

# Fifty years of chasing lizards: new insights advance optimal escape theory

Diogo S. M. Samia<sup>1\*</sup>, Daniel T. Blumstein<sup>2</sup>, Theodore Stankowich<sup>3</sup>  
and William E. Cooper Jr.<sup>4</sup>

<sup>1</sup>*Laboratory of Theoretical Ecology and Synthesis, Federal University of Goiás, CP. 131, 74001-970 Goiânia, Brazil*

<sup>2</sup>*Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, U.S.A.*

<sup>3</sup>*Department of Biological Sciences, California State University, 1250 Bellflower Blvd., Long Beach, CA 90840, U.S.A.*

<sup>4</sup>*Department of Biology, Indiana University Purdue University Fort Wayne, Fort Wayne, IN 46835, U.S.A.*

## ABSTRACT

Systematic reviews and meta-analyses often examine data from diverse taxa to identify general patterns of effect sizes. Meta-analyses that focus on identifying generalisations in a single taxon are also valuable because species in a taxon are more likely to share similar unique constraints. We conducted a comprehensive phylogenetic meta-analysis of flight initiation distance in lizards. Flight initiation distance (FID) is a common metric used to quantify risk-taking and has previously been shown to reflect adaptive decision-making. The past decade has seen an explosion of studies focused on quantifying FID in lizards, and, because lizards occur in a wide range of habitats, are ecologically diverse, and are typically smaller and differ physiologically from the better studied mammals and birds, they are worthy of detailed examination. We found that variables that reflect the costs or benefits of flight (being engaged in social interactions, having food available) as well as certain predator effects (predator size and approach speed) had large effects on FID in the directions predicted by optimal escape theory. Variables that were associated with morphology (with the exception of crypsis) and physiology had relatively small effects, whereas habitat selection factors typically had moderate to large effect sizes. Lizards, like other taxa, are very sensitive to the costs of flight.

*Key words:* antipredator behaviour, escape behaviour, escape distance, flight initiation distance, lizards, meta-analysis, optimal escape theory, phylogenetic meta-analysis.

## CONTENTS

I. Introduction .....	350
II. Methods .....	351
(1) Literature survey .....	351
(2) Estimating effect sizes .....	351
(3) Analyses .....	352
III. Results .....	352
(1) Comparison between categories of effects .....	352
(2) Predatory effects .....	353
(3) Habitat selection effects .....	353
(4) Cost of fleeing effects .....	354
(5) Physiological and morphological effects .....	355
(6) Experiential effects .....	355
(7) Correlation with other escape responses .....	355
IV. Discussion .....	355
(1) Predatory effects .....	356
(2) Habitat selection effects .....	357

\* Address for correspondence (Tel: +55 62 35211203; E-mail: diogosamia@gmail.com).

(3) Cost of fleeing effects .....	357
(4) Physiological and morphological effects .....	358
(5) Experiential effects .....	360
(6) Correlation with other escape responses .....	361
(7) Phylogenetic effects .....	361
(8) Future directions .....	361
V. Conclusions .....	362
VI. Acknowledgements .....	363
VII. References .....	363
VIII. Supporting Information .....	366

## I. INTRODUCTION

Predation risk exerts a strong selective force on prey to escape predators because failure to do so can result in death and termination of any future contribution to fitness. Escaping too early, however, can also result in a loss of fitness-enhancing benefits that may emerge from finding food or a mate. This creates a potential conflict: when is the best moment to flee from an approaching predator? Optimal escape theory (OET) states that prey must counterbalance risks and costs when fleeing from predators (Ydenberg & Dill, 1986; Cooper & Frederick, 2007). A large literature has evaluated the predictions of OET in a variety of taxa (Jordão & Oliveira, 2001; Martín *et al.*, 2004; Rodríguez-Prieto & Fernández-Juricic, 2005; Stankowich, 2008; Moller, Christiansen & Mousseau, 2011; Weston *et al.*, 2012). Most of these studies use flight initiation distance (FID), the distance between the predator and prey when prey begin to flee, as the metric to quantify risk-taking.

Lizards are extremely well represented in the OET literature. Rand (1964) was the first to demonstrate that lizards make trade-offs in escape decisions when he showed that lizards permitted closer approach by predators as body temperature increased, explaining this result by noting that warmer lizards were faster and more agile and, therefore, were able to accept more risk before fleeing. Other studies of lizard escape behaviour trickled in over the following decades (e.g. Heatwole, 1968; Bauwens & Thoen, 1981; Martín & López, 1995b; Cuadrado, Martín & López, 2001), but the past decade has been especially notable in the rapid accumulation of lizard OET studies. Indeed, of the 236 studies on OET that we found as part of the present study, 105 tested OET predictions in lizards; the remaining studies were distributed across mammals, birds, snakes, frogs, fishes, and arthropods. Notably, when examining the lizard studies, 69 were published in the last decade—an increase of 92% in relation to the previous 40 years combined.

A previous systematic review of OET (Stankowich & Blumstein, 2005) included studies published up to 2003. Given the proliferation of OET studies over the past decade, an updated comprehensive evaluation of OET predictions is warranted. Additionally, since the previous systematic review (Stankowich & Blumstein, 2005), new methods have been developed both to account for the phylogenetic relatedness among species and to test the effect of multiple

factors acting simultaneously on the prey (Lajeunesse, 2009; Nakagawa & Santos, 2012). Ignoring the evolutionary history of taxa can lead one to biased conclusions if species' behaviour is similar due to shared phylogeny (Blomberg, Garland & Ives, 2003). Additionally, most studies of OET use a reductionist approach, testing the effect of an isolated factor on FID when, in reality, prey consider multiple factors when making escape decisions. For example, an animal must account for both its distance to a refuge and the speed of a predator's attack in order to escape successfully. A broad understanding of how prey adjust escape behaviour under realistic scenarios for immediately dangerous interactions with predators is lacking.

To advance our current knowledge about OET, we conducted a comprehensive meta-analysis using lizards as model organisms. Here we avoid biased conclusions by explicitly accounting for potential phylogenetic effects. By using new meta-analytic algorithms, we were able to model decision-making by prey as a function of multiple factors. We focused on variables related to a species' morphology and natural history, differences in predator behaviour, and differences between environments. The results of our meta-analyses help to shed light on the mechanisms underlying optimal escape decisions and provide fruitful insights to the theory.

Several practical and biological reasons make lizards an ideal model organism for our study. First, as previously stated, a considerable proportion of the OET literature has focused on lizards. For this reason, lizard studies are those that present the most empirical evidence for many of the variables we examined.

Second, comparison of results from lizards, which are ectothermic poikilotherms, with those from homeothermic endotherms (i.e. mammals and birds) is important because temperature strongly affects performance and escape strategy of lizards and is predicted to affect escape decisions more strongly in lizards compared to homeotherms.

Third, most of the studied lizards are much smaller than those species of birds and mammals studied to date. Since we know that body size is a major determinant of FID (Scrimgeour, Cash & Culp, 1997; Kelt, Nabors & Forister, 2002; Blumstein, 2006; Fernández-Juricic *et al.*, 2006; Gotanda, Turgeon & Kramer, 2009), studies of smaller-bodied animals are essential to determine whether findings from larger-

bodied animals are generalisable to smaller prey – lizards in particular. This is especially important because small-bodied animals are more sensitive to reduced foraging success than are larger animals (Møller, 2009). It is, therefore, essential to study trade-offs between physiological requirements and predation risk.

Fourth, because many lizards rely somewhat on crypsis as an antipredatory defence (Heatwole, 1968; Stuart-Fox, Moussalli & Whiting, 2008), it is important to know to what extent animals relying on crypsis permit closer approaches by their predators.

Fifth, because parental care of hatchlings or neonates is virtually absent in most lizard species (Clutton-Brock, 1991), it is possible to determine whether perception of risk changes during ontogeny when the potentially confounding effects of parental protection are excluded.

Sixth, lizards have an unusual antipredator ability: they are able to autotomise their tails when threatened or attacked by a predator. Interestingly, tail autotomy may have opposing influences on escape decisions (Cooper & Frederick, 2010). On one hand, it could increase predation risk since autotomy cannot be used to distract a predator until the tail has been regenerated and because tail-less individuals may have reduced agility and sprint speed (Wilson, 1992; Chapple & Swain, 2002). On the other hand, autotomy could increase the cost of fleeing since the loss of energy stored in the tail and diversion of energy to regenerate the tail reduce fitness (Dial & Fitzpatrick, 1981; Maginnis, 2006), as does loss of social status following autotomy. The balance of such effects on predation risk, fitness, and costs associated with fleeing determines the effect of autotomy on FID predicted by OET (Cooper & Frederick, 2010). Following autotomy lizards may alter their habitat use, stay closer to a refuge to compensate for reduced speed and/or rely more on crypsis, all of which are expected to reduce FID. By examining data from a variety of lizards, we can ask whether autotomised individuals take more risks to compensate for the energetic costs of tail loss and reduced fitness, or, conversely, whether they take less risk because they are more vulnerable to predation.

Seventh, while most mammalian and avian OET studies have focused on prey species without reference to their foraging modes, carnivorous lizards have two distinctive foraging modes and these differences affect many aspects of morphology and behaviour (Huey & Pianka, 1981; Vitt *et al.*, 2003). Species that are active foragers move through the habitat searching for prey and spend a relatively high percentage of the time moving. By contrast, sit-and-wait (ambush) foragers spend much of the time motionless while waiting for prey to approach them. Ambushers have lower energetic costs of foraging than active foragers (Anderson & Karasov, 1981) and incur an increased risk of being detected by a predator during their occasional movements. By contrast, because of their movement, active foragers are readily detectable to visually oriented predators much of the time (Cooper, 2005b, 2008a). Furthermore, abandoning profitable ambush posts to flee might be costly for ambushers more often than

abandoning sites where prey have been located is for active foragers. Given the differences between foraging modes that might affect predation risk and cost of fleeing, we examined the lizard data to detect a possible difference in effect size between foraging modes.

## II. METHODS

### (1) Literature survey

We first compiled all studies cited in Stankowich & Blumstein's (2005) review. Next, we used the *Web of Science*, *Scopus*, and *Google Scholar* databases to search for papers published before 31 December 2013 that cited Ydenberg & Dill (1986) and Stankowich & Blumstein (2005). We searched in the same databases using the terms 'flight initiation distance', 'FID', 'flight distance', 'escape distance', 'approach distance', 'flushing distance', and 'response distance'. We checked all references of the retained papers to identify studies not located by our survey. Among the papers evaluated, we included in our data set studies testing the effect of some factor on the FID of lizards. The full data set consists of 274 effect-size estimates from 96 studies across 76 species (see online supporting information Fig. S1). The complete data set is provided in Table S1.

### (2) Estimating effect sizes

We used the Pearson's product–moment correlation coefficient,  $r$ , as our measure of effect size. For the factors related to the risk,  $r$  is the magnitude of the difference between FID under a low-risk condition and FID under a high-risk condition (e.g. prey close to refuge *versus* prey far from refuge). For the factors related to the cost of fleeing,  $r$  is the magnitude of the difference between FID under a low-cost condition and FID under a high-cost condition (e.g. absence of food *versus* presence of food). Therefore, positive  $r$ -values mean that lizards had larger FIDs under situations assumed to impose a higher risk (for risk factors) or a lower cost (for cost factors), whereas negative  $r$ -values mean that lizards had shorter FIDs in these situations. In the ecological literature  $r$ -values of 0.1, 0.3, and 0.5 are considered small, medium, and large effect sizes, respectively (Cohen, 1992; Jennions & Møller, 2002). When possible, we tabulated  $r$  directly from published correlation coefficients. Otherwise, we used formulae in Rosenthal (1991) to calculate  $r$  in the following order of preference from published statistics: mean and variance of treatments, statistical results ( $t$ ,  $F$ ,  $\chi^2$ ,  $z$ ), and exact  $P$ -values reported with sample sizes. When the experimental design of a study included more than two levels (e.g. predator approaching with slow speed, intermediate speed, and fast speed), we used the extreme levels to make the effect size comparable with those from most of the studies. The only exception was in the directness of approach effects where we contrasted the direct approach with the indirect approach using the shortest bypass distance. We did this because very few (in

some cases, none) of the lizards fled at the largest bypass distances. When necessary, we collected data from the graphs of the paper (mean and S.E.M.) using WebPlotDigitizer v. 2.6 (<http://arohatgi.info/WebPlotDigitizer/>). We contacted several authors directly for missing information (see Section VI). For analysis,  $r$ -values were transformed to Fisher's  $z$ .

### (3) Analyses

Our meta-analyses were calculated as both random-effects models and mixed-effects models. The latter permitted us to test the effect of both categorical variables (ANOVA-like test) and continuous variables (meta-regression) on the effect sizes (Borenstein *et al.*, 2009). Because more closely related taxa are expected to respond more similarly than phylogenetically distant taxa, we conducted both standard and phylogenetic meta-analyses on each evaluated model (Lajeunesse, 2009; Nakagawa & Santos, 2012). We reconstructed the phylogenetic relationships of the species using the most recent time-calibrated phylogeny of Squamata (Pyron & Burbrink, 2014). When a species in our data set was not included in this broad phylogeny, we used a closely related (congeneric) species as a substitute. The trees were pruned using the R package *picante* (Kembel *et al.*, 2010). The phylogenetic tree of the taxa included in the study is provided in Fig. S2.

