CHAPTER FIVE

FEAR, Spontaneity, and Artifact in Economic Escape Theory: A Review and Prospectus

William E. Cooper, Jr.[*,1], **Diogo S.M. Samia**[§], **Daniel T. Blumstein**[¶]
[*]Department of Biology, Indiana University and Purdue University, Fort Wayne, IN, USA
[§]Laboratory of Theoretical Ecology and Synthesis, Federal University of Goiás, Goiânia, Brazil
[¶]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA
[1]Corresponding author: e-mail address: cooperw@ipfw.edu

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1. INTRODUCTION

Decision-making by prey about when to begin fleeing when approached by a predator have been and are being studied intensively, producing a large theoretical and empirical literature (Cooper & Blumstein, 2015). Here, we review the cost-benefit models of economic escape theory, their successes, and some recent developments that challenge them. Escape theory, until very recently, has been limited to predictions about a single aspect of escape: the decision about when to start fleeing. However, that

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is only one aspect of escape. Escape occurs in a broader context of antipredatory defenses that include the signals some prey give to predators before fleeing, the distance at which prey flee predators, the choice of escape direction and speed, the choice of whether to use a refuge and, if so, how long to remain there, strategies used during pursuit, and defenses available if overtaken by a predator. The scope of economic escape theory has mostly been limited to studying flight initiation distance (FID = predator–prey distance when escape begins) and hiding time (the length of time that prey remain in a refuge or burrow after fleeing to it).

Economic escape theory provides many testable predictions. The use of researchers as simulated predators, which is feasible because many species view people as predators and flee from them (Frid & Dill, 2002), has facilitated study of escape decisions. The ease of collecting data and the tight linkage between empirical studies and the predictions of economic models have led to rapid advances and created a remarkably comprehensive understanding of the adaptive basis of the decision by prey as to when to begin fleeing.

Although major predictions of the economic escape theory are well supported, some new observations and theoretical considerations have emerged over the past decade. Prior to 2003, researchers had assumed that FID was unrelated to predator starting distance (SD, which is the distance of the prey from the predator at the initiation of approach), and paid little attention to the prey's awareness of and vigilance toward predators, which is estimated empirically by alert distance (AD, which is the distance from the predator when the prey responds by looking toward it). Another important point raised recently was how the movements of prey that are unrelated to the presence of a predator might affect conclusions about the predictions of economic escape theory. Understanding the relationships among FID, AD, SD, and spontaneous movements unrelated to presence of a predator has become increasingly important in the last decade and researchers have grappled with their theoretical and practical implications. Here, we briefly outline the history of escape theory, examine the new and currently unresolved issues, and identify studies that may settle remaining issues.

2. A BRIEF HISTORY OF ECONOMIC ESCAPE THEORY

Escape behavior is a long-standing topic of biological interest. Darwin (1868) noted the loss of escape behavior in domesticated animals and the loss of some types of fleeing behaviors by animals that experienced frequent human interactions. By the end of the first third of the twentieth century, the literature on escape behavior was large enough to warrant a synthetic paper in which Hedigeer (1934) discussed the distances from predators at which prey became alert and at which they fled. Published information about escape behavior continued to accumulate over the next 50 years. While many studies identified factors that affected how closely a prey allowed a predator to approach before fleeing, they were not based on general theoretical principles.

With the demonstration of the utility of economic theory to behavioral ecology (e.g., Thornhill & Alcock, 1983; Stephens & Krebs, 1986), biologists began to think about escape behavior in terms of the competing effects of costs and benefits. It has long been clear that predation risk exerts strong natural selection on prey because the failure escape typically has disastrous consequences: death and loss of all future contribution to lifetime fitness. To that understanding was added the realization that fleeing too soon can result in a loss of fitness-enhancing benefits, such as finding food or courting a potential mate (Cooper, 1999, 2000). This loss is an opportunity cost. The opposing fitness consequences create a conflict that requires prey to decide the best moment at which to flee from an approaching predator. Natural selection is most likely to have favored those individuals who behaved optimally by escaping with the lowest opportunity cost.

These ideas led Ydenberg and Dill (1986) to develop a seminal graphical model of escape that was initially published in *Advances in the Study of Behavior*, and which still underpins our understanding of the economics of escaping from predators. More recently, models, in which prey make explicitly optimal escape decisions, have added to our understanding of escape and provided new predictions (Cooper & Frederick, 2007, 2010). All of these optimality models predict how close prey will permit predators to come before starting to flee (FID), where FID is determined by a trade-off between predation risk, costs of fleeing (i.e., the benefits lost by fleeing), and the prey's fitness as assessed by the prey while monitoring the predator's approach.

In the Ydenberg and Dill (1986) model, FID is predicted graphically from curves that relate the cost of not fleeing (which is primarily attributable to predation risk) and the cost of fleeing, to predator-prey distance (Figure 1(a)). In the following, we refer frequently to predation risk as a substitute for the cost of not fleeing. As a predator approaches, the risk increases. However, by fleeing when the predator is farther away, the prey forgoes

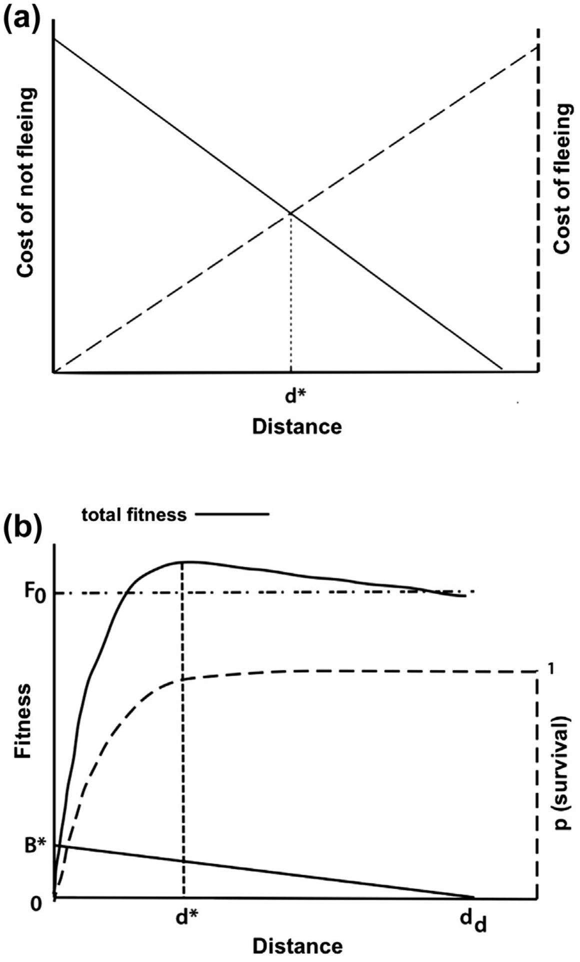

Figure 1 Graphs depicting the two main models of economic escape theory in which a prey monitors an approaching predator and selects a flight initiation distance (FID). (a) According to Ydenberg and Dill's (1986) graphical model, FID occurs when the predator reaches a distance where the cost of not fleeing and cost of fleeing are equal. *(After Cooper and Blumstein (2014).)* (b) Cooper and Frederick's (2007) optimality model of escape behavior predicts that prey select the FID that maximizes expected lifetime fitness at the end of the encounter. Fitness at any given distance is the prey's initial fitness (F_0) plus benefits gained during the approach by not fleeing (lower line ending with B*, the maximum benefit obtainable by not fleeing), conditioned by the probability of survival if the prey flees at a given distance. The total fitness can exceed F_0. The optimal FID occurs where the total fitness is maximized. *(After Cooper and Frederick (2007).)*

benefits to fitness that might be obtained by not fleeing. Therefore, as predator–prey distance increases, the risk curve decreases and the cost of fleeing curve increases. The predicted FID occurs at the intersection of the two curves, where risk and costs are equal (Figure 1(a)). The other economic (cost–benefit) model (Cooper & Frederick, 2007, 2010) predicts that prey select the FID that maximizes their expected fitness at the conclusion of the predator–prey encounter (Figure 1(b)). Prey, theoretically, can achieve higher fitness in this optimality model than in the graphical model, but the fitness components of the two models have not been measured. Regardless of their quantitative differences, these models make identical predictions at the ordinal level when the Ydenberg and Dill (1986) model is modified to take the prey's fitness into account (Cooper, 2015).

