = 0.41$). The effect size of age-sex group was small ($\eta^2 = 0.06$).

Distance Fled

Distance fled for all lizards was 45 ± 3 cm, but differed significantly between foraging situations ($F_{2,93} = 22.29, p < 0.001$; Fig. 2). Distance fled did not differ significantly age/sex classes ($F_{2,93} = 1.00, p = 0.37$), and the interaction between foraging situation and age-sex classes was not significant ($F_{4,93} = 0.6349, p = 0.64$). Distance fled was significantly shorter for

lizards foraging above ground on *C. corymbosa* (28 ± 2 cm) than both for lizards on *C. corymbosa* inflorescences at ground level (61 ± 3 cm; Tukey's HSD test, $p < 0.001$) and for lizards foraging on the ground without *C. corymbosa* (57 ± 6 cm; Tukey's HSD test, $p < 0.001$). Distance fled did not differ significantly between lizards foraging on the ground with and without *C. corymbosa* ($p = 0.84$).

Discussion

Foraging situations affected escape, but patterns of differences between situations were very different for FID and DF. Age/sex differences affected FID, but not DF. The results reveal differences in factors affecting FID and DF.

Flight Initiation Distance

Foraging groups

The differences in FID between experimental groups cannot be explained by differences in predation risk alone or in opportunity cost of fleeing alone. Each experimental group had a unique combination of cost of not fleeing and cost of fleeing. Therefore, factors that account for differences in FID themselves differ between pairs of experimental groups. FID was greater for lizards foraging on inflorescences on intact plants than for lizards foraging on cut inflorescences on the ground although both suffered loss of feeding opportunity upon fleeing. This finding verifies the

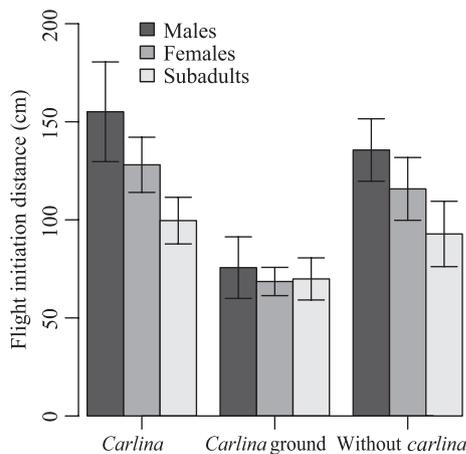


Fig. 1: Mean values of flight initiation distance (FID) of *Podarcis lilfordi* for each age-sex class and situation. *Carlina*, lizards eating on *Carlina corymbosa* inflorescences above ground; *Carlina ground*, lizards eating on *C. corymbosa* inflorescences cut at ground level; *Without Carlina*, active lizards on ground without *C. corymbosa*. Error bars represent ± 1 SE.

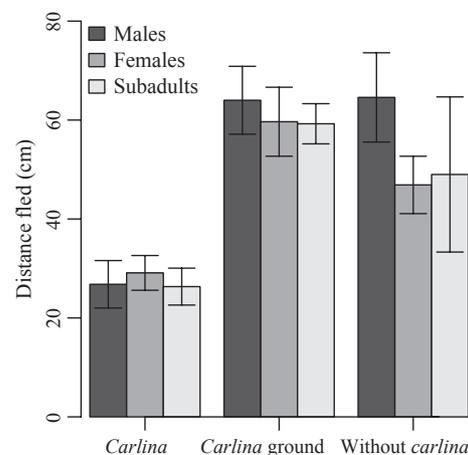


Fig. 2: Mean values of distance fled (DF) of *Podarcis lilfordi* for each age-sex class and situation. *Carlina*, lizards eating on *Carlina corymbosa* inflorescences above ground; *Carlina ground*, lizards eating on *C. corymbosa* inflorescences cut at ground level; *Without Carlina*, active lizards on ground without *C. corymbosa*. Error bars represent ± 1 SE.

prediction based on the greater risk of lizards foraging on inflorescences above ground, where their black bodies are viewed against yellow flowers, than on the ground next to cut inflorescences where the background is the soil rather than flowers.

For the groups on the ground, risk was similar, but only lizards foraging on cut inflorescences had an opportunity cost. The shorter FID by the group foraging on cut inflorescences than lizards on the ground without inflorescences supports the prediction based on opportunity cost. We made no prediction about the difference in FID between lizards foraging on flowers above ground and lizards foraging away from flowers on the ground because the cost of fleeing was lower, but the cost of not fleeing was also lower for lizards on the ground without flowers because they are less conspicuous. The lack of difference for these two experimental groups suggests that their differences in costs of fleeing and of not fleeing were approximately equal. *Podarcis lilfordi* accepts greater risk to gain the benefits of foraging on inflorescences high on thistle plants.

Our finding of shorter FID for lizards on the ground with than without flowers adds to a growing body of empirical evidence for effects of food presence consistent with predictions of economic models of FID (Ydenberg & Dill 1986; Lima & Dill 1990; Cooper & Frederick 2007; lizards – Cooper 2000; Cooper et al. 2003). In previous studies of *P. lilfordi*, lizards permitted closer approach when fruit or animal prey were present than absent (Cooper & Pérez-Mellado 2004; Cooper et al. 2006). In addition, there are several studies that titrate food and safety with diverse species of invertebrates (e.g. Nonacs & Dill 1990), fish (e.g. Abrahams & Dill 1989), birds (e.g. Todd & Cowie 1990) or mammals (e.g. Kotler & Blaustein 1995). This kind of experiments showed that individuals accepted foraging on the riskier patch if food was more abundant or easier to obtain than in the safer patch, balancing costs and benefits of each option (Brown & Kotler 2004).