The overall effects of the models (i.e. the mean of the effect sizes weighted by the inverse of their variance) were considered significant if their 95% confidence interval (CI) did not include zero (Borenstein *et al.*, 2009). We used  $I^2$  as a measure of heterogeneity for the standard meta-analyses (Higgins *et al.*, 2003) and a modified version of  $I^2$  for the phylogenetic meta-analyses (Nakagawa & Santos, 2012).  $I^2$  represents the proportion of observed variation in data that is not due to random error (25% low variation; 50% medium variation; 75% high variation) (Higgins *et al.*, 2003). We used the Egger regression test to estimate publication bias; intercepts significantly different from zero suggest potential publication bias (Egger *et al.*, 1997; Robert & Stanley, 2006). Additionally, we calculated the fail-safe number, the number of unpublished studies with no effect that would be needed to eliminate an observed effect (Rosenthal, 1979), to assess the robustness of the results. All analyses were conducted using the R package *metafor* v.1.9-2 (Viechtbauer, 2010).

A large literature documents how interspecific differences in morphology and natural history, predator's behaviour (represented here by methodological inconsistency), as well as environmental factors, can greatly influence antipredator behaviours (Martín & López, 1995b; Losos *et al.*, 2002; Blumstein, 2006; Vervust, Grbac & Damme, 2007; Cooper & Sherbrooke, 2013). We expected that such variables will influence the trade-off between costs and benefits facing individuals when determining the moment to flee (Ydenberg & Dill, 1986). Thus, we tested the combined effect of several covariates on those factors manipulated by experimenters in source studies. Covariates were: foraging mode (ambush foraging, active foraging or herbivorous), species size (mean snout-vent length), predator's (experimenter's) approach

speed (in m/min), altitude [m above sea level (a.s.l.)], and 'other covariates'. The latter were tested exclusively for some factors: difference between slow and fast approach speed (in m/min) for 'approach speed', bypass distance (in m) of the indirect approach for 'directness of approach', lizard ecomorph (bush-grass or semi-arboreal) for 'height of perch', and source of the crypsis (body camouflage or partially concealed by vegetation) for 'crypsis'. Details about the covariates and their predictions are provided in Appendix S1. Continuous covariates were  $\log_{10}$ -transformed to improve normality.

We ran the analyses in two parts. First, to identify situations in which lizards were more responsive, we combined their effect sizes and compared five groups: predatory effects, habitat selection effects, cost of fleeing effects, physiological and morphological effects, and experiential effects. Second, we ran meta-analyses on the 20 factors for which we had a minimal number of three estimated effect sizes (Table 1). Of these factors, we tested the effect of the covariates in a subset of seven factors (all with  $N \geq 13$ ; Table 2). In addition to the problem of lack of degrees of freedom, factors with  $N < 13$  showed high multicollinearity among covariates ( $r > 0.6$ ), which made isolation of key variables difficult. We used Akaike's information criteria corrected for small sample size (AICc) to evaluate the set of candidate models (standard *versus* phylogenetic meta-analyses; models including covariates). Models with covariates were considered plausible only if they were better ( $\Delta\text{AICc} > 2$ ) than the null model (i.e. the intercept-only model; AICc values are presented in Table 1). Models with  $\Delta\text{AICc} < 2$  were considered equally parsimonious (Burnham & Anderson, 2002). For simplicity, when standard and phylogenetic models had  $\Delta\text{AICc} < 2$ , we discussed results based on standard models (although our conclusions were the same regardless of the model chosen; see online Tables S2 and S3).

## III. RESULTS

### (1) Comparison between categories of effects

Effect type significantly influenced lizard responsiveness ( $Q_b = 82.88$ , d.f. = 4,  $P < 0.001$ ,  $r^2 = 0.32$ ). Factors related to costs of fleeing had the strongest effects on lizard responses ( $z$ -tests, all  $P < 0.046$ ; Table 1). Conversely, lizards were barely affected by their morphology and physiology (Table 1), which had the lowest overall effect among the five categories investigated ( $z$ -tests,  $P < 0.001$ ). There were medium-to-large effects of predators, habitat selection factors, and prey experience (Table 1), but they were not statistically different from each other ( $z$ -tests,  $P > 0.181$ ). Nevertheless, the five categories were quite heterogeneous ( $I^2 > 81.5\%$ ), and this justified more detailed analyses of their associated factors.

Only four factors were better supported by the phylogenetic meta-analyses: distance to refuge, substrate temperature, density of predators, and sequential attacks

Table 1. Summary results of the standard meta-analyses. Overall effect ( $r$ ), 95% confidence interval (CI), number of replicates ( $N$ ), total number of individuals tested ( $N_{within}$ ), degree of heterogeneity in effect size ( $I^2$ ), the number of studies reporting no effect required to nullify the observed effect (fail-safe  $N$ ), Egger's regression test to assess possible bias in publication ( $P$ -values), and the corrected Akaike's information criterion of the model (AICc)

Factor	$r$	CI	$N$	$N_{within}$	$I^2$ (%)	Fail-safe $N$	Egger's $P$	AICc
<i>Predatory effects</i>								
Combined	0.41	0.32–0.49	59	2831	85.00	8368	0.153	90.4
Approach speed	0.59	0.49–0.68	24	806	73.60	2737	0.797	25.0
Directness of approach	0.35	0.24–0.46	22	1164	72.29	829	0.080	16.9
<i>Excluding artifact</i>	0.37	0.25–0.47	21	1152	72.60	858	0.031	14.5
Predator's gaze	0.23	0.10–0.36	4	372	42.20	23	0.277	11.1
Predator's size	0.56	0.19–0.79	3	155	73.33	36	0.366	17.5
<i>Habitat selection effects</i>								
Combined	0.46	0.37–0.53	52	3401	86.79	10313	>0.001	70.7
Distance to refuge	0.40	0.31–0.48	28	1835	77.58	2486	0.004	23.7
Height of perch	0.50	0.29–0.66	16	928	91.41	855	0.059	32.4
Amount of cover	0.57	0.27–0.77	6	528	93.87	289	0.145	17.9
<i>Cost of fleeing effects</i>								
Combined	0.65	0.53–0.74	14	785	81.5	2103	0.287	11.7
Food availability	0.69	0.53–0.80	5	264	72.35	301	0.698	10.5
Social interactions	0.63	0.45–0.76	9	521	85.51	805	0.366	11.6
<i>Physiological and morphological effects</i>								
Combined	0.09	0.02–0.17	107	9304	87.79	885	0.009	132.1
Crypsis	0.60	0.46–0.71	13	850	84.35	1247	0.013	14.0
Ontogeny	–0.33	–0.52 to –0.11	11	911	90.86	187	0.003	19.6
Prey's body size	0.22	0.13–0.30	11	548	4.87	82	0.837	–3.7
Autotomy	–0.06	–0.27 to 0.16	10	734	87.36	0	0.868	11.9
Female reproductive state	–0.28	–0.35 to –0.19	9	976	22.29	141	0.066	–3.5
Body temperature	0.42	0.23–0.58	12	397	75.01	274	0.620	17.0
Substrate temperature	–0.07	–0.26 to 0.11	12	581	79.05	0	0.657	11.4
Air temperature	0.01	–0.07 to 0.09	26	1531	49.23	0	0.043	–2.1
<i>Experiential effects</i>								
Combined	0.50	0.39–0.59	28	1864	85.04	4521	0.684	22.2
Density of predators	0.53	0.36–0.67	11	1229	91.43	1371	0.996	13.0
Sequential attacks	0.50	0.33–0.64	14	486	77.81	633	0.655	15.8
<i>Correlation with other escape response</i>								
Distance fled	0.05	–0.07 to 0.17	9	801	61.48	0	0.709	2.0

(see online Table S2). However, all models that included covariates were better supported by the standard meta-analysis (Tables 2 and S3). Detailed results are described below.

## (2) Predatory effects

The overall strength of predatory effects on escape behaviour ranged from small to large (Table 1). The predator's approach speed was the factor with the largest overall effect in this category (Table 1); lizards approached faster fled at greater distances. The best model to explain the variation in predator's approach speed included species body size as a covariate (Table 2); lizards were more responsive to the speed of approach as body size increased ( $b = 1.35$ ,  $P = 0.015$ ,  $r^2 = 0.16$ ; Fig. 1). The effect of the directness of approach was moderate (Table 1); lizards approached directly fled at greater distances than lizards approached tangentially. A sensitivity analysis that excluded one artifactual effect size (*Rhoptopus boultoni*) in which the

authors (Cooper & Whiting, 2007b) set FID equal to the predator's bypass distance for individuals that did not flee did not alter our conclusions (Table 1). Therefore, the analyses with covariates were conducted with the full data set ( $N = 22$ ). The bypass distance used in the indirect approach influenced lizard responsiveness (Table 2): FID from direct and indirect approaches converged as bypass distance increased ( $b = -0.67$ ,  $P = 0.002$ ,  $r^2 = 0.20$ ; Fig. 2). The effect of the predator's gaze was small, but significant: lizards fled at a greater distance when predators looked directly at them (Table 1). Predator size, on the other hand, had a large overall effect; larger predators elicited larger FIDs in lizards (Table 1). Despite the relatively small sample size for these two last factors, the fail-safe number indicates that results were robust (Table 1).

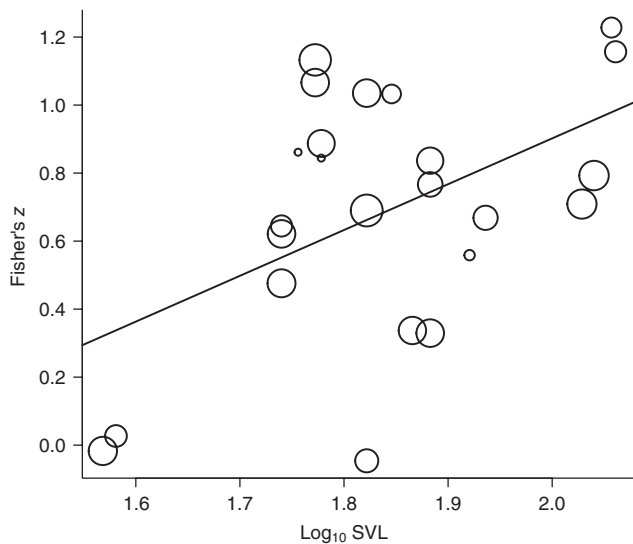
## (3) Habitat selection effects

The three risk factors related to habitat selection had large and positive overall effects (Tables 1 and S2). In

Table 2. Corrected Akaike's information criteria of the mixed-effect standard meta-analyses including the indicated covariates. Column 'other covariates' refers to covariates tested with a given factor (from top to bottom): difference between slow and fast approach speed, bypass distance of the indirect approach, lizard's ecomorph, and source of the crypsis (see text and online Appendix S1 for details)

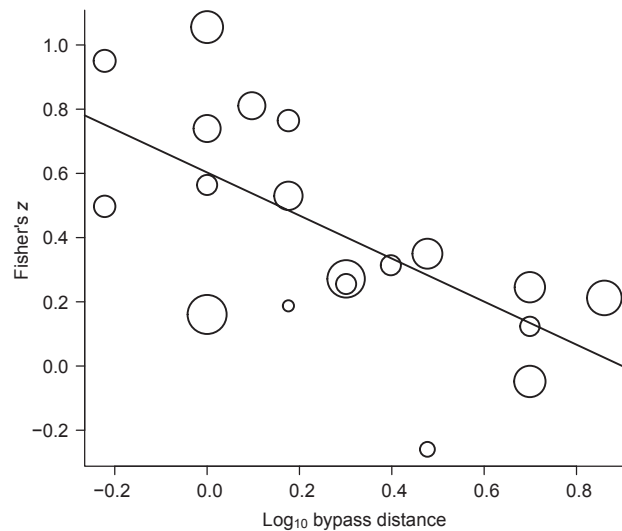
Factor	Foraging mode	Species size	Predator's speed	Altitude	Other covariates
Approach speed	26.1	21.8*	27.4	27.6	27.6
Directness of approach	21.6	17.2	14.4	18.1	11.1*
Distance to refuge	26.3	25.7	27.4	17.7*	—
Height of perch	35	31.7	33.2	34.1	21.7*
Crypsis	17.5	14.5	2.0	14.3	-1.6*
Air temperature	0.5	-0.1	6.1	-1.3	—
Sequential attacks	13.8	18.1	19.3	4.7*	—

\*Best models.



