

# Fear in animals: a meta-analysis and review of risk assessment

Theodore Stankowich<sup>1,\*</sup> and Daniel T. Blumstein<sup>2</sup>

<sup>1</sup>*Animal Behavior Graduate Group, Department of Psychology, University of California, One Shields Avenue, Davis, CA 95616, USA*

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

The amount of risk animals perceive in a given circumstance (i.e. their degree of 'fear') is a difficult motivational state to study. While many studies have used flight initiation distance as a proxy for fearfulness and examined the factors influencing the decision to flee, there is no general understanding of the relative importance of these factors. By identifying factors with large effect sizes, we can determine whether anti-predator strategies reduce fear, and we gain a unique perspective on the coevolution of predator and anti-predator behaviour. Based on an extensive review and formal meta-analysis, we found that predator traits that were associated with greater risk (speed, size, directness of approach), increased prey distance to refuge and experience with predators consistently amplified the perception of risk (in terms of flight initiation distance). While fish tolerated closer approach when in larger schools, other taxa had greater flight initiation distances when in larger groups. The presence of armoured and cryptic morphologies decreased perception of risk, but body temperature in lizards had no robust effect on flight initiation distance. We find that selection generally acts on prey to be sensitive to predator behaviour, as well as on prey to modify their behaviour and morphology.

**Keywords:** anti-predator behaviour; fear; flight initiation distance; meta-analysis; risk perception

## 1. INTRODUCTION

Flight initiation distance is the distance at which an animal begins to flee from an approaching predator (Ydenberg & Dill 1986). Because it is relatively easy to systematically approach animals until they flee, and because flight initiation distance is correlated with other key aspects of escape behaviour (e.g. scanning rate—Fernández-Juricic & Schroeder 2003; alert distance (i.e. distance at which prey become alert to an approaching threat)—Blumstein *et al.* 2005), flight initiation distance is an excellent metric with which to quantify an individual's fearfulness in a particular circumstance. This easy-to-measure metric has spawned a considerable theoretical literature, with a main goal being to evaluate hypotheses about optimal escape theory (Ydenberg & Dill 1986). Wildlife managers also use flight initiation distance to identify set-back zones—areas beyond which species are not impacted by humans (Rodgers & Smith 1995; Fernández-Juricic *et al.* 2005).

Despite this large literature, there has been no attempt at a synthesis to identify the relative importance of various factors that influence fearfulness in animals. Thus, we do not generally know the degree to which prey behaviour or conditional changes (e.g. in morphology or experience) reduce perceptions of risk (i.e. the current probability of being captured during a predatory encounter) compared to changes in predator behaviour. If prey defences coevolve with predator hunting tactics, we might expect them to have similar effect sizes. Moreover, we currently do not know how prey respond to changes in predator behaviour (Lima 2002).

We do know that there are species-specific effects for many factors and it is thus difficult to draw generalizations about these factors. For instance, some reptiles tolerate closer approach when warm (*Anolis lineatopus*, Rand 1964; *Tropidurus oreadicus*, Rocha & Bergalo 1990), which is consistent with greater agility and a greater ability to escape; other species, when cool, tolerate closer approach before fleeing (*Lophognathus temporalis*: Blamires 1999), which itself is consistent with another strategy of relying on crypsis when the cost of locomotion is high. At this point it is premature to conclude how temperature influences flight. Another issue is identifying the effect of group size on fearfulness. Do animals generally feel safer in large groups, as would be predicted by some models of predation hazard assessment (e.g. risk dilution models: Foster & Treherne 1981; Godin 1986)? Empirical evidence is mixed because some species tolerate a closer approach when in larger groups (Spottail shiner *Notropis hudsonius*; Seghers 1981), while other species are seemingly better able to detect approaching threats in groups and thus, initiate flight at a greater distance (brent geese *Branta bernicla*, Owens 1977; house sparrow *Passer domesticus*, Barnard 1980; *Macaca* spp., Schaik *et al.* 1983). The high variance in the effect of group size on flight initiation distance has been attributed to the fact that many other variables contribute to optimal group size (Ydenberg & Dill 1986).

We conducted a formal meta-analysis, where we estimated the effect sizes of various factors known to influence flight initiation distance. We asked the following broad questions.

\* Author for correspondence (tstankowich@ucdavis.edu).

- (i) Are animals relatively more responsive to characteristics associated with their predators, or with external factors, such as group size and the distance they are from a refuge, over both of which they have control? This is an important question because it identifies the degree to which factors like habitat selection impact the effectiveness of different anti-predator strategies.
- (ii) How important are physical condition and morphological adaptations like armour or crypsis in explaining variation in flight initiation distance? While it is generally assumed that crypsis and armour make animals safer, do these morphological adaptations generally increase the perceived level of safety?
- (iii) A large literature has examined the effects of body temperature or ambient temperature on reptile escape behaviour. How important is this? Are reptiles at lesser or greater at risk as temperature increases and locomotor ability increases?
- (iv) How important is the experience with predators for flight initiation distance? Individuals may habituate or sensitize (i.e. perceive greater risk) to repeated exposure. Can any generalizations be drawn about the effect of experience with predators?

