16 Best practice for the study of escape behavior

Daniel T. Blumstein, Diogo S. M. Samia, Theodore Stankowich, and William E. Cooper, Jr.

Escape decisions have been studied in a remarkably Tinbergian way that has included examination of both proximate and ultimate questions, including questions about the evolution of escape behavior. Evolutionary studies have been made possible by developing large comparative data sets. Methodological differences, however, may impede our ability to combine studies to create comparative databases that can be, and have been, used to ask both evolutionary questions and questions of management relevance. Evolutionary comparative studies and meta-analyses both depend on animals being studied in relatively consistent ways, yet astute readers of the primary literature will have noticed that there is great variation in the ways in which studies of escape have been conducted. We wish to discuss some of the variation in how escape has been studied, and to recommend best practices for moving forward. We discuss several key details below, focusing primarily on flight initiation distance (FID).

In part because escape theory is now capable of predicting many aspects of escape behavior and in part because hypothesis-driven research is an efficient way to advance our understanding, the use of focused hypotheses and predictions is a fundamental feature of best practices for escape studies. Beyond this key feature, we make many recommendations that apply to a wide range of studies. Our recommendations, however, do not apply universally. In some cases, researchers should ignore our suggestions if, for instance, they wish to study the consequences of a recommendation. In other cases it may be essential to alter the approach protocol to ask other focused questions. Thus researchers should view our recommended practices as guidelines, not scripture.

16.1 Behavior of prey as a trial begins

Before measuring the escape of an individual, many key data must be collected. What animals are doing before they are experimentally approached influences both flight decisions (e.g., level of alertness, fighting with conspecifics, foraging in a profitable patch, sleeping or lying down: reviewed in Stankowich & Blumstein 2005) and hiding time decisions (Blumstein & Pelletier 2005). *We suggest that animals be relaxed yet not*

sleeping, as opposed to highly vigilant, when initiating an experimental approach. Relaxed behavior might include sitting and looking, or being perched, singing or producing other non-alarm vocalizations or signals, self-grooming, or foraging. Some protocols (including some of ours) require humans to identify a subject from a given distance and then wait quietly for five to ten seconds before initiating an experimental approach. In theory this is fine, but some species (e.g., browsing ungulates) move quickly through an area and the opportunity to approach might be lost if there is a lengthy delay before approach. In practice, animals may continue monitoring us, albeit in a relaxed way, and animals that were alert to the approacher prior to the initiation of the approach may make flight decisions differently than unaware subjects with different information about the approacher (Stankowich & Coss 2006). This requires a decision about whether or not to include immediate flushes when the experimental approach begins. Ultimately, this decision may rest on the exact question being asked. For example, immediate flushes may be of particular interest when testing the flush early and avoid the rush (FEAR) hypothesis (Blumstein 2010; Chapter 2).

These recommendations apply to many birds and mammals, but cannot be followed readily in some other taxa, including lizards, especially those that are ambush foragers in which it is often not possible to discern signs of vigilance (Cooper 2008a, b). For such prey, an experimenter approaches to some starting distance (SD) and position at which the prey is presumed to have detected the experimenter, stops for a brief interval, and then begins an experimental approach. Thus, SD equals alert distance (AD), and only questions related to zones I and II (Blumstein 2003) can be studied because the subject is already aware of the threat. It would be preferable to include approaches beginning at longer SDs when the examination of effects of spontaneous movements and the flushing early hypothesis are of interest. Inclusion of longer SDs would make lizard studies more comparable to those on birds and mammals, but the issue of degree of vigilance remains problematic. This might be addressed by monitoring focal animals for physiological correlates of vigilance (_sensu_ Blumstein & Bouskila 1996). Another advantage of including long SDs is that in FID should begin to asymptote at the boundary of zone II, where prey monitor predators, and zone III, where they do not.

16.2   Number of humans

The vast majority of FID experiments have used a single experimenter to flush individuals. Unless the objective is to study the effects of multiple observers (Geist _et al._ 2005; Cooper _et al._ 2007_), we suggest that future studies use a single observer_. By doing so, we ensure that future data will be maximally comparable to previously collected data. Sometimes a second person is called in to watch the animals from afar and record behavior. This practice should be fine as long as there is only a single person experimentally approaching the subject. Ideally, the second person is at a distance far enough to not influence the escape behavior of the animal (since the number of predators can affect the subject's flight decision), but close enough to guarantee the accuracy of their records.

