Morphological traits affect escape behaviour of the Balearic lizards (*Podarcis lilfordi*)

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Abstract. Escape theory predicts that a prey should start escaping (flight initiation distance = FID) from a predator when the costs of fleeing and the cost staying are equal or until future fitness is maximized. Consequently, prey escape performances and current reproductive asset can affect FID. We tested effects of body condition, morphology, and whether the tail was regenerated or original on FID in the Balearic lizard (*Podarcis lilfordi*) by ourselves simulating predators. Lizards with better body condition had longer FID and lizards with longer intact tails had shorter FID. Lizards with regenerated tail presented shorter FID than lizards with intact tails. These results suggest that impaired escape performance is counterbalanced by fitness costs of tail regeneration or by alteration of escape behaviour. The weak association between morphology, body condition and FID suggest that escape performances and asset protection have relatively small effect on *P. lilfordi* escape decisions.

Keywords: antipredatory behaviour, escape, flight initiation distance, predation risk, refuge, Squamata.

Escape theory predicts that a prey should start to escape from an approaching predator when the costs of fleeing (primarily opportunity costs) and not fleeing (due to predation risk) are equal (Ydenberg and Dill, 1986) or until expected fitness is maximized (Cooper and Frederick, 2007). Flight initiation distance (= FID, distance between predator and prey when escape starts) is predicted to be shorter when cost of escaping increases or risk of delaying escape decreases. These predictions have been verified in various taxa (reviewed by Stankowich and Blumstein, 2005) for many environmental factors affecting risk, including predator approach speed (Cooper, 1997a; Cooper et al., 2003), number and relative attack angles of predators (Cooper, Pérez-Mellado and Hawlena, 2007) proximity of refuge (Cooper, 1997b), and weather conditions (Rand, 1964; Hertz, Huey and Nevo, 1982), as well as factors affecting the costs of fleeing such as loss of feeding and social opportunities (Cooper, 1999, 2000b; Diaz-Uriarte, 1999; Martín, López and Cooper, 2003a; Cooper, Pérez-Mellado and Hawlena, 2006; Cooper and Wilson, 2007).

Risks and costs can vary as a consequence of variation in morphological traits and body condition of the prey (Stankowich and Blumstein, 2005). Prey that can escape faster or more efficiently have lower cost of not fleeing when at a given distance from a predator, but slower maximum speed might be associated with a change in escape tactics toward greater reliance of crypsis due to immobility to avoid being detected and attacked (Cooper et al., 1990). Faster speed alone would predict shorter predicted FID due to lower risk at a given distance, but a switch to greater crypsis would predict shorter FID. In lizards running speed increases as body size and hind limb length increase; tail length is also expected to affect speed (Warner and Shine, 2006; Cooper and Wilson, 2008). Consequently in the absence of change in tactics, escape theory predicts that individuals having greater body length (snout-vent length = SVL) and longer hind limbs will have shorter FID than conspecifics with shorter SVL and limbs.

Effects of body condition on FID are difficult to predict because body condition may affect both escape ability and initial fitness. Poor body condition associated with decreased speed

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or stamina may impair escape ability, requiring prey in poor condition to initiate escape attempts sooner to have a probability of escape equal or more nearly equal to that of individuals in better body condition. Observations of woodpigeons attacked by goshawks conforms with this expectation of greater FID for individuals in poorer condition (Kenward, 1978). On the other hand, prey that suffer from poor body condition may experience higher cost of fleeing than healthier individuals, and have low initial fitness; they are thus expected by the asset protection principle (Clark, 1994) to have shorter FID. Additionally, prey of poorer body condition may suffer higher missed opportunity costs relatively to individuals with better body condition. Because body condition and running speed are not strongly related in lacertid lizards (Vervust et al., 2008), asset protection and missed opportunities might be more important, leading to longer FID by individuals in better condition.