**Fig. 1.** Relationship between species body size (snout-vent length, SVL) and effect size (Fisher's  $z$ ). Effect size represents the difference in flight initiation distance between a slow and a fast approach of the predator. Responsiveness of the lizards to the predator's approach speed increases with body size. The size of points is proportional to the inverse of the variance of the effect size.

all studies analysed, lizards far from a refuge fled at greater distances than lizards close to a refuge (phylogenetic model:  $r = 0.52$ , CI: 0.17–0.75; see online Table S2). However, this effect became progressively weaker as altitude increased ( $b = -0.002$ ,  $P = 0.003$ ,  $r^2 = 0.11$ ; Table 2 and Fig. 3). Perch height on rocks, vegetation or other substrates strongly affected FID: overall, lizards on low perches fled at greater distances than those that were perched higher up (Table 1). However, analysis of subgroups revealed that the direction of the effect depended on the species' ecomorph ( $Q_b = 12.06$ , d.f. = 1,  $P < 0.001$ ,  $r^2 = 0.30$ ; Table 2): bush-grass lizards tended to flush at greater distances when on higher perches ( $r = -0.37$ , CI: -0.76 to 0.22), while semi-arboreal species systematically flushed at greater distances when they were perched closer to the ground ( $r = 0.66$ , CI: 0.49–0.78). The overall effect of the amount of cover shows that lizards

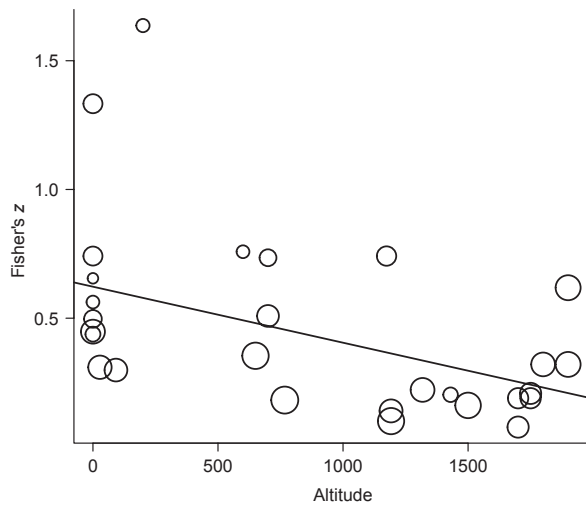


**Fig. 2.** Relationship between bypass distance used in the predator's indirect approach and effect size (Fisher's  $z$ ). Effect size represents the difference in flight initiation distance between a direct and an indirect approach of the predator. Responsiveness of the lizards to the directness of the approach decreases as bypass distance increases. The size of points is proportional to the inverse of the variance of the effect size.

were substantially more responsive in open areas (Table 1). Although the sample size is modest, this result is highly robust as indicated by the fail-safe number (Table 1).

#### (4) Cost of fleeing effects

Effect sizes from factors related to costs of flight were large and positive, indicating that lizards delayed escape when engaging in potentially fitness-enhancing activities (Table 1). Indeed, their overall effects were the greatest among the 20 factors analysed in the present study (Table 1). Lizards fled at greater distances when patches contained no food, but permitted predators to get substantially closer when food was present (Table 1). Lizards also permitted much closer approach by the predator when interacting with other lizards than when alone (Table 1).



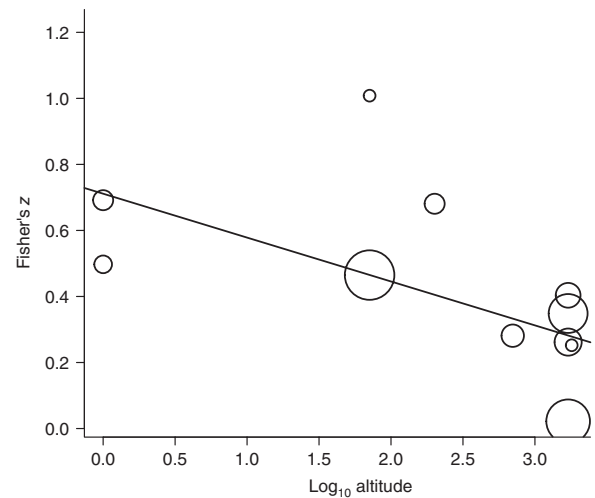
**Fig. 3.** Relationship between altitude and effect size (Fisher's  $z$ ). Effect size represents the difference in flight initiation distance between lizards approached close to a refuge and far from a refuge. Responsiveness of lizards due to distance to refuge decreases as altitude increases. The size of points is proportional to the inverse of the variance of the effect size.

#### (5) Physiological and morphological effects

The effects of physiology and morphology on lizard responsiveness were highly varied (Table 1). Cryptic lizards systematically permitted closer approach by predators than did conspicuous lizards (Tables 1 and S1). Lizards partially concealed by the vegetation permitted even closer approach than individuals that relied on body camouflage (camouflage:  $r = 0.37$ , CI: 0.27–0.46; partially concealed by vegetation:  $r = 0.76$ , CI: 0.69–0.82;  $Q_b = 44.04$ , d.f. = 1,  $P < 0.001$ ,  $r^2 = 0.95$ ; Table 2). Ontogeny had a moderate and negative effect size (Table 1), suggesting that juvenile lizards tended to be more prone to taking risks than adult lizards. Presence or absence of tail autotomy did not appear to affect FID (Table 1). Responsiveness increased with an individual's body size, and gravid females tolerated closer approaches than non-gravid females although both effect sizes were weak (Table 1). Effects of an individual's body size were highly homogeneous ( $I^2 = 4.87\%$ ). Interestingly, although air temperature (Table 1) and substrate temperature (phylogenetic model:  $r = -0.03$ , CI:  $-0.5$  to  $0.44$ ; see online Table S2) are often used as proxies for body temperature in lizard studies, their overall effects differed substantially ( $Q_b = 23.41$ , d.f. = 2,  $P < 0.001$ ; Table 1). Body temperature, but not substrate or air temperature, affected lizard behaviour in a reliable way (Table 1). All but one species tested fled at greater distances when their bodies were colder than when warmer (Tables 1 and S1).

#### (6) Experiential effects

Both predator density, and whether the individual was sequentially attacked, had large and significant effect sizes. All species tested had greater FIDs in locations with a



**Fig. 4.** Relationship between altitude and effect size (Fisher's  $z$ ). Effect size represents the difference in flight initiation distance from the first to the second attack of the predator. Responsiveness to the second attack decreases as altitude increases. The size of points is proportional to the inverse of the variance of the effect size.

higher predator density (phylogenetic model:  $r = 0.56$ , CI: 0.19–0.79; see online Table S2). Likewise, all species had greater FIDs when approached a second time compared to the first approach (phylogenetic model:  $r = 0.54$ , CI: 0.06–0.82; see online Table S2). However, altitude was an important predictor of lizard response to sequential attacks (Table 2): the difference between FIDs from the first to the second approach decreased as altitude increased ( $b = -0.13$ ,  $P = 0.024$ ,  $r^2 = 1$ ; Fig. 4). Because more than 20% of the variance in sequential attack was due to random error ( $I^2 = 77.81$ ), the model fit for altitude diverged notably from the observed data points.

#### (7) Correlation with other escape responses

In some species, distance fled is related to FID (e.g. Cooper, 2000a). However, the meta-analysis showed that overall, the relationship between FID and distance fled after an attack was not significant (Table 1).

## IV. DISCUSSION

OET predicts that prey must counterbalance risks and costs to decide the best moment to escape from predators. Fifty years of research since the first study testing economic aspects of FID in lizards have permitted a deep examination of factors (and combinations of factors) affecting prey escape decisions. Through a comprehensive meta-analysis, we found that variables that reflected costs of escape (lost opportunities for social interactions and hunting/eating) had the largest effects on prey response. Lizard escape decisions were also strongly affected by previous experience with the predator as

well as certain predatory effects (predator size and approach speed) and habitat selection effects (perch height and amount of cover). By contrast, effect sizes of variables associated with morphology and physiology had, in general, relatively small effects. Contrary to a previous meta-analysis (Stankowich & Blumstein, 2005), however, we found that body temperature is an important factor affecting lizard flight decisions. We also found novel interactions between the factors manipulated in the source studies and other covariates linked to prey's morphology (body size, ecomorph, and source of crypsis), predator behaviour (bypass distance of indirect approach), and the environment (altitude).

Publication bias can lead a meta-analysis to misleading conclusions (Egger *et al.*, 1997; Koricheva, Gurevitch & Mengersen, 2013). The Egger's regression test results of four of the 20 factors investigated were significant, suggesting potential publication biases for these factors (Table 1). However, FID was of secondary interest in many of these studies because some tested OET predictions using other antipredatory metrics (e.g. McConnachie & Whiting, 2003; Whiting *et al.*, 2003; Punzo, 2007), or tested other hypothesis not directly related to OET (e.g. Stone, Snell & Snell, 1994; Vervust *et al.*, 2007; Brecko *et al.*, 2008). Thus, we do not believe that our FID results, *per se*, were biased. Regardless, some caution is warranted when interpreting certain results.

Below we discuss the results of our meta-analyses by effect type, focussing specifically on: (i) how our knowledge about OET has changed after 10 years of new evidence since the last systematic review (Stankowich & Blumstein, 2005); (ii) new insights gained from our meta-analyses; and (iii) new challenges to OET as well as suggestions about ways to test them in the future. We briefly consider the absence or relatively small effect of phylogenetic influences on lizard escape decisions.

### (1) Predatory effects

Our results reaffirm that both behavioural and morphological traits are important cues that prey use to estimate the risk posed by an approaching predator. Namely, lizards perceived themselves under a greater risk of predation when predators: (i) approached rapidly; (ii) attacked in a straight line that led directly to the prey; (iii) looked directly at them; and (iv) were bigger. Because most lizards are small animals preyed upon by a number of non-specialist predators, lizards must have been selected to interpret these widespread signals as generic indications of imminent attack and risk if attacked. By responding to these factors, lizards improve their evaluation of the predation threat, making it possible for them to make appropriate escape decisions to diverse potential predators with varied motivations to attack.

Among the predatory factors tested, approach speed had the greatest influence on lizard escape decision. The effect of approach speed was positive, as seen in other taxa (Dill, 1974; Lord *et al.*, 2001; Hemmi, 2005; Cooper, 2006c). Prey may interpret rapid approach as indicating that the predator is already attacking, or that risk is greater because a prey has less time to reach a refuge once it begins to flee. Additionally,

as speed increases, prey have less time to evaluate the situation, which might affect the accuracy of economic escape decisions. Natural selection may have favoured prey that over-estimate risk (Bouskila & Blumstein, 1992), such that by fleeing sooner than might be 'optimally' predicted would be the least costly decision (Johnson *et al.*, 2013). Moreover, the best model that explained the effect size variation for approach speed revealed that effect sizes increased as lizard body size increased: smaller prey were more weakly affected by increasing approach speeds. This relationship is consistent with current evidence that has reported differential risk-taking among small and large species (Scrimgeour *et al.*, 1997; Kelt *et al.*, 2002; Blumstein, 2006; Fernández-Juricic *et al.*, 2006; Gotanda *et al.*, 2009). We will discuss probable mechanisms behind this relationship in Section IV.4.

The exploration of the directness of approach raised a relevant methodological issue. For *R. boultoni*, Cooper & Whiting (2007) set FID equal to the minimum bypass distance for individuals that did not flee at all when approached indirectly. While lizards approached directly ran on average at 2.6 m, a lizard that remained immobile when approached tangentially at 3 m was assigned a FID equal to 3 m. Thus, the experimental design excluded the possibility of detecting any effect in the predicted direction because the minimum bypass distance was longer than the FID for direct approach. Because field time was limited, tests using shorter minimum bypass distances could not be conducted. Therefore, results from this species are not comparable to those of the remaining species because use of the long bypass distance inadvertently created an artifact in which an indirect approach seemed to be assessed by prey as indicating greater risk than a direct approach. Our sensitivity analysis showed that inclusion of this artifactual result did not alter substantially the magnitude of the effect. However, conclusions could be reversed if more species with artifactual effect sizes were inadvertently included in the data set. This artifactual problem can be avoided in future by experimenters carefully selecting the appropriate minimum bypass distance, which often requires collection of pilot data to determine FID for direct approach (W. E. Cooper, personal observations).

Unexpectedly, differences in FID under direct and indirect approach decreased as bypass distance increased. Cryptic prey, such as ambush foragers, may use qualitatively different escape strategies influenced by the likelihood that (i) the predator has seen them, and (ii) the predator is attacking directly. If the prey determines that the predator is on a trajectory to intercept it directly or bypass it by a wide margin, a long FID may be the best strategy to avoid being detected. If, on the other hand, the predator is on a trajectory to bypass the prey at a closer distance where there is a higher probability of being detected if the prey moves, prey may adopt a cryptic strategy and wait to flee until the conditions for economically predicted FID are met. Alternatively, bypass distance selected by experimenters might increase as the wariness of the species increases. For wary species, assessed risk at short bypass distances may be so high that FID remains close to that for direct approach and very large samples might



be required to detect any effect between direct and indirect approaches. At longer bypass distances, effect sizes may still be small because the wariest individuals flee at long FIDs even when approached indirectly. At even longer bypass distances few, if any, individuals flee because risk is very low. Studies including finer differences over a wider range and larger sample sizes are needed to test the hypothesised changes with bypass distance.

Our findings verify that FID was longer when a predator's gaze was direct. A prey that can see a predator's eyes may assess itself as being in the predator's field of view and at greater risk of being or having been detected than when the predator's eyes cannot be seen. Predators that look directly at prey by turning towards them are likely to be using binocular vision to maximise acuity and depth perception. They are likely to have detected the prey and to be focusing on it (Burger, Gochfeld & Murray, 1992). However, the effect size of predator's gaze was small, presumably because risk remained high while the predator continued to approach directly and because a predator's averted gaze is likely to revert to a direct one as it approaches. Studies are needed to determine whether a predator's head orientation and direction of eye gaze independently affect FID, as they influence the decision that starlings (*Sturnus vulgaris*) make about when to resume feeding after a disturbance (Carter *et al.*, 2008).

The relationships between a predator's body size and risk to a particular prey type are complex (Dickman, 1988; Costa, 2009). For a prey of fixed size, very small potential predators may pose no threat, but above some threshold size, predation risk may increase as predator body size increases. However, as the predator's body size continues to increase, the prey's attractiveness to the predator (in terms of energetic reward) may decline, even to the point that the predator will not attack a small-bodied prey.

Studies reported here cover the range in size of approaching stimuli, from small 'prey'-sized stimuli that are attacked by the lizard, to large 'predator'-sized stimuli from which the lizard flees. The large effect of approacher body size is, therefore, a direct result of the wide range of predator size used in the studies. The strongest effects were detected in a study using model insects as predators, which allowed greater size variation relative to lizard body size (Cooper & Stankowich, 2010) than is possible in studies using human beings as predators. No studies of lizards have directly examined the effects of increasing predator size over the range in which predators' become less likely to attack as they grow larger relative to the prey. However, the shorter FIDs of hatchling than adult lizards (see Section IV.4) may in part reflect a lower likelihood of being attacked by very large predators.