16.3   Group size

The prey's group size can influence antipredator behavior and escape responses. Models of predation risk assessment predict that FID decreases as group size increases for two possible reasons: (1) either risk to the individuals decreases as group size increases because the predator has more choices (risk dilution hypothesis; Roberts 1996) or (2) an individual's risk decreases because at least one group member will detect the predator before it can overtake any member of the group (many-eyes hypothesis; Roberts 1996), permitting escape. These hypotheses are not mutually exclusive. Indeed, a variety of studies demonstrate that group size influences FID (Fernández-Juricic *et al.* 2004; Stankowich & Coss 2006), but the strength of the effect is widely variable, even within taxa (Stankowich & Blumstein 2005; Stankowich 2008). As species get larger, the area around them that they monitor increases (Blumstein *et al.* 2004). *Thus it is essential to collect information on the number of conspecifics and, if interested, heterospecifics, within a biologically relevant distance and use these values as covariates in subsequent analyses.*

16.4   Starting distance and alert distance

Starting distance has one of the largest effects on FID for many species (Samia *et al.* 2013), and serves as a proxy for the real biologically relevant measure, alert distance (Blumstein 2003). The main difference between these variables is that SD is determined by the experimenter, whereas AD is determined by the focal animal. Despite this key difference, it is impossible to test the effect of AD without varying the SD because of a mathematical constraint that links these two variables (i.e., SD ≥ AD; see detailed discussion in section 16.9 below). In some studies of lizards, SDs have been systematically varied to include observations over a wide range of values (Cooper 2005, 2008; Cooper *et al.* 2009). And while some large data sets exist on birds and mammals that have a variety of SDs, many of these have been collected in an *ad hoc* manner; systematic variation in their collection is needed. Indeed, it is desirable to include approaches beginning at longer SD when studying the effects of spontaneous movements or when testing the FEAR hypothesis. Inclusion of longer SDs would make lizard studies more comparable to those on birds and mammals, but the issue of degree of vigilance (AD) remains problematic as does the ability to observe a relatively tiny lizard in shrubby habitat. This might be addressed by monitoring focal animals for physiological correlates of vigilance.

We recognize that several issues arise when initiating experimental approaches at variable distances. There may be distances beyond which animals will not flee from an approaching person, possibly because it is simply not worth it or because the human is not detected (zone III: Blumstein 2003; Chapter 3). Thus initiating experimental flushes at relatively long distances may mean that the experimenter walks toward an animal until

s/he is detected or enters a "zone of awareness" where the animal begins assessing risk (zone II). Given that animals are constrained in their ability to scan in all directions at all times, an approacher starting from outside the zone of awareness (D_{max}) and walking directly toward the animal may be able to approach nearer the subject before it becomes alert than an approacher milling around at D_{max}, where the subject might eventually become alert before approach begins. This effect could lead to shorter ADs in zone II and a general quadratic effect between SD and FID (Stankowich & Coss 2006; Chapter 3: Figure 3.1). In addition to this effect, a predator approaching in a prey's field of view may well be detected while farther from the prey than one that is out of the field of view. Similarly, prey may detect predators farther away if they approach from within a binocular vs. monocular field of view, in taxa that have both, such as birds. In lizards, detection is easier when the predator is in one of the lateral fields of view than when in front of or behind the lizards (Cooper 2008a, b).

