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Original Article

Novel effects of monitoring predators on costs of fleeing and not fleeing explain flushing early in economic escape theory

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Economic escape theory predicts flight initiation distance (FID, predator–prey distance when fleeing from an approaching predator begins), but currently cannot account for an observed increase in FID as alert distance (AD, predator–prey distance when a prey becomes alert to a predator), or its surrogate, starting distance (SD, predator–prey distance when approach begins) increases. The flush early and avoid the rush hypothesis suggests that FID increases as AD increases due to costs of monitoring the predator. However, the AD–FID relationship and the cost of monitoring have been questioned. Nevertheless, recent evidence shows that FID remains correlated with AD even when spontaneous movements are removed. We discuss possible effects of monitoring that might explain the AD–FID relationship and ways to improve understanding of the influence of spontaneous movements. We disentangle possible effects of 3 distinct phenomena associated with monitoring predators and incorporate them into escape theory. Cost of fleeing might increase as an attentional monitoring cost increases as duration of approach increases. Cost of not fleeing might increase as AD increases due to a physiological cost of monitoring and because assessed risk might increase as duration of approach increases. The attentional cost and effect on assessed risk occur in addition to the effect of decreasing distance in prey that do not account for duration of approach, while assessing costs of fleeing and not fleeing. Some of these effects may operate simultaneously. We describe research needed to better understand the flush early hypothesis and proposed costs associated with monitoring approaching predators.

Key words: **alert distance, escape behavior, escape theory, flight initiation distance, starting distance.**

INTRODUCTION

From 1986 until 2003, economic escape theory (Ydenberg and Dill 1986) successfully predicted relationships between flight initiation distance (FID, predator–prey distance when a prey begins to flee from an approaching predator) and various factors that affect the prey's assessment of the cost of not fleeing (predations risk) and the cost of fleeing (loss of opportunities). The finding that FID in many bird species increases as starting distance (SD, predator–prey distance when the predator begins to approach) increases (Blumstein 2003) could not be explained readily by the existing theory. Since then, the relationship has been studied in many species, especially of birds and lizards (reviewed by Samia et al. 2013). One hypothesis is that FID increases as SD increases because prey may move spontaneously during approaches, especially if unaware of the predator. Chamaillé-Jammes and Blumstein (2012) have demonstrated that in some prey species the relationship between FID and SD persists when the effects of spontaneous movement have been removed. The flush early and avoid the rush hypothesis (Blumstein 2010) proposes that costs associated with monitoring a predator as it approaches underlie the relationship between FID and SD. In this paper, we consider the nature of such costs.

Economic models of escape behavior (Ydenberg and Dill 1986; Cooper and Frederick 2007, 2010) predict FID (the predator–prey distance when a prey begins to flee from an approaching predator). The predictions are based on 1) the cost of not fleeing, which is primarily expected loss of fitness due to predation, 2) the cost of fleeing, which is largely the cost incurred by prey when abandoning opportunities to enhance fitness in order to flee, and 3) the prey's fitness at the outset of its encounter with the predator. FID is predicted to increase as the cost of not fleeing and initial fitness increases, and to decrease as the cost of fleeing increases.

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In Ydenberg and Dill's (1986) model, only cost of not fleeing and cost of fleeing affect FID. In Figure 1, the predicted FID, d*, occurs when these costs are equal. Blumstein (2003) and Stankowich and Coss (2006) proposed and empirically confirmed that in the scenario of the Ydenberg and Dill (1986) model, prey responds differently to predators in 3 distance intervals (Figure 1). In zone III, predators are far enough away that they are not detected or do not warrant intense monitoring. At shorter predator–prey distances in zone II, prey monitor predators and make escape decisions based on the predation risk and the cost of fleeing. On detecting predators at still shorter distances in zone I, prey flees immediately. A large body of empirical knowledge strongly supports these predictions for diverse prey, and identifies many factors that affect predation risk and cost of fleeing (Stankowich and Blumstein 2005; Cooper 2010a). However, the relationship between assessed risk and FID may sometimes not extend to interspecific comparisons. For example, European bird species that have shorter FIDs are more likely to be killed when attacked by European sparrow hawks (*Accipiter nisus*) than are species having longer FIDs (Møller et al. 2008). This comparative finding does not contradict escape theory because FID is free to vary within species, increasing as assessed risk increases.

Blumstein (2003) reported that FID increases as SD (the distance between a predator and a prey when the predator begins to approach) increases in many avian species. This finding was somewhat controversial for several reasons. First, SD was not correlated with FID in some lizards, or SD had a very low positive correlation with FID only at fast predator approach speed (Cooper 2005a). Second, when SD is very long, prey initially may be unaware of the predator. Third, as SD increases, the likelihood of spontaneous movement unrelated to predation risk increases, especially for prey that has not detected the predator. Finally, and most importantly in the current context, how SD might affect costs of not fleeing and of fleeing are, at present, unclear.

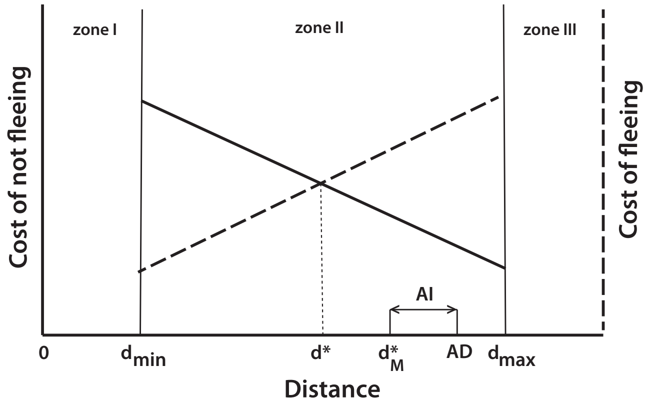

Figure 1

In a modified version of Ydenberg and Dill's (1986) economic model of FID, prey flees immediately in zone I ($0 \le d \le d_{min}$, where d is the distance, and d_{min} is the shortest distance, where escape is immediate), assess costs of fleeing and of not fleeing in zone II ($d_{min} \le d \le d_{max}$, where d_{max} is the greatest predator–prey distance at which prey begin to assess costs), and do not monitor and may not detect predators in zone III ($d > d_{max}$). The predicted FIDs are d* for a prey whose escape decisions are not influenced by AD and d^*_M for prey whose FID is affected by monitoring the predator's approach. The distance over which the prey monitors the predator is the AI, shown for prey whose FID is longer due to monitoring. Modified and expanded from Blumstein (2003).