By answering these four broad questions, we attempt to identify general factors that influence fearfulness in animals, and the degree to which they are generally important across taxa. We will identify those taxa in which homogeneous effects are found, and we will identify species or studies that have idiosyncratic results. Thus, our review and meta-analysis allow us to begin to identify those factors that influence the evolution of flight initiation distance and fearfulness in animals in general, and determine the relative importance of each effect in predicting flight responses.

## 2. MATERIAL AND METHODS

### (a) *Data collection*

To obtain data, we first gathered the studies cited in Ydenberg & Dill's (1986) original review of flight initiation distance and searched the Web of Science ([isiknowledge.com](http://isiknowledge.com)) for all references citing the review. In the literature, flight initiation distance has also been termed 'flight distance' (e.g. Hediger 1964), 'approach distance' (e.g. Cooper 1997), 'reaction distance' (e.g. Hurley & Hartline 1974), 'escape distance' (e.g. Handeland *et al.* 1996) and 'flush distance' (e.g. Holmes *et al.* 1993), and the ambiguity in the literature regarding these terms has come under recent scrutiny (Taylor & Knight 2003). We searched Biosis reviews for papers citing these terms and extracted relevant citations from papers gathered through these means. We found 116 publications, published prior to 31 December 2003, which examined the influence of any environmental, predatory or prey condition-based factor on flight initiation distance. We included both studies that presented empirical tests of each factor and their statistical results and studies that simply reported an observational effect of a factor on flight distance. We then pre-identified a list of factors (see electronic supplementary material: 'factors investigated') to be analysed with meta-analysis. For the analysis, we selected factors that: (i) have been studied in a wide range of species, (ii) seemed to have some consistency

(i.e. low experimental variation; Osenberg *et al.* 1999) in the way they were measured (e.g. consistent: predator speed usually contrasted fast versus slow approaches; inconsistent: numerous measures of habitat type) and (iii) were likely to be targets of natural selection based on the economic theory of flight (Ydenberg & Dill 1986), specifically, factors that directly and most strongly should affect variation in the level of threat posed during predatory encounters. The final list included: predator speed, size, directness of approach, prey distance to refuge, prey group size, presence of armour or crypsis, temperature in reptiles, predator population density, and sequential approaches by the predator. A full description and rationale for each factor studied is described in the electronic supplementary material. Sixty-one (53%) of the original 116 studies were used in our meta-analyses. Full tables of all relevant references collected, their findings, and the  $r$  and  $N$  values gathered from each are given in the electronic supplementary material.

### (b) *Analyses*

The Pearson's product-moment correlation coefficient,  $r$ , was chosen as an appropriate measure of effect size (Hunter *et al.* 1982; Rosenthal 1991), since it has been shown recently to be appropriate for analysing results from behavioural and psychological studies (Fiske *et al.* 1998; Møller & Saino 2004; Segerstrom & Miller 2004) and the question being addressed in this study concerned an immediate effect (Osenberg *et al.* 1999) on flight decisions. For our studies,  $r$  is the magnitude of the effect on perceived risk of moving from a low-risk condition (control) to a high-risk condition (treatment). *Sensu* Segerstrom & Miller (2004), coefficients were obtained for each study, when possible, in the following ways (in order of preference): (i) direct reporting of  $r$ ,  $R^2$ , or partial correlation; (ii) mean and variance data (s.e. or s.d.) reported in the text or figures converted to  $r$  using methods in Rosenthal (1991); (iii) other test statistics (e.g.  $F$ ,  $U$ ,  $t$ ,  $\chi^2$ ) converted to  $r$  using methods in Rosenthal (1991); (iv) exact  $p$ -values converted to  $r$  using META-ANALYSIS 5.3 (Ralf Schwarzer: [http://userpage.fu-berlin.de/~health/meta\\_e.htm](http://userpage.fu-berlin.de/~health/meta_e.htm)). Studies that simply reported that there 'was an effect' or there 'was no effect',  $p > 0.05$  or  $p < 0.05$ , or only stated observationally that there was or was not a difference in flight initiation distance were excluded from analyses.

We performed meta-analyses by the Schmidt-Hunter method (Hunter & Schmidt 1990), where effect sizes from individual studies are weighted by their sample size to the proportion of the total sample size of the meta-analysis; weighted tests are the most precise and powerful meta-analytic procedures (Gurevitch & Hedges 1999). We estimated the observed standard deviation of effect sizes (Hunter & Schmidt 1990) and tested the significance of results using the  $Z$  test (Rosenthal 1984). Some studies report flight initiation data broken down by year, site, or other treatment effect; when combination of results across categories was inappropriate or not possible, we treated these results as independent studies in our analyses (*sensu* Fiske *et al.* 1998). For each weighted mean  $r$ , we calculated the fail-safe number of studies with an overall mean effect size equal to zero that would need to be filed away (i.e. unpublished) in order to reduce the observed effect size to a non-significant level ( $p < 0.05$ ; Rosenthal 1991). To test for the homogeneity (i.e. the amount of constancy or variation in  $r$ -scores) of results across studies, we calculated the  $I^2$  statistic (following Higgins *et al.* 2003). Negative values of  $I^2$  were set