Because animals may look up and move at the start of natural bouts of vigilance and intermittent locomotion (here named as "spontaneous behaviors"), mistakenly scoring spontaneous behaviors as AD or FID is theoretically more likely for experiments with large SD (Cooper 2008a, b; Cooper & Blumstein 2014). *As long as the experimenter is attuned to eventual natural threats or distractions (such as social behavior), long approaches will likely not produce spurious data.* Despite their potential to confound the study of escape, we do not believe these are often "real" issues because it is usually very obvious when an animal alerts or flees from an approaching human. *We recommend that if an observer is unsure of whether the animal is responding to their experimental approach, they should simply not record data for that approach.* Although some models have shown that spontaneous behaviors could potentially bias the conclusions that are drawn (Chamaillé-Jammes & Blumstein 2012), our experience with over 15,000 experimental approaches on lizards, birds, and mammals, suggests that it is very unlikely that we have been making systematic mistakes scoring escape decisions. Moreover, the influence of spontaneous behaviors on final results may be in itself of particular interest. With knowledge of natural patterns of vigilance and locomotion, it is possible to develop null models (Williams *et al.* 2014) that allow one to eliminate those experimental approaches that are possibly "tainted." Even without such knowledge, it is possible to develop null models that eliminate the suspicion of spurious relationship caused by tainted observations (Samia *et al.* 2013).

Some investigators have used a fixed or narrow range of SDs to study effects of factors that affect the cost of not fleeing and the cost of fleeing. These distances are intended to be long enough to avoid creating situations in which escape is immediate (Cooper 1998, 2012), yet short enough to ensure that the prey has detected the predator before the approach begins (e.g., Møller & Garamszegi 2012 and almost all lizard studies). *If SD is fixed or has a narrow range, there must be some justification for selecting a particular distance and the experimenters must clearly describe their rationale for selecting this distance. When working with an unfamiliar species or situation, we recommend that pilot data be collected to ensure that the SD is appropriate.* It is important to ensure the prey is monitoring the predator during the entire approach, which is necessary for the

predator–prey encounter to match the scenario of the economic escape models of Ydenberg and Dill (1986) and Cooper and Frederick (2007).

16.5   Flight initiation distance

Many of our recommendations are designed to properly measure FID. When animals are on the ground, FID is readily measured as the straight line separating the experimenter and the animal when the escape begins. To identify the exact point at which FID (and other variables) occurs, many experimenters drop weighted flags or other objects along the path of approach. Typically markers are placed (1) at the starting point of the experimental approach; (2) at the approacher's position when the prey becomes alert and responds to the approacher; (3) at the point where the prey began to flee; and (4) at the point where prey was located at the start of the experiment. The distance between markers 1 and 4 is SD; that between markers 2 and 4 is AD, and that between markers 3 and 4 is FID. Additionally, beyond the preferred method of measuring FID using a measuring-tape or laser rangefinder, it is also a common practice for experimenters to convert the number of paces into meters to record the escape variables (e.g., SD, AD, FID; Blumstein 2006).

However, when studying many birds, lizards, or arboreal mammals, the focal animal may be perched above the ground. Two procedures have been developed to measure the FID for animals off the ground.

The first is to test all individuals, and then determine the boundary height, which is assumed to represent the maximum height at which the animals perceive themselves to be at risk (*c.* two to three meters for some lizards approached by human investigators; Cooper 1997; Cooper & Avalos 2010). Flight initiation distance is calculated as if all individuals are at ground level (i.e., no adjustment is made for differences in predator–prey distance among perch heights). The relationship between perch height and FID is studied in the range 0 m to boundary height. At typical SDs and FIDs, this has a relatively small effect on estimates of distance. However, as perch height increases, the proportion of the Euclidean distance between predator and prey that is attributable to perch height increases substantially. To our knowledge, only lizards have been tested using this boundary height approach to date.

A second, more generally correct, method has been used to study many birds and arboreal mammals that flee when perched at greater heights, where perch height may account for a large portion of the Euclidean distance. Birds are usually tested using the "direct" FID, which is calculated as the Euclidian distance between experimenter and focal animal (i.e., the square root of the sum of the squared horizontal distance and the squared height of perch; Blumstein 2006). Because height in tree may (or may not) affect risk perception (Blumstein *et al.* 2004), *our conservative suggestion is that height should be estimated and the direct FID (FID$_{direct}$) should be calculated using the Pythagorean theorem.* It should be noted, however, that because FID$_{direct}$ depends on the height an individual is in a tree, it is possible that when there are immediate or near immediate flushes, FID$_{direct}$ may be greater than SD. This would contradict the envelope constraint (where SD > AD > FID).