Autotomy, the voluntary severing of a body part, is an important defence mechanism in many lizards, which sever their tails to permit escape when overtaken by a predator (Arnold, 1984). Autotomy often has the immediate benefit of survival, but is costly. Energy stored in the tail is lost, and energy must be invested to regenerate the tail (Vitt, Congdon and Dickson, 1977). Moreover, autotomy may increase risk of predation due to decrease in escape speed and manoeuvrability (Ballinger, Nietfeldt and Krupa, 1979; Punzo, 1982; Brown, Taylor and Gist, 1995; Cooper, Wilson and Smith, 2009) and to temporary loss of the ability to autotomize the tail (Wilson, 1992). Tailless lizards can compensate for the increased risk by becoming more cryptic (Formanowicz, Brodie and Bradley, 1990) or by increasing the FID (Cooper and Wilson, 2008). Most lizards can regenerate the tail after autotomy, but regenerated tails differ in many ways from the originals (Hughes and New, 1959; Clark, 1971; Bellairs and Bryant, 1985; Duffy et al., 1992; Naya et al., 2007). As a result lizards may fail to regain the original tail capacities even after full regeneration (Arnold, 1988; Brown, Taylor and Gist, 1995), making them more vulnerable to predators. Effects of autotomy on FID are difficult to predict because autotomy affects risk of being overtaken, lethality of predators if overtaken, and the prey's fitness at the outset of the encounter, as well as defensive strategy. After autotomy, lizards might move less and/or stay closer to refuge to reduce probability of being detected and captured (Cooper, 2003). The duration of effects of autotomy is unknown for the vast majority of species, but in *Sceloporus virgatus*, FID increased immediately after autotomy (Cooper, 2007; Cooper and Wilson, 2008), but no effect of autotomy on FID was detected when lizards with intact tails were compared with those having tails that had regenerated in the field after breakage that occurred at unknown times (Smith, 1996; Rugiero, 1997).

We examined possible effects of variation in morphological characteristics (SVL, body mass, hind limb length, and tail length) on FID in the Balearic lizard (*Podarcis lilfordi*). We evaluated the effect of previous tail breakage (as indicated by regeneration) on FID without predicting any effect of regeneration.

We observed escape by *P. lilfordi* on the islet of Aire off the coast of Menorca in May 2005 on sunny days when lizards were fully active. The study site is characterised by numerous potential lizard refuges (low bushes and exposed rocks). High refuge abundance limited variation among individuals in distance to refuge and made our attempts to measure the distance between a lizard to what we considered the nearest refuge meaningless. Balearic lizards are easily observed due to dark coloration on paler backgrounds. Natural predators of *P. lilfordi* on Aire are rare, including Kestrels (*Falco tinnunculus*) that frequently visit the islet and Shrikes (*Lanius* spp.) that visit occasionally. Seagulls (*Larus michahellis*) are abundant, but very rarely eat lizards (Pérez-Mellado, unpublished data). No mammalian or ophidian predators occur on Aire (Pérez-Mellado, 1989). Human beings are larger than typical predators on Balearic lizards, but *P. lilfordi* responds to approaching human beings by attempting to escape and often by hiding under bushes and in rock crevices.

We simulated predatory attacks by approaching the lizards ourselves. This method is effective and is commonly used to escape by diverse prey (justification: Cooper (2008); review for diverse taxa: Stankowich and Blumstein (2005); lizards: (e.g., Cooper, 1997b, 2000a; Martín and López, 1999; Martín, López and Cooper, 2003b; Cooper and Wilson, 2007)). To standardize our approach speed, we practiced our walking speed until it was consistent (80.7 + 0.126 m/min) before conducting trials.

We located Balearic lizards by searching visually while walking slowly through the study site. We did not approach lizards that were engaged in social interaction. To begin a trial, we moved slowly to a position allowing direct approach and affording the lizard a clear view of the investigator. We approached and recorded FID to the nearest cm using 30 m measuring tape. We captured lizards by noosing and measured SVL, tail length (TL-distance from the cloaca to the tail tip), and hind limb length (HLL-distance from groin to tip of distal claw) using a transparent ruler (±1.0 mm). We recorded whether the tail was intact or regenerated, measured the lengths of the original and regenerated tail portions, and weighed the lizard using a spring scale (±0.1 g). We failed to noose only negligible number of the observed lizards. Thus, our data represent a random subset of *P. lilfordi* adults on the islet of Aire. We included only adult males in all analyses.

