

# Escape behavior: dynamic decisions and a growing consensus

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There has been a recent flurry of theoretical, empirical, and comparative research in the remarkably integrative field of animal escape behavior. We highlight several new insights, mostly those that have emerged from the economic study of flight initiation distance (FID). Recent theoretical developments have shown that the logic applied to understanding FID also applies to other situations and that escape behavior is influenced by its benefits and costs, but the importance of these factors varies by taxa. In some cases, escape behavior is part of a compensatory response animals use to manage risk. Escape behavior varies geographically and can be used to inform wildlife management.

## Addresses

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## Introduction

Since virtually all animals are vulnerable to predation at some point in their lives, those that are ambulatory will likely use escape as an antipredator strategy. Successful escape is essential and predation risk should create a strong incentive for making wise escape decisions. Since 1986 when Ydenberg and Dill's seminal paper on the economics of escape behavior was published [1<sup>•</sup>], the hypothesis that individuals trade-off the costs and benefits of escape has been overwhelmingly supported. Most of the work has focused on the distance a threatening stimulus (often a human) can approach a prey before it begins to flee, the flight initiation distance (FID). A recent edited volume that synthesized and reviewed contemporary literature on escape behavior reported that annual numbers of published escape papers and citations are rapidly increasing [2<sup>••</sup>, Fig. 1.1]. We focus this review on novel insights into escape decisions published since 2013, emphasizing FID. After reviewing recent theoretical and

empirical advances, we summarize a series of emerging conclusions.

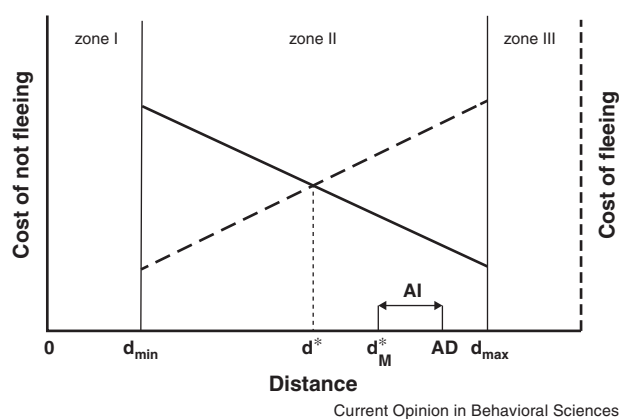
## New theoretical insights

Economic models predicting FID from costs of fleeing and not fleeing are more fully developed than models of other escape variables (e.g., escape trajectory, distance fled, latency to flee, hiding time in refuge, etc.), and have been strongly supported by extensive empirical work [2<sup>••</sup>, 3<sup>•</sup>]; (Box 1). Perhaps the greatest challenge for the economic model of FID was faced over a decade ago [4] when many studies found that FID of most taxa increases positively with alert distance, which is the distance the prey first responds by looking toward a predator. But whether this finding is consistent with an economic decision by prey was uncertain. Nevertheless, a recent model, seemingly supported by empirical evidence, provides an economic explanation for this ubiquitous relationship: FID increases with alert distance because of increased attentional costs of monitoring an approaching predator [5<sup>•</sup>]. It occurs because potential benefits of current activity (e.g., foraging) decreases while prey redirect their limited attention to monitoring an approaching predator and because perceived risk increases as the duration of a predator's approach increase [5<sup>•</sup>]. Proper methods to quantify the effect of alert on FID have been developed recently [6].