16.6 Approach speed and angle

We know that the speed at which an individual is approached may influence both the decision to flee and the decision to hide. Thus it is important for researchers to report clearly the approach speed. Many data have been collected by approaching animals between 0.5 and 1.0 m/s (Blumstein 2006; Gulbransen *et al.* 2006). As humans speed up (e.g., 0.5 to 1.0 m/s vs. 2 to 3 m/s in Stankowich & Coss 2006; Chapter 5), speed has detectable effects on escape. While it is essential to vary approach speed to determine whether animals are maintaining a spatial margin of safety or a temporal margin of safety (Cárdenas *et al.* 2005), and to study joint effects of approach speed and other factors that may affect FID, *we recommend a default approach speed of 0.5 to 1.0 m/s to ensure data are maximally comparable with other studies.* In comparative studies, if animals are approached at different speeds, approach speed could be used as a covariate (e.g., Cooper *et al.* 2014). And speed can be varied during approach to study effects of changes during approach on FID (Cooper 2006), but investigators should realize that these will not be generally comparable with other studies.

The angle and directness of approach also may affect escape decisions (Fernández-Juricic *et al.* 2005; Cooper *et al.* 2010; Chapter 5). Interestingly, while many species are more tolerant of tangential approaches compared to direct approaches, birds studied in a high-elevation grassland in Argentina were more sensitive to tangential approaches (Fernández-Juricic *et al.* 2005). *Unless it is of interest to study the effect of directness of approach or the approacher is restricted to established trails in sensitive wildlife areas, we recommend that researchers directly approach experimental subjects.* In some cases it may be prudent to add the bypass distance (for tangential approaches) as a covariate in models explaining variation in FID.

16.7 When to stop approaching

Once an animal flees, a relevant question is whether to stop approaching toward the location where animal was, continuing to walk up to its initial location, or continue approaching the prey past its initial location. Pragmatically, to properly measure SD, it is important to know precisely the location of the subject. Additionally, if it is desirable to measure the distance fled, or the distance to the nearest refuge, it is essential to go to the subject's initial location. *Our recommendation is that approaches should be terminated in one of two places, the predator's location when escape begins or the prey's location when escape begins. If the predator continues to the initial position where the subject was at the start of the experimental approach, the prey will likely flee a longer distance and/or be more likely to enter refuge than if the predator stops moving as soon as the prey flees.* The choice between these stopping points sometimes may be dictated by the escape tendencies of the prey, the need to continue observations on the animal (i.e., escape into refuge or out of the area is undesirable), or the need to maintain comparability with previously collected data.

If the approacher continues to the prey's initial location, distance fled will depend on the additional risk implied by the continued approach and will very likely vary with the directness of approach during flight (i.e., on the angle between the approach path and the flight path). With continued approach, distance fled, probability of refuge entry, and hiding time may increase. The correlation between distance to refuge and distance fled may also be greater than when the predator stops approaching when escape begins. We also note that sometimes it may be essential to follow an animal *until* it hides, if the goal is to study hiding time. Stopping as soon as the prey flees may be realistic in portraying reactions of predators that stop approaching when they assess that they will not be able to capture the prey. Experimentally pursuing prey might be the most realistic way to simulate attacks by pursuing predators, but pursuit introduces uncontrolled variation in risk and costs that may affect distance fled and hiding time. Continuing to approach, but only to the prey's initial location, may be a compromise between these extremes and has the advantage of being more likely to induce prey to enter refuge if hiding time is of interest.

16.8   Data to collect

At the very minimum, data sheets should permit the collection of location, date, time, species, sex, initial behavior, starting distance, alert distance, flight initiation distance, and the number of conspecifics (and potentially heterospecifics) within a biologically relevant distance. Of course, additional questions can be asked with additional data and some researchers (and for some questions) have collected data on how far animals were from refugia when an experimental approach began, details about the type of movement during escape, and the distance fled. Some researchers have examined subsequent escape decisions that have included the dynamics of the second flush (which sometimes happens), and the dynamics of hiding, the type of escape behavior performed, the distance fled, or the latency to resume initial behavior. Analyses that include such additional information can provide a richer understanding of escape, but we recommend that investigators also collect the initial data to ensure maximum comparability.