Table 1. Effect size ( $r$ ), standard deviation of effect size (s.d.),  $Z$  score to test for significant differences from zero,  $I^2$  to judge degree of heterogeneity in effect sizes, total number of studies ( $K$ ), total combined sample size for all studies (total  $N$ ), fail-safe number: the number of studies with a mean effect of zero to make the observed effect insignificant ( $p > 0.05$ ), and a correlation between the effect size and  $\log(n)$  of each study to test for heterogeneity of results (Spearman's  $\rho$ ). ( $N$ , total sample size of all studies combined;  $n$ , sample size of an individual study.)  
(\* $p < 0.05$ , \*\* $p < 0.001$ ; na: sample size too small for test.)

factor	$r$	s.d.	$Z$	$I^2$	$K$	total $N$	fail-safe no.	spear $\rho$
predatory effects (combined)	0.32	0.26	10.24**	68.7%	28	958	902 <sup>a</sup>	0.05
predator speed	0.38	0.36	6.89**	84.1%	10	315	140 <sup>a</sup>	0.03
exclude mammals	0.60	0.17	9.66**	32.0%	8	210	171 <sup>a</sup>	0.44
reptiles only	0.67	0.07	9.75**	0%	4	159	102 <sup>a</sup>	-0.80
predator directness	0.29	0.19	5.49**	32.0%	11	356	84 <sup>a</sup>	0.21
excluding outlier	0.31	0.14	5.90**	0%	10	344	112 <sup>a</sup>	0.10
predator size	0.34	0.10	5.75**	0%	7	277	66 <sup>a</sup>	0.04
refuge distance	0.43	0.26	13.59**	87.3%	17	907	1302 <sup>a</sup>	-0.48
group size	-0.01	0.31	-0.33	82.4%	16	964	-5	-0.41
exclude fish	0.15	0.19	4.00**	60.0%	12	689	100 <sup>a</sup>	-0.69*
fish only	-0.42	0.07	-7.22**	0%	4	275	48 <sup>a</sup>	-0.60
prey defence (combined)	0.34	0.09	8.66**	0%	7	613	181 <sup>a</sup>	-0.46
presence of armour crypsis	0.33	0.16	3.99**	55.8%	3	138	17	na
crypsis	0.34	0.05	15.28**	0%	4	475	82 <sup>a</sup>	-0.60
temp. in lizards	0.05	0.31	1.72*	87.2%	18	1096	-18	0.37
experience (combined)	0.38	0.26	28.42**	92.0%	44	5141	8997 <sup>a</sup>	-0.01
predator density	0.33	0.24	20.65**	89.3%	30	3701	3893 <sup>a</sup>	-0.11
sequential approach	0.47	0.41	8.96**	93.7%	7	330	99 <sup>a</sup>	0.21

<sup>a</sup> robust effect (Rosenthal 1991).

to 0% so that  $I^2$  varied between 0% (no heterogeneity: little variation in individual  $r$ -scores) and 100% (large heterogeneity: high variation in individual  $r$ -scores). We also used the rank correlation test of Begg & Mazumdar (1994) to examine the relationship between standardized effect size and sample size; negative correlations indicate that there were fewer than expected studies with negative effects at low sample sizes, another indication of heterogeneity in effect size. When results were found to be heterogeneous, we examined individual study effect sizes using cluster analyses. For these, we used META-ANALYSIS 5.3 and interpreted clusters at the 5% level of significance. When appropriate, we subdivided taxonomic groups either by exclusion or inclusion of certain taxa. We then reran the meta-analyses as described above. All meta-analyses were computed using META-ANALYSIS 5.3.

### 3. RESULTS

In most cases, we found medium (Cohen 1988) estimates of effect size (table 1) and our analyses were robust in that fail-safe numbers were substantial. Below we address our main questions.

**(a) Are animals more responsive to characteristics associated with their predators, or with external factors over which they have more control, such as group size, or their distance from a refuge?**

In general, animals are sensitive to both predator behaviour and external factors over which they have more control when assessing predation risk. The distance of prey from their refugia had a large ( $r = 0.43$ ), significant ( $p < 0.0001$ ), and positive effect on flight initiation distance; animals far from their refugia systematically

fled at greater distances. We also found a number of studies reporting effects of patch quality and costs of leaving. Typically, non-territorial animals and non-feeding animals initiate flight sooner (i.e. they have larger flight initiation distances) than individuals engaged in combat, guarding territories or mates, or feeding (electronic supplementary material). The effect of refuge distance was larger than the effects of predator speed ( $r = 0.38$ ), or directness ( $r = 0.29$ ), or all predatory effects combined ( $r = 0.32$ ; table 1). However, reptiles were exceptionally sensitive to the speed at which predators approached them ( $r = 0.67$ ). Relative predator size had a modest effect size ( $r = 0.34$ ) with larger predators inducing greater flight initiation distances than smaller predators. Many studies also reported an effect of predator species or type on flight initiation distance (electronic supplementary material), however, since most were comparisons between humans and animals or machines, conclusions about the degree of threat posed are less clear. Overall, while group size had no significant effect size ( $r = -0.01$ ,  $p > 0.05$ ), when group size was subdivided along taxonomic lines, we found that fish tolerated closer approach when grouped ( $r = -0.42$ ,  $p < 0.001$ ), and other taxa were more sensitive when grouped and fled at greater distances ( $r = 0.15$ ,  $p < 0.001$ ).