Current economic models [1<sup>•</sup>, 7] cannot predict FID exactly because their currency is fitness and the exact relationship between model variables and fitness are unknown. However, a recent experiment operationalized fitness by using the probability of prey's survival as a proxy for fitness [8]. The result of this study indicated that the shape of the cost of not fleeing curve matched the first economic [1<sup>•</sup>] and optimality models [7], but also suggested that the relationship between FID and survival was quadratic rather than exponential [8]. Although converting probability of survival curves to cost of not fleeing curves is a promising approach, some important points must be clarified. The Ydenberg and Dill economic model [1<sup>•</sup>], being graphical, does not imply any specific functional relationship between FID and cost of not fleeing. And, although the optimality model specifies the functional relationships for fitness consequences of each possible choice of FID, these relationships are theoretical and illustrative, rather than being based on empirical evidence. Moreover, the survival curve from the optimality model appears to have been inappropriately treated as a cost of fleeing curve in this recent study [Fig. 4 in 8]. Predictions

**Box 1 When a predator encounters a prey it must make a number of decisions.**

The prey may detect it but elect to not respond in an overt way, respond in an overt way by modifying its current behavior and focusing its attention on the predator, and flee. Once the prey flees, it must make additional decisions about its escape angle, how far to flee, how long to remain hidden (for those that hide), as well as how long to wait before resuming its previous behavior. All of these decisions can be modeled using the logic initially developed by Ydenberg and Dill [1\*]. In economic models of flight initiation distance (FID), prey flee immediately in zone I ( $0 \leq d \leq d_{\min}$ , where  $d$  is distance and  $d_{\min}$  is the shortest distance where escape is immediate), assess costs of fleeing and of not fleeing in zone II ( $d_{\min} \leq d \leq d_{\max}$ , 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 flight initiation distances are  $d^*$  for a prey whose escape decisions are not influenced by alert distance (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 assessment interval (AI), shown for prey whose FID is longer due to monitoring. The shape of the curves is idealized; many factors can influence the costs of not fleeing and the costs of fleeing. Based on [1\*] and [4]. Figure and legend modified from [5\*].



of the two models are much more similar when both are based on cost of fleeing.

Traditional economic models predict FID when a predator approaches an immobile prey [1\*,8] and time spent hiding (hiding time) in a refuge after an approach [9]. New models extend predictions to three other scenarios: (1) latency to flee is predicted when an immobile prey detects an immobile predator; (2) the closest approach distance is predicted for a prey approaching an immobile predator, and (3) FID is predicted when the predator and prey approach each other [10\*\*]. These scenarios require more empirical tests.

Since escape is a game between predators and prey, game theory is a useful way to understand escape decisions. Recent models have shown that the probability that a predator attacks is reduced if a prey honestly signals its escape ability [10\*\*]. This reduced risk implies that FID should be shorter for signaling prey [10\*\*]. More work

needs to focus on the predator's interactive response to prey. Here we consider a related, but slightly separate issue, the advances in understanding how prey integrate multiple aspects of their overall antipredator response to predators. Another application of game theory posits that prey subject to being discovered and pursued by a predator may choose to be hard to find or to occupy sites where they are hard to catch if attacked. The model predicts that hiding in random locations is predicted to be increasingly favored as the frequency of being pursued increases. Being hard to catch is favored when the frequency of being attacked is low [11\*].

**Are escape behaviors repeatable and are they part of an escape syndrome?**

The literature on personality and behavioral syndromes has rapidly expanded in recent years and FID is a common way to measure 'boldness' [12]. If statistically repeatable [13], boldness (FID) may be considered a personality trait. If boldness is correlated with other traits, it may be part of a behavioral syndrome.

Considerable evidence shows that FID can be repeatable. For instance, FID of Namibian rock agamas (*Agama planiceps*) is repeatable within and between wet and dry seasons [14]. Burrowing owls (*Athene cunicularia*) have remarkably high FID repeatabilities throughout their adulthood [15]. Such repeatable traits may influence later survival as nicely shown by earlier mortality during the hunting season of bold male captive-reared pheasants (*Phasianus colchicus*) released into the wild compared to females [16\*]. Moreover, pheasants males that died of natural causes (including disease) were bolder than their counterparts that were shot. Crickets too have repeatable FID associated with survival: bold animals had shorter lifespans [17]. Similarly, pigeons (*Columba livia*) that tolerated closer approach were more likely to be preyed upon while homing [18\*]. More studies need to examine fitness consequences of FID.