16.9   Statistical analysis of FID data

16.9.1   Use of SD or AD as covariate or study of interactions involving the SD x FID relationship

There are many statistical issues associated with analyzing FID data. A key feature of the analysis of FID data is that variance in both AD and FID increases as a function of SD. This happens because these variables are subject to a constraint envelope relationship where $SD \geq AD \geq FID$. Logically, a prey cannot flee from a predator (FID) at a greater distance than where it was detected (AD) and, similarly, prey cannot

become alert to a predator before the predator initiates its approach (SD). We note that there are situations where AD > SD are possible, but, because true AD is not measurable when animals are alerted to the experimenter prior to the start of the approach, such observations do not typically exist in FID data sets or AD is set to equal SD. For example, SD = AD in experiments in which all approaches begin at relatively short SDs at which prey are already aware of the predator's presence. The constraint envelope is an unavoidable statistical issue in FID studies and has implications as to how data may be analyzed.

Our first statistical recommendation is: *if starting distances vary and alert distances are not available, starting distance must be added as covariate in subsequent statistical models. However, starting distance is unrelated to FID in some species, especially at slow approach speeds. For studies of single species for which it is known that SD and FID are unrelated, SD should not be used as a covariate.* Starting distance is a proxy for AD and it likely explains a considerable proportion of the variance in FID (Blumstein 2010; Samia *et al.* 2013; Samia & Blumstein 2014). This creates a statistical issue about whether the effect of other variables should be tested as main effects or as interactions between SD and the other variables. When interpreting a two-way interaction, the question becomes "does a variable of interest influence the expected relationship between SD and FID?" Researchers have tested these both ways and *we recommend thorough examination leading to an understanding of the nature of a data set before making a decision about whether to focus on interpreting main effects or interactions.*

16.9.2 Should the FID x SD regression be forced through the origin?

Another important decision one must make is whether or not to include an intercept in statistical models of data sets that include SD. Because FID cannot be greater than the distance where an experimental approach begins, FID is zero when SD is zero. Some investigators prefer to force though the origin and other do not when using regression models. It is important to note that the slopes and estimated intercepts of fitted regression models likely differ in zones I, II, and III (Blumstein 2003; Stankowich & Coss 2006; Chapter 3), and that it may be more appropriate to conduct separate regressions in the different zones. *If you know your data are exclusively in zone I, you should force the fitted model through the origin (i.e., exclude the intercept – unless you want to test the hypothesis that the intercept differs from 0). If you suspect that your data spans zones I and II, you should consider fitting a piecewise linear regression where you can look for a breakpoint. If you suspect your data spans only zones II and III, you should consider exploring both linear and non-linear models (e.g., logarithmic) with intercepts included, as the predicted relationship between SD and FID changes with increasing SD.* The remaining residual error can then be used to test for whatever factor effects were included in the study. Please note that while the idea of three zones is conceptually useful, focused empirical studies are needed to properly define these zones in a given species.

16.9.3   Spontaneous movements and the decision to keep observations of immediate flight

Another issue is whether or not to remove values where SD = FID. In zone I immediate flushing is predicted, but in zone II prey are predicted to monitor the predator's approach prior to fleeing. Situations where SD = FID may be the result of animals flushing immediately at the start of the experimental approach if the SD happens to be the FID for that individual, which occurs at the boundary of zones I and II or may occur if an animal is particularly wary. At longer SDs, flushing may also be attributable to spontaneous movements (Williams *et al.* 2014). *We generally suggest that investigators only remove data if they believe that the movement is not in response to a predator and to otherwise keep cases where SD = FID.*

In cases where SD varies considerably, *FID studies can profitably employ quantile regression*, particularly if one is concerned that long SD values may influence the relationship between SD or AD and FID (Chamaillé-Jammes & Blumstein 2012). Quantile regression estimates how subsets of the data vary. Thus if one is concerned that at large SDs, larger FIDs may reflect spontaneous movement (see below), one could focus on quantiles that did not include these data. Quantile regression cannot be used if SD is fixed. And quantile regression requires a substantial amount of data to profitably employ it.