Compared to optimal foraging theory (Stephens & Krebs, 1986), and sexual selection theory (Andersson, 1994), where there has been a highly productive interplay between theoreticians and empiricists, the successes of economic escape theory have been relatively ignored by researchers in other fields and textbook authors. This is remarkable because it illustrates a similarly productive integration of theory and empirical research (Cooper & Blumstein, 2015).

Indeed, the cost–benefit models have stimulated hundreds of studies that support the predictions for predation risk and cost of fleeing, and the trade-off between risks and costs, for diverse prey and causal factors (see compilations in Stankowich & Blumstein, 2005; Samia, Blumstein, Stankowich, & Cooper, 2015). For example, robust evidence shows how the prey's decision to flee is affected by the directness of approach (Burger & Gochfeld, 1981; Fernández-Juricic, Venier, Renison, & Blumstein, 2005; Møller & Tryjanowski, 2014), approach speed (Lord, Waas, Innes, & Whittinghan, 2001; Hemmi, 2005), and persistence of predators (Cooper, 2010; Møller, 2010), as well as by the prey's conspicuousness (Martín & López, 1999; Ozel & Stynoski, 2011), distance from refuge (Dill, 1990; Cooper, 2000; Martín & López, 2003), body size (Plasman, Duchateau, & Macedonia, 2007; Gotanda, Turgeon, & Kramer, 2009), and locomotor abilities (Hawlena, Pérez-Mellado, & Cooper, 2009; Bateman & Fleming, 2011). These studies show that, within limitations imposed by the sensory capacities of prey, FID increases as risk increases. Fewer studies have focused on the cost of fleeing, but they show that prey have shorter FID when fleeing requires the abandonment of social (Brick, 1998; Cooper, 2009) or feeding opportunities (Scrimgeour & Culp, 1994; Cooper, Pérez-Mellado, & Hawlena, 2006).

For practical reasons, most studies of escape use human beings as simulated predators. Using human surrogate predators permit researchers to standardize the approaches across trials and easily control (or vary) levels of risk across experimental treatments. The latter is almost impossible to set up with natural predators. Although some prey have predator-specific escape responses (Stuart-Fox, Moussalli, & Whiting, 2008), the behavior of prey that are approached by humans generally matches the predictions of economic escape theory (Frid & Dill, 2002; Møller, Nielsen, & Garamszegi, 2007; Cooper, 2008a; Møller, Erritzøe, & Nielsen, 2010; Blumstein, Samia, Stankowich, & Cooper, 2015).

In addition to this theoretical success, the predictions of economic escape theory also have applied importance. As Blumstein and Fernandez-Juricic (2010) have pointed out, economic escape theory can be useful in identifying and defining set-back zones in parks, reserves, and recreation areas visited by people to reduce human impacts on wildlife. By determining factors that influence FID, FID can be used to identify locations within a managed area in which animals are not likely to respond to humans. By doing so, managers can create evidence-based buffer areas. The creation of large data sets of FID that have been collected for birds (e.g., Weston, McLeod, Blumstein, & Guay, 2012; McLeod, Guay, Taysom, Robinson, & Weston, 2013), and some other taxa (e.g., Stankowich & Blumstein, 2005; Samia et al., 2015) facilitates the creation of suggested buffer areas for many species. Additionally, it is possible to identify the human footprint on wildlife by understanding how human visitation influences FID (e.g., Li, Monclús, Maul, Jiang, & Blumstein, 2011; Blumstein, 2014). By this, we mean that animals naturally respond to humans at different distances and some habituate to certain types of human visitation while others sensitize. Again, these large databases of FID that have been collected permit managers to identify how and where species will respond negatively to humans in natural landscapes.

3. CURRENT CHALLENGES TO ECONOMIC ESCAPE THEORY

Despite the success of the economic models, studies of optimal escape decisions are complicated by factors that were not considered when the models were initially developed. One unpredicted recent discovery, that, in birds, the prey's FID was positively correlated with the predator's SD emerged after decades of field studies of escape behavior (Blumstein, 2003). Subsequent to the initial report (Blumstein, 2003), the same positive relationship between FID and SD or between FID and AD has been found in diverse taxa. A formal meta-analysis demonstrated that such effects are relatively large (Samia, Nomura, & Blumstein, 2013; Samia & Blumstein, 2015).

Initially, SD was used as a surrogate for AD, since, in some species, it is difficult to know whether a predator has been detected and is being monitored, as required by the economic models. Nevertheless, animals must base their escape decisions on AD, not SD. To incorporate the effect of the predator's SD on FID, Blumstein (2003) and Stankowich and Coss (2007) modified the Ydenberg and Dill (1986) model to include three ranges (zones) of predator-prey distance (Figure 2). In both models, prey in zone 3, where distances are longest, may be unaware of a predator or perceived risk may be too low to warrant continuous vigilance. In an intermediate range of predator-prey distance (zone 2), prey assess the risk and cost of fleeing as expected by the economic models. In zone 1, the closest of the three ranges, flight occurs immediately when a predator is detected. Immediate flight is interpretable by economic models as a response to risk greater than at the economic FID. The empirical finding that the slope of FID and AD or SD is one for very short predator-prey distance is consistent with the existence of zone 1 (e.g., Cooper, 2008b).

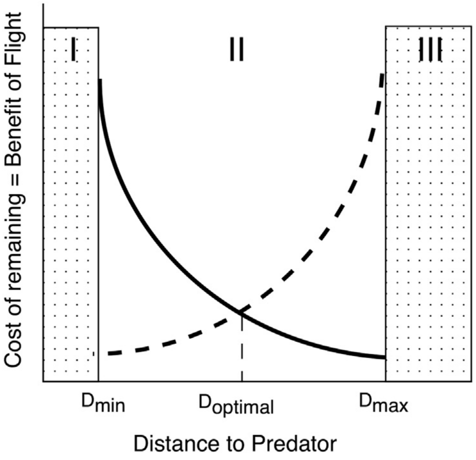

Figure 2 The three zones of predator-prey distance. In zone III the prey does not detect the predator or risk is too low to warrant monitoring. In zone II the prey makes economic decisions about FID based on costs of fleeing and or not fleeing. In zone I prey flee immediately upon detecting a predator. *From Blumstein (2003).*

The apparently simple finding of a positive relationship between FID and AD or SD has had unexpected important theoretical and practical implications for economic escape studies. The most immediate effect was that when testing the effect of a given risk or cost of fleeing factor on FID (e.g., speed of the predator's approach), researchers began to control for effects of AD or SD, either statistically (using it as a covariate in analyses; e.g., Blumstein, 2006; Glover, Weston, Maguire, Miller, & Christie, 2011), or experimentally (by standardizing the SD for experiments, using trials with fixed SD values to define experimental groups; e.g., McCleery, 2009; Cooper & Stankowich, 2010; Møller, 2012). While such statistical procedures are necessary to assess effects of risk and cost of fleeing on FID when SD varies, they do not explain how and why AD or SD affects the prey's decision to flee. We explore these issues by asking the four key questions about the relationships between FID, AD, and SD in the context of economic escape theory.

First, does the positive relationship between FID and AD or SD contradict the trade-off between predation risk and costs of fleeing predicted by economic escape theory? Does it imply that prey decisions take into account only reduction of risk by fleeing sooner? What is the underlying cause of the positive relationship between FID and AD or SD?

Second, the relationships among SD, AD, and FID are constrained by an envelope in which SD $\geq$ AD $\geq$ FID (Figure 3). For this reason, it has been suggested that positive relationships among these variables might constitute a mere mathematical artifact (Dumont, Pasquaretta, Réale, Bogliani, & Von Hardenberg, 2012). According to this idea, one would expect a positive relationship between FID and its constraining variables (i.e., AD and SD) even if there were no biologically meaningful relationships between them. This has important implications for both theory and methods of study. We explore these matters by asking whether the positive relationship between FID and its constraining variables is an artifact. If it is, what methodological approaches are needed to determine if a nonartifactual relationship exists?