Of the many factors related to FID, SD may have the most variable relationship to FID and has required the most effort to understand. Since Blumstein (2003) first reported the relationship between SD on FID in many bird species, SD has been shown to be correlated with FID in mammals (Stankowich and Coss 2006), a crab (Blumstein 2010; hiding initiation distance), and some lizard species (Cooper 2005a, 2008; Cooper et al. 2009; Cooper and Sherbrooke 2013). Among lizards, FID did not vary with SD in several species of ambush foragers that were approached slowly (Cooper 2005a; Cooper and Sherbrooke 2013), but increased markedly as SD increased for active foragers (Cooper 2008; Cooper et al. 2009) and slightly in 1 ambushing species, the latter only when approached rapidly (Cooper 2005a). Even in birds, the relationship between SD and FID may be variable (Blumstein 2003). Møller (2010) and Díaz et al. (2013) found weakly negative interspecific relationships for large numbers of avian species between SD and FID when SDs < 30 m were excluded. Previous studies have focused on why SD related to FID between species; we expand this discussion to the nature of the relationship within species as well.

Lack of apparent fit between risk and cost factors led to doubt about the general importance of SD. Was it an artifact of spontaneous movement? Did it affect economic escape decisions? We have identified several previously unconsidered ways in which monitoring an approaching predator might affect escape decisions, including energetic cost of monitoring and influences of monitoring on perceived risk and cost of fleeing. We present these new ideas, briefly review empirical findings and theoretical models about effects of SD, and present some novel consideration of ways in which assessment of cost of not fleeing and of fleeing may depend on SD.

SD, ALERT DISTANCE, FLUSHING EARLY, AND SPONTANEOUS MOVEMENT

How can these differences be explained and how can SD affect assessment of predation risk or cost of fleeing, as required by economic escape models? When approach begins at long SD, a prey may move spontaneously before it has detected the predator, in which case the apparent relationship between SD and FID could be an artifact of spontaneous movement. High rates of spontaneous movement by active foragers and very low rates in ambush foragers might account for some of the differences in the relationship between SD and FID in lizards (Caro 2005; Cooper 2008), but in other taxa, researchers frequently ignore movements that are not obviously in response to the experimental approach. Moreover, because many prey appear to suppress movement while monitoring predators (Cooper et al. 2008), the relationship between SD and FID cannot be entirely due to spontaneous movement. Finally, spontaneous movements are very unlikely to completely account for the SD–FID correlation when a prey has detected the predator.

The flush early hypothesis (Blumstein 2010) suggests that prey begin to flee from approaching predators soon after they have detected and identified the predators to reduce or minimize cost of monitoring while the predator approaches. Many prey do not flee immediately on detecting predators, and a recent model suggests that cryptic prey should flee immediately or not at all (Broom and Ruxton 2005). According to the flush early hypothesis, FID increases as SD increases because monitoring costs increase as SD increases. The nature of the proposed monitoring costs has not been clear. Our goal is to identify ways in which monitoring might affect costs of not fleeing and of fleeing.

The relationship between SD and escape behavior is problematic when the prey is unaware of the predator. Fortunately, some preys indicate awareness of a predator by looking toward and often turning to orient toward it. Alert distance (AD) is the predator–prey distance at which this occurs (Blumstein et al. 2005). Alerting responses may be delayed for some time after the prey has become aware of the predator. This is especially likely to occur in zone III of Blumstein's (2003) model where prey may detect, but do not monitor predators to assess risk, but might also occur in the monitoring interval (zone II) if prey are aware for a time before showing the alerting response. This difficulty could be at least partially overcome by monitoring physiological parameters that track the autonomic nervous activity (such as heart rate, pupillary responses, or galvanic skin responses) during approach. By monitoring less attentively at longer distances, prey might incur a hidden monitoring cost before becoming alert. Furthermore, alerting responses not only indicate that the prey has detected the predator, but also serve as pursuit-deterrent signals in some prey (Holley 1993; Ruxton et al. 2004; Caro 2005). Zebra-tailed lizards (*Callisaurus draconoides*) that were aware of an approaching predator did not signal until the predator approached to a distance that increased as predation risk increased (Cooper 2010b, 2010c, 2010d, 2011), showing that awareness sometimes precedes signaling. Despite its limitations, AD is less subject to effects of spontaneous movement than SD, and, like SD, is positively correlated with FID (Stankowich and Coss 2006).

Once the prey is alert, it monitors the approaching predator during some interval until it flees. This interval is called assessment time (Stankowich and Coss 2006). The corresponding spatial assessment interval (AI) is AD − FID. In these intervals, the prey monitors the approaching predator and matches the scenario of economic models of FID. SD may serve as a substitute for AD for prey that do not perform alerting responses, but is more subject to a potentially spurious relationship with FID due to spontaneous movement and statistical constraints (Dumont et al. 2012).

Dumont et al. (2012) showed that there must be a positive correlation between AD and FID because AD is always ≥ FID, but no such relationship exists in some studies (e.g., Cooper 2005a; Cooper and Sherbrooke 2013; some species in Blumstein 2003; Chamaillé-Jammes and Blumstein 2012). In such cases, FID is not causally related to AD and does not exhibit the artifactual relationship identified by Dumont et al. (2012), which occurs if FIDs are selected as random numbers ≤ AD. FID is economically, not randomly, selected by prey. Its mean value is constant unless the distance and duration approached by a predator affects costs of fleeing and/or not fleeing. Researchers routinely discard data if uncertain that the focal animal fled in response to the approach. The potential for a statistical artifact exists, but we expect that it is rare in practice.