16.9.4   Other statistical issues associated with studying FID

Because correlational statistics are sensitive both to expected heteroscedasticity (caused by the constraint envelope) and to outliers with high leverage, such effects can lead to potentially erroneous conclusions about whether observations support the FEAR hypothesis or not. Samia and Blumstein (2014) developed an index (phi, Φ) designed to test the 1:1 expectation in an SD–FID or an AD–FID relationship in a way that avoids the above statistical pitfalls. Moreover, in addition to allowing the proper evaluation of the FEAR hypothesis, the index permits one to determine if a species is flushing later or with no predetermined strategy.

Recently, there have been some concerns about the use of SD as proxy for AD (Dumont *et al.* 2012). If SD is not a good proxy for AD, conclusions drawn from studies using SD rather than AD might be suspect. It could be even more critical to studies of lizards for which AD is difficult to determine. However, a further comparative study with 75 avian species showed that the use of SD is a conservative alternative to using AD as a covariate in FID studies (Samia & Blumstein 2014). By conservative, we mean that while a low and/or non-significant SD–FID relationship is inconclusive, a large and/or significant SD–FID is robust support of the influence that AD has on FID.

Computational simulations and null models have been recently used to study FID. Specifically, computational simulations have been used to model the effect of spontaneous behaviors on FID (Chamaillé-Jammes & Blumstein 2012), to filter the data according with a baseline rate of spontaneous behaviors observed in natural conditions (Williams *et al.* 2014), to eliminate the suspicion of spurious data in the AD–FID relationship caused by the envelope constraint (Dumont *et al.* 2012; Samia *et al.*

2013), and to simulate null distributions of metrics developed to test the FEAR hypothesis (Samia & Blumstein 2014). The already available algorithms can be valuable when one tests the FEAR hypothesis, but we argue that further benefits can be obtained by using computational simulations. For example, the conceptual zones that Blumstein (2003) proposed influence escape behavior. Because it is difficult to identify such zones in natural conditions, mathematical and computational models can help us better understand their roles in dynamic decision-making of prey. *We expect that future advances in our understanding of escape will rely on developing specific null models and using computational simulations to evaluate empirical data.*

16.10   Comparative studies and meta-analyses: a complementary way to study escape

Many hypotheses about escape theory have been studied using a comparative or meta-analytical approach (Stankowich & Blumstein 2005; Blumstein 2006; Møller 2008; Samia *et al.* 2013). Because the evolutionary history of taxa renders species not statistically independent, most of these studies use phylogenetically informed models to account for the non-independence (Garland & Ives 2000; Felsenstein 2004; Lajeunesse 2009; Nakagawa & Santos 2012). Some recent studies, however, show remarkable plasticity in escape behavior that seems rather unconstrained by phylogeny (e.g., Cooper *et al.* 2014) and different populations of the same species often vary greatly in their flight responses based on their experience with natural predators or humans. *Thus we recommend that in comparative studies, authors provide a measure of the phylogenetic signal of the FID.* To date, we have little evidence to assess whether FID is a conserved or a species-specific trait. This is because, although most interspecific studies control the phylogenetic effect, few studies provide a measure of phylogenetic signal such as Pagel's lambda or Bloomberg's K (for exceptions, see Møller & Garamszegi 2012; Samia *et al.* 2013). In the absence of such measures, the superiority of phylogenetic models, as indicated by adjusted r^2 or Akaike's information criterion, indicates that a phylogenetic signal occurs, but does not quantify its strength (Cooper *et al.* 2014). It is also important to realize that phylogenetic models are not indicated when there is no phylogenetic signal present because there is increased uncertainty about parameter estimates (Revell 2010).

Our final suggestion is one that has brought us all together. We think that while there is a lot to learn from single-species studies of escape, *we encourage others to present their findings either in the context of meta-analysis or to present them in ways that facilitate future meta-analyses* ("meta-analytic thinking"; Cumming & Finch 2001; Nakagawa & Cuthill 2007; Borenstein *et al.* 2009). This requires a bit of a paradigm shift and we have two recommendations to facilitate this shift. *In primary studies, we suggest that inferences should be based on the magnitude of the effect; thus researchers should present the effect size along with its confidence interval. Second, we encourage researchers to present results in sufficient detail so that the calculation of the effect size can be made easily (e.g., provide the sample size and the exact P-values of statistics).*

16.11 Conclusions

We are thrilled and excited by both the number of studies and the diversity of studies of escape behavior. We hope that our suggestions for standardizing some of the ways that escape is studied will lead to even more comparative studies and meta-analyses. Indeed, we believe that it is through these sorts of studies that generalizations emerge. Creating such data sets is typically beyond the scope of a single researcher or a single study. As we also wrote, there are reasons to ignore some of our suggestions and researchers that do so will invariably discover new ways that animals manage predation risk through the dynamics of their escape behavior. We look forward to reading those studies in the future!