Third, when the economic models were proposed, the possibility that prey may move spontaneously (i.e., for reasons other than the presence of the predator) as a predator approaches was ignored. Therefore, the positive relationship between FID and its constraining variables may arise from a "biological" artifact because a prey's spontaneous behavior may be recorded inaccurately as FID (Cooper, 2005). Movements made during a predator's approach, but before the prey has detected the predator (i.e., spontaneous

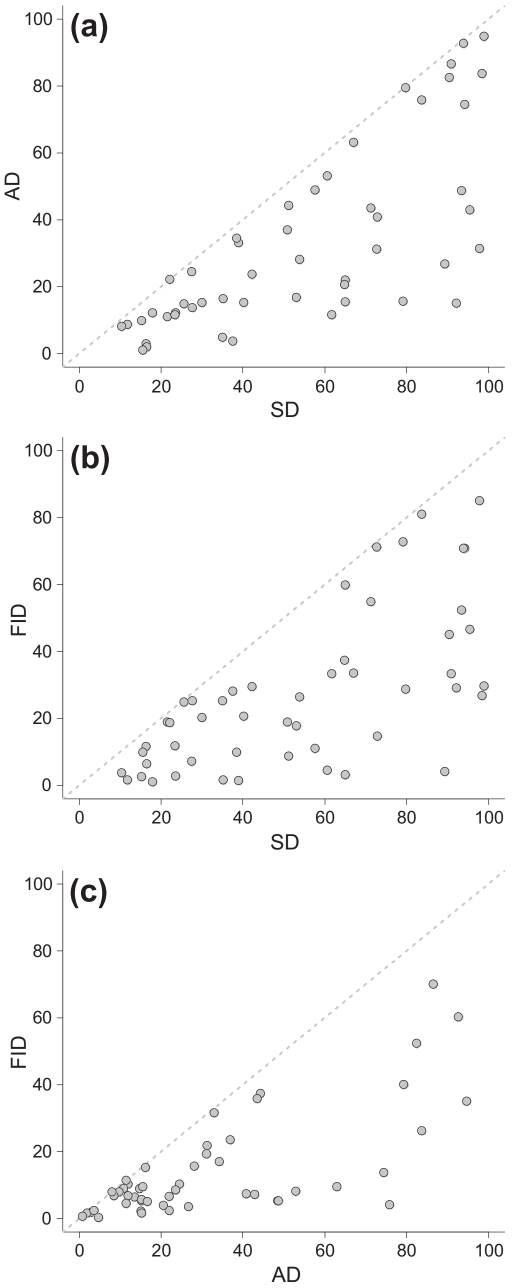

Figure 3 The envelope constraint between starting distance (SD), alert distance (AD), and flight initiation distance (FID). Relationships between (a) SD-AD, (b) SD-FID, and (c) AD-FID were generated with 50 random values extracted from a uniform distribution respecting the constraint SD $\geq$ AD $\geq$ FID. Variables were simulated as SD $\sim$ U(10, 100), AD $\sim$ U(0, SD), FID $\sim$ U(0, SD) for the SD-FID relationship, and FID $\sim$ U(0, AD) for the AD-FID relationship, where U(x, y) is the value for the variable by random selection from a uniform distribution. The dashed line identifies the 1:1 relationship that forms the upper boundary of the envelope in each graph.

movements), fall outside the scenario of economic escape theory, which applies to aware prey that are monitoring the predator. We use empirical evidence to assess whether spontaneous movement accounts for the positive relationship between FID and its constraining variables.

Fourth, it is sometimes difficult to know when a prey has detected a predator. Although SD is of real interest in some contexts (e.g., to test hypotheses related to spontaneous behaviors; Williams, Samia, Cooper, & Blumstein, 2014), SD is almost always used as a proxy for AD. This is important for work on many taxa, including reptiles and amphibians, where alertness does not often obviously increase as a predator approaches. Despite the high correlations that are typically found, the use of SD as a proxy for AD has been criticized recently (Dumont et al., 2012). It was suggested that different conclusions could be drawn about the effects of other factors (e.g., predator intensity) on FID, depending on which constraining variable was used as a covariate. If such an effect applies generally, it could invalidate past studies that used SD as a proxy for AD, as well as prevent future studies about optimal escape using taxa that do not express vigilance by alerting. The obvious question, then, is whether SD is a good proxy for AD in economic escape studies.

4. PUTATIVE BIOLOGICAL CAUSE OF THE FID-AD RELATIONSHIP: COSTS ASSOCIATED WITH MONITORING AN APPROACHING PREDATOR

Given the accumulation of studies that identified a positive relationship between FID and SD, Blumstein (2010) proposed the flush early and avoid the rush (FEAR) hypothesis. The FEAR hypothesis states that FID increases as AD increases because prey incur attentional costs while monitoring the predator's approach (Blumstein, 2010). Because attention has a limited capacity (Dukas, 2004), monitoring the predator decreases the prey's ability to eat, forage or engage in social activities. The cost of fleeing is then lowered progressively because the benefits that remain to be gained by not fleeing decrease as the length of the predator's approach increases (Blumstein, 2010; Cooper & Blumstein, 2014).

Empirical tests have verified that prey flush earlier when the predator's approach begins further away. The first broad meta-analytical evaluation of the relationship between FID and SD showed that mammals and birds tend to flush early, whereas, for lizards, early flushing is contingent on their hunting methods and the predator's approach speed (Samia et al., 2013).

Most lizards studied are ambush foragers, which have low monitoring costs because they can simultaneously forage and monitor predators (Anderson & Karasov, 1981; Cooper, 2008a), the result of the meta-analysis is consistent with the hypothesized causal mechanism of FEAR (i.e., monitoring cost; Samia et al., 2013). Recently, many other empirical studies have shown that flushing early also occurs in other taxa, including a variety of mammals and other species of birds not initially studied (Clucas, Marzluff, Mackovjak, & Palmquist, 2013; Guay, Lorenz, Robinson, Symonds, & Weston, 2013; Guay, McLeod, et al., 2013; McGiffin, Lill, Beckman, & Johnstone, 2013; McLeod et al., 2013; Price, Strombom, & Blumstein, 2014; Symonds, Weston, Robinson, & Guay, 2014; Williams et al., 2014).

However, the ability of attentional costs to explain flushing early was considered to be unclear for two reasons (e.g., Cooper, 2005, 2008b). First, it was thought to be unlikely that the neurological costs of monitoring are sufficiently large to completely account for the strong effects of AD and SD on FID. Second, it was not known how the proposed attentional cost might relate to economic escape theory because ways in which they might affect cost of not fleeing or cost of fleeing were not immediately apparent. Using the Ydenberg and Dill (1986) model as a basis for considering how monitoring might affect the predation risk and cost of fleeing, Cooper and Blumstein (2014) identified four ways in which FID can increase with AD: two that affect predation risk and two that affect the cost of fleeing (Figure 4) (Cooper & Blumstein, 2014).

First, there could be a physiological cost of monitoring that increases with the duration of monitoring (Figure 4(a)). This neurological cost increases the cost of not fleeing as distance decreases, and can be added to the cost of not fleeing due to predation risk to obtain the total cost of not fleeing. However, the physiological cost must be quite small during brief predator-prey encounters; presumably it is too small relative to the other potential effects of monitoring to have a readily detectable effect on FID.

Second, as a predator continues to approach a prey, the perceived threat increases not only as predator-prey distance decreases, as in classical escape models, but also as a consequence of the length or duration of the predator's approach. The longer a predator approaches, the more likely it is to continue on the path leading to the prey and to have already detected the prey and be attacking. Therefore, as a predator continues to approach, the risk curve is higher for a prey that uses duration of approach as a cue to risk than for one that uses only predator-prey distance. Because the curve for assessed