Chamaillé-Jammes and Blumstein (2012) modeled effects of spontaneous movement and monitoring costs on the relationship between SD and FID. The model incorporates d_{min}, which separates Blumsteins' (2003) zone I, where flight is immediate, from zone II, where escape decisions are based on economic considerations; it is the shortest distance where flight is immediate (Blumstein 2003). In zone II, SD may or may not be related to FID. These possibilities are both permitted by assuming that the predator–prey distance at which cost of monitoring is great enough to elicit escape is proportional to SD: $d^*_M = d_{min} + \beta SD$, where d^*_M is the distance at which prey flee based on monitoring cost. Note that $d^*_M > d^*$ for monitoring cost >0 (Figure 1).

Preys are assumed to move spontaneously with a random Poisson distribution at rate λ s^{-1}, which can be expressed in m^{-1}. Spontaneous movement is allowed between SD and the FID predicted by monitoring cost, that is, when $d^* < SD$. If the rate of spontaneous movement is constant, the proportion of prey that have moved spontaneously increases exponentially with duration and distance approached by the predator. The predicted FID is the greater of the FIDs based on economic considerations and on spontaneous movement. Analysis of data by quantile regression, in which many individuals that move spontaneously are excluded in the lower quantiles, showed that FID increased as SD increase for 2 of 4 avian species (Chamaillé-Jammes and Blumstein 2012). Large data sets are required for quantile regressions, and no relationship may be detected with insufficient data even if a relationship between FID and SD exists.

ROLES OF SD AND AD IN ECONOMIC ESCAPE

Preliminary considerations

In current cost-benefit models (Ydenberg and Dill 1986; Cooper and Frederick 2007, 2010), monitoring is assumed to occur while the predator approaches, but is not otherwise known to affect predation risk or cost of fleeing, as required by the flush early hypothesis (Blumstein 2010; Chamaillé-Jammes and Blumstein 2012). In this section, we propose novel effects of AD on FID and incorporate some ideas from the model by Chamaillé-Jammes and Blumstein (2012) into existing economic escape theory. If $d_{min} > 0$, prey may not flee immediately in the portion of zone II to the left of the intersection of the cost curves in Blumstein's (2003) model (Figure 1) on which the SD model of Chamaillé-Jammes and Blumstein (2012) is based. Note that if $d_{min} = 0$, zone I does not exist, making the model spatially equivalent to the Ydenberg and Dill (1986) and Cooper and Frederick (2007, 2010) models. In this case, if a prey detects an approaching predator at any distance in the range $0 \le d \le d^*$, it flees immediately in the economic models. No opportunity exists for dynamic adjustment of FID during the predator's approach at these short distances. Therefore, dynamic adjustment based on monitoring costs can occur only in the interval $d^* < d_{max}$, which separates zone II from zone III, the zone of longer distances where prey may or may not detect predators, but do not assess risk while monitoring them (Figure 1).

The effect of spontaneous movements on predictions of escape theory depends on the relationship between monitoring and spontaneous movement. If moving is likely to cause the predator to detect and attack the prey, the prey may suppress spontaneous movement while monitoring. Spontaneous movements would then occur only in zone III, where $d > d_{max}$ (Figure 1). In this case, the natural rate of leaving, λ, is only applicable for very long SDs. Such movements do not alter estimates of FID when the prey is aware of the predator at distances where prey makes economic assessments that affect escape decisions. In the model of Chamaillé-Jammes and Blumstein (2012), spontaneous movement occurs during the entire interval between the SD and the FID based on monitoring cost, d^*_M. In that case, spontaneous movements inflate estimates of FID, but their effect on economically predicted FID, d^*, can be removed if rates of spontaneous movements are known.

How might monitoring affect escape decisions in the cost-benefit escape models?

Stankowich and Coss (2006) showed that time spent assessing an approaching predator increased as SD increased, suggesting that any cost associated with duration of monitoring should increase as SD increases. The cost of fleeing is primarily an opportunity cost (OC), which increases as FID increases because by fleeing at longer distances, the prey has less time to complete beneficial activities. The cost of not fleeing is primarily based on predation risk, which increases as the predator draws nearer. Monitoring may have complex effects, but they have not been thoroughly examined theoretically or empirically. Here, we identify 4 ways in which monitoring AD and its proxy, SD, might affect FID, one of which underlies the flush early hypothesis. Two of these costs would affect the cost of not fleeing and 2 might affect cost of fleeing.

Cost of not fleeing

The cost of not fleeing could be affected by AD in 2 ways. First, the physiological cost of monitoring should increase with the duration of the approach. Second, increasing perception of risk also might occur as duration of approach increases.

Physiological costs of monitoring

The physiological cost of monitoring (which we specifically define as the energetic expenditure required to focus attention on the predator) is presumably largely a neurological cost due to sensory processing and cognitive function, but may include cost of postural adjustments and movements required for monitoring. It potentially can be measured empirically, but it is likely to be very small during brief predator–prey encounters. This physiological cost of monitoring increases as the duration of monitoring increases, and therefore increases as SD increases. Physiological monitoring costs can be added to the cost of not fleeing due to predation risk to obtain a total cost of not fleeing (Figure 2). Because the physiological cost is likely to be very small compared with fitness consequences of predation risk and any large OCs of fleeing and to simplify presentation, it will not be included in subsequent figures.