## (2) Habitat selection effects

The three factors related to habitat selection (i.e. distance to refuge, perch height, and habitat openness) had large effects on lizard responsiveness, indicating that habitat structure has a large effect on lizard risk assessment. The influence of

distance to refuge on FID was demonstrated by Stankowich & Blumstein (2005). With a data set containing eight lizard species, they found an intermediate overall effect of distance to refuge on FID. Here, with data from 28 species, we found that distance to refuge has a large overall effect on FID. A novel effect revealed by our study is that the magnitude of the distance to refuge effect is significantly affected by altitude: the effect decreases as altitude increases. This is consistent with evidence suggesting lower predation risk at high altitudes (Shaffer, 1978; Diego-Rasilla, 2003b). The reduced perception of risk at higher altitudes might select for bolder individuals who assess less risk at a given distance from a refuge than lizards at lower altitudes.

The effect of perch height had not previously been formally studied with a meta-analysis. One could expect that lizards perched higher always permitted a closer approach because they were less likely to be caught by non-aerial or non-arboreal predators such as human beings (Frid & Dill, 2002). We found this to be true for most species in our data set: semi-arboreal species flushed at greater distances when they were perched closer to the ground, whereas grass-bush lizards flushed at greater distances when on higher perches. Such a divergent escape strategy may be related to distance from the nearest refuge: grass-bush species typically occupy low perches a short distance above their ground-level refuges, whereas semi-arboreal species may have to flee from ground level to heights above the reach of terrestrial predators (Cooper, 2006b). Because humans are the simulated predators in experimental studies, semi-arboreal species must climb to heights greater than the maximum perch heights of grass-bush species to reach safety (Cooper, 2006b).

Habitat openness was also not studied in the previous meta-analysis. Here we show that lizards in open areas tolerate less risk, presumably because individuals in open areas are more conspicuous to predators. More conspicuous species are intermediate to large in size and live in relatively open areas. In mammals, these species are at greater risk of predation and may be more likely to evolve specialised antipredator morphologies or behavioural strategies (Stankowich & Caro, 2009; T. Stankowich, unpublished data).

## (3) Cost of fleeing effects

A major new insight from our analysis is that the cost of fleeing has a profound effect on lizard flight decisions. Given that OET states that prey must counterbalance cost of fleeing with cost of not fleeing (risk) to decide the best moment to flee, the consistent effects of cost of fleeing in the primary studies support the trade-off predicted by OET (Ydenberg & Dill, 1986). Although theoretically expected, this result is critically important for OET since empirical evidence showing that the decision to flee is influenced by costs is comparatively rare.

Lizards consistently permit closer approaches by predators when in presence of food or conspecifics, which is consistent with the opportunity cost hypothesis. Alternatively, the effect

could also be explained by the limited attention of prey (Dukas, 2004). The ‘distracted prey hypothesis’ suggests that prey can be distracted by factors that divert the prey’s attention away from an approaching predator, such as noises or presence of conspecifics (Chan *et al.*, 2010). The experimental design of the primary studies, however, provides clues about the real causal effect. For example, researchers studying food availability compared the FID of lizards presented with a food item (e.g. a piece of fruit) with the FID of lizards presented with an unpalatable object with similar dimensions as a control (e.g. a rock: Cooper *et al.*, 2003). If the distraction hypothesis was adequate to explain prey behaviour, one would expect similar FIDs in both situations, since both objects would theoretically capture the prey’s attention (initially, at least). However, results showed that lizards systematically had much smaller FIDs when a food item was presented than when a control stimulus was presented, supporting the opportunity cost hypothesis. Nevertheless, we note that these competitive hypotheses are not mutually exclusive. Distraction can have an additive or multiplicative effect on prey escape decisions. Combined effects could be tested further through an experimental design with three levels: without any stimuli beyond the predator’s approach (control), presenting an unpalatable object (the distraction treatment), and presenting a food item (the cost treatment).

Unlike the distracted prey hypothesis, the ‘flush early and avoid the rush’ hypothesis suggests that reducing attentional costs is an integral part of optimal escape – thus individuals escape soon after detecting an approaching threat to reduce on-going monitoring costs (Blumstein, 2010; Cooper & Blumstein, 2013; Williams *et al.*, 2014). For lizards, but not birds and mammals, individuals only flushed early when approached rapidly, suggesting that the early response in lizards was triggered by higher assessed risk rather than monitoring costs (Samia, Nomura & Blumstein, 2013). Because most lizard species tested were ambush foragers, which we assume have low monitoring costs for foraging because they can continue to scan for prey while monitoring (Cooper, 2008*a,b*), the lizard results reinforce the idea of monitoring costs as the underlying mechanism of the flush-early phenomenon.

#### (4) Physiological and morphological effects

Overall, physiological and morphological traits of the prey had weak influences on FID of the lizards in our data set. With the exception of crypsis, these factors had overall effect sizes that ranged from non-significant to moderate in both directions. Effects of physiology and morphology on FID are particularly rich in competitive causal hypotheses. We will cite each of them and discuss which hypothesis seems to be best supported by the available data.

Cryptic lizards permit closer approach by predators than conspicuous lizards. Because cryptic morphology must be accompanied by equally cryptic behaviour (Ruxton, Sherratt & Speed, 2004), cryptic lizards likely permit a closer approach of predators as consequence of the immobility required for

effective camouflage. For example, *Chamaeleo chamaeleon* is so highly cryptic that it permits very close approach from predators without fleeing. Indeed, approach was so close that FID could not be used to study its antipredator responses (Cuadrado *et al.*, 2001). However, even highly cryptic body camouflage is usually ineffective when a predator is very close (Ruxton *et al.*, 2004; Tullberg, Merilaita & Wiklund, 2005; Bohlin, Tullberg & Merilaita, 2008). Therefore, lizards must have been selected to adopt an alternative antipredatory strategy (flee) when a predator is close to this danger threshold.

Interestingly, our results suggest that individuals partially concealed by vegetation assess themselves as being considerably safer from predation than camouflaged animals in open areas. However, it would be premature to conclude that partial concealment is more important for reducing risk than cryptic colouration. In only two studies were there unquestionable differences in crypsis between the cryptic and conspicuous lizards: those of *Phrynosoma modestum* (a highly cryptic horned lizard; Cooper & Sherbrooke, 2010*a*) and *Plestiodon laticeps* (Cooper, 1998). Furthermore, two of the remaining studies by Johnson (1970) and Heatwole (1968) do not conform to current methodological and statistical standards; the qualitative assignments of relative conspicuousness in these studies are both ambiguous and highly debatable. The differences in conspicuousness for the other species for which crypsis is a factor are real, but these species are not specialised for crypsis and the differences studied are intraspecific. Additional studies of lizards specialised for crypsis are needed to determine the strength of its effect on FID.

Both ontogenetic stage and body size affect FID. The intraspecific ranges of body size are larger in ontogenetic studies than in those restricted to adults, which may be a major factor accounting for the larger effect size of ontogeny than adult body size. In some species, the effect size of ontogeny was large, but in others it ranged from non-significant to small to moderate. This variation presumably has several bases. Studies may differ in whether they included hatchlings *versus* juveniles, the latter being larger than hatchlings relative to adults. Effect sizes are likely to be larger when hatchlings are included. Because they are considerably smaller, hatchlings are more difficult to detect at a given distance and may therefore have a reduced risk of predation. Furthermore, very small prey, such as hatchlings, may not be selected to attend to predators as large as human beings because the energetic reward to a predator of detecting and capturing such small prey will likely be very low. Finally, in some species, adults and hatchlings also differ in microhabitat selection (Stamps, 1983; Cooper & Wilson, 2007) and juveniles remain relatively closer to their refugia (Cooper, 2010*a*). All of these factors are expected to lead to shorter FIDs by hatchlings, and all may contribute to the effect size we report here.

Prey body size had a small, but significant, effect on FID: as body size increases, lizards flush at greater distances. Importantly, we excluded the confounding effect of ontogeny

by calculating effect sizes only for adult lizards. Body size is perhaps the most ubiquitous factor affecting FID, showing a large effect size in diverse taxa (Scrimgeour *et al.*, 1997; Kelt *et al.*, 2002; Fernández-Juricic *et al.*, 2006; Gotanda *et al.*, 2009). However, support for the positive body size–FID relationship came from interspecific comparisons in which differences in body size usually span a wide range of sizes, as is the case for lizards (Cooper, Pyron & Garland, 2014). Intraspecifically, differences in body sizes of adult lizards have much narrower ranges (often on the order of a few millimeters). Since data consistently show that body size and FID are linearly related, small effect sizes of intraspecific comparisons fit well with our expectations.

The mechanism underlying the positive body size–FID relationship is unclear. Several hypotheses seek to explain this relationship. First, larger prey are more conspicuous to predators and therefore have longer FIDs to compensate for the greater risk of attack (Blumstein, 2006). Second, because larger prey are usually less agile, having a longer turning radius than smaller prey, large prey require more time to escape successfully (Marden, 1987; Witter, Cuthill & Bonser, 1994). Third, as body size decreases animals are more sensitive to loss of foraging opportunities because their energetic requirements are more immediate (Bennett & Harvey, 1987). Therefore, smaller animals would be more prone to accept risk to compensate for their greater metabolic rates (Bennett & Harvey, 1987). Fourth, small individuals in the same habitats as adults may tend to stay closer to refuges (Stiller, 2011) because they are socially subordinate or are potential prey of adults. By remaining close to their refugia, they attempt to remain inconspicuous to larger territory holders.

The first two hypotheses may account for some, but not much, intraspecific variation in FID because the size ranges of adult lizards is restricted. In the first hypothesis, a few more millimeters are unlikely to have led to a substantial increase in predation pressure that would lead to natural selection favouring substantially longer FIDs by slightly larger prey. The second hypothesis is implausible because substantial differences in agility are unlikely for prey that differ only slightly in body size. However, the second hypothesis could account for the body size–FID relationship interspecifically because species often differ morphologically and physiologically in ways that affect agility. For instance, interspecific variation exists in the relative sizes of limbs, cross-sectional areas of limb muscles, and variation in types of muscle fibres that differ physiologically (Bonine & Garland, 1999). Whether such differences should systematically influence the effect of body size variation within adults of the same species is unknown.

The metabolic constraints hypothesis is attractive because it can explain both interspecific and intraspecific differences in FID. Metabolic rate increases with body mass (both intra- and interspecifically) with a scaling factor between 2/3 and 3/4 (White & Seymour, 2003; Nagy, 2005). The decrease in the surface area:volume ratio as size increases should diminish the

effects of morphological and physiological idiosyncrasies of species. The fourth hypothesis could be important for explaining intraspecific variation in territorial species. Smaller adults, especially males, may lack territories and remain unobtrusive to permit undetected copulation and avoid aggression by territorial males (Stapley & Keogh, 2004). This could lead them to stay relatively closer to refuges thereby reducing FID. To date no study has tested these hypotheses directly, but we hope that our findings will help guide future research aiming to elucidate the mechanism(s) of the ubiquitous increase in FID as body size increases in the context of OET in lizards and in other taxa.

The effects of tail autotomy on FID are unpredictable without detailed knowledge of its multiple effects in a particular species. In OET (Cooper & Frederick, 2010), FID can increase after autotomy because predation risk increases because most species suffer a decreased sprint speed after tail loss (Bateman & Fleming, 2009; McElroy & Bergmann, 2013). In addition, once a tail has been shed, lizards are unable to use autotomy as a defence until the tail has been regenerated. Tail loss can also affect the cost of fleeing, resulting in shorter FID. Loss of the tail reduces fitness at the outset of the predator–prey encounter, which is predicted to lead to greater risk-taking (shorter FID; Clark, 1994; Cooper & Frederick, 2010) due to loss of stored energy, increased risk of starvation, decreased clutch size, and/or decreased social status affecting the ability to mate (Bateman & Fleming, 2009). Another complication is that autotomised lizards may alter their strategies by staying closer to refugia to compensate for reduced running speed and/or rely more on crypsis conferred by immobility to avoid being detected (Cooper, 2003c; Bateman & Fleming, 2009; Cooper & Frederick, 2010). Further complicating predictions, tails were experimentally autotomised within a few days before lizards were tested for FID in some studies, but in others tails had been autotomised naturally weeks or months before testing for FID. The effects of autotomy on running speed and on other relevant variables are expected to decrease with time since autotomy if speed and agility are regained through experience running with a short tail and through regeneration of the tail, but the time course of changes in speed is known for only a few species.

Overall, autotomy had no effect on lizard escape decisions, which is not surprising because the balance of the various factors influencing FID after autonomy is likely to vary among species. Although most of the effect sizes are very close of zero, some species showed medium-to-large effect sizes in both directions. Current sample sizes did not permit more detailed evaluation of effects of autotomy. Predicting the direction and magnitude of effects of autotomy will be difficult because it requires not only knowledge of multiple factors that affect FID, but also knowledge of the magnitudes or relative magnitudes of the effects of these factors on fitness, which is the currency of optimal escape theory (Cooper & Frederick, 2007, 2010).