**(b) How important are physical condition and morphological adaptations like armour or crypsis in explaining variation in flight initiation distance?**

Morphological and behavioural defences against predators effectively reduce prey's perception of risk. We found a medium-sized effect ( $r = 0.34$ ) when we combined defences and consistent results for both the presence of armour and crypsis when examined alone. Additionally, the majority of studies found that large animals and

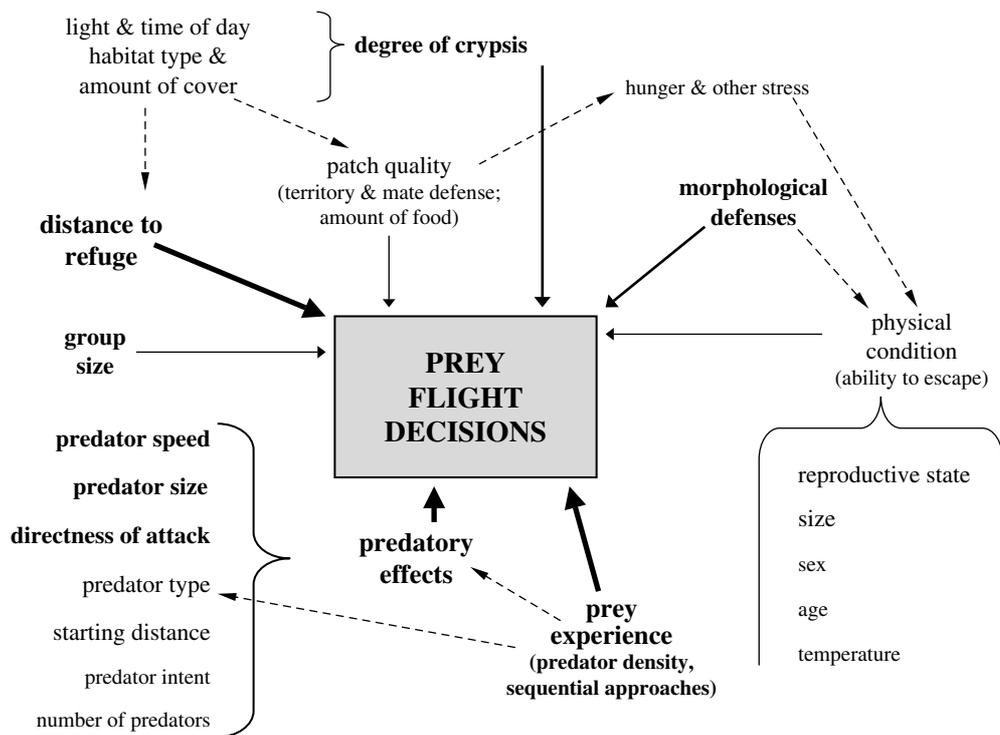


Figure 1. Summary of potential factors identified to influence flight initiation distance in animals. Boldness and size of solid lines and fonts indicate the relative strengths of statistical and theoretical support for each relationship (i.e. bold and larger fonts indicate more important factors). Dotted lines indicate possible indirect relationships between factors.

animals in good condition (i.e. lizards with intact tails) have longer flight initiation distances than shorter animals or those in poor condition (electronic supplementary material). There appeared to be no cross-taxon effects of sex or reproductive state of the animal on flight initiation distance.

**(c) How generally important is body or ambient temperature in lizards?**

There was no consistent effect of body or ambient temperature in lizards ( $r=0.05$ ). Some species fled at greater distances when warm, others at shorter distances. There were no consistent effects in other taxa (electronic supplementary material).

**(d) How important is experience with predators on flight initiation distance?**

Overall, experience with predators increased the perception of risk by 38%. Prey were more sensitive to predators when predator density is reduced ( $r=0.33$ ), and when they were sequentially approached by predators ( $r=0.47$ ). Also there are consistent observational reports in avian species of greater flight initiation distances during hunting seasons than during other months (electronic supplementary material).

#### 4. DISCUSSION

The results of both the review and the meta-analyses suggest that predatory, environmental, conditional and experiential factors all have significant effects on flight initiation distance and that prey's responses to predator's threats are sensitive to variation in predator behaviour. While some specific effects are ubiquitous (e.g. refuge distance), others are taxon- or species-specific (e.g. group size). We summarize the results of our review graphically,

and identify how each factor directly and/or indirectly influences flight decisions in animals (figure 1). The combination of factors that are influential for any given species probably differs because prey can pay attention only to a limited number of external variables. Selection favours paying attention to one or a few factors by weighting or de-emphasizing factors to streamline decision-making (Bernays & Wcislo 1994). Certainly, rapid assessment and decision-making are important when confronted by a potential predator (Bouskila & Blumstein 1992). We have grouped factors into four main categories for analysis and review: aspects of the predator, physical condition of the organism, environmental factors and effects of experience and learning.