Small neurological monitoring costs do not imply that energetic expenditure is unrelated to AD and FID. FID increases as basal metabolic rate (BMR) increases in 76 avian species, presumably because predation risk imposes selection favoring wariness requiring higher BMR (Møller 2009). This relationship has not been demonstrated intraspecifically. Even if it were to exist, monitoring a predator would not affect an individual's BMR: whether or not a prey monitors a predator during approach, its BMR will not vary. During brief approaches by predators lasting only a few seconds, energetic expenditure due to BMR and any non-neurological increase in metabolic rate must be very small. BMR appears to evolve in response to long-term differences in predation risk, but the evidence (Møller 2009) links BMR with FID, not with monitoring cost. Higher BMR might enhance escape ability in species that require long FIDs. It might also affect the ability of prey to remain vigilant and monitor predators while conducting other activities. However, during brief approaches by predators that last only a few seconds, differences in energetic expenditure related to BMR and neurological costs of monitoring must be quite small.

AD and assessed predation risk

Prey dynamically and rapidly adjust assessed risk in response to changes in predator behavior during approaches (Cooper 2005b) and exhibit longer FID when predators indicate their persistence by approaching repeatedly (Stankowich and Blumstein 2005). These findings and the increase of FID as AD increases suggest that assessed risk increases as the duration and distance moved by the predator increase. This can be considered another effect of predator persistence. The longer a predator approaches, the greater the likelihood that it has detected or will soon detect the prey and the greater the likelihood that the predator will attack.

In this view, AD could be an important indirect predation risk factor. The true factor that affects assessed risk is duration or distance approached (AD – d), whereas AD marks the beginning of intense risk assessment. As AD increases, the length of approach and, therefore, the assessed risk at any given predator–prey distance increases. Consider a risk curve in which duration of monitoring does not affect assessed risk. If the curve is linear, assessed risk is on the same line regardless of AD (Figure 3).

By contrast, if assessed risk at a given distance increases with the duration of monitoring, a curve representing this effect will be above the line for no effect of monitoring duration on assessed risk

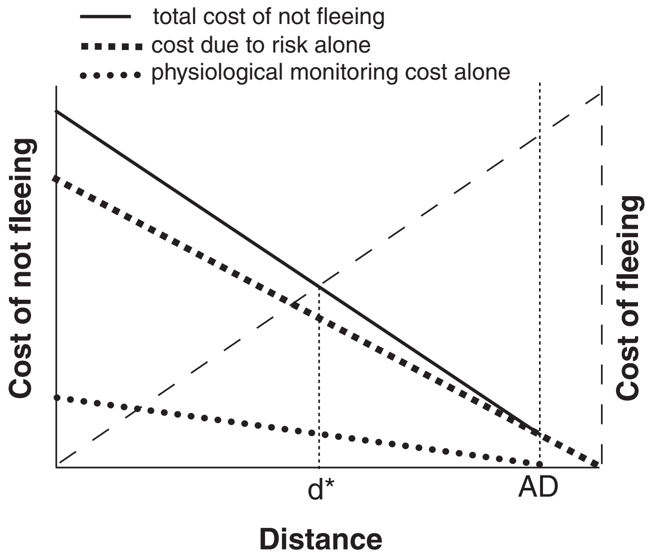

Figure 2
When the physiological cost of monitoring is added to predation risk, the predicted FID, d*, is increased.

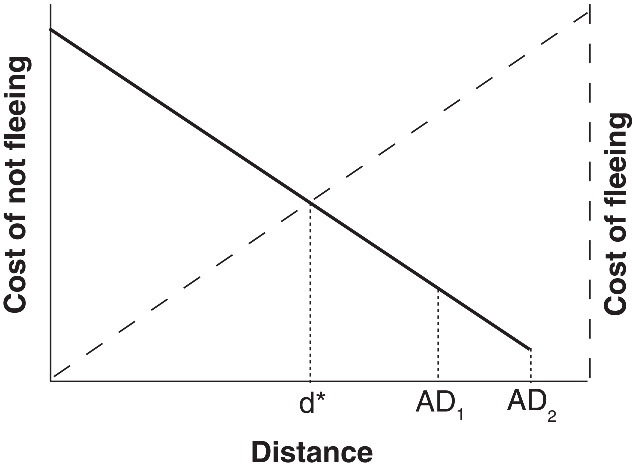

Figure 3
Flight initiation is unaffected by AD if the cost of not fleeing curve is the same for both ADs. This occurs if assessed risk is not affected by monitoring duration. Similarly, if cumulative monitoring costs do not affect cost of fleeing, predicted FID, d*, does not vary with AD. The graph depicts the Ydenberg and Dill (1986) model with addition of ADs.

for all distances ≤ AD. Such a curve must be concave downward because it must intersect the line representing no effect of monitoring duration both at AD and at d = 0 (Figure 4A). After an initial period of increasing rate of gain in assessed risk as the predator's approach is monitored, the rate of gain must be attenuated because as d becomes short, risk approaches a maximum at d = 0 that is not affected by AD, only by the expected loss of fitness on contact with the predator. Predicted FIDs are d^*_N when AD does not affect assessed risk and d^*_R when assessed risk increases as AD increases. Because the intersection of the cost of fleeing with the cost of not fleeing is at a longer predator–prey distance when assessed risk increases as AD increases, $d^*_R > d^*_N$.

Suppose that AD differs for 2 preys that perceive similar increases in risk as the duration of approach increases (Figure 4B). The curve for the prey having longer AD, AD_2, is above the curve for the shorter AD_1 everywhere except at d = 0, where the cost of not fleeing is equal for both ADs (Figure 4B). Therefore, monitoring may differentially influence the optimal FID in 2 ways. First, for a fixed AD, FID is longer when assessed risk increases as approach duration increases than when it does not. Second, FID increases as AD increases when the duration of approach affects assessed risk.