Gravid females had shorter FID than non-gravid females. The most frequent hypothesis to explain this pattern

states that, because gravid females have reduced maximal sprint speeds (Garland, 1985; Van Damme, Bauwens & Verhey, 1989), gravid females alter their antipredatory strategy by remaining immobile and thereby enhancing crypsis (Bauwens & Thoen, 1981; Schwarzkopf & Shine, 1992; Bulova, 1994). This idea is plausible because fleeing may trigger attack by a predator that had not previously detected the prey, placing gravid females at greater risk due to decreased sprint capacity. However, the relationship between maximal sprint speed and escape ability is complex because factors other than speed (especially agility, turning radius, and changes in speed and direction) are important for evasion. Most studies showing reduced maximal sprint speeds in gravid females are conducted in laboratories (e.g. Van Damme *et al.*, 1989; Sinervo, Hedges & Adolph, 1991). However, because running speed during escape in the field is typically slower than the maximal sprint speed and because natural terrain is much less uniform, the relevance of reduced maximal sprint speed is uncertain (Brecko *et al.*, 2008). Nevertheless, the large reductions in maximal sprint speed observed in gravid females of some species indicate reduced sprint capacity when being overtaken by a predator.

An alternative hypothesis attempts to explain shorter FIDs in gravid females by changes in habitat use. Gravid females may compensate for the risk attributable to reduced sprinting ability by remaining closer to refugia, reducing their time required to escape to safety. Thus, the effect of gravidity on FID may reflect a change in strategy of habitat selection rather than greater reliance on crypsis *via* immobility. This hypothesis is supported by some empirical evidences (Braña, 1993; Husak, 2006). In *Holbrookia propinqua*, gravid females stay closer to refugia, but the FIDs of gravid and non-gravid females are the same (Cooper, 2003c). This suggests that gravid females of this species stay close enough exactly to compensate for the added risk due to their reduced locomotor ability. Maintaining a shorter distance to refuge may overcompensate for the increased risk. Apparent overcompensation could occur if staying close to a refuge is beneficial to gravid females in other ways (e.g. there is increased access to food near a refuge or there is the ability to escape into the refuge to avoid unwanted copulations). The crypsis and distance to refuge hypotheses are not mutually exclusive: increased reliance on crypsis and staying closer to a refuge could differ among species and both might operate simultaneously to different degrees.

The effect size of body temperature on FID was moderate. Presumably, as lizards become cooler, their ability to escape by running decreases progressively (Marsh & Bennett, 1986; Van Berkum, 1988). At temperatures that are suboptimal for achieving maximum running speed, but sufficiently warm that running can aid in escape, lizards appear to compensate by initiating escape when the predator is further from them. FID is greater at lower body temperatures for all species tested except one, *P. modestum*, a highly cryptic species that has short FIDs even at warm temperatures. At cooler body temperatures they appear to rely more on

crypsis, often delaying escape until a predator has reached them (Cooper & Sherbrooke, 2010b). Additionally, our analyses showed that although air temperature and substrate temperature have been used frequently as surrogates for body temperature (because lizards need not be captured to measure them), they are often weakly correlated with body temperature (e.g. Powell & Russell, 1985). Our finding provides robust evidence that air and substrate temperature are poor surrogates for body temperature, and, therefore their use must be avoided in studies of escape behaviour.

For ectotherms, temperature strongly affects physiological and behavioural activities (Huey, 1982). Counter-intuitively, however, Stankowich & Blumstein's (2005) meta-analysis indicated that temperature (substrate, air, and body temperatures combined in a single analysis) had no effect on lizard FID. However, our current analysis contains substantially more data (from 18 to 40 species), and we analysed these temperature measures separately. Thus, we now find that body temperature, but not substrate or air temperature, affects lizard escape decisions. We believe that the moderate effect size is likely an underestimate because all lizards were studied at peak activity periods when they were within their optimal temperature ranges. Body temperature can have more striking effects on FID outside the optimal range. For example, when low body temperature prevents escape by running, some lizards switch strategy from escape to aggressive defence (Hertz, Huey & Nevo, 1982) and when body temperature is too high, some species (e.g. *Holbrookia propinqua*, *Aspidozelis sexlineatus*) switch from escaping on the surface to running into burrows (Cooper, 2000a).

##### (5) Experiential effects

In the intraspecific comparisons included in our data set, some of which included data for only two to several populations that differed substantially in predator density, FID was consistently longer in populations exposed to denser predator populations. A likely reason why effect sizes varied is that predator density was measured crudely and may not always reflect actual predation intensity. Furthermore, differences in actual predation intensity varied among studies, which presumably accounted for some variation in effect size among studies. Even so, effect sizes were large in over half of the studies, indicating that lizards under greater risk of predation due to high density of predators have longer FIDs, as predicted by escape theory. This agrees with the findings of a comparative study of 65 lizard species which showed that FID is longer in mainland species than in island species (where predator density is expected to be reduced) and that the difference increased as distance from the mainland increased (Cooper *et al.*, 2014).

In populations exposed to more intense predation, natural selection must favour individuals that are warier, and defensive behaviours are heritable (Brodie, 1989), suggesting that a longer FID is an adaptive response to higher predation intensity. Experience also affects escape behaviour through learning, sometimes rapid learning by prey that have been attacked (Marcellini & Jenssen, 1991) or *via* habituation

when contact with predators is frequent, but predators do not attack (Cooper, 2010a; Cooper & Avalos, 2010a). Experience with predators that attack may contribute to the effect size of predator density, the large effect sizes resulting from a combination of natural selection and experience by individuals that have survived attacks or seen other animals attacked. The relative importance of these factors should depend on the intensity and duration of natural selection and the efficiency of predators.

FID was consistently longer after second attacks with short latency than after first attacks. When attacked by the same predator a second time after the initial attack, lizards appeared to assess the predator as being more dangerous, and consequently exhibited longer FIDs. The novel finding that the effect of repeated attacks decreased as altitude increased suggests lower predation intensity at higher altitudes (Shaffer, 1978; Diego-Rasilla, 2003b). This could indicate that sequential attacks are more frequent at lower altitudes, leading to greater increase in perceived risk due to experience or natural selection than at higher altitudes.

#### (6) Correlation with other escape responses

Our comprehensive meta-analysis provided no evidence that lizard FID was correlated with distance fled (i.e. the distance travelled by a prey after initiation of flight). Distance fled should be affected by factors such as prey distance to refuge, obstacles along the path, the presence of other predators along the path, the capacity for uninterrupted sprinting, among others (Bulova, 1994). These factors make it difficult to predict the relationship between FID and distance fled.

However, FID is positively correlated with two other variables related to predator–prey encounter: starting distance (predator–prey distance when the attack begins), and alert distance (predator–prey distance when prey become aware of the predator’s approach). Indeed, this positive relationship is predicted by the ‘flush early and avoid the rush’ hypothesis discussed in Section IV.3. Studies showing the starting distance–FID or alert distance–FID relationship were not explored further here because this topic was comprehensively examined in a recent meta-analysis (Samia *et al.*, 2013). No new evidence for lizards has been published since then.

#### (7) Phylogenetic effects

Lineages of lizards differ greatly in many ecologically important traits, including methods of prey apprehension, foraging modes, and related morphological features (Huey & Pianka, 1981; Vitt *et al.*, 2003). Because such traits tend to be fairly to very stable in large squamate taxa, even in families and suborders, phylogenetic analyses are necessary to detect influences of behavioural traits such as foraging mode on other related traits, such as chemosensory behaviours and related morphological features (Cooper, 1995). In such cases, non-phylogenetic analyses may yield inflated estimates of correlations between traits because values tend to be

similar among more closely related species, but differ among distantly related taxa.

In a previous analysis of the effect of predation intensity on FID of lizards, no phylogenetic signal was detected (Cooper *et al.*, 2014). This finding suggests that FID is somewhat labile and responsive to natural selection exerted by predation. In our meta-analysis, a phylogenetic model was superior to a non-phylogenetic model for only 4 out of 20 factors and relationships examined. Thus, for most factors that affect FID, ecological trait values influence FID in similar ways across lizard taxa. This suggests an important role of phenotypic plasticity in explaining variation in FID across species. Another reason for the lack of phylogenetic effects could be that risk assessment algorithms to predators are similar to those of the common ancestor of lizards and have not changed because the basic escape strategies of lizards have not changed. The mechanisms of risk assessment and escape undoubtedly were refined by natural selection during a long history of predation avoidance and have remained effective to the present. This hypothesis seems plausible for lizards included in our studies because only species that flee when approached and are terrestrial, scansorial, or semi-arboreal were included. Fossorial species are unrepresented, as are extremely cryptic species (such as chameleons) that typically do not run from predators (Cuadrado *et al.*, 2001). When FID data become available for a broader range of ecologically and morphologically specialised lizard taxa, phylogenetic effects may become more important in explaining variation in FID.

Phylogeny influenced effect sizes of distance to refuge, substrate temperature, predator density, and sequential attacks on FID. Many hypotheses could be generated as possible explanations for phylogenetic influences on these effects. However, we believe that it may be premature to state them because it is uncertain whether real phylogenetic effects have been detected. Substrate temperature, which had the second largest  $\Delta\text{AICc}$  among the four factors, did not significantly explain variation in FID in either model. This hints that although differences for the four factors met our criterion that  $\Delta\text{AICc}$  be at least 2.0, such differences may not indicate any meaningful difference in explanatory power of the phylogenetic and non-phylogenetic models. This failure to detect clear and large phylogenetic effects corroborates findings for the remaining factors, further supporting findings that FID is largely determined by ecological, morphological and physiological factors rather than by phylogenetically stable differences among taxa in escape behaviour.

#### (8) Future directions

In the economic escape model proposed by Ydenberg & Dill (1986), prey begin to flee when fitness costs of fleeing and not fleeing are equal. In the optimal escape model proposed by Cooper & Frederick (2007), prey begin to flee when the balance of the prey’s fitness at the start of the encounter, predation risk, and cost of fleeing provides the greatest expected fitness at the end of the encounter. The qualitative predictions of the two models are largely identical, and have

been strongly supported by extensive data for lizards and other taxa.

Because fitness is the currency of both models, their quantitative predictions are very difficult to test and compare. Only the optimal escape model predicts the effect of the prey's initial fitness. Therefore, one apparent way to distinguish between models is to conduct tests of the effects of the prey's initial fitness on FID. However, Ydenberg & Dill's (1986) model can be extended to include the effect of initial fitness without making it an optimality model. Another approach might be to use surrogate currencies for fitness and to compare the shapes of the empirically determined cost of fleeing and cost of not fleeing curves to those in the models. Nevertheless, this method is not feasible because the shapes of the curves and their underlying mathematical functions are purely illustrative. In Ydenberg & Dill's (1986) model and its more recent adaptations, the two curves are linear or curvilinear and intersect (Cooper & Vitt, 2002). In Cooper & Frederick's (2007, 2010) models, the mathematical functions for the curves were selected somewhat arbitrarily to match biological aspects of the scenario. The exact shapes of the curves are unknown for both models and cannot be used to distinguish between models. Thus, we believe that the greatest advance in our theoretical understanding would come from direct measurements of fitness components of escape models in a way that would permit critical comparisons between them.

Most lizards for which escape behaviour has been studied are sit-and-wait predators. One reason for this bias is that behaviours of ambush foragers conform well to the scenario of escape theory in which an immobile prey monitors an approaching predator. Active foragers spend a high proportion of the time moving, and often have short inter-movement intervals while foraging; both of which make it difficult to conduct field observations to test economic escape theory. Another source of bias is that many studies of lizard escape have been conducted in areas of North America and southern Africa where the most observable and sometimes most abundant species are ambushers. Although predictions and findings are comparable for ambushers and active foragers, we encourage future researchers to study escape responses of a wide taxonomic range of active foragers because many aspects of lizard behaviour, ecology, morphology and physiology are affected by foraging mode (Huey & Pianka, 1981; McBrayer, Miles & Reilly, 2007).

How community composition affects FID is virtually unknown. However, the diversity and abundance of predators appears to affect FID, as indicated by studies showing that lizards exhibit island tameness in that they have shorter FIDs on islands than on the mainland, which increases as distance from the mainland increases (Cooper & Pérez-Mellado, 2012; Cooper *et al.*, 2014). Because actively foraging predators are more likely to consume ambushing prey, and ambushing predators are more likely to predate actively foraging prey, the foraging modes of predators in a community may differentially affect the FID of prey having

different foraging modes. These are unexplored topics for future investigation.

The vast majority of studies of FID in all taxa have used human researchers as surrogate predators. Having people approach prey has the great practical advantages of affording control of aspects of the approach, such as speed, directness and direction of gaze, in natural habitats where the use of natural or robotic predators is difficult or impossible. Frid & Dill (2002) suggested that animals often respond to people as predators. But do prey respond to people as they do to their natural predators? The method is widely accepted, but remains subject to the caveat that some prey may have predator-specific antipredator responses that might include behaviours that would not be elicited by human beings (e.g. Stuart-Fox *et al.*, 2008). However, tests with model raptors and snakes revealed no qualitative differences in the responses of the lizard *Sceloporus virgatus* among the model predators and human approachers (Cooper, 2008*b*). We encourage future researchers to use natural predators or realistic predator models under field conditions when this is possible, but expect that such studies will continue to remain rare.

The lack of evidence for some factors prevented us from asking additional potentially interesting questions. For example, factors with fewer than three replicates cannot be used meta-analytically to answer the following questions: does perception of risk increase with number of predators? Do lizards with greater limb length accept more risk? Are environmental factors, such as wind speed and time of day, taken into account in making escape decisions? In some cases, reduced sample sizes prevented us from testing effects of covariates potentially important for some factors we tested. Do smaller individuals permit predators to draw nearer than larger individuals when presented with a food item? Does the energetic value of the food item matter? Does body temperature influence FID more strongly at higher altitudes? Future studies that test these questions in a variety of species will enable the next meta-analysis comprehensively to address them.