Predatory effects combined were found to contribute significantly and substantially to prey flight decisions because attributes of a predator directly relate to the perceived threat of the situation. Specifically, the non-mammalian prey are particularly sensitive to the increased speed of an approaching predator: the perceived risk of non-mammals increases by 60% when a predator increases its speed—a strong cue that it poses a significant threat. Curiously, we found no empirical evidence in the literature that this effect holds in mammals. However, this result is not convincing. For example, Hutson (1982) found no effect of variable approach speed when merino sheep (*Ovis aries*) were tightly enclosed in a pen, which left only one study of no effect on which to base conclusions. We also found ubiquitous, homogeneous effects of directness of approach; perception of risk decreased by 31% when a predator appeared to be on a trajectory that bypassed the target prey. Directness of the path of approach is a strong indicator of the intent of the predator to attack or to bypass the focal animal. Interestingly, since we conducted our extensive literature review, new data have become available showing that in alpine birds found

in an open tussock grass community, four out of five species initiated flight at *greater* distances in response to an indirect approach (Fernández-Juricic *et al.* 2005). However, the publication of four negative results would be insufficient to overcome the original, large fail-safe number of studies (84) that would be required to eliminate or change our conclusion. The body size of the threat increases perceived risk. Larger size will emphasize the apparent size differences between predator and prey and can significantly increase the perceived loom rate of the predator (i.e. 'the rate of change of the angle subtended by the predator at the prey's eye'; Dill 1974a; 711), a proposed mechanism of speed assessment by prey.

Other possible measures of predator threat level are less supported in our review and meta-analysis. There is no evidence that predator posture during approach affects perceived risk. The only empirical study included in the review of number of predators (Scrimgeour *et al.* 1997) found no effect (but see Geist *et al.* 2005), and most studies comparing types of predators focused on the response to humans rather than natural predators.

Two studies, however, found that the degree of exposure of a predator's face can affect perceived risk (Burger & Gochfeld 1993), and that prey assign different levels of risk to different predator species, potentially based on hunting styles (Walther 1969). Prey seem also to evaluate the distance at which a predator begins its approach (Blumstein 2003). This nearly universal phenomenon is seen by the significant relationship between alert distance and flight initiation distance in many species (Fernández-Juricic *et al.* 2001; Blumstein 2003; Blumstein *et al.* 2004; Blumstein *et al.* 2005). Aspects of the predator's behaviour have a significant effect on the perceived risk of prey.

The meta-analysis clearly suggests that species that use refugia to escape from danger take into account the distance between themselves and safety when making flight decisions. Perceived risk increases by 43% when prey are far from rather than near a potential refuge. While the effect sizes were heterogeneous, the effect indicates that prey have some zone of safety around refugia, and when they venture farther from those refugia, their assessment of fear increases. This refuge-based perception of safety is strengthened by numerous studies showing longer flight initiation distances in more open habitats than when cover is greater (see 'Habitat Type/Amount of Cover'; electronic supplementary material, section C). Modelling and empirical data suggest that this positive relationship between refuge and flight initiation distance is stronger (greater slope) when the refuge is between the predator and prey, and weaker (smaller slopes) when the prey is between the predator and refuge (Kramer & Bonenfant 1997).

While the effect of refuge distance on flight initiation distance is highly consistent, the effect size of group size is varied to an equal extent: effect sizes ranged from  $-0.49$  to  $+0.81$ . There are many confounding effects on group size: dilution and food density effects have negative impacts on flight initiation distance and increased vigilance levels of a group have positive effects. There is no consensus among the studies, but looking at how fish respond, we see that larger groups resulted in smaller flight initiation distances: individuals gained an increased perception of safety when aggregated. Perhaps fish use

coordinated shoaling behaviour to systematically decrease risk differently than do other species: shoaling fish, in response to an increase in predation risk, perform a compaction response (Seghers 1974; Magurran & Pitcher 1987). If so, species that use coordinated defence (e.g. musk ox; *Ovibos moschatus*) against predators should feel safer when in larger groups and tolerate closer approach (n.b., however, there we found no examples of this effect), while other species, that use conspecific behaviour as cues about predation risk (e.g. water birds) should flush at greater distances when in larger groups (e.g. Owens 1977).

Varying levels of investment in a particular site or high heterogeneity in patch quality can also impact flight decisions (Ydenberg & Dill 1986). Animals defending territories, mates or young were more likely to have reduced flight initiation distances but this effect was not universal (e.g. Rodgers & Smith 1997). Males engaged in combat have reduced flight initiation distances due to reduced vigilance/attention to predators. There was very little empirical evidence for territory defence, but territory-guarding individuals allowed closer approach than non-territorial animals (Walther 1969; Shallenberger 1970). Patch quality is also dependent upon how much food it holds. When there are large or numerous food items available, an animal will be less likely to leave, since it is less likely to find such a resource elsewhere (Cooper *et al.* 2003). Between the strong effect of refuge distance in most species and more species-specific evidence of effects of group size, habitat type and patch quality, there is significant evidence that the state of the surrounding environment can have a profound effect on the perception of fear by prey animals in predatory encounters.