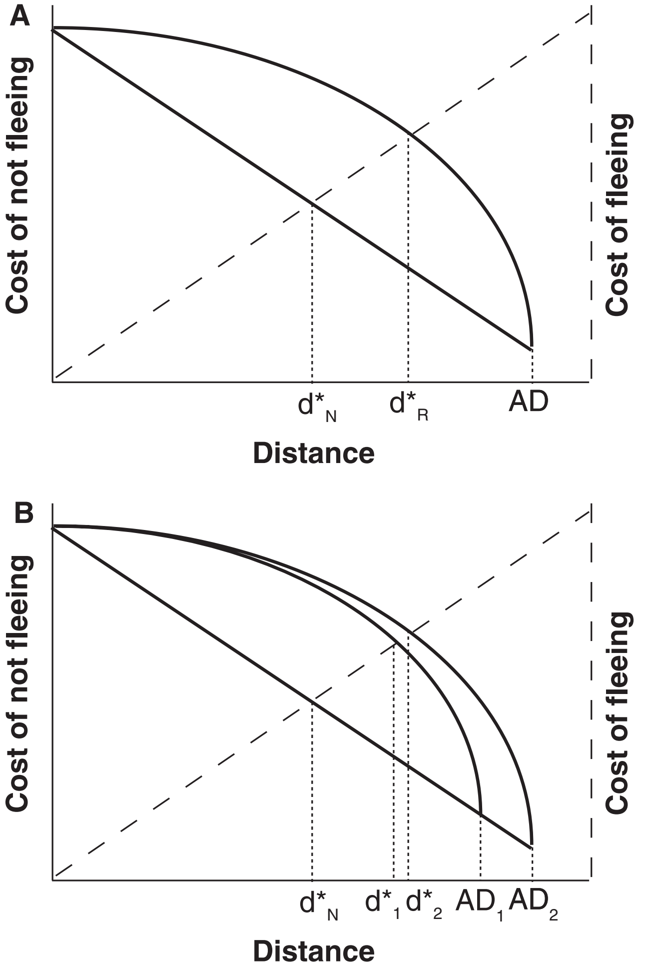

Figure 4

The cost of not fleeing line represents a prey that does not change its assessment of risk based on duration/distance that the predator approaches. (A) In the upper curve, assessed risk increases to maximum at d = 0 as the duration/length of approach increases. FID is longer for prey that interpret continued approach as indicating greater risk. Predicted FIDs are d^*_N if AD does not affect assessed risk and d^*_R if assessed risk increases as AD increases. (B) Among prey that assess increasing risk as the distance approached by the predator increases, FID is longer for the longer of 2 ADs.

Cost of fleeing

Effects of monitoring on the cost of fleeing also could contribute to the relationship between AD and FID. Monitoring may cause a loss of some benefits that might be obtained at any given distance (i.e., reduce OC of not fleeing) by nonmonitoring prey, and this monitoring cost may cumulatively increase as the duration of approach increases.

Relationships between AD and cost of fleeing

AD might influence the cost of fleeing in several ways, including differences in magnitude of benefits that prey might obtain among ADs and impaired ability to enhance fitness while monitoring. First, at the shorter of 2 ADs, the benefit that the prey might obtain by fleeing immediately is smaller than at the longer AD along the same monotonically increasing cost of fleeing curve (Figure 3). Because the same FID is predicted for all AD > d*, this relationship is not relevant to economic escape decisions.

Next, suppose that a monitoring prey cannot gain fitness as rapidly as nonmonitoring prey because its attention is distracted by the predator (Chan and Blumstein 2011). The effect of this distraction is to lower the OC at all distances. Compared with a prey that does not incur an attentional cost, potential benefits available to a monitoring prey are lowered to a degree depending on the degree of distraction and the magnitude of the potential benefit. If a monitoring prey can obtain no benefits, its effective OC is 0, which predicts longer FID.

We begin by considering 2 unlikely cases in which cumulative monitoring costs do not occur. The case in which monitoring has no effect on cost of fleeing is represented by a single cost of fleeing curve or line with 2 ADs (Figure 2). Because OC of fleeing increases as d increases, the OC is greater at the longer of the 2 ADs. However, because these ADs are on the same cost of fleeing curve, the intersection of the cost of not fleeing and cost of fleeing curves is identical for the 2 ADs (Figure 2). On the other hand, any monitoring cost incurred cumulatively before reaching the predicted FID at the intersection would be greater for the longer AD. Because monitoring cannot affect FID in this scenario, any relationship between AD and FID cannot be attributed to monitoring cost.

In another unlikely scenario, monitoring cost might vary with distance and differ between prey or situations, but not in a cumulative manner. This scenario can be represented by a family of cost of fleeing curves, the highest of which represents the case in which monitoring does not reduce OC (i.e., no attentional cost). Assume that the costs of not fleeing are linear (Figure 5; although they might be any monotonically increasing functions that do not intersect in zone II). As the degree of reduction of OC increases, the line becomes lower and its intersection with the cost of not fleeing curve occurs at a longer predicted FID (Figure 5). An attentional cost, such as that depicted in Figure 5, is unlikely because the difference between the 2 lines is greatest at AD, whereas the instantaneous cost of monitoring should be the same for prey that do or do not incur cumulative monitoring cost.

Finally, consider a scenario in which there is a cumulative attentional cost that leads to longer FIDs when there are longer ADs. In this scenario, 2 curves increase monotonically as predator–prey

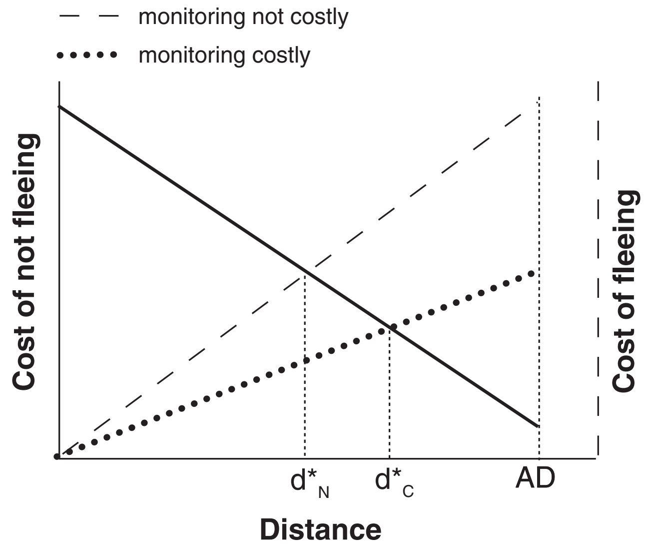

Figure 5

Reduced rate of obtaining benefits while monitoring lowers the cost of fleeing and therefore increases FID. This plot shows an upper cost of fleeing curve for a prey that incurs no monitoring cost and a lower curve in which monitoring costs are lower at all distances because benefits obtainable are reduced. Predicted FIDs are d^*_N when monitoring does not impair ability to obtain benefits and d^*_C when benefits that can be gained are reduced for monitoring prey.