The assumption of homogeneity of variance was examined using Levene's test; that of normality was assessed using the Kolgomorov-Smirnov test with Lilliefors significance correction. Data that did not meet the assumptions were logarithmically transformed prior to analysis. We used multiple regressions with backward stepwise procedure and stepping method criteria of 0.05-entry and 0.1-removal to test what lizard characteristics (SVL, body condition, relative HLL, and relative TL) significantly affect $\log_{10}$ FID, in lizards with intact tails. We used un-standardized residuals resulted from linear regression of $\log_{10}$ SVL against $\log_{10}$ transformed body mass, HLL and TL as relative variables. We repeated the same procedure in lizards with regenerated tails.

We used one-way analysis of covariance (ANCOVA) to examine the effect of tail status (original or regenerated) on *P. lilfordi* $\log_{10}$ FID. We conducted a multiple regression with backward stepwise procedure on a dataset that included all lizards regardless of their tail status to identify any covariates for the analysis of tail status. We used lizard HLL as a covariate since this was the only variable that had a significant effect on $\log_{10}$ FID. Significance tests were two-tailed at $\alpha = 0.05$.

Prior to the regression analysis of effects of morphological variables in lizards having intact tails, we $\log_{10}$ transformed FID to achieve a normal distribution ($d = 0.138$, df $= 20$, $P = 0.20$). Using backward stepwise multiple regression, the best model (R^2 adj $= 0.298$, $F_{2,15} = 4.614$, $P = 0.027$) included the body condition ($t = 2.58$, $\beta = 0.539$, $P = 0.021$) and relative tail length (TL) ($t = -2.142$, $\beta = -0.447$, $P = 0.049$). FID increased as body condition increased and decreased as relative TL increased. The SVL and the relative HLL did not affect FID. In the analysis of data restricted to lizards having regenerated tails, log 10 transformed FID was not significantly related to any of the morphological variables in the best model, which retained only the relative HLL ($F_{1,16} = 3.666$, $P = 0.074$).

Variances of FID were homogeneous between lizards with original and regenerated tails (Levene's $F_{1,34} = 2.599$; $P = 0.116$). HLL had a significant effect on $\log_{10}$ FID (R^2 adj $= 0.115$, $F_{1,34} = 4.423$, $P = 0.043$) and the slopes were homogenous for lizards with regenerated and intact tails ($t = 0.540$, $P = 0.593$). Using one-way ANCOVA to examine the effect of tail regeneration on FID we found that the covariate relative HLL and the tail status (i.e., original or regenerated) significantly affected FID ($F_{1,33} = 6.415$, $P = 0.016$; $F_{1,33} = 7.736$, $P = 0.009$, respectively). Male *P. lilfordi* with regenerated tails had shorter FID than males with original tails at a given HLL (fig. 1), and males with longer hind legs had longer FID. The model including HLL and tail condition explained 21.4% of the variance in FID.

Our primary findings are that (1) FID increased with body condition and decreased with increase in tail length in lizards having intact tails; (2) none of the morphological variables affected FID in lizards having regenerated tails;

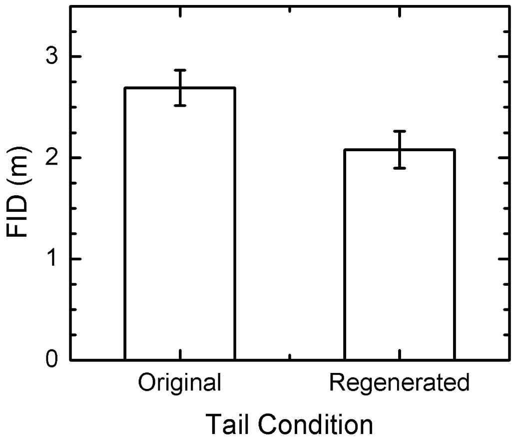

Figure 1. The effect of tail condition on FID (flight initiation distance) by *Podarcis lilfordi* for a given relative HLL. Error bars show 1.0 SE.

(3) FID increased as hind limb length increased for all lizards; (4) FID was shorter in lizards having regenerated than intact tails; and (5) none of the reported effects was strong.

Because body condition in lacertid lizards is weakly related or unrelated to running speed (Vervust et al., 2008), greater speed by lizards in better condition is unlikely to account for the relationship between body condition and FID. The increase in FID as body condition increases might indicate that individuals in better body condition have greater assets to protect (Clark, 1994) and relatively less profitable foraging opportunities to loose. This association can vary between species that live in different environments and vary in their social behaviour (Cabido et al., 2009).