In some circumstances FID may not be repeatable. For instance, variable FIDs by incubating Eurasian curlews (*Numenius arquata*) has been interpreted as part of an unpredictable 'surprise strategy' [19]. Repeatability also may vary over an animal's lifetime. For instance, FID was repeatable in yearling, but not in juvenile or adult yellow-bellied marmots (*Marmota flaviventris*) [20]. Such age-specific variation might be explained by juveniles being uniquely constrained to gain mass before hibernation so there is selection against behavioral variation (all individuals should be relatively bold). Similarly, adults might be selected for behavioral variation across years accounting for the lost repeatability.

FID is often correlated with other traits, but it need not be [21]. Some studies correlate various behaviors systematically, but are not strongly hypothesis-driven. For instance,

in coyotes (*Canis latrans*), FID is correlated with latency to approach a novel object, but not other measured traits [22]. Concrete predictions about syndrome structure can be made if FID is viewed as a way to compensate for vulnerability. For instance, a risk-compensation hypothesis was rejected in yellow-bellied marmots: marmots that ran more slowly than others also tolerated closer approaches [23<sup>\*</sup>]. Similarly, brightly colored birds did not flee at greater distances [24].

## Biogeographic aspects in prey escape decisions

### Island tameness

Darwin famously conjectured in 1839 that prey on islands are less wary than their mainland relatives because predation pressure is reduced on islands [25]. Empirical interest in this phenomenon has grown because FID provides a convenient metric for wariness. Island tameness was recently confirmed by a comparative study of 66 lizard species [26<sup>\*\*</sup>]. Controlling for effects of predator approach speed and prey body size and using phylogenetically informed statistical analysis, FID was shorter for island than mainland lizards and decreased as distance from the mainland increased.

New data confirm that FID varies among populations intraspecifically in lacertid lizards as predicted by level of predation risk on main islands and associated islets [27<sup>\*</sup>,28]. Effects were stronger for avian and mammalian than other predators [27<sup>\*</sup>]. The decrease of FID in populations increased as the duration of isolation from predators increased [27<sup>\*</sup>]. In populations exposed to cat predation, lizards were found closer refuges, another indication that wariness increases in populations under strong predation pressure [28].

### Geographic variation in fearfulness

A few recent studies have documented geographic variation of FID. In a study of 714 populations of 159 species of European birds, FID decreased as latitude increased, in parallel with a clinal reduction in abundance of their primary predator—raptors [29]. A pattern consistent with a latitudinal cline in fearfulness was also found for 447 bird species on three continents [30]. These findings are consistent with the biogeographical pattern of reduced predation pressure at higher latitudes [31]. However, novel findings have demonstrated that effects of latitude differ between sexes, presumably because of different pressures on the sexes [30,32]. For example, only female lizards reduce their FID as latitude increases, probably because sex-specific environmental constraints more strongly affect the reproductive effort of females than males [32].

## Using escape behavior as a conservation tool

A number of advances have occurred in understanding how escape behavior can be used as a wildlife management tool [33<sup>\*</sup>]. For instance, recent studies have shown

that when exposed to humans, animals modify their physiology and escape behavior [34–37] and, importantly, that there can be cascading effects on their populations and communities. Given that animals commonly flee from humans, chronic exposure to humans should negatively alter fitness if individuals increase allocation of limited energy to escape instead of reproduction. Three empirical studies correlating a population's FID with its population trends provide some support for this prediction. Declining species are generally less tolerant of humans [38<sup>\*\*</sup>,39<sup>\*</sup>,40]. However, the magnitude and, sometimes, the direction of the effect may differ among geographical locations [39<sup>\*</sup>,40].

A comprehensive meta-analysis including 212 species showed that most birds, mammals and lizards avoid fitness cost of chronic disturbance by increasing tolerance (i.e., reducing their FID) to non-lethal human presence [41<sup>\*\*</sup>]. For birds, the best studied taxon, the two main predictors of tolerance were habitat contrasts (urban versus rural, rural versus suburban, etc. — the most urban birds were the most tolerant) and body size (larger species