Age-sex differences

The lack of interaction between foraging situation and age-sex groups indicates that the relative magnitudes of FID for age-sex groups were similar among foraging situations. FID was slightly longer for adult males than subadults, but otherwise similar among age-sex groups. In some species, juveniles allow closer approach than adults (Lima & Dill 1990; Martín & López 2003; Whiting et al. 2003; Cooper 2011b). Differences were more pronounced in most of these studies than in ours

(e.g. FID in *Sceloporus jarrovi* neonates was only 0.42 as long as that of adults; Cooper 2011b). In interspecific comparisons, FID increases as body size increases in lizards (own data). Because subadults were closer to adult body size in our study, differences in FID between ages may have been minimized.

Potential reasons why FID was shorter for subadults than adult males are lower risk of being attacked by a large predator, greater ability to escape if attacked, lower expected residual reproductive value (if subadult survival is lower than that of adults), greater cost of fleeing for subadults and assessment of lower risk by subadults due to their lesser experience with predators. Greater escape ability by subadults seems unlikely. A substantial difference in fitness at the outset of the experiment is unlikely because predation intensity is low on Aire and because subadults had already survived the initial period of high vulnerability of hatchlings to cannibalism by adults. Even if flowers of *C. corymbosa* were to provide greater benefit to subadults than adult males, the longer FID of adult males than subadults on the ground away from flowers cannot be explained by a food-related difference in cost of fleeing.

We cannot discount differences in predation risk or experience. Because they are more readily detected due to larger size and are more likely to be attacked by a larger predator (Cooper & Stankowich 2010), risk may be greater for adult males, the largest size class, than for subadults. During approaches juvenile lizards may remain immobile, relying on crypsis, longer than adults (Martín & López 2003). Some lizards rapidly alter their escape behaviour after one encounter with a predator that is very threatening (Marcellini & Jenssen 1991). On the other hand, habituation to the presence of human beings that do not attack leads to shortened FID in many species (Stankowich & Blumstein 2005; Cooper 2010). Relative effects of habituation and predatory attacks on subadults and adult males are unknown. In the absence of knowledge regarding effects of experience in the two age-sex classes, we tentatively attribute the observed difference in FID to greater risk of adult males.

Distance Fled

The pattern of DF among foraging situations does not clearly correspond to predictions of optimal escape theory adapted to DF, but is explicable in a manner consistent with theory. The shorter DF by lizards foraging on inflorescences above ground on thistles is a consequence of fleeing down towards the ground

and often taking refuge among the spiny leaves at the base of the plant. In some, lizard species that flee towards ground from elevated perches, including the grass-bush anoles *Anolis krugi* and *Anolis pulchellus* and the phrynosomatid lizard *Sceloporus occidentalis* when on fence posts (Johnson 1970; Cooper 2006), FID is directly correlated with perch height. These species often are more conspicuous over a high perch than on ground, but the authors believed that the increase in distance from refuge as perch height increased is the major reason that FID increases as perch height increases (Cooper 2006). *Podarcis lilfordi* flees downwards from elevated perches on *C. corymbosa*, but does not flee to ground and then away from the predator as do the species discussed above. Instead, they usually flee down the plant, stopping on the ground at the base of the plant among its branches and spiny leaves. Thus, a lizard foraging on *C. corymbosa* is just above a secure refuge of thistle leaves where they are inaccessible avian predators. Because their perch heights were typically lower than the DF in the other groups, DF presumably was determined primarily by perch height or distance to refuge, which were tightly correlated. It is not possible to determine even the qualitative effects of cost of fleeing and risk in this circumstance.

Lizards in the ground-foraging groups fled away from the predator on the ground and usually did not enter refuges, accounting for longer distances fled than for lizards above ground on *C. corymbosa*. For groups on the ground, greater cost of fleeing from inflorescences predicts shorter DF, but DF did not differ. *Podarcis lilfordi* exhibited shorter DF in the presence than absence of maggots and pear (Cooper & Pérez-Mellado 2004; Cooper et al. 2006). However, the effect for maggots was detected only when at least eight maggots were present. Maggots and pears are rarely, if ever, available. The maggots might have escaped if lizards fled too far. Scarcity, large nutritional benefit and potential for escape or consumption by other lizards may affect opportunity cost for DF. *Carlina corymbosa* is immobile and abundant. Other inflorescences are available nearby, obviating the need to return to cut inflorescences. Distance fled may be affected only by large opportunity costs that occur for resource that are scarce and likely to be lost by fleeing too far. FID may be more sensitive to opportunity cost, requiring smaller opportunity cost to be shortened. No differences in DF occurred between age-sex groups. Because no effects of differences in cost of fleeing were observed and proximity to refuge varied between the foraging groups, the possibility remains

that age-sex group may differ in DF if costs of fleeing and of not fleeing are pronounced.

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