References

Blumstein, D. T. (2003). Flight initiation distance in birds is dependent on intruder starting distance. *Journal of Wildlife Management*, **67**, 852–857.

Blumstein, D. T. (2006). Developing an evolutionary ecology of fear: How life history and natural history traits affect disturbance tolerance in birds. *Animal Behaviour*, **71**, 389–399.

Blumstein, D. T. (2010). Flush early and avoid the rush: A general rule of antipredator behavior? *Behavioral Ecology*, **21**, 440–442.

Blumstein, D. T. & Bouskila, A. (1996). Assessment and decision making in animals: A mechanistic model underlying behavioral flexibility can prevent ambiguity. *Oikos*, **77**, 569–576.

Blumstein, D. T. & Pelletier, D. (2005). Yellow-bellied marmot hiding time is sensitive to variation in costs. *Canadian Journal of Zoology*, **83**, 363–367.

Blumstein, D. T., Runyan, A., Seymour, M. *et al*. (2004). Locomotor ability and wariness in yellow-bellied marmots. *Ethology*, **110**, 615–634.

Borenstein, M., Hedges, L. V., Higgins, J.P.T. & Rothstein, H.R. (2009). *Introduction to Meta-Analysis*. John Wiley & Sons, Ltd., Chichester, UK.

Cárdenas, Y. L., Shen, B., Zung, L. & Blumstein, D. T. (2005). Evaluating temporal and spatial margins of safety in galahs. *Animal Behaviour*, **70**, 1395–1399.

Chamaillé-Jammes, S. & Blumstein, D.T. (2012). A case for quantile regression in behavioral ecology: Getting more out of flight initiation distance data. *Behavior Ecology and Sociobiology*, **66**, 985–992.

Cooper, W. E., Jr. (1997). Escape by a refuging prey: The broad-headed skink (*Eumeces laticeps*). *Canadian Journal of Zoology*, **75**, 943–947.

Cooper, W. E., Jr. (1998). Direction of predator turning, a neglected cue to predation risk. *Behaviour*, **135**, 55–64.

Cooper, W. E., Jr. (2005). When and how do predator starting distances affect flight initiation distances? *Canadian Journal of Zoology*, **83**, 1045–1050.

Cooper, W. E., Jr. (2006). Dynamic risk assessment: Prey rapidly adjust flight initiation distance to changes in predator approach speed. *Ethology*, **112**, 858–864.

Cooper, W. E., Jr. (2008a). Visual monitoring of predators: Occurrence, cost and benefit for escape. *Animal Behaviour*, **76**, 1365–1372.

Cooper, W. E., Jr. (2008b). Strong artifactual effect of starting distance on flight initiation distance in the actively foraging lizard *Aspidoscelis exsanguis. Herpetologica*, **64**, 200–206.

Cooper, W. E., Jr. (2012). Risk, escape from ambush, and hiding time by the lizard *Sceloporus virgatus. Herpetologica*, **68**, 505–513.

Cooper, W. E., Jr. & Avalos, A. (2010). Escape decisions by the syntopic congeners *Sceloporus jarrovii* and *S. virgatus*: comparative effects of perch height and of predator approach speed, persistence, and direction of turning. *Journal of Herpetology*, **44**, 425–430.

Cooper, W. E., Jr. & Blumstein, D. T. (2014). Novel effects of monitoring predators on costs of fleeing and not fleeing explain flushing early in economic escape theory. *Behavioral Ecology*, **25**, 44–52.

Cooper, W. E., Jr. & Frederick, W. G. (2007). Optimal flight initiation distance. *Journal of Theoretical Biology*, **244**, 59–67.