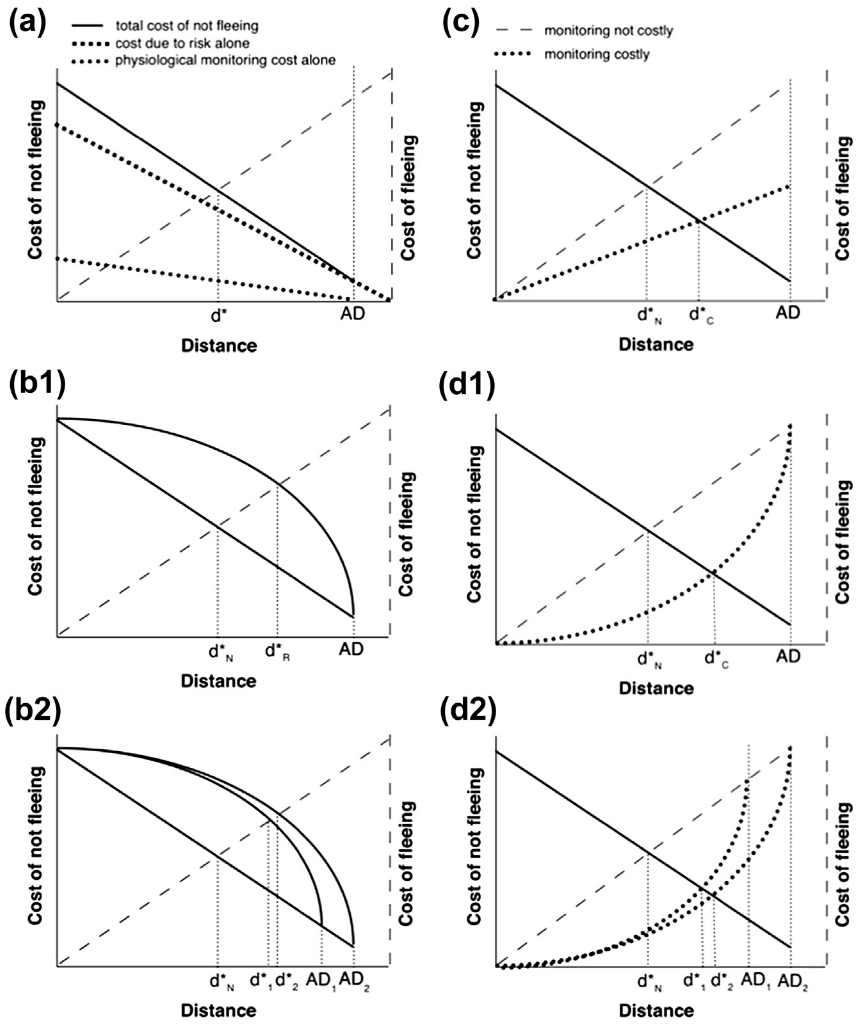

Figure 4 The flush early and avoid the rush (FEAR) hypothesis predicts that FID increases as AD increases. Flushing early can be accommodated escape theory via its hypothesized effects of monitoring the approaching predator on the cost of not fleeing and the cost of fleeing in the Ydenberg and Dill (1986) model. (a) Monitoring must exact a small physiological cost, which might stem from neural costs of focusing and possibly costs of postures maintained while focusing. The physiological cost increases the cost of not fleeing slightly. d*, predicted FID. (b1) Continued approach by a predator may indicate increased risk that the predator is attacking or will attack. For prey that use duration or length of approach as a cue to risk, assessed risk increases dynamically during approaches. Both the physiological cost of monitoring and dynamic risk assessment elevate the cost of not fleeing curve, which causes it to intersect with the cost of fleeing curve at a longer FID. AD, alert distance; d^*_N, FID without dynamic risk

risk is higher using dynamic risk assessment, FID increases as AD increases (Figure 4(b1) and (b2)).

Third, the cost of fleeing for prey that cannot monitor an approaching predator efficiently and engage simultaneously in fitness-enhancing behaviors, such as foraging, might be lower at all predator-prey distances (Figure 4(c)). The reduced rate of obtaining benefits while monitoring causes the cost of fleeing curve to be lower even when the prey begins to monitor than for a prey that suffers no decrease in its ability to gain benefits by monitoring. This lower cost of fleeing predicts longer FID in comparison to prey that can monitor the predator without reducing the rate of gaining benefits.

Finally, as the prey monitors the predator, the rate of obtaining benefits is reduced. This causes the potential benefits that would be lost by fleeing to decrease with increasing monitoring duration or length of the predator's approach. In this case, the cost of fleeing for prey that do and do not have reduced ability to obtain benefits while monitoring is identical at AD, where monitoring begins, although during an approach the potential gain of not fleeing decreases cumulatively (Figure 4(d1) and (d2)).

Formal experiments are needed to tease apart the relative magnitude of each of these effects in explaining the relationship between AD and FID. In a study in which costs of fleeing were negligible, initial results indicated that SD strongly affected FID (Cooper, Hawlena, & Pérez-Mellado, 2009). Because the physiological cost of monitoring is trivial, this finding provides

assessment; d^*_R, FID with dynamic risk assessment. (b2) For prey that dynamically adjust assessed risk, the predicted FID is longer for longer AD. (c) If monitoring is costly because it decreases the prey's rate of gaining benefits during the approach, FID will be longer than if monitoring does not affect ability to gain benefits, i.e., $d^*_C > d^*_N$. (d1) The prey's rate of gaining benefits is reduced while monitoring, which lowers the cost of fleeing and, therefore, to longer FID. The dashed line is cost of fleeing for a prey that does not incur any decrease in ability to gain benefits while monitoring. The dotted curve shows cost of fleeing for a prey that incurs a monitoring cost for gaining benefits. The dotted curve is lower than the line for no monitoring cost at all points except the origin and AD, indicating a smaller opportunity cost of fleeing. The cost of monitoring increases initially as the predator approaches, but after some point the difference between the curves for monitoring cost and no monitoring cost decreases because benefits that might be obtained decrease as predator-prey distance decreases. Predicted FID is longer for the dotted curve representing no monitoring cost (d^*_C) than for the upper line in which monitoring does not impairs ability to obtain benefits (d^*_N). (d2) For a given degree of impairment of obtaining benefits while monitoring, FID is longer for the longer of two ADs, i.e., $d^*_2 > d^*_1$. *Graphs from Cooper and Blumstein (2014).*

evidence for the proposed effect of dynamic risk assessment. Experimental studies that vary the magnitude of benefits that may be obtained, while holding effects of dynamic risk assessment constant, are needed to test the hypothesized effect of monitoring on cost of fleeing. An energetic cost of monitoring might be determined by comparisons of physiological measurements of prey that are unaware of a predator and those that are monitoring.

5. IS THE POSITIVE RELATIONSHIP BETWEEN FID AND ITS CONSTRAINING VARIABLES ONLY A MATHEMATICAL ARTIFACT?

5.1 Constraint on FID Values by Alert and Starting Distances

Contrary to the four biological explanations for the positive relationship between FID and its constraining variables (Cooper & Blumstein, 2014), the most parsimonious explanation for this relationship is that it is a mathematical artifact (Dumont et al., 2012). Because SD $\geq$ AD $\geq$ FID, a graph of the relationship of FID to either AD or SD approximates a right triangle with vertices at (0, 0), (0, SD), and (FID = SD). The upper limiting line segment connects (0,0) and (FID, SD), while the lower limiting line segment represents possible values of SD (Figure 3). Because the possible range of FID increases as its constraining variables increase, data may be heteroscedastic. If so, the constraint envelope may yield a positive relationship between FID and either of its constraining variables solely by chance. The mathematical constraint has an impact on traditional null hypothesis testing because it violates the assumption of linear regression that variances will be equal throughout the range of FID. For this reason, Dumont et al. (2012) suggested that the observed slope of FID on one of the constraining variables should be compared with slopes generated from a null model that includes the constraint SD $\geq$ AD $\geq$ FID.

Although a spurious relationship is theoretically possible, its magnitude and importance must be evaluated relative to predicted biological effects of AD or SD on FID because both artifactual and biological effects may operate simultaneously. A key step to evaluating this is to examine empirical evidence to ascertain whether all or considerable parts of the positive relationships reported in the literature are spurious. In Dumont et al.'s (2012) paper, the positive relationship between FID and its constraining variables was stronger than that generated by their null model. This finding shows that FID varies nonrandomly with AD, suggesting the presence of an underlying biological effect (Dumont et al., 2012).

A meta-analysis found that only 7 of 95 estimates of the relationship between FID and AD or SD could potentially be attributed to the artifact (Samia et al., 2013). In a recent empirical study testing AD-FID relationships in yellow-bellied marmots (*Marmota flaviventris*), we filtered data by removing potential observations that may have resulted from spontaneous vigilance; these generated 28 different data sets based on different assumptions about how spontaneous vigilance was defined (see Section 6 for more discussion about spontaneous vigilance). All of the 28 slopes estimated between AD and FID differed significantly from the null expectation. Therefore, although a mathematical artifact is conceptually possible, a large body of empirical evidence is not consistent with the proposition that the relationship between AD and FID is entirely artifactual. Indeed, effect sizes of SD and AD on FID are typically among the largest observed for a wide range of factors affecting FID and are much larger than could be explained by the artifact (Samia et al., 2013).