## V. CONCLUSIONS

(1) The reciprocally illuminating nature of model generation and development, combined with empirical studies testing predictions of OET models have demonstrated that many predictions of OET are upheld in lizards.

(2) In lizards, costs of flight have a profoundly important effect on escape decisions while physiological and morphological factors have, overall, a surprisingly small effect.

(3) Future studies testing prey's escape decisions using natural predators, examining how different factors interact with each other, and determining the specific shape of fitness functions are needed to advance our understanding of escape decisions.

(4) Our comprehensive meta-analysis has highlighted empirical research lacunae that, once filled, should permit a more comprehensive understanding of the role of environmental factors on escape decisions.

## VI. ACKNOWLEDGEMENTS

D.S.M.S. is grateful for support from CAPES. D.T.B. is supported by the NSF. We are very grateful to José Martín, Geoffrey Smith, Matthew Lattanzio, Leonardo Vignoli, Miguel Molina-Borja, Viktoria and Igor Majlath, Jerry Husak, and Antonieta Labra for providing unpublished data. We are also grateful to Shinichi Nakagawa and Viechtbauer Wolfgang for clarifications about phylogenetic meta-analysis. We thank two anonymous reviewers for valuable comments.

## VII. REFERENCES

References marked with asterisk have been cited within the supporting information.

- \*AMO, L., LÓPEZ, P. & MARTÍN, J. (2005). Flexibility in antipredatory behavior allows wall lizards to cope with multiple types of predators. *Annales Zoologici Fennici* **42**, 109–121.
- \*AMO, L., LÓPEZ, P. & MARTÍN, J. (2006). Nature-based tourism as a form of predation risk affects body condition and health state of *Podarcis muralis* lizards. *Biological Conservation* **131**, 402–409.
- \*AMO, L., LÓPEZ, P. & MARTÍN, J. (2007). Habitat deterioration affects antipredatory behavior, body condition, and parasite load of female *Psammotromus algirus* lizards. *Canadian Journal of Zoology* **85**, 743–751.
- ANDERSON, R. & KARASOV, W. (1981). Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia* **49**, 67–72.
- BATEMAN, P. W. & FLEMING, P. A. (2009). To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. *Journal of Zoology* **277**, 1–14.
- BAUWENS, D. & THOEN, C. (1981). Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *Journal of Animal Ecology* **50**, 733–743.
- BENNETT, A. F. & HARVEY, P. H. (1987). Active and resting metabolic rate in birds: allometry, phylogeny and ecology. *Journal of Zoology* **213**, 327–363.
- \*BERGER, S., WIKELSKI, M., ROMERO, L. M., KALKO, E. K. V. & RÖDL, T. (2007). Behavioral and physiological adjustments to new predators in an endemic island species, the Galápagos marine iguana. *Hormones and Behavior* **52**, 653–663.
- \*BLAMIRE, S. J. (1999). Factors influencing the escape response of an arboreal agamid lizard of tropical Australia (*Lophognathus temporalis*) in an urban environment. *Canadian Journal of Zoology* **77**, 1998–2003.
- \*BLÁZQUEZ, M. C., RODRÍGUEZ-ESTRELLA, R. & DELIBES, M. (1997). Escape behavior and predation risk of mainland and island spiny-tailed iguanas (*Ctenosaura hemilopha*). *Ethology* **103**, 990–998.
- BLOMBERG, S. P., GARLAND, T. & IVES, A. R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745.
- BLUMSTEIN, D. T. (2006). Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour* **71**, 389–399.
- BLUMSTEIN, D. T. (2010). Flush early and avoid the rush: a general rule of antipredator behavior? *Behavioral Ecology* **21**, 440–442.
- BOHLIN, T., TULLBERG, B. S. & MERILAITA, S. (2008). The effect of signal appearance and distance on detection risk in an aposematic butterfly larva (*Parnassius apollo*). *Animal Behaviour* **76**, 577–584.
- BONINE, K. E. & GARLAND, T. Jr. (1999). Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *Journal of Zoology* **248**, 255–265.
- BORNESTEIN, M., HEDGES, L. V., HIGGINS, J. P. T. & ROTHSTEIN, H. R. (2009). *Introduction to Meta-Analysis*. John Wiley & Sons, Chichester.
- BOUSKILA, A. & BLUMSTEIN, D. T. (1992). Rules of thumb for predation hazard assessment: predictions from a dynamic model. *American Naturalist* **139**, 161–176.
- BRAÑA, F. (1993). Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. *Oikos* **66**, 216–222.
- BRANCH, B. (1998). *Field Guide to Snakes and other Reptiles of Southern Africa*. Ralph Curtis Books, Sanibel Island.
- \*BRAUN, C. A., BAIRD, T. A. & LEBEAU, J. K. (2010). Influence of substrate temperature and directness of approach on the escape responses of juvenile collared lizards. *Herpetologica* **66**, 418–424.
- BRECKO, J., HUYGHE, K., VANHOODONCK, B., HERREL, A., GRBAC, I. & VAN DAMME, R. (2008). Functional and ecological relevance of intraspecific variation in body size and shape in the lizard *Podarcis melisellensis* (Lacertidae). *Biological Journal of the Linnean Society* **94**, 251–264.
- BRODIE, E. D. I. (1989). Genetic correlations between morphology and antipredator behavior in natural populations of the garter snake *Thamnophis ordinoides*. *Nature* **342**, 542–543.
- BULOVA, S. J. (1994). Ecological correlates of population and individual variation in antipredator behavior of two species of desert lizards. *Copeia* **1994**, 980–992.
- \*BURGER, J. & GOCHFELD, M. (1990). Risk discrimination of direct versus tangential approach by basking black iguanas (*Ctenosaura similis*): variation as a function of human exposure. *Journal of Comparative Psychology* **104**, 388–394.
- \*BURGER, J. & GOCHFELD, M. (1993). The importance of the human face in risk perception by black iguanas, *Ctenosaura similis*. *Journal of Herpetology* **27**, 426–430.
- \*BURGER, J., GOCHFELD, M. & MURRAY, B. G. Jr. (1991). Role of a predator's eye size in risk perception by basking black iguana, *Ctenosaura similis*. *Animal Behaviour* **42**, 471–476.
- BURGER, J., GOCHFELD, M. & MURRAY, B. G. Jr. (1992). Risk discrimination of eye contact and directness of approach in black iguanas (*Ctenosaura similis*). *Journal of Comparative Psychology* **106**, 97–101.
- BURNHAM, K. P. & ANDERSON, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Second Edition. Springer, New York.
- \*CAPIZZI, D., LUISELLI, L. & VIGNOLI, L. (2007). Flight initiation distance in relation to substratum type, sex, reproductive status and tail condition in two lacertids with contrasting habits. *Amphibia-Reptilia* **28**, 403–407.
- \*CARRETERO, M. A., VASCONCELOS, R., FONSECA, M., KALIONTZOPOULOU, A., BRITO, J. C., HARRIS, D. J. & PERERA, A. (2006). Escape tactics of two syntopic forms of the *Lacerta perspicillata* complex with different colour patterns. *Canadian Journal of Zoology* **84**, 1594–1603.
- CARTER, J., LYONS, N. J., COLE, H. L. & GOLDSMITH, A. R. (2008). Subtle cues of predation risk: starlings respond to a predator's direction of eye gaze. *Proceedings of the Royal Society B* **275**, 1709–1715.
- CHAN, A. A. Y.-H., GIRALDO-PÉREZ, P., SMITH, S. & BLUMSTEIN, D. T. (2010). Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. *Biology Letters* **6**, 458–461.
- CHAPPLE, D. G. & SWAIN, R. (2002). Effect of caudal autotomy on locomotor performance in a viviparous skink, *Neoscincus metallicus*. *Functional Ecology* **16**, 817–825.
- CLARK, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology* **5**, 159–170.
- CLUTTON-BROCK, T. H. (1991). *The Evolution of Parental Care*. Princeton University Press, Princeton.
- COHEN, J. (1992). A power primer. *Psychological Bulletin* **112**, 155–159.
- CONANT, R. & COLLINS, J. T. (1993). *A Field Guide to Reptiles and Amphibians: Eastern/Central North America*. Houghton Mifflin, New York.
- COOPER, W. E. Jr. (1995). Foraging mode, prey chemical discrimination, and phylogeny in lizards. *Animal Behaviour* **50**, 973–985.
- \*COOPER, W. E. Jr. (1997a). Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Canadian Journal of Zoology* **75**, 943–947.
- \*COOPER, W. E. Jr. (1997b). Factors affecting risk and cost of escape by the broad-headed skink (*Eumeces laticeps*): predator speed, directness of approach, and female presence. *Herpetologica* **53**, 464–474.
- COOPER, W. E. Jr. (1998). Effects of refuge and conspicuousness on escape behavior by the broad-headed skink (*Eumeces laticeps*). *Amphibia-Reptilia* **19**, 103–108.
- \*COOPER, W. E. Jr. (1999a). Escape behavior by prey blocked from entering the nearest refuge. *Canadian Journal of Zoology* **77**, 671–674.
- \*COOPER, W. E. Jr. (1999b). Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, *Eumeces laticeps*. *Behavioral Ecology and Sociobiology* **47**, 54–59.
- COOPER, W. E. Jr. (2000a). Effect of temperature on escape behaviour by an ectothermic vertebrate, the keeled earless lizard (*Holbrookia propinqua*). *Behaviour* **137**, 1299–1315.
- \*COOPER, W. E. Jr. (2000b). Tradeoffs between predation risk and feeding in a lizard, the broad-headed skink (*Eumeces laticeps*). *Behaviour* **137**, 1175–1189.
- \*COOPER, W. E. Jr. (2003a). Effect of risk on aspects of escape behavior by a lizard, *Holbrookia propinqua*, in relation to optimal escape theory. *Ethology* **109**, 617–626.
- \*COOPER, W. E. Jr. (2003b). Risk factors affecting escape behavior by the desert iguana, *Dipsosaurus dorsalis*: speed and directness of predator approach, degree of cover, direction of turning by a predator, and temperature. *Canadian Journal of Zoology* **81**, 979–984.
- COOPER, W. E. Jr. (2003c). Shifted balance of risk and cost after autotomy affects use of cover, escape, activity, and foraging in the keeled earless lizard (*Holbrookia propinqua*). *Behavioral Ecology and Sociobiology* **54**, 179–187.
- COOPER, W. E. Jr. (2005a). The foraging mode controversy: both continuous variation and clustering of foraging movements occur. *Journal of Zoology* **267**, 179–190.