Cooper, W. E., Jr., Pérez-Mellado, V. & Hawlena, D. (2007). Number, speeds, and approach paths of predators affect escape behavior by the Balearic lizard, Podarcis lilfordi. *Journal of Herpetology*, **41**, 197–204.

Cooper, W. E., Jr., Hawlena, D. & Pérez-Mellado, V. (2009). Interactive effect of starting distance and approach speed on escape behavior challenges theory. *Behavioral Ecology*, **20**, 542–546.

Cooper, W. E., Jr., Hawlena, D. & Pérez-Mellado, V. (2010). Influence of risk on hiding time by Balearic lizards (*Podarcis lilfordi*): Predator approach speed, directness, persistence, and proximity. *Herpetologica*, **66**, 131–141.

Cooper, W. E., Jr., Pyron, R. A. & Garland, J. T. (2014). Island tameness: living on islands reduces flight initiation distance. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, **281**, 20133019.

Cumming, G. & Finch, S. (2001). A Primer on the understanding, use, and calculation of confidence intervals that are based on central and noncentral distributions. *Educational Psychology and Measurement*, **61**, 532–574.

Dumont, F., Pasquaretta, C., Réale, D., Bogliani, G. & Hardenberg, A. (2012). Flight initiation distance and starting distance: Biological effect or mathematical artefact? *Ethology*, **118**, 1–12.

Felsenstein, J. (2004). *Inferring Phylogenies*. Sunderland, MA: Sinauer Associates, Inc.

Fernández-Juricic, E., Vaca, R. & Schroeder, N. (2004). Spatial and temporal responses of forest birds to human approaches in a protected area and implications for two management strategies. *Biological Conservation*, **117**, 407–416.

Fernández-Juricic, E., Venier, M. 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. *Biological Conservation*, **125**, 225–235.

Garland, T. & Ives, A. R. (2000). Using the past to predict the present: Confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist*, **155**, 346–364.

Geist, C., Liao, J., Libby, S. & Blumstein, D. T. (2005). Does intruder group size and orientation affect flight initiation distance in birds? *Animal Biodiversity and Conservation*, **28**, 69–73.

Gulbransen, D., Segrist, T., del Castillo, P. & Blumstein, D.T. (2006). The fixed slope rule: An inter-specific study. *Ethology*, **112**, 1056–1061.

Lajeunesse, M. J. (2009). Meta-analysis and the comparative phylogenetic method. *American Naturalist*, **174**, 369–381.

Møller, A. P. (2008). Flight distance and blood parasites in birds. *Behavioral Ecology*, **19**, 1305–1313.

Møller, A. P. & Garamszegi, L. Z.(2012). Between individual variation in risk-taking behavior and its life history consequences. *Behavioral Ecology*, **23**, 843–853.

Nakagawa, S. & Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: A practical guide for biologists. *Biological Reviews of the Cambridge Philosophical Society*, **82**, 591–605.

Nakagawa, S. & Santos, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, **26**, 1253–1274.

Revell, L. J. (2010). Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, **1**, 319–329.

Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour*, **51**, 1077–1086.

Samia, D. S. M. & Blumstein, D. T. (2014). Phi index: A new metric to test the flush early and avoid the rush hypothesis. *PLoS One*, **9**, e113134.

Samia, D. S. M., Nomura, F. & Blumstein, D. T. (2013). Do animals generally flush early and avoid the rush? A meta-analysis. *Biology Letters*, **9**, 20130016.

Stankowich, T. (2008). Ungulate flight responses to human disturbance: a review and meta-analysis. *Biological Conservation*, **141**, 2159–2173.

Stankowich, T. & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society B*, **272**, 2627–34.

Stankowich, T. & Coss, R. G. (2006). Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. *Behavioral Ecology*, **17**, 246–254.

Williams, D. M., Samia, D. S. M., Cooper, W. E., Jr. & Blumstein, D. T. (2014). The flush early and avoid the rush hypothesis holds after accounting for spontaneous behavior. *Behavioral Ecology*, **25**, 1136–1147.

Ydenberg, R. C. & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior*, **16**, 229–247.