The shorter FID of lizards having longer intact tails may be a consequence of greater running speed and/or manoeuvrability that reduce risk (Ballinger, Nietfeldt and Krupa, 1979; Punzo, 1982; Cooper, Pérez-Mellado and Vitt, 2004; Cooper, Wilson and Smith, 2009). The lack of relationship between FID and any of the morphological variables in lizards having regenerated tails hints that long term effects of autotomy may alter the importance of body condition and other morphological traits. This might occur if the cost of tail regeneration is dependent on the level of regeneration, offsetting the effect of body condition. Another hypothesis is that the effect of autotomy on FID is relatively long-lasting and overrides the lesser effects of body condition and tail length on FID. However, in *S. virgatus*, speed decreases and FID increases immediately after tail loss, but FID does not differ between lizards having intact tails or tails that have been regenerated (Smith, 1996; Cooper, 2007; Cooper and Wilson, 2008; Cooper, Wilson and Smith, 2009). A long-lasting deficit in running speed occurs after autotomy in the skink *Niveoscincus metallicus* (Chapple and Swain, 2002), and might account for relatively long lasting differences in effects of morphological variables on FID between individuals having intact and regenerated tails in *P. lilfordi*.

That FID increased with hind limb length is counterintuitive because individuals with longer legs should have greater speed and be at reduced risk at a given distance from a predator. They would, therefore, be predicted to have shorter, not longer FID. This effect of hind limb length on FID is small, but significant. That it was detected in the entire data set, but not in intact lizards alone or those with regenerated tails, suggests that the larger sample size was required to detect a small effect. Running speed might not be very important for escape by *P. lilfordi* on Aire. The lizards are usually close to vegetation or rocks that can be used as cover. Perhaps more importantly, during 5 million years before human inhabited this archipelago *P. lilfordi* experienced very little risk of predation (Pérez-Mellado, Corti and LoCascio, 1997). Even today predation is rare in the Aire population (Pérez-Mellado, 1989; Cooper and Pérez-Mellado, 2004). Consequently, it is possible that *P. lilfordi* lost part of its antipredator capabilities (Pérez-Mellado, Corti and LoCascio, 1997). If hind leg length affects running speed, but lacks a strong effect on escape ability, the observed relationship might be a consequence of relationships between hind limb length and other traits that affect escape decisions. For example, faster lizards having longer legs might venture further from refuges, requiring longer FID (Cooper, 1997b). Alternatively, longer hind leg length might be associated with greater dominance or other social advantage affecting fitness, leading to greater FID to protect the asset.

The shorter FID for lizards having regenerated than intact tails might seem paradoxical if one were to consider only the effect of tail loss on running speed and manoeuvrability (Cooper, Pérez-Mellado and Vitt, 2004) or the role of the tail as a distraction mechanism to predators (Naya et al., 2007). However, the complex effects of tail loss include facets predicted to shorten FID, as well as those predicted to increase it. Lower expected fitness at the outset of an encounter and changes in escape strategy are the main factors that may lead to shorter FID. For lizards that do not change escape strategy, shorter FID is predicted because lower fitness is expected from Clark's (1994) asset protection principle: prey with higher fitness should be more conservative, i.e., have longer FID. If escape ability is sufficiently impaired by tail loss, lizards may permit closer approach because they rely more on immobility to avoid being detected and/or they stay closer to refuges (Cooper, 1997b, 2003). Thus, a long lasting deficit in escape ability may account for the shorter FID by lizards having regenerated tails. Further research on *P. lilfordi* is needed to determine immediate effects of autotomy on FID, to discover the time course of recovery of running speed, and to ascertain whether escape strategy changes after autotomy.

Overall, morphological variation had relatively small effects on escape decisions by Balearic lizards. This could be due to the low impact those factors have on escape ability relative to the impact of environmental factors (e.g., escape path, refuge quality) or to offsetting effects on escape ability and initial fitness. Alternatively, lizards with impaired escape performance might compensate behaviourally by diverting their activity to safer microhabitats. Future studies should test those possibilities in greater detail.

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