Many physical aspects of prey have been hypothesized to affect flight initiation distance and risk perception in general. Meta-analyses showed that the presence of defensive armour and cryptic coloration decrease the amount of risk perceived by an animal in a given predatory encounter. There is also related evidence that increased crypsis via low lighting (electronic supplementary material, section D; Effect of Time & Light) and greater habitat cover (electronic supplementary material, section C; Effect of Habitat) can also decrease perceived risk and flight initiation distance. Clearly, the perception of having not been seen reduces fear in prey, and cryptic prey act as though potential predators will not detect them if they remain still. The physical condition of the animal affects its normal ability to escape in terms of speed, agility and endurance. Very few studies have directly addressed measures of condition (good versus poor). There is evidence from studies of tail autotomy in lizards suggesting that individuals with intact tails have longer flight initiation distances than those with autotomized tails, however, some studies found no effect of tail autotomy. The presence of a tail facilitates flight, and those lacking tails should have slower escape speeds; tail loss might thus result in a switch to a crypsis-based anti-predator strategy (but for further debate, see Burger & Gochfeld 1990; Kelt *et al.* 2002; Cooper 2003). Conversely, Kenward (1978) found that woodpigeons (*Columba palumbus*) in poor overall condition had longer flight initiation distances than those in good overall condition; this may indicate that in species where crypsis is not a viable strategy, animals with reduced ability to escape must flee sooner than those that are fully capable.

Other evidence for effects of the physical state of the animal on risk assessment are less robust; there is some consistency in the effect of large animals having longer flight initiation distances than small animals (larger animals may be at greater risk due to increased visibility, higher quality as potential prey, or reduced escape speeds) and there is no consistent effect of sex, age, stress or temperature. An individual's reproductive state may indeed play a role in perception of risk: in reptiles, gravid females had shorter flight initiation distances than other animals, and in mammals, females with young had longer distances than others. These results may indicate that a switching of anti-predator strategy occurs when pregnant or immediately after having given birth due to decreased locomotor abilities (gravid reptiles) or the need to encourage young with undeveloped escape tactics to flee sooner, allowing more time to reach safety. While some aspects of an animal's physical state have clear effects on risk perception (armour, cryptic colouration/habitat, and physical condition), most other factors that have been studied show marginal, if any, impacts on an animal's state of fear.

Habituation and experience with a predator significantly influences the perception of fear. While inter-species variation was high ( $I^2=89.3\%$ ), there was a moderate effect ( $r=0.33$ ) of predator density on flight initiation distance. Typically, populations with few predators flushed at longer distances than those where predators were common. All of the predator density studies classified humans as the predator and measured differences in flight initiation distance between populations that differed in human density. If these populations with high human density have become habituated to humans in a non-threatening context (e.g. in a park or recreation area), they are likely to perceive less risk when approached by a human than would an individual from a population where contact with humans is rare. However, if the prey have not become habituated to the predator, and the predatory species, whether at high density or low density, is always a potential threat, animals that are more experienced or live in higher density areas should perceive higher risk and have higher flight initiation distances. Dill's (1974b) study of zebra danios (*Brachydanio rerio*) demonstrates this point: fish with more experience with predators had longer flight initiation distances than fish with less experience. Likewise, most studies of populations where hunting by humans occurs, found that animals have longer flight initiation distances during months when hunting was permitted (electronic supplementary material; for reviews see Smit & Visser 1993; Fox & Madsen 1997). Therefore, in times or places where human presence is typically non-threatening, animals have generally lower flight initiation distances. While there is evidence of genetic effects on fear (beef cattle breeds had longer flight initiation distances than dairy breeds and switching rearing type had no effect on this outcome, Murphey *et al.* 1980), risk assessment appears to be a plastic process for predator-savvy prey. Similarly, the more certain an animal is that the approaching predator intends to attack, the more risk it will perceive: most animals have longer flight initiation distances on the subsequent approaches than they do on the initial approach ( $r=0.47$ ). However this effect is not universal (Paulissen 1995; Rodgers & Smith 1995).

Using meta-analyses of a systematic literature review, we have identified key factors associated with risk

perception in animals. We have shown that prey can reduce their perception of risk and fear via behavioural, morphological or experiential modifications to the same degree that predator behaviour can increase the perception of risk in prey. Life history experience with predators and natural selection sensitize prey to cues from predator behaviour that reveal something about the predator's intent or motivation, and to modify their own behaviour and morphology to reduce the level of threat a given predator poses. It is likely that an animal pays attention to a small subset of the factors we have reviewed to generate an estimate of the relative risk in any given predatory encounter. Future studies should focus on this complex decision making process and identify the trade-offs individuals make when assessing risk. Specifically, future research must be aimed at studying the interactions between these factors (e.g. Cooper *et al.* 2003) and must go beyond simply identifying significant factors to examine the relative importance of significant factors. Additionally, we believe that attention should be given to modelling risk assessment and flight decisions using Bayesian or dynamic state techniques in order to elucidate how the continuous influx of information about an approaching predator (e.g. behaviour, state, etc.) affects the likelihood that an animal will flee.

We thank T. Caro, J. Stankowich, and two anonymous reviewers for comments on a previous version. T.S. was supported by Block Grant Fellowships from the University of California-Davis. D.T.B. thanks the UCLA Division of Life Sciences for support.