- COOPER, W. E. JR. (2005b). When and how do predator starting distances affect flight initiation distances? *Canadian Journal of Zoology* **83**, 1045–1050.
- \*COOPER, W. E. JR. (2006a). Dynamic risk assessment: prey rapidly adjust flight initiation distance to changes in predator approach speed. *Ethology* **112**, 858–864.
- COOPER, W. E. JR. (2006b). Risk factors affecting escape behaviour by Puerto Rican *Anolis* lizards. *Canadian Journal of Zoology* **84**, 495–504.
- COOPER, W. E. JR. (2006c). Risk factors and escape strategy in the grasshopper *Dissosteira carolina*. *Behaviour* **143**, 1201–1218.
- \*COOPER, W. E. JR. (2007a). Compensatory changes in escape and refuge use following autotomy in the lizard *Sceloporus virgatus*. *Canadian Journal of Zoology* **85**, 99–107.
- \*COOPER, W. E. JR. (2007b). Escape and its relationship to pursuit-deterrent signalling in the Cuban curly-tailed lizard *Leiocephalus carinatus*. *Herpetologica* **63**, 144–150.
- \*COOPER, W. E. JR. (2007c). Foraging modes as suites of coadapted movement traits. *Journal of Zoology* **272**, 45–56.
- COOPER, W. E. JR. (2008a). Strong artifactual effect of starting distance on flight initiation distance in the actively foraging lizard *Aspidoscelis exanguis*. *Herpetologica* **64**, 200–206.
- COOPER, W. E. JR. (2008b). Visual monitoring of predators: occurrence, cost and benefit for escape. *Animal Behaviour* **76**, 1365–1372.
- \*COOPER, W. E. JR. (2009a). Fleecing and hiding under simultaneous risks and costs. *Behavioral Ecology* **20**, 665–671.
- \*COOPER, W. E. JR. (2009b). Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). *Behavioral Ecology and Sociobiology* **63**, 1765–1771.
- \*COOPER, W. E. JR. (2009c). Optimal escape theory predicts escape behaviors beyond flight initiation distance: risk assessment and escape by striped plateau lizards *Sceloporus virgatus*. *Current Zoology* **55**, 123–131.
- COOPER, W. E. JR. (2010a). Escape tactics and effects of perch height and habituation on flight initiation distance in two Jamaican anoles (Squamata: Polychrotidae). *Revista de Biología Tropical* **58**, 1199–1209.
- \*COOPER, W. E. JR. (2010b). Pursuit deterrence varies with predation risks affecting escape behaviour in the lizard *Callisaurus draconoides*. *Animal Behaviour* **80**, 249–256.
- \*COOPER, W. E. JR. (2011a). Age, sex and escape behaviour in the striped plateau lizard (*Sceloporus virgatus*) and the mountain spiny lizard (*Sceloporus jarrovi*), with a review of age and sex effects on escape by lizards. *Behaviour* **148**, 1215–1238.
- \*COOPER, W. E. JR. (2011b). Influence of some potential predation risk factors and interaction between predation risk and cost of fleeing on escape by the lizard *Sceloporus virgatus*. *Ethology* **117**, 620–629.
- \*COOPER, W. E. JR. (2012). Risk factors affecting escape behavior by the Jamaican lizard *Anolis lineatopus* (Polychrotidae, Squamata). *Caribbean Journal of Science* **46**, 1–12.
- COOPER, W. E. JR. & AVALOS, A. (2010a). Escape decisions by the syntopic congeners *Sceloporus jarrovi* and *S. virgatus*: comparative effects of perch height and of predator approach speed, persistence, and direction of turning. *Journal of Herpetology* **44**, 425–430.
- \*COOPER, W. E. JR. & AVALOS, A. (2010b). Predation risk, escape and refuge use by mountain spiny lizards (*Sceloporus jarrovi*). *Amphibia-Reptilia* **31**, 363–373.
- COOPER, W. E. JR. & BLUMSTEIN, D. T. (2013). Novel effects of monitoring predators on costs of fleeing and not fleeing explain flushing early in economic escape theory. *Behavioral Ecology* **25**, 44–52.
- COOPER, W. E. JR. & FREDERICK, W. G. (2007). Optimal flight initiation distance. *Journal of Theoretical Biology* **244**, 59–67.
- COOPER, W. E. JR. & FREDERICK, W. G. (2010). Predator lethality, optimal escape behavior, and autotomy. *Behavioral Ecology* **21**, 91–96.
- \*COOPER, W. E. JR., HAWLENA, D. & PÉREZ-MELLADO, V. (2009a). Effects of predation risk factors on escape behavior by Balearic lizards (*Podarcis lilfordi*) in relation to optimal escape theory. *Amphibia-Reptilia* **30**, 99–110.
- \*COOPER, W. E. JR., HAWLENA, D. & PÉREZ-MELLADO, V. (2009b). Islet tameness: escape behavior and refuge use in populations of the Balearic lizard (*Podarcis lilfordi*) exposed to differing predation pressure. *Canadian Journal of Zoology* **87**, 912–919.
- \*COOPER, W. E. JR. & PÉREZ-MELLADO, V. (2004). Tradeoffs between escape behavior and foraging opportunity by the Balearic lizard (*Podarcis lilfordi*). *Herpetologica* **60**, 321–324.
- \*COOPER, W. E. JR. & PÉREZ-MELLADO, V. (2011). Escape by the Balearic lizard (*Podarcis lilfordi*) is affected by elevation of an approaching predator, but not by some other potential predation risk factors. *Acta Herpetologica* **6**, 247–259.
- COOPER, W. E. JR. & PÉREZ-MELLADO, V. (2012). Historical influence of predation pressure on escape behavior by *Podarcis* lizards in the Balearic Islands. *Biological Journal of the Linnean Society* **107**, 254–268.
- COOPER, W. E. JR., PÉREZ-MELLADO, V., BAIRD, T., BAIRD, T. A., CALDWELL, J. P. & VITT, L. J. (2003). Effects of risk, cost, and their interaction on optimal escape by nonrefuging Bonaire whiptail lizard, *Cnemidophorus murinus*. *Behavioral Ecology* **14**, 288–293.
- \*COOPER, W. E. JR., PÉREZ-MELLADO, V. & HAWLENA, D. (2006). Magnitude of food reward affects escape behavior and acceptable risk in Balearic lizards, *Podarcis lilfordi*. *Behavioral Ecology* **17**, 554–559.
- \*COOPER, W. E. JR., PÉREZ-MELLADO, V. & HAWLENA, D. (2007). Number, speeds, and approach paths of predators affect escape behavior by the Balearic lizard, *Podarcis lilfordi*. *Journal of Herpetology* **41**, 197–204.
- COOPER, W. E. JR., PYRON, R. A. & GARLAND, T. (2014). Island tameness: living on islands reduces flight initiation distance. *Proceedings of the Royal Society B* **281**, 20133019.
- COOPER, W. E. JR. & SHERBROOKE, W. C. (2010a). Crypsis influences escape decisions in the round-tailed horned lizard (*Phrynosoma modestum*). *Canadian Journal of Zoology* **88**, 1003–1010.
- COOPER, W. E. JR. & SHERBROOKE, W. C. (2010b). Initiation of escape behavior by the Texas horned lizard (*Phrynosoma cornutum*). *Herpetologica* **66**, 23–30.
- \*COOPER, W. E. JR. & SHERBROOKE, W. C. (2010c). Plesiomorphic escape decisions in cryptic horned lizards (Phrynosoma) having highly derived antipredatory defenses. *Ethology* **116**, 920–928.
- COOPER, W. E. JR. & SHERBROOKE, W. C. (2013). Effects of recent movement, starting distance and other risk factors on escape behaviour by two Phrynosomatid lizards. *Behaviour* **150**, 447–469.
- COOPER, W. E. JR. & STANKOWICH, T. (2010). Prey or predator? Body size of an approaching animal affects decisions to attack or escape. *Behavioral Ecology* **21**, 1278–1284.
- COOPER, W. E. JR. & VITT, L. J. (2002). Optimal escape and emergence theories. *Comments on Theoretical Biology* **7**, 283–294.
- \*COOPER, W. E. JR. & WHITING, M. J. (2007a). Effects of risk on flight initiation distance and escape tactics in two southern African lizard species. *Acta Zoologica Sinica* **53**, 446–453.
- \*COOPER, W. E. JR. & WHITING, M. J. (2007b). Universal optimization of flight initiation distance and habitat-driven variation in escape tactics in a Namibian lizard assemblage. *Ethology* **113**, 661–672.
- COOPER, W. E. JR. & WILSON, D. S. (2007). Beyond optimal escape theory: microhabitats as well as predation risk affect escape and refuge use by the phrynosomatid lizard *Sceloporus virgatus*. *Behaviour* **144**, 1235–1254.
- \*COOPER, W. E. JR. & WILSON, D. S. (2008). How to stay alive after losing your tail. *Behaviour* **145**, 1085–1099.
- COSTA, G. C. (2009). Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology* **90**, 2014–2019.
- CUADRADO, M., MARTÍN, J. & LÓPEZ, P. (2001). Camouflage and escape decisions in the common chameleon *Chamaeleo chamaeleon*. *Biological Journal of the Linnean Society* **72**, 547–554.
- DIAL, B. E. & FITZPATRICK, L. C. (1981). The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). *Oecologia* **51**, 310–317.
- \*DÍAZ-URIARTE, R. (1999). Anti-predator behaviour changes following an aggressive encounter in the lizard *Tropidurus hispidus*. *Proceedings of the Royal Society of London B* **266**, 2457–2464.
- DICKMAN, C. R. (1988). Body size, prey size, and community structure in insectivorous mammals. *Ecology* **69**, 569–585.
- \*DIEGO-RASILLA, F. J. (2003a). Human influence on the tameness of wall lizard, *Podarcis muralis*. *Italian Journal of Zoology* **70**, 225–228.
- DIEGO-RASILLA, F. J. (2003b). Influence of predation pressure on the escape behaviour of *Podarcis muralis* lizards. *Behavioural Processes* **63**, 1–7.
- DILL, L. M. (1974). The escape response of the zebra danio (*Brachydanio rerio*) I. The stimulus for escape. *Animal Behaviour* **22**, 711–722.
- DUKAS, R. (2004). Causes and consequences of limited attention. *Brain, Behavior and Evolution* **63**, 197–210.
- EGGER, M., DAVEY SMITH, G., SCHNEIDER, M. & MINDER, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *BMJ* **315**, 629–634.
- \*EIFLER, D. (2001). *Egernia cunninghami* (Cunningham's skink). *Herpetological Review* **32**, 40.
- FERNÁNDEZ-JURICIC, E., BLUMSTEIN, D. T., ABRICA, G., MANRIQUEZ, L., ADAMS, L. B., ADAMS, R., DANESHRAH, M. & RODRIGUEZ-PRieto, I. (2006). Relationships of anti-predator escape and post-escape responses with body mass and morphology: a comparative avian study. *Evolutionary Ecology Research* **8**, 731–752.
- FRID, A. & DILL, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* **6**, 1–11.
- GARLAND, T. (1985). Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *Journal of Zoology* **207**, 425–439.
- \*GOODMAN, B. A. (2007). Divergent morphologies, performance, and escape behaviour in two tropical rock-using lizards (Reptilia: Scincidae). *Biological Journal of the Linnean Society* **91**, 85–98.
- GOTANDA, K. M., TURGEON, K. & KRAMER, D. L. (2009). Body size and reserve protection affect flight initiation distance in parrotfishes. *Behavioral Ecology and Sociobiology* **63**, 1563–1572.
- GRISMER, L. L. (2002). *Amphibians and Reptiles of Baja California Including its Pacific Islands and Islands in the Sea of Cortés*. University of California Press, Berkeley.
- \*HAWLENA, D., PÉREZ-MELLADO, V. & COOPER, W. E. JR. (2009). Morphological traits affect escape behaviour of the Balearic lizards (*Podarcis lilfordi*). *Amphibia-Reptilia* **30**, 587–592.
- HEATWOLE, H. (1968). Relationship of escape behavior and camouflage in anoline lizards. *Copeia* **1968**, 109–113.
- HEMMI, J. M. (2005). Predator avoidance in fiddler crabs: 2. The visual cues. *Animal Behaviour* **69**, 615–625.