distance increases and both have 0 OC when d = 0 ($OC_0 = 0$) and identical OC > 0 at AD, OC_{AD} (Figure 6A). The curve with no reduction in OC due to monitoring is the higher one throughout $0 < d < AD$. Each point on the lower cost of fleeing curve in Figure 6A represents OC, which decreases as d decreases and is discounted by attentional costs. The lower curve intersects the cost of not fleeing at a longer predicted FID (Figure 6A). Thus, for fixed AD, FID is longer for a prey that has lower OC because it incurs greater attentional cost of fleeing. The attentional cost can be calculated by integration as the area between the 2 curves between AD and $d \geq d^*_c$, the predicted FID for a prey that incurs attentional cost.

Attentional cost is not incurred until the prey is alert and increases as approach continues. Therefore, the attentional cost at a given predator–prey distance is greater for the longer of 2 ADs. In Figure 6B, the curve for the longer of 2 ADs is lower at all points $0 < d \leq AD_1$, the shorter AD (Figure 6B). For prey that accumulates increasing intentional cost as a predator approaches, longer FID is predicted for longer AD. The shapes of the functions shown are arbitrary, and the relationships discussed apply to monotonically increasing functions and their differences in attentional and OCs.

Consider Figure 6B when the OC is the same for 2 costs of fleeing curves having different attentional costs at a fixed predator–prey distance. The point of equal OC_d can be visualized in Figure 6B by imagining a horizontal line segment of equal cost of not fleeing passing from the point where the curve for shorter AD ends at the line to the curve for the shorter AD. Between the shorter AD and d = 0, cost of fleeing is lower at all points along the curve with the longer AD.

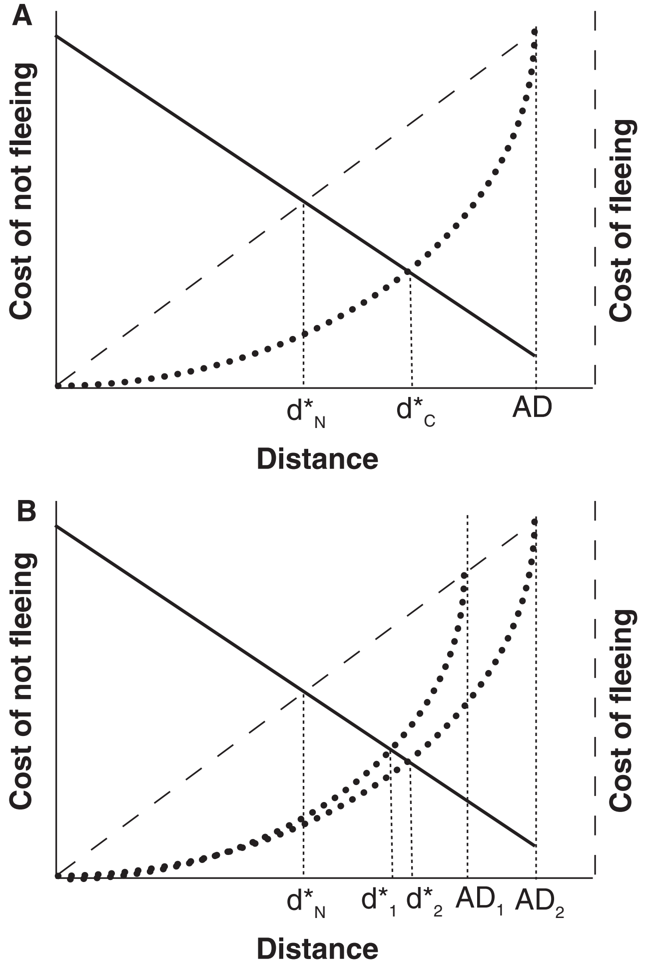

Figure 6

(A) Reduced rate of obtaining benefits while monitoring lowers the cost of fleeing and therefore increases FID. This plot shows an upper OC of fleeing line for a prey that incurs no monitoring cost and a lower curve. In the upper line, the OC, which is OC_0 at d = 0 and OC_{AD} at AD. Monitoring cost is 0 for both curves at the origin and at the AD, but greater for the lower curve at all distances between them, which lowers OC of fleeing. In this case, the cost of monitoring increases as the predator approaches, but its effect is diminished as benefits remaining to be obtained shrink as predator–prey distance decreases. The predicted FID is shorter for the upper line representing no monitoring cost (d^*_N) than for the curve in which monitoring impairs ability to obtain benefits (d^*_C). (B) For 2 ADs lying along the line for which monitoring costs do not affect cost of fleeing, let monitoring cost increase at the same rate as duration of approach increases. The cost of fleeing discounted for monitoring cost and adjusted for decrease in remaining benefits as the predator approaches is shown as curves through the origin to 2 ADs. The curve for the longer AD is always lower than that of the shorter AD in the interval $0 < d \leq AD_1$, the shorter AD. Therefore, d* is greater for the longer AD. Confirmation of this effect of monitoring on cost of fleeing would strongly support the flush early hypothesis.