5.2 Methodological Issues

Although the positive relationships between SD, AD, and FID were not attributed to mathematical artifact in most of the earlier studies, the constraint among the variables exists and it represents a real methodological challenge to studies of economic escape theory. As the relationship among the variables is mathematically constrained, it is expected that variance increases as the constraining variable increases, thereby violating the homoscedasticity assumption of parametric tests (Sokal & Rohlf, 1995; Zar, 2010). This increase in the variance of residuals could be explicitly modeled by a generalized least squares (GLS) regression, ensuring the estimation of unbiased parameters (Zuur, Ieno, Walker, Saveliev, & Smith, 2009; Cleasby & Nakagawa, 2011). For example, for a simple linear function between FID and AD (i.e., $\text{FID} = \beta_0 + \beta_1 AD_i + \varepsilon_i$), one could use the following variance function to estimate the error variance: $\varepsilon_i \sim N\,(0, \sigma^2 \times \text{AD})$. However, whereas a GLS would overcome the concern about heteroscedasticity in residuals, it would not address another problem: the null expectations of these slopes differ from zero. Figure 5 illustrates how the null expectation of constrained and nonconstrained relationships diverges from zero. Importantly, because the null expectation is not zero, the usual significance testing for correlational analyses is not appropriate.

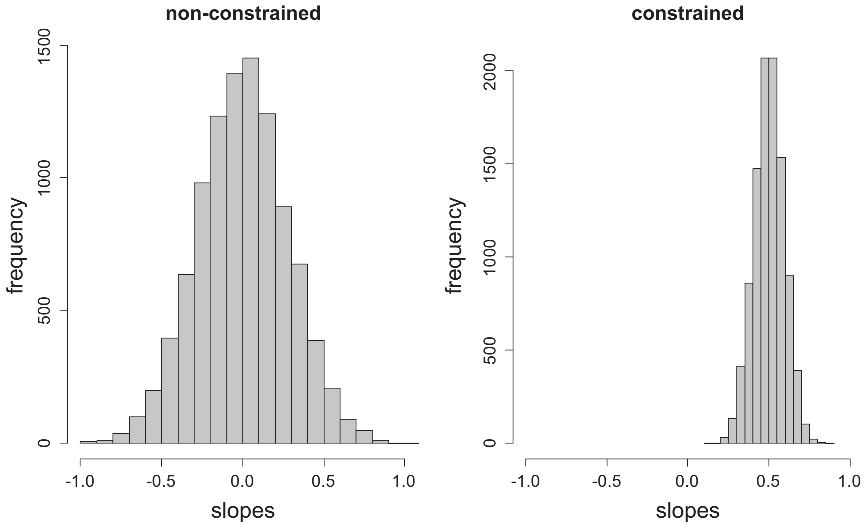

Figure 5 Null expectation of the slope of a nonconstrained and a constrained relationship. The null expectations were constructed by sampling 50 simulated X values from a uniform distribution bounded between 10 and 100. Then, for each X_i, a simulated Y value was sampled from a uniform distribution. For the nonconstrained relationships, we permitted Y_i to range from -100 to 100, whereas for the constrained relationships Y_i varied between 0 and X_i. Given the vectors of X and Y, the slope was calculated. This process was repeated 10,000 times. Note how the mean expectation diverges from zero in the constrained relationships.

These peculiarities in SD–AD–FID relationship have led researchers studying economic escape theory to propose alternative ways to quantify the effect of SD and AD on FID appropriately. The three suggested approaches are based on Monte Carlo simulations, quantile regressions, and an index developed to test the FEAR hypothesis.

The first method estimates the slope between FID and its constraining variable and compares this estimate to a distribution of slopes generated from a null model that respects the constraint SD $\geq$ AD $\geq$ FID (Dumont et al., 2012). The applicability of this approach is not limited to linear regressions; other nonlinear functions such as quadratic and cubic functions are also possible (e.g., Stankowich & Coss, 2006). However, some caution is needed to ensure that this Monte Carlo-based approach yields reliable results.

First, the fact that there is an envelope constraint means that there will be substantial heterogeneity of variance. This is because the variation at large SD is much greater than the variation at small SD. For this reason, the estimated slopes are very susceptible to leverage effects caused by outliers, which can lead to overestimation or underestimation of the real effects. In the Monte Carlo approach, the variance of the estimated slope is not taken into account in the evaluation of the significance of the relationship between AD and FID. Instead, the confidence interval of the "simulated" slopes is used: if the observed slope falls outside the range of 95% of simulated slopes, significance is inferred. Outliers can therefore lead to either Type I (false positive) or Type II (false negative) errors (Figure 6). If data transformations are unable to homogenize the variances, one can explore analyses that are more robust to outliers, such as robust regression (Sokal & Rohlf, 1995; Ellison & Gotelli, 2004; Zar, 2010). Importantly, estimated and simulated parameters must be measured on the same scale; if, for example, $\log_{10}$ transformation is used on the observed data, the same transformation should be applied to the simulated data (Gotelli & Graves, 1996).

Second, when evaluating how different functions fit the data, model comparison using Akaike's information criterion (AIC) may sometimes generate misleading conclusions. Although AIC identifies which models are "better" among a set of candidate models, it does not tell us how "good" they are. If all models are poor, the AIC will merely inform us which is the least poor model (frequently the model with the fewest parameters) (Burnham & Anderson, 2002). Therefore, we suggest the use of r^2 both to evaluate the adequacy of the best model and as a measure of the effect size of the relationship. A large literature has shown that effect sizes are the biologically meaningful measure by which scientists should base their inferences (Nakagawa & Cuthill, 2007; Stephens, Buskirk, & del Rio, 2007; Koricheva, Gurevitch, & Mengerson, 2013).

Third, regressions of AD against FID with equal slopes but very different intercepts illustrate different strategies that prey employ (Figure 7). If, for example, the researcher predicts that a prey will flee as soon as it detects the predator, an estimated $\beta_1 \approx 1$ will not reflect such a strategy unless $\beta_0 = 0$. Thus, forcing the models through the origin (i.e., setting $\beta_0 = 0$) may, in some cases, be mandatory (Blumstein et al., 2015). Exclusion of the intercept is statistically justifiable if FID $= 0$ when AD or SD $= 0$.

The second method proposed to evaluate relationships between FID and its constraining variables employs quantile regression (Chamaillé-Jammes & Blumstein, 2012). Quantile regression overcomes the problem of heterogeneity of variance by fitting linear regressions on different conditional quantiles of the range of a response variable (Koenker & Bassett, 1978; Cade & Noon, 2003). To evaluate the FEAR hypothesis, it might be preferable to

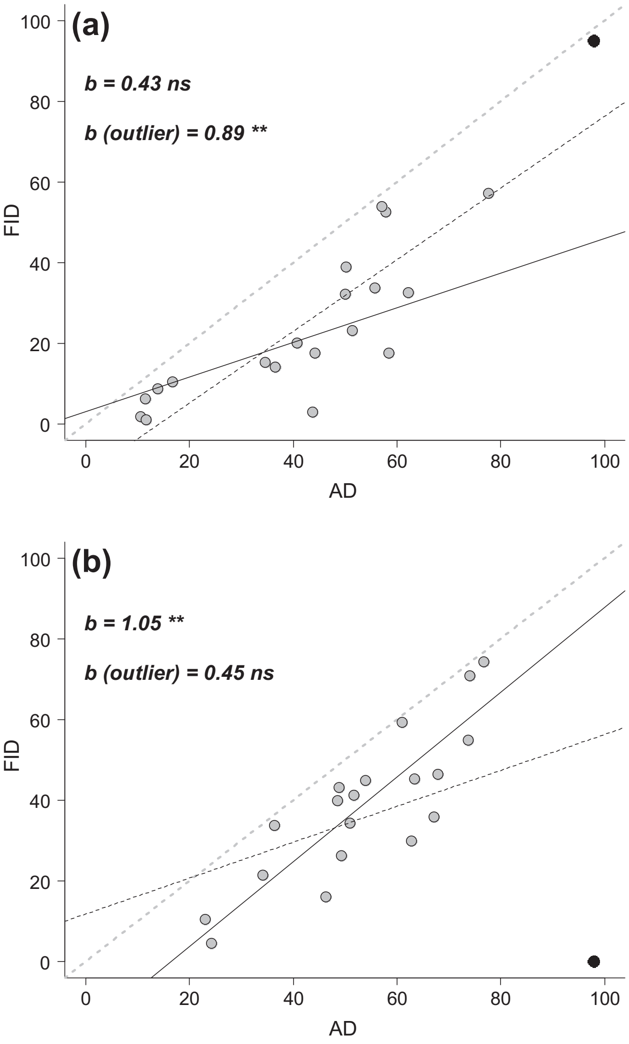

Figure 6 Examples of how a single outlier could (a) overestimate or (b) underestimate a relationship between alert distance (AD) and flight initiation distance (FID). Black points are the outliers; solid line, regression line without the outlier; black dashed line, regression line with the outlier; gray dashed line delimits the 1:1 relationship between AD and FID. Values of the slope coefficients (b) and their significances (ns, nonsignificant; **, significant) are shown in each plot.