## REFERENCES

- Barnard, C. J. 1980 Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Anim. Behav.* **28**, 295–309.
- Begg, C. B. & Mazumdar, M. 1994 Operating characteristics of a rank correlation test for publication bias. *Biometrics* **50**, 1088–1101.
- Bernays, E. A. & Wcislo, W. T. 1994 Sensory capabilities, information processing, and resource specialization. *Q. Rev. Biol.* **69**, 187–204.
- Blamires, S. J. 1999 Factors influencing the escape response of an arboreal agamid lizard of tropical Australia (*Lophognathus temporalis*) in an urban environment. *Can. J. Zool.* **77**, 1998–2003. (doi:10.1139/cjz-77-12-1998.)
- Blumstein, D. T. 2003 Flight-initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manag.* **67**, 852–857.
- Blumstein, D. T., Fernandez-Juricic, E., LeDee, O., Larsen, E., Rodriguez-Prieto, I. & Zugmeyer, C. 2004 Avian risk assessment: effects of perching height and detectability. *Ethology* **110**, 273–285.
- Blumstein, D. T., Fernández-Juricic, E., Zollner, P. A. & Garity, S. C. 2005 Interspecific variation in anti-predator behaviour and human-wildlife coexistence. *J. Appl. Ecol.*
- Bouskila, A. & Blumstein, D. T. 1992 Rules of thumb for predation hazard assessment: predictions from a dynamic model. *Am. Nat.* **139**, 161–176. (doi:10.1086/285318.)
- 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. *J. Comp. Psychol.* **104**, 388–394. (doi:10.1037//0735-7036.104.4.388.)
- Burger, J. & Gochfeld, M. 1993 The importance of the human face in risk perception by black iguanas, *Ctenosaura similis*. *J. Herpetol.* **27**, 426–430.