- HERTZ, P. E., HUEY, R. E. & NEVO, E. (1982). Fight versus flight: body temperature influences defensive responses of lizards. *Animal Behaviour* **30**, 676–679.
- HIGGINS, J. P. T., THOMPSON, S. G., DEEKS, J. J. & ALTMAN, D. G. (2003). Measuring inconsistency in meta-analyses. *BMJ* **327**, 557–560.
- \*HOTCHKIN, P. & RIVEROLL, H. (2005). Comparative escape behavior of chihuahuan desert parthenogenetic and gonochoristic whiptail lizards. *The Southwestern Naturalist* **50**, 172–177.
- HUEY, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In *Biology of the Reptilia, Volume 12, Physiology C: Physiological Ecology* (eds C. GANS and F. H. POUGH), pp. 25–91. Academic Press, London.
- HUEY, R. B. & PIANKA, E. R. (1981). Ecological consequences of foraging mode. *Ecology* **62**, 991–999.
- HUSAK, J. F. (2006). Do female collared lizards change field use of maximal sprint speed capacity when gravid? *Oecologia* **150**, 339–343.
- \*HUSAK, J. F. & ROUSE, M. N. (2006). Population variation in escape behavior and limb morphology of collared lizards (*Crotaphytus collaris*) in Oklahoma. *Herpetologica* **62**, 156–163.
- JENNIONS, M. & MØLLER, A. P. (2002). How much variance can be explained by ecologists and evolutionary biologists? *Oecologia* **132**, 492–500.
- JOHNSON, C. R. (1970). Escape behavior and camouflage in two subspecies of *Sceloporus occidentalis*. *American Midland Naturalist* **84**, 280–282.
- JOHNSON, D. D. P., BLUMSTEIN, D. T., FOWLER, J. H. & HASELTON, M. G. (2013). The evolution of error: error management, cognitive constraints, and adaptive decision-making biases. *Trends in Ecology & Evolution* **28**, 474–481.
- JORDÃO, J. M. & OLIVEIRA, R. F. (2001). Sex differences in predator evasion in the fiddler crab *Uca tangeri* (Decapoda: Ocypodidae). *Journal of Crustacean Biology* **21**, 948–953.
- KELT, D. A., NABORS, L. K. & FORISTER, M. L. (2002). Size-specific differences in tail loss and escape behavior in *Liolaemus nigromaculatus*. *Journal of Herpetology* **36**, 322–325.
- KEMBEL, S. W., COWAN, P. D., HELMUS, M. R., CORNWELL, W. K., MORLON, H., ACKERLY, D. D., BLOMBERG, S. P. & WEBB, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–1464.
- KORICHEVA, J., GUREVITCH, J. & MENGENSEN, K. (eds) (2013). *Handbook of Meta-Analysis in Ecology and Evolution*. Princeton University Press, Princeton.
- LAJEUNESSE, M. J. (2009). Meta-analysis and the comparative phylogenetic method. *The American Naturalist* **174**, 369–381.
- \*LATTANZIO, M. (2009). Escape tactic plasticity of two sympatric *Norops* (Beta, *Anolis*) species in Northeast Costa Rica. *Amphibia-Reptilia* **30**, 1–6.
- LORD, A., WAAS, J. R., INNES, J. & WHITTINGHAM, M. J. (2001). Effects of human approaches to nests of northern New Zealand dotterels. *Biological Conservation* **98**, 233–240.
- LOSOS, J. B., MOUTON, P. L. F. N., BICKEL, R., CORNELIUS, I. & RUDDOCK, L. (2002). The effect of body armature on escape behaviour in cordylid lizards. *Animal Behaviour* **64**, 313–321.
- MAGINNIS, T. L. (2006). The costs of autotomy and regeneration in animals: a review and framework for future research. *Behavioral Ecology* **17**, 857–872.
- MARCELLINI, D. L. & JENSEN, T. A. (1991). Avoidance learning by the curly-tailed lizard, *Leiocephalus schreibersi*: implications for anti-predator behavior. *Journal of Herpetology* **25**, 238–241.
- MARDEN, J. H. (1987). Maximum lift production during takeoff in flying animals. *Journal of Experimental Biology* **130**, 235–238.
- MARSH, R. L. & BENNETT, A. F. (1986). Thermal dependence of sprint performance of the lizard *Sceloporus occidentalis*. *Journal of Experimental Biology* **126**, 79–87.
- \*MARTÍN, J. & LÓPEZ, P. (1995a). Escape behaviour of juvenile *Psammotromus alginus* lizards: constraint of or compensation for limitations in body size? *Behaviour* **132**, 181–192.
- MARTÍN, J. & LÓPEZ, P. (1995b). Influence of habitat structure on the escape tactics of the lizard *Psammotromus alginus*. *Canadian Journal of Zoology* **73**, 129–132.
- \*MARTÍN, J. & LÓPEZ, P. (1999). Nuptial coloration and mate guarding affect escape decisions of male lizards *Psammotromus alginus*. *Ethology* **105**, 439–447.
- \*MARTÍN, J. & LÓPEZ, P. (2000a). Costs of refuge use affect escape decisions of Iberian rock lizards *Lacerta monticola*. *Ethology* **106**, 483–492.
- \*MARTÍN, J. & LÓPEZ, P. (2000b). Fleeing to unsafe refuges: effects of conspicuousness and refuge safety on the escape decisions of the lizard *Psammotromus alginus*. *Canadian Journal of Zoology* **78**, 265–270.
- \*MARTÍN, J. & LÓPEZ, P. (2003a). Changes in the escape responses of the lizard *Acanthodactylus erythrinus* under persistent predatory attacks. *Copeia* **2003**, 408–413.
- \*MARTÍN, J. & LÓPEZ, P. (2003b). Ontogenetic variation in antipredator behavior of Iberian rock lizards (*Lacerta monticola*): effects of body-size-dependent thermal-exchange rates and costs of refuge use. *Canadian Journal of Zoology* **81**, 1131–1137.
- MARTÍN, J., NEVE, L., FARGALLO, J. A., POLO, V. & SOLER, M. (2004). Factors affecting the escape behaviour of juvenile chinstrap penguins, *Pygoscelis antarctica*, in response to human disturbance. *Polar Biology* **27**, 775–781.
- MCBRAYER, L. D., MILES, D. B. & REILLY, S. M. (2007). The evolution of the foraging mode paradigm in lizard ecology. In *Lizard Ecology: The Evolutionary Consequences of Foraging Mode* (eds S. M. REILLY, L. D. MCBRAYER and D. B. MILES), pp. 508–521. Cambridge University Press, New York.
- MCCONNACHIE, S. & WHITING, M. J. (2003). Costs associated with tail autotomy in an ambush foraging lizard, *Cordylus melanotus melanotus*. *African Zoology* **38**, 57–65.
- MCELROY, E. J. & BERGMANN, P. J. (2013). Tail autotomy, tail size, and locomotor performance in lizards. *Physiological and Biochemical Zoology* **86**, 669–679.
- MEIRI, S. (2010). Length-weight allometries in lizards. *Journal of Zoology* **281**, 218–226.
- MØLLER, A. P. (2009). Basal metabolic rate and risk-taking behaviour in birds. *Journal of Evolutionary Biology* **22**, 2420–2429.
- MØLLER, A. P., CHRISTIANSEN, S. S. & MOUSSEAU, T. A. (2011). Sexual signals, risk of predation and escape behavior. *Behavioral Ecology* **22**, 800–807.
- NAGY, K. A. (2005). Field metabolic rate and body size. *Journal of Experimental Biology* **208**, 1621–1625.
- NAKAGAWA, S. & SANTOS, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology* **26**, 1253–1274.
- PERRY, G. (1999). The evolution of search modes: ecological versus phylogenetic perspectives. *American Naturalist* **153**, 98–109.
- \*PLASMAN, M., DUCHATEAU, M. J. H. M. & MACEDONIA, J. M. (2007). Anti-predation behaviour of Dickerson's collared lizard, *Crotaphytus dickersonae*. *Animal Biology* **57**, 231–246.
- POWELL, L. G. & RUSSELL, A. P. (1985). Field thermal ecology of the eastern short-horned lizard (*Phrynosoma douglassi brevirostre*) in southern Alberta. *Canadian Journal of Zoology* **63**, 228–238.
- PUNZO, F. (2007). Sprint speed and degree of wariness in two populations of whiptail lizards (*Aspidoscelis tessellata*) (Squamata: Teiidae). *Ethology Ecology & Evolution* **19**, 159–169.
- PYRON, R. A. & BURBRINK, F. T. (2014). Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecology Letters* **17**, 13–21.
- RAND, A. S. (1964). Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology* **45**, 863–864.
- \*REGALADO, R. (1998). Approach distance and escape behavior of three species of Cuban *Anolis* (Squamata, Polychrotidae). *Caribbean Journal of Science* **34**, 211–217.
- ROBERT, C. J. & STANLEY, T. D. (2006). *Meta-Regression Analysis: Issues of Publication Bias in Economics*. Blackwell Publishing, Oxford.
- \*ROCHA, C. F. D. & BERGALLO, H. G. (1990). Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria, Iguanidae) in an area of Amazonian Brazil. *Ethology Ecology & Evolution* **2**, 263–268.
- \*RÖDL, T., BERGER, S., MICHAEL ROMERO, L. & WIKELSKI, M. (2007). Tameness and stress physiology in a predator-naïve island species confronted with novel predation threat. *Proceedings of the Royal Society of London Series B* **274**, 577–582.
- RODRÍGUEZ-PRIETO, I. & FERNÁNDEZ-JURICIG, E. (2005). Effects of direct human disturbance on the endemic Iberian frog at individual and population levels. *Biological Conservation* **123**, 1–9.
- ROSENTHAL, R. (1979). The file drawer problem and tolerance for null results. *Psychological Bulletin* **86**, 638–641.
- ROSENTHAL, R. (1991). *Meta-Analytic Procedures for Social Research* (Rev. ed.). Second Edition. Russel Sage Foundation, New York.
- RUXTON, G. D., SHERRATT, T. N. & SPEED, M. P. (2004). *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals, and Mimicry*. Oxford University Press, New York.
- SAMIA, D. S. M., NOMURA, F. & BLUMSTEIN, D. T. (2013). Do animals generally flush early and avoid the rush? A meta-analysis. *Biology Letters* **9**, 20130016.
- SCHWARTZ, A. & HENDERSON, R. W. (1991). *Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History*. University of Florida Press, Gainesville.
- SCHWARZKOPF, L. & SHINE, R. (1992). Costs of reproduction in lizards: escape tactics and susceptibility to predation. *Behavioral Ecology and Sociobiology* **31**, 17–25.
- SCRIMGEUR, G. J., CASH, K. J. & CULP, J. M. (1997). Size-dependent flight initiation by a lotic mayfly in response to a predatory fish. *Freshwater Biology* **37**, 91–98.
- SHAFFER, H. B. (1978). Relative predation pressure on salamanders (Caudata: Plethodontidae) along an altitudinal transect in Guatemala. *Copeia* **1978**, 268–272.
- \*SHALLENBERGER, E. W. (1970). *Tameness in insular animals: a comparison of approach distances of insular and mainland Iguanid lizards*. PhD Dissertation in Zoology: University of California Los Angeles.
- SINERVO, B., HEDGES, R. & ADOLPH, S. C. (1991). Decreased sprint speed as a cost of reproduction in the lizard *Sceloporus occidentalis*: variation among populations. *Journal of Experimental Biology* **336**, 323–336.
- \*SMITH, G. R. (1996). Correlates of approach distance in the striped plateau lizard (*Sceloporus virgatus*). *Herpetological Journal* **6**, 56–58.
- \*SMITH, D. G. (1997). Ecological factors influencing the antipredator behaviors of the ground skink, *Scincella lateralis*. *Behavioral Ecology* **8**, 622–629.
- \*SMITH, G. R. & LEMOS-ESPINAL, J. A. (2005). Comparative escape behavior of four species of Mexican Phrynosomatid lizards. *Herpetologica* **61**, 225–232.
- \*SNELL, H. L., JENNINGS, R. D., SNELL, H. M. & HARCOURT, S. (1988). Intrapopulation variation in predator-avoidance performance of Galapagos lava lizards: the interaction of sexual and natural selection. *Evolutionary Ecology* **2**, 353–369.
- \*SREEKAR, R. & QUADER, S. (2013). Influence of gaze and directness of approach on the escape responses of the Indian rock lizard, *Psammophilus dorsalis* (Gray, 1831). *Journal of Biosciences* **38**, 829–833.

- STAMPS, J. A. (1983). The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). *Behavioral Ecology and Sociobiology* **12**, 19–33.
- STANKOWICH, T. (2008). Ungulate flight responses to human disturbance: a review and meta-analysis. *Biological Conservation* **141**, 2159–2173.
- STANKOWICH, T. & BLUMSTEIN, D. T. (2005). Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society of London Series B* **272**, 2627–2634.
- STANKOWICH, T. & CARO, T. (2009). Evolution of weaponry in female bovids. *Proceedings of the Royal Society B* **276**, 4329–4334.
- STAPLEY, J. & KEOGH, J. S. (2004). Exploratory and antipredator behaviours differ between territorial and nonterritorial male lizards. *Animal Behaviour* **68**, 841–846.
- STEBBINS, R. C. (2003). *A Field Guide to Western Reptiles and Amphibians*. Houghton Mifflin, Boston.
- STILLER, R. B. (2011). *The Ontogeny of Escape Responses and Locomotor Performance in *Sceloporus woodi**. Georgia Southern University, Statesboro.
- STONE, P. A., SNELL, H. L. & SNELL, H. M. (1994). Behavioral diversity as biological diversity: introduced cats and lava lizard wariness. *Conservation Biology* **8**, 569–573.
- STUART-FOX, D., MOUSSALLI, A. & WHITING, M. J. (2008). Predator-specific camouflage in chameleons. *Biology Letters* **4**, 326–329.
- \*THAKER, M., LIMA, S. L. & HEWS, D. K. (2009). Alternative antipredator tactics in tree lizard morphs: hormonal and behavioural responses to a predator encounter. *Animal Behaviour* **77**, 395–401.
- TULLBERG, B. S., MERILAITA, S. & WIKLUND, C. (2005). Aposematism and crypsis combined as a result of distance dependence: functional versatility of the colour pattern in the swallowtail butterfly larva. *Proceedings of the Royal Society of London Series B* **272**, 1315–1321.
- VAN BERKUM, F. H. (1988). Latitudinal patterns of thermal sensitivity of sprint speed in lizards. *American Naturalist* **132**, 327–343.
- VAN DAMME, R., BAUWENS, D. & VERHEY, R. F. (1989). Effect of relative clutch mass on sprint speed in the lizard *Lacerta vivipara*. *Journal of Herpetology* **23**(4), 459–461.
- VERVUST, B., GRBAC, I. & VAN DAMME, R. (2007). Differences in morphology, performance and behaviour between recently diverged populations of *Podarcis sicula* mirror differences in predation pressure. *Oikos* **116**, 1343–1352.
- VIECHTBAUER, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* **36**, 1–48.
- VITT, L. J., PIANKA, E. R., COOPER, W. E. JR. & SCHWENK, K. (2003). History and the global ecology of squamate reptiles. *American Naturalist* **162**, 44–60.
- WESTON, M. A., MCLEOD, E. M., BLUMSTEIN, D. T. & GUAY, P. J. (2012). A review of flight-initiation distances and their application to managing disturbance to Australian birds. *Emu* **112**, 269–286.
- WHITE, C. R. & SEYMOUR, R. S. (2003). Mammalian basal metabolic rate is proportional to body mass<sup>2/3</sup>. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 4046–4049.
- WHITING, M. J., LAILVAUX, S. P., REANEY, L. T. & WYMAN, M. (2003). To run or hide? Age-dependent escape behaviour in the common flat lizard (*Platysaurus intermedius wilhelmi*). *Journal of Zoology* **260**, 123–128.
- WILLIAMS, E. E. (1972). The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. *Evolutionary Biology* **6**, 47–89.
- WILLIAMS, E. E. (1983). Ecomorphs, faunas, island size, and diverse end points in island radiations of Anolis. In *Lizard Ecology: Studies of a Model Organism* (eds R. B. Huey, E. R. Pianka and T. W. Schoener), pp. 326–370. Harvard University Press, Cambridge.
- WILLIAMS, D. M., SAMIA, D. S. M., COOPER, W. E. JR. & BLUMSTEIN, D. T. (2014). The flush early and avoid the rush hypothesis holds after accounting for spontaneous behavior. *Behavioral Ecology* **25**, 1136–1147.
- WILSON, B. S. (1992). Tail injuries increase the risk of mortality in free-living lizards (*Uta stansburiana*). *Oecologia* **92**, 145–152.
- WITTER, M. S., CUTHILL, I. C. & BONSER, R. H. C. (1994). Experimental investigations of mass-dependent predation risk in the European starling, *Sturnus vulgaris*. *Animal Behaviour* **48**, 201–222.
- YDENBERG, R. C. & DILL, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior* **16**, 229–247.
- \*ZANI, P. A., JONES, T. D., NEUHAUS, R. A. & MILGROM, J. E. (2009). Effect of refuge distance on escape behavior of side-blotched lizards (*Uta stansburiana*). *Canadian Journal of Zoology* **87**, 407–414.

## VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

**Figure S1.** PRISMA flow diagram describing the literature search.

**Figure S2.** Phylogenetic tree of lizards used in the phylogenetic meta-analysis.

**Table S1.** Complete data set used for meta-analysis.

**Table S2.** Summary results of the phylogenetic meta-analyses.

**Table S3.** Corrected Akaike's information criteria of the mixed-effect phylogenetic meta-analyses including the indicated covariates.

**Appendix S1.** Details and predictions of the covariates used in the analyses.

(Received 22 July 2014; revised 28 November 2014; accepted 11 December 2014; published online 25 January 2015)