examine the 0.1th quantile (i.e., 10% lowest y-values), rather than the average response (as ordinary least squares (OLS) does). Figure 8 illustrates how OLS can lead to misleading conclusions when testing for an effect of AD (or SD) on FID. Although OLS regressions yield almost identical

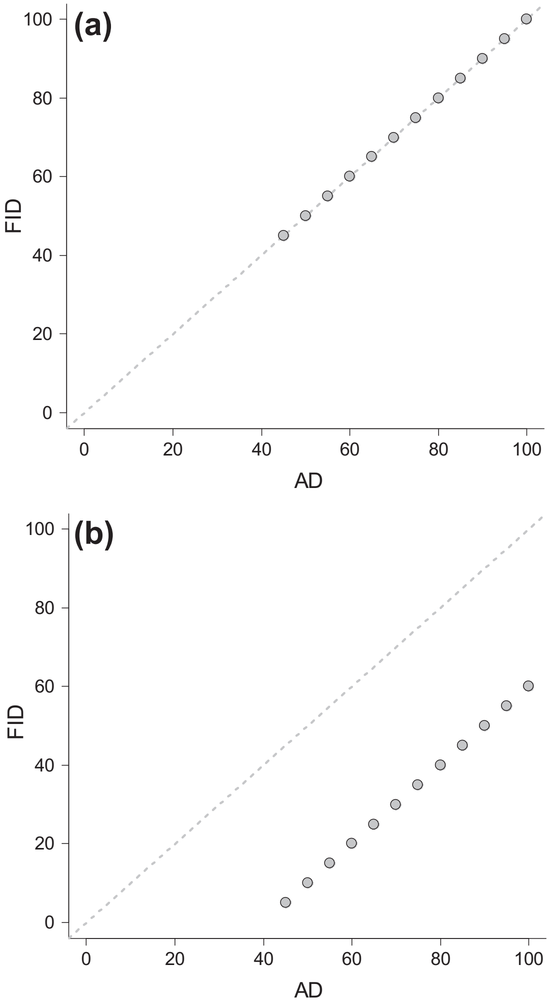

Figure 7 Examples of different antipredatory strategies that result in identical slope values ($b = 1$), but different intercept values in the relationship between alert distance (AD) and flight initiation distance (FID). Panel (a) shows a prey that flushes as soon as a predator is detected (intercept = 0), whereas panel (b) shows a prey that systematically waits for predators to travel 40 m before initiating flight (intercept <0 m). Dashed line identifies the 1:1 relationship.

estimates both on nonrandom and random AD–FID relationships, quantile regressions on the 0.1th FID quantile differ substantially between the models.

Like the Monte Carlo approach, quantile regression has the flexibility of using nonlinear functions to fit data, and it has two additional advantages: it

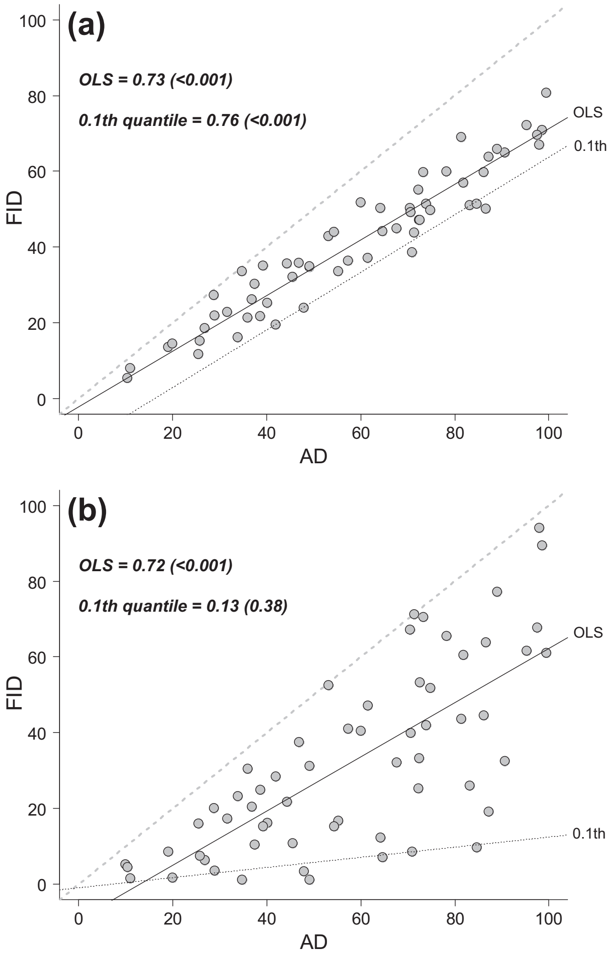

Figure 8 Examples of applications of quantile regression on the relationship between alert distance (AD) and flight initiation distance (FID). Panel (a) shows a hypothetical species that flushes early, whereas panel (b) shows a random AD-FID relationship. Although ordinary least square (OLS) regressions (solid line) are almost identical in both relationships, quantile regressions on the 0.1th FID quantiles (black dashed lines) differ widely between random and nonrandom data. Estimated slopes and their associated p-values (in parenthesis) are shown in each plot. Gray dashed line delimits the 1:1 relationship.

does not require any assumptions about the distribution of the regression residuals (e.g., normality), and it is robust to outliers (Cade & Noon, 2003). Quantile regression is similar to OLS regression in that sample size affects the accuracy of the estimate for a quantile (Cade & Noon, 2003).

However, the power analysis available to OLS is not easily determined for quantile regression. In quantile regression, the accuracy of estimates varies among quantiles. The best estimates are obtained for quantiles closest to the median and the worst estimates are obtained for extreme quantiles (i.e., those closest to zero or one; Cade & Noon, 2003). This implies that use of the first quantile, which we recommend because it is the most biologically meaningful quantile to test effect of SD or AD on FID, requires a larger sample size for its proper estimation.

By conducting analyses using increasingly larger subsamples of their data sets, Chamaillé-Jammes and Blumstein (2012) found that a sample size of at least 50 is usually needed to obtain consistent results. The requirement of such large sample sizes limits the applicability of quantile regression in interspecific studies of FID because sampling intensity varies among species and obtaining a sufficiently large sample may be difficult or impossible for rare species. For example, only 45% of 97 species included in the meta-analysis testing effect of SD or AD on FID had $N > 50$ (Samia et al., 2013).

An additional problem associated with quantile regression is related to the null expectation that is used to assert significance of the quantiles ($\beta = 0$). As with any frequentist analysis, statistical significance is a function of effect size and sample size (Nakagawa & Cuthill, 2007). In terms of the FEAR hypothesis, this means that with sufficient sample size, even a slope of 0.1 in the 0.1th quantile would be significant. Such small effects might be attributable entirely to the mathematical constraint on FID by AD, or small effects might indicate that animals flush very slightly earlier than expected in the absence of attentional costs.

A third way to identify a relationship between FID and its constraining variable, the phi (Φ) index, has been developed specifically to test the FEAR hypothesis (Samia & Blumstein, 2014). Inspired by the Pearson's chi-square statistic (χ^2), Φ can be considered a goodness-of-fit metric to test for flushing early in the constraint envelope. However, contrary to χ^2, Φ is not disproportionally influenced by deviance of FIDs at the largest ADs (caused by the constraint envelope) because observed expected deviances are standardized by the expected outcome, resulting in deviance varying from 0 to 1. Because Φ has a fixed null expectation ($\Phi = 0.5$; analogous to a zero relationship in most traditional statistics), its distribution is known to be normal and, as it is a standardized index, Φ can be used as an effect size metric (Koricheva et al., 2013). Specifically, Φ-values that deviate from 0.5 are robust indications that prey adopt a flush later (<0.5) or a flush early (>0.5) strategy. When $\Phi = 1$, all FID = AD. When $\Phi = 0$, all FID = 0.