SPONTANEOUS MOVEMENT: EFFECT ON ECONOMICALLY PREDICTED FID

If prey continues to move spontaneously while monitoring, estimates of predator-induced FID are erroneously inflated to a degree determined by λ, the natural leaving rate. Fortunately for experimental studies, if AD is held constant, spontaneous movement does not affect ordinal level predictions about effects of cost of not fleeing and cost of fleeing factors on FID in a single population provided that monitoring costs are equal or randomly distributed among experimental treatments. These restrictions ensure that the rates of spontaneous movement are the same across treatments. Consider the effect of assessed risk. The longer of 2 observed mean FIDs includes some spontaneous movement plus a component based on assessed risk. Because prey in the treatment having shorter FID are subject to spontaneous movement to the same degree between AD and initiation of flight, assessed risk must be greater for the longer FID. If a third treatment is added, prey in the second and third treatments has equal time for spontaneous movement when the second FID occurs, so assessed risk is greater for the second treatment and so on. Similar considerations apply for the effect of cost of fleeing, but longer FID is associated with lower cost of fleeing.

Spontaneous movement within populations does not alter ordinal level predictions about effects of predation risk and cost of not fleeing factors on FID. However, interpopulational and interspecific differences in natural leaving rates could lead to misinterpretations in experimental comparative studies for constant AD. For example, a species having a very high λ might have a shorter economic FID, but a longer observed FID than a species having a lower λ. The same is true for comparative studies using regression analysis for constant AD. When AD is variable within species, the outcomes of experimental studies will not be affected if ADs do not differ among treatments. Typically, variation in AD would be equal across treatments. Therefore, it would increase experimental error variance, but not the treatment variance.

When AD is variable among species and is related to FID, differences in spontaneous movement rates and AD among taxa, as well as their economically determined FIDs, can affect apparent FID and its relative magnitude among taxa. This does not invalidate comparative studies, but it makes their interpretation more difficult. Ideally, SD, AD, λ, and the effect of monitoring on λ should be known and used to adjust raw FID data, but we are just beginning to understand how these variables are related to FID. Some comparative studies already include estimates of SD. Future studies that also include estimates of λ and determine effects of monitoring on spontaneous movement will permit assessment of the effects of interspecific differences in these variables in comparative studies. We suspect that the broad findings of comparative FID studies are likely valid despite these possible complications, but more knowledge about λ values will permit better resolution, which may be important when such information is used in wildlife management.

If a prey has not detected an approaching predator in the assessment zone (zone II) or at longer distance (zone III), spontaneous movements occur, but no monitoring costs are incurred at distances greater than the distance at which the prey becomes aware of the predator. Suppose that AD is that distance. Once the prey detects the predator, it may both move spontaneously and incur monitoring costs before reaching the economically predicted FID. The main advantage of using AD rather than SD is that spontaneous movements, while the prey is not attentively assessing risks and costs, are eliminated. However, because awareness is indicated by behavior, prey might be aware for variable times before performing the behaviors. This would increase variances of AD and its relationship with FID. The proportion of individuals that leave spontaneously may be expressed as $1 - e^{-\lambda(\mathrm{SD} - d)}$, $\lambda \geq 0$. The observed FID overestimates the economically based FID to a degree that increases as λ increases and as the difference between SD and the economically based FID increases.

There are several potential ways to estimate the contributions of economically determined FID and spontaneous movements to FID calculated from raw data. When FID is normally distributed, the economically predicted FID should have the greatest frequency. This will be apparent for distributions skewed to the right by spontaneous movements unless the rate of spontaneous movement is so great that few prey remain when the economically predicted FID is reached. At less drastic natural leaving rates, spontaneous movement skews the distribution to the right, but a large fraction of prey do not move before the predator reaches the economically predicted FID. The modal FID presumably represents d*, the economically decided FID. A mean FID reduced to account for spontaneous movement would be preferable to a mode. A caveat regarding FID distributions: differences in factors such as personality, age, and sex might lead to multimodal distributions, and studies have just begun to explore heterogeneities among individuals and their influence on the distribution of FID (Møller and Garamszegi 2012).

A second approach to estimating the economically based FID focuses on $d \leq d^*$. Spontaneous movement need not be considered at distances below the predator-induced FID because prey that detects predators there flees immediately. The slope of FID on SD in this range is 1.0, and the slope at longer distances usually differs from 1.0. FID can be estimated as the maximum distance for which the slope of FID on SD is 1.0. The difference between this estimated and the observed FID shows the magnitude of increase in apparent FID caused by spontaneous movement. This method is feasible, yields an estimated mean d*, and avoids the need to adjust mathematically for spontaneous movement.

Two other methods require knowledge of the natural leaving rate. The third, and our preferred, method for estimating the economically determined FID is to adjust the empirical FID data for the natural leaving rate. This requires measurement of the movement rate of prey when not being approached by a predator. In the literature on foraging, MPM is the number of movements per minute (Huey and Pianka 1981; Perry 1999; Cooper 2005b, 2007). Published MPM values for many species, especially of lizards and some birds, can be converted easily to λ in s^{-1}. Movement data can be collected readily for other species by focal observations (Cooper 2005a). Estimates improve as the duration and number of focal observation increase (Perry 2007). The foregoing assumes that λ does not vary with predator–prey distance within a particular habitat, but research is needed to assess possible variation in the rate of spontaneous movement across predator–prey distance. Whether λ is constant or varies over distance, expected numbers of individuals leaving spontaneously can be calculated for a set of intervals from SD to $d = 0$. The expected numbers of individuals would then be removed at random from the data for each distance interval. Finally, the mean FID would be calculated from the remaining data.

A last alternative estimate of FID might be obtained by comparing the expected proportions of individuals that leave due to spontaneous movement with the actual proportions that leave in each interval. Doing so would reveal an interval in which the observed proportion that leaves exceeds the expected proportion to the greatest degree. Because immediate escape occurs at distances below the economically predicted FID, the longest distance having the largest excess over that predicted by spontaneous movement could be used as a rough estimate of the true FID.