- Cohen, J. 1988 *Statistical power analysis for the behavioral sciences*. Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Cooper Jr, W. E. 1997 Escape by a refuging prey, the broad-headed skink (*Eumeces laticeps*). *Can. J. Zool.* **75**, 943–947.
- Cooper Jr, W. E. 2003 Shifted balance of risk and cost after autotomy affects use of cover, escape, activity, and foraging in the keeled earless lizard (*Holbrookia propinqua*). *Behav. Ecol. Sociobiol.* **54**, 179–187.
- Cooper Jr., W. E., 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 lizards, *Cnemidophorus murinus*. *Behav. Ecol.* **14**, 288–293.
- Dill, L. M. 1974a The escape response of the zebra danio (*Brachydanio rerio*). I. The stimulus for escape. *Anim. Behav.* **22**, 711–722.
- Dill, L. M. 1974b The escape response of the zebra danio (*Brachydanio rerio*). II. The effect of experience. *Anim. Behav.* **22**, 723–730.
- Fernández-Juricic, E. & Schroeder, N. 2003 Do variations in scanning behavior affect tolerance to human disturbance? *Appl. Anim. Behav. Sci.* **84**, 219–234.
- Fernández-Juricic, E., Jimenez, M. D. & Lucas, E. 2001 Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environ. Conserv.* **28**, 263–269.
- Fernández-Juricic, E., Venier, P., Renison, D. & Blumstein, D. T. 2005 Sensitivity of wildlife to spatial patterns of recreationist behavior: a critical assessment of minimum approaching distances and buffer areas for grassland birds. *Biol. Conserv.* **125**, 225–235. (doi:10.1016/j.biocon.2005.03.020.)
- Fiske, P., Rintamäki, P. T. & Karvonen, E. 1998 Mating success in lekking males: a meta-analysis. *Behav. Ecol.* **9**, 328–338.
- Foster, J. B. & Treherne, J. E. 1981 Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* **293**, 466–467. (doi:10.1038/293466a0.)
- Fox, A. D. & Madsen, J. 1997 Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. *J. Appl. Ecol.* **34**, 1–13.
- Geist, C., Liao, J., Libby, S. & Blumstein, D. T. 2005 Does intruder group size and orientation affect flight initiation distance in birds? *Anim. Biodivers. Conserv.* **28**, 67–71.
- Godin, J.-G. J. 1986 Risk of predation and foraging behaviour in shoaling banded killifish (*Fundulus diaphanous*). *Can. J. Zool.* **64**, 1675–1678.
- Gurevitch, J. & Hedges, L. V. 1999 Statistical issues in ecological meta-analyses. *Ecology* **80**, 1142–1149.
- Handeland, S. O., Järvi, T., Fernö, A. & Stefansson, S. O. 1996 Osmotic stress, antipredator behaviour, and mortality of Atlantic salmon (*Salmo salar*) smolts. *Can. J. Fish. Aquat. Sci.* **53**, 2673–2680.
- Hediger, H. 1964 *Wild animals in captivity*. New York: Dover Publications Inc.
- Higgins, J. P. T., Thompson, S. G., Deeks, J. J. & Altman, D. G. 2003 Measuring inconsistency in meta-analyses. *BMJ* **327**, 557–560. (doi:10.1136/bmj.327.7414.557.)
- Holmes, T. L., Knight, R. L., Stegall, L. & Craig, G. R. 1993 Responses of wintering grassland raptors to human disturbance. *Wildl. Soc. Bull.* **21**, 461–468.
- Hunter, J. E. & Schmidt, F. L. 1990 *Methods of meta-analysis: correcting error and bias in research findings*. Newbury Park, CA: Sage Publications.
- Hunter, J. E., Schmidt, F. L. & Jackson, G. B. 1982 *Meta-analysis: cumulating research findings across studies*. Beverley Hills, CA: Sage Publications.
- Hurley, A. C. & Hartline, P. H. 1974 Escape response in the damselfish *Chromis cyanea* (Pisces: Pomacentridae): a quantitative study. *Anim. Behav.* **22**, 430–437.
- Hutson, G. D. 1982 'Flight distance' in merino sheep. *Anim. Prod.* **35**, 231–235.
- Kelt, D. A., Nabors, L. K. & Forister, M. L. 2002 Size-specific differences in tail loss and escape behavior in *Lidolaemus nigromaculatus*. *J. Herpetol.* **36**, 325–327.
- Kenward, R. E. 1978 Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *J. Anim. Ecol.* **47**, 449–460.
- Kramer, D. L. & Bonenfant, M. 1997 Direction of predator approach and the decision to flee a refuge. *Anim. Behav.* **54**, 289–295. (doi:10.1006/anbe.1996.0360.)
- Lima, S. L. 2002 Putting predators back into behavioral predator-prey interactions. *Trends Ecol. Evol.* **17**, 70–75.
- Magurran, A. E. & Pitcher, T. J. 1987 Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. *Proc. R. Soc. B* **229**, 439–465.
- Møller, A. P. & Saino, N. 2004 Immune response and survival. *Oikos* **104**, 299–304. (doi:10.1111/j.0030-1299.2004.12844.x.)
- Murphey, R. M., Duarte, F. A. M. & Penedo, M. C. T. 1980 Approachability of bovine cattle in pastures: breed comparisons and a breed × treatment analysis. *Behav. Genet.* **10**, 171–181. (doi:10.1007/BF01066267.)
- Osenberg, C. W., Sarnelle, O., Cooper, S. D. & Holt, R. D. 1999 Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* **80**, 1105–1117.
- Owens, N. W. 1977 Responses of wintering brent geese to human disturbance. *Wildfowl* **28**, 5–14.
- Paulissen, M. A. 1995 Comparative escape behavior of parthenogenic and gonochoristic *Cnemidophorus* in southern Texas. *Copeia* **1995**, 223–226.
- Rand, A. S. 1964 Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology* **45**, 863–864.
- Rocha, C. F. D. & Bergalo, H. G. 1990 Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria Iguanidae) in an area of Amazonian Brazil. *Ethol. Ecol. Evol.* **2**, 263–268.
- Rodgers Jr, J. A. & Smith, H. T. 1995 Set-back distances to protect nesting bird colonies from human disturbance in Florida. *Conserv. Biol.* **9**, 89–99. (doi:10.1046/j.1523-1739.1995.09010089.x.)
- Rodgers Jr, J. A. & Smith, H. T. 1997 Buffer zone distances to protect foraging and loafing waterbirds from human disturbance in Florida. *Wildl. Soc. Bull.* **25**, 139–145.
- Rosenthal, R. 1984 *Meta-analytic procedures for social research*, 1st edn. Newbury Park, CA: Sage Publications.
- Rosenthal, R. 1991 *Meta-analytic procedures for social research*, 2nd edn. New York: Russell Sage Foundation.
- Schaik van, C. P., van Noordwijk, M. A., Warsono, B. & Sutriano, E. 1983 Party size and early detection of predators in Sumatran forest primates. *Primates* **24**, 211–221.
- Scrimgeour, G. J., Cash, K. J. & Culp, J. M. 1997 Size-dependent flight initiation by a lotic mayfly in response to a predatory fish. *Freshwater Biol.* **37**, 91–98. (doi:10.1046/j.1365-2427.1997.d01-537.x.)
- Segerstrom, S. C. & Miller, G. E. 2004 Psychological stress and the human immune system: a meta-analytic study of 30 years of inquiry. *Psychol. Bull.* **130**, 601–630. (doi:10.1037/0033-2909.130.4.601.)
- Seghers, B. H. 1974 Schooling behavior in the guppy: an evolutionary response to predation. *Evolution* **28**, 486–489.
- Seghers, B. H. 1981 Facultative schooling behavior in the spottail shiner (*Notropis hudsonius*): possible costs and

- benefits. *Environ. Biol. Fish.* **6**, 21–24. (doi:10.1007/BF00001795.)
- Shallenberger, E. W. 1970 Tameness in insular animals: a comparison of approach distances of insular and mainland iguanid lizards. Ph.D. dissertation in zoology, UCLA, pp. 1–131.
- Smit, C. J. & Visser, G. J. M. 1993 Effects of disturbance on shorebirds: a summary of existing knowledge from the Dutch Wadden Sea and Delta area. *Wader Study Group Bull.* **68**, 6–19.
- Taylor, A. R. & Knight, R. L. 2003 Behavioral responses of wildlife to human activity: terminology and methods. *Wildl. Soc. Bull.* **31**, 1263–1271.
- Walther, F. R. 1969 Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Geunther 1884). *Behaviour* **34**, 184–221.
- Ydenberg, R. C. & Dill, L. M. 1986 The economics of fleeing from predators. *Adv. Study Behav.* **16**, 229–249.

The electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2005.3251> or via <http://www.journals.royalsoc.ac.uk>.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.