The Φ index seems to overcome most of the drawbacks cited for the other two methods. First, as mentioned before, Φ is an effect size measure, permitting an intuitive inference concerning the magnitude and direction of the effect of SD or AD on FID. Second, it is a distribution-free metric, which means that it does not require any assumptions about the distribution of data, such as normality or homogeneity of variance. Third, Φ is very robust to outliers because it is based on the standardized deviance between observed and expected outcomes. Fourth, Type I and II error tests indicate that it is a powerful metric, yielding reliable estimates even with very small sample sizes (see Samia & Blumstein, 2014).

We suggest two approaches to improve our inferences about the biological effect of SD or AD on FID. The first, and easier to apply, is to combine the philosophies of the first two methods, i.e., to test the significance of the 0.1th quantile of an SD-FID or AD-FID relationship using a null model respecting the constraint SD $\geq$ AD $\geq$ FID. This approach would overcome both the outlier problem from the Monte Carlo-based method and provide a better cutoff for the significance of slopes in the 0.1th FID quantiles.

Our second and more challenging suggestion is to develop more realist null models with which to compare the observed parameters. Dumont et al. (2012) proposed the use of uniform distributions to generate the random FID values (see notation on Figure 3). Although it is perhaps the most parsimonious alternative, since it requires only setting the maximum (SD or AD) and minimum (usually zero) FID, the underlying assumption of this model is that prey do not behave optimally. Given the substantial empirical evidence that prey trade-off risk and costs even when their FID is positively related with SD or AD (see Section 3), this nonoptimality assumption may be excessively unrealistic to be useful. Moreover, because simulations using uniform distributions distribute the simulated FIDs over the whole possible range of FID (see Figures 3 and 8(b)), there is a risk that the null distribution overestimates variability in FID, making the test more prone to Type II errors. For example, an AD-FID relationship with the same parameters as those used in the simulation of Figure 5, a slope as large as 0.71 would be needed to assert a potential biological effect of AD on FID. Therefore, we suggest that studies using null models should incorporate the trade-offs in FID. Doing so provides a more realistic baseline for comparing the observed parameters, which will improve inferences concerning the biological effect of SD or AD on FID. The modeling approach proposed by Chamaillé-Jammes and Blumstein (2012) therefore offers a starting point from which to develop more realistic null models.

In this section, we have demonstrated that some statistical issues affect methods needed to study the relationships between FID and its constraining variables, SD and AD. One important issue is that data are not homogenously distributed when there is a constraint envelope. In some cases, heterogeneity of variance can be eliminated by data transformations. When this is not possible, two techniques, one based on Monte Carlo simulation and the other on quantile regression, have been proposed to address these statistical concerns. Both have merits and shortcomings. A third approach, using the Φ index, may avoid some of the statistical pitfalls in the previous two methods when testing the FEAR hypothesis. If the goal of a study is to determine the relationship between SD or AD and FID, it is essential to select a method that will not lead to rejection of the hypothesis of a relationship on spurious statistical grounds.

6. CAN SPONTANEOUS BEHAVIOR ACCOUNT FOR THE POSITIVE RELATIONSHIP BETWEEN FID AND ITS CONSTRAINING VARIABLES?

Cooper (2005) suggested that the relationship between SD and FID might be a consequence of a biological effect that is unrelated to predation. Because the duration of the predator's approach increases as SD increases, prey may be more likely to move spontaneously at longer SD, in a manner unrelated to the predator's approach (Cooper et al., 2009). Given that spontaneous locomotion might be erroneously recorded as FID, the relationship between FID and SD could then be an artifact of spontaneous movement (Cooper, 2005). Spontaneous behaviors are theoretically most likely to occur in zone 3 (Figure 2), where the predator is so far away that prey are either incapable of detecting it or the risk is too low to warrant continuous vigilance (Blumstein, 2003; Stankowich & Coss, 2006).

Studying the actively forager lizard, *Aspidoscelis exsanguis*, Cooper (2008b) demonstrated that a positive relationship between SD and FID could emerge from spontaneous behavior erroneously being recorded as FID. This finding was corroborated by a model that illustrated how spontaneous behaviors could inflate the positive relationship between SD and FID (Chamaillé-Jammes & Blumstein, 2012). The model also showed that the magnitude of the artifactual effect increased with an increase in the natural movement rate of prey that have not detected a predator (Chamaillé-Jammes & Blumstein, 2012) and suggested that artifacts due to spontaneous movements may be more common in actively foraging animals.

Williams et al. (2014) conducted the first empirical test of the effect of spontaneous movement on AD-FID relationships, using estimates of the rate at which spontaneous behaviors naturally occurred in yellow-bellied marmots to remove potential artifactual observations from a series of AD-FID regressions. The positive AD-FID relationships remained strong and significant in all regressions after exclusion of the potentially spurious data (explaining 73—100% of variance of FID). This suggests that, if present, spontaneous behaviors were far too infrequent to account for the positive FID-AD relationship in the marmots (Williams et al., 2014).

Additional studies, similar to that of Chamaillé-Jammes and Blumstein (2012) and Williams et al. (2014), are needed to assess the importance of the possible effects of spontaneous movement in taxonomically and ecologically diverse prey. Controlling both for rates of spontaneous movement and any mathematical artifact due to constrained relationships will permit the estimation of the true effect sizes of AD or SD. Rates of spontaneous movement might differ at distances before and after a prey begins to monitor a predator because spontaneous movements may be suppressed while the prey continuously monitors in zone 2, which could be determined by comparing movement rates in zone 3 and the adjacent portion of zone 2. A more direct method is to compare movement rates between SD and AD with rates obtained while the prey monitors the predator, i.e., between AD and FID. This is possible because spontaneous movements are readily distinguished from escape in the field.

Although flushing early may not occur in all prey species at all risk levels, it has already been shown to be a common strategy. Some spontaneous movements occur in field observations, but most authors routinely discard data for trials in which it is not clear that the prey is fleeing in response to an experimental approach (see suggestions for good practice in Blumstein et al., 2015). Usually, it is obvious whether a movement is spontaneous or associated with fleeing. For instance, relatively rapid movement away from the approaching threat indicates flight. Following flight, refuging animals either stop at their refuge or escape into them. Spontaneous movement that precedes ongoing foraging or a social interaction is not likely to indicate escape. When data are retained only for trials in which the prey are judged to be fleeing, spontaneous movement should have very little or no effect on reported relationships between FID and AD or SD.

7. IS SD A GOOD PROXY FOR AD IN ECONOMIC ESCAPE STUDIES?

When a predator begins to approach a prey, the prey might initially either be aware or unaware of the predator. As SD increases, both the duration and length of approach increase. Therefore, as the approach continues, the probability that an unaware prey will detect the advancing predator increases for two reasons. First, as it approaches, a predator, initially in zone 3, moves into zone 2 where it is within the prey's detection or attention range. Sometimes, a predator may initially be concealed, and then suddenly enter the prey's field of view, either in zone 1 or 2. Second, the predator may be sighted during prey's routine bouts of vigilance, which are likely to occur at higher rates as predation pressure increases (Frid, 1997; Li et al., 2011).

Economic escape theory assumes that animals do not necessarily flush immediately on detecting a predator but may employ some decision-making process prior to fleeing in which risk and cost of fleeing are taken into account (Ydenberg & Dill, 1986). In order to estimate the distance at which monitoring begins, many researchers record AD (e.g., Fernández-Juricic, Jimenez, & Lucas, 2001; Stankowich & Coss, 2006; Whitfield & Rae, 2014). Some prey signal awareness by stopping their ongoing activities and detectably modifying their posture, usually by turning their heads and bodies toward the predator (Blumstein et al., 2015). Such alerting behavior indicates to the observer that the prey has detected the predator and is vigilant. Although it is sometimes uncertain whether a prey has detected a predator before adopting the alert posture, and recent studies show that attention can be focused on an approaching threat before there is an overt behavioral response (Tyrrell & Fernández-Juricic, 2015), once there is an overt behavioral response, we can be certain that there is an opportunity for dynamic risk assessment.