CONCLUSIONS AND FUTURE RESEARCH

In the decade since the SD–FID correlation was first reported (Blumstein 2003), its underlying causes, its implications for escape theory, and the misleading effects of spontaneous movement have been studied intensively. Research on SD, AD, and related variables has progressed rapidly due to the combined theoretical and empirical efforts of behavioral ecologists, and has led to rapid advances in our understanding of adaptive flight decisions. We now know that spontaneous movements may sometimes strongly affect the relationship between SD and FID, and that the relationship between SD or AD and FID often remains when spontaneous movements have been taken into account. In hopes that these proposed relationships may have heuristic value for future studies, we have outlined several ways in which AD, or its proxy SD, might affect escape decisions.

Much remains to be discovered about the influence of spontaneous movement on FID estimated from raw data and about roles and monitoring in determining cost of fleeing and of predation risk that lead to flushing early. We have suggested some avenues for research on spontaneous movement. Another variable that deserves attention is the rate of spontaneous looking toward a predator. Usually, spontaneous looking and associated postural changes would bring about awareness, but perhaps not in zone III. A high spontaneous rate of looking might lead to estimated AD > actual AD.

A recent meta-analysis (Samia et al. 2013) showed that FID is related to SD (or AD) in diverse prey taxa. However, the mechanisms underlying this relationship are not entirely clear. Two plausible mechanisms point to increasing attentional costs of monitoring and increasing perceived risk with continued approach. Future research must focus on estimating the magnitude of the cost of distraction to prey monitoring predators, which decreases the magnitude of the cost of not fleeing (OC) and is accumulated as the predator draws nearer.

Research is also needed to assess effects of possible dynamic increases on assessed predation risk during approach that would lead to longer FID. Some available information hints that in some cases, the effect of AD on perceived risk may lead to increase in FID as AD increases. The OC of fleeing was presumably small in lizard studies included in the meta-analysis (Samia et al. 2013) that showed a correlation between SD on FID because no food or conspecifics were visible. Moreover, because lizards were aware when the approach started, SD = AD. SDs in these studies were too short for spontaneous movement to have had a substantial effect. In these cases, dynamically increasing perceived risk probably accounts for the effect of AD. Studies including large OCs of fleeing may clarify effects of AD on FID via monitoring costs of fleeing.

In the model of Chamaillé-Jammes and Blumstein (2012), the effect of SD and AD not attributable to spontaneous movement was called monitoring cost. In light of the above discussion, a possibly major effect of increasing length of the approach is to increase assessed risk. Provided that spontaneous movements do not occur during monitoring, our new interpretation incorporates effects on FID of monitoring cost of fleeing and the effect of monitoring on assessed predation risk associated with AD at distances $d \leq d_{max}$.

We have proposed an attentional monitoring cost that might affect cost of fleeing and have identified other effects of monitoring that may influence the cost of not fleeing (the physiological cost of monitoring and assessment of increasing risk as duration or distance of the approach increases). All or some combination of these effects of monitoring might operate in some prey. Critical tests are needed to distinguish among the possible effects of AD on FID. In a recent experimental study, FID increased as the difficulty of monitoring increased (Camp et al. 2012). The authors assumed that the prey had detected the approaching researcher before the approach began, but no SD or AD values were reported. The major challenge remaining is to devise experiments to identify, distinguish between, or exclude the hypothesized effects of AD on assessed risk and cost of fleeing.

In the absence of experimental verification of the proposed effects, we can only speculate about their relative theoretical and empirical importance. Because monitoring may affect cost of fleeing, attentional costs might be construed to be the critical basis for the flush early hypothesis. However, monitoring might also affect assessed risk cumulatively and affect total cost of fleeing via physiological cost of monitoring. All of these effects of monitoring have been conflated as monitoring cost until now. Among them, increases in assessed risk based on distance approached in excess of the increase in risk associated with decreasing predator–prey distance and any attentional costs of monitoring both might have large effects on FID, whereas physiological costs are likely to be small and have limited effect on FID.

Attentional costs are typically likely to be small, but their cumulative effect may increase OCs. In some circumstances, attentional costs may be large, especially if they interfere with rare mating opportunities, chances to protect fertilizations, or rare feeding opportunities by hungry prey. Generally, in many short-term predator–prey encounters, we expect that the OC of flight is very small, and risk is the primary determinant of FID. Therefore, frequent, substantial effects of AD on FID in the absence of obvious OCs suggest that effects of distance/duration of approach on assessed risk may account for much of the observed effect of AD.

Empirical investigation of the proposed costs related to monitoring is needed to separate the possible costs and to determine their relative importance. In any given situation, physiological cost, dynamic increases in assessed risk, and attentional cost might operate simultaneously. The physiological cost of monitoring could be measured as the difference in energy expended by monitoring and nonmonitoring prey initially engaged in the same activity during approach. Prey could be approached from a direction in which detection of the predator is difficult or while the prey's vision is blocked by a barrier or blindfold. If the physiological cost of not fleeing is very small, its effect on FID may be difficult to detect. It must be trivial compared with the overall effect of AD on FID.

The 2 major effects hypothesized are the dynamic increase in assessed risk and attentional cost, that is, decrease in opportunity by monitoring prey, as AD increases. Suppose that a prey is satiated or that little or no food is present and that the prey has no social opportunities during the approach. In such cases, the OC of fleeing is very small. Because the attentional cost is less than or equal to the OC, it must be very small, too. Demonstration of a large effect of AD on FID when OC is very low would strongly suggest that dynamic increase in assessed risk as AD increases has occurred. If another group of prey for which OC of fleeing is larger is added, any effect of dynamic increase in assessed risk will be constant if the approach is identical. If the relationship between AD and FID is stronger in the second group, attentional cost would be inferred. In a complementary design, the OC of fleeing and any associated attentional costs could be held constant. If the relationship between AD and FID is stronger for approaches during high-risk than low-risk approaches, dynamic increase in assessed risk as AD increases is implied.

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