It is important to understand that a different methodology is sometimes employed. Some human simulated predators slowly position themselves so as to standardize SD before initiating a direct approach toward prey that have already detected them (Blumstein et al., 2015). In this case, SD is the distance from which the researcher begins to approach an aware prey. Therefore, for species which perform alerting responses, and for researchers who initiate their experimental approach after this, SD $\leq$ AD. It is important to note that there may indeed be a second AD that follows this and researchers may record this as AD which is $\leq$SD.

In general, though, AD ≤ SD. If so, why use SD rather than AD? First, for some taxa, AD is not obvious—some lizards, frogs, fishes, and insects do not obviously turn their heads toward the approaching predator. Second, before 2012, there was no concern about using it; Dumont et al. (2012) were the first to suggest that SD may be a poor proxy of AD. In a study of Alpine marmots, *Marmota marmota*, Dumont et al. (2012) argued that the observed relationship between SD and AD (i.e., between the constraining variables) did not differ significantly from the expectation of the null model, and that different terms of their model explaining variation in FID were significant if SD versus AD was used.

We suggest, however, that the findings and the conclusion that SD is a poor proxy for AD are based on flawed analyses and assumptions, which we have discussed in part above. Here we discuss why SD may indeed be a useful proxy for AD.

First, a variable and its proxy need not be significantly related statistically. That the SD-AD relationship is not significant does not preclude use of SD instead of AD. Moreover, it is incorrect to use null hypothesis significance testing to infer the strength of a relationship (Nakagawa & Cuthill, 2007; Stephens et al., 2007). Furthermore, despite Dumont et al.'s (2012) interpretation, their results showed that, even if an AD-SD relationship was not significant, one could use SD to infer the effect of AD on FID (both SD-FID and AD-FID differed from the null predictions in their study).

Second, Dumont et al. (2012) stated that SD has no biological relationship to AD, but this is not a valid reason to dismiss the use of a potential proxy. The only relevant issue for selecting a proxy is whether the proxy yields conclusions similar to those that would be obtained by using the real causal variable. Imagine that one found that by regressing FID against the square root of the distance between the head and toe of an animal multiplied by nine minus pi always yielded exactly the same slope as the AD-FID relationship. We suggest that this admittedly strange statistic would be a valid proxy.

Third, whereas different conclusions depending on the constraining variable used would be a valid concern, we argue that Dumont et al.'s (2012) conclusions about the biological factors affecting FID are questionable because they stem from incorrect analyses. They tested the effects of three factors (previous activity, distance to burrow, and presence of conspecifics) on FID by estimating the slope of each level of these factors separately. To estimate the slope between AD and FID of the level "foraging marmots" from the "previous activity" factor, they selected the subset of the total ($N = 102$) data set in which marmots were observed foraging, and then used this subset of data to estimate the slope. The error was that the authors compared the slope of each level of the factors (e.g., foraging marmots) with the 95% confidence interval estimated from the "total" data set (see results, Figures 3 and 5 of Dumont et al., 2012). In contrast, the correct null hypothesis test to determine whether the observed slope differs from that expected from the mathematical artifact would compare the observed slope of each level with the 95% confidence interval yielded with its "own" parameters (i.e., sample size, identity of individuals (because a linear mixed-effects model was used), SD, and AD values) (Gotelli & Graves, 1996).

Finally, we know from comparative studies (Samia et al., 2013) that the strength of the relationship between AD or SD and FID varies. Thus, even if the Dumont et al. (2012) study had correctly demonstrated that SD was not a good proxy for AD, this result would be based on data collected from a single species and might not apply to others.

The relationship between SD and AD is clear. Although the prey may or may not be unaware of the predator between SD and AD, SD includes the interval 0—AD. This alone makes SD a potentially meaningful proxy for AD. Presumably, the utility of SD as a proxy increases as SD approaches AD. Even if SD is much longer than AD, conclusions about FID could be altered from those obtained by using AD only by spontaneous movements by unaware prey. However, we have argued that spontaneous movements are unlikely to occur in data sets due to the practice of including only trials in which the prey clearly flees from the predator.

8. CONCLUSIONS AND FUTURE DIRECTIONS

Economic escape theory rivals optimal foraging theory and sexual selection theory in the extent to which the interplay of theoretical models and empirical studies has rapidly and successfully produced a corpus of results with both theoretical and applied relevance. The predictions that prey base escape decisions on trade-offs involving predation risk, cost of fleeing, and the prey's expected fitness have been resoundingly validated. Many of the issues challenging escape theory that we have reviewed have arisen quite recently. Although rapid advances have been and continue to be made in our theoretical understanding of escape behavior and the evaluation of theoretical predictions, some issues remain to be resolved.

One of the most pressing needs is empirical studies of the recently hypothesized four ways by which monitoring a predator can cause early escape (i.e., the FEAR hypothesis) to determine whether they exist and evaluate their importance. If future tests verify that AD affects FID via its influence of monitoring on the risks and costs of fleeing, AD will be established as a major factor affecting escape decisions. This would place the FEAR hypothesis even more firmly within the scope of economic escape theory. In contrast, if the predictions are refuted, the effects of spontaneous movement would remain as the only known contributor to the SD-FID and AD-FID relationship. The FEAR hypothesis would either have to be abandoned or a new basis for it identified. We encourage researchers to make testing predictions of the proposed effects of monitoring on FID, a priority.

Studies are also needed to identify whether spontaneous movements occur while prey monitor approaching predators. In species that perform obvious alerting behaviors (such as the marmots described above), it will be possible to compare rates of spontaneous movement in the absence of predators to rates at distances between SD and AD. If fleeing were indistinguishable from spontaneous movement, it would be more difficult to do so between AD and FID, but spontaneous movements typically differ from escape movements in direction and activity upon completion of the movement. If the spontaneous movement rate is lower in SD-AD than when no predator is nearby, it could be inferred that prey are aware of the predator to some degree prior to alerting. If the spontaneous movement rate is lower in FID-AD than AD-SD, it could be concluded that spontaneous movement is suppressed during continuous monitoring.

Simulations and empirical studies are needed to determine the effect of the relative magnitudes of AD and SD on the correlation between them. In addition to these novel studies, we call for studies of more species so that we can examine the effects of the constraint envelope in diverse taxa.

Relationships between FID and various factors that affect the cost of not fleeing and the cost of fleeing have been studied experimentally and by observational methods. Slopes of relationships between FID and other variables determined in the observational studies have been reported in many cases (e.g., Blumstein, 2003; Dumont et al., 2012). In one paper, slopes have been used theoretically and empirically to establish a relationship between FID escape decisions and the positions of prey and predator with respect to refuge (Kramer & Bonenfant, 1997). However, little is known about the factors that influence the shape of the curves. Relationships between predator-prey distance and FID and relationships between predator-prey distance and costs of fleeing and not fleeing may be linear or nonlinear, but these relationships have rarely been studied (but see

Stankowich & Coss, 2006). Research regarding slopes and shapes of the relationships between predator-prey distance and model components is likely to provide important new insights into escape decisions.

Economic escape theory has focused on FID by a prey that has remained immobile while monitoring an approaching predator. More recently, researchers have begun to develop and test models of escape in new scenarios. Models successfully predict latency to flee from an immobile predator by an immobile prey and time spent hiding in refuge using economic logic similar to that of theory for FID, but consideration of cases in which a prey approaches and immobile predator or both predator and prey are moving have barely begun to be considered (Cooper, 2015). We encourage studies of escape decisions using these scenarios, and predict that they will lead to more comprehensive understanding of risk assessment and trade-offs between costs of fleeing and not fleeing.

Ydenberg and Dill (1986) seminal publication in *Advances in the Study of Behavior* stimulated decades of escape research that has successfully identified the adaptive value of escape. We expect that in the forthcoming decades we will obtain a much more integrated understanding of escape, which will be of particular value if we wish to manage wildlife behavior in order to protect threatened populations or control overabundant populations. Regardless of whether we wish to apply knowledge or not, integrative, Tinbergian studies of escape behavior that integrate a mechanistic understanding of escape with its ultimate benefits will provide compelling textbook examples of adaptive behavior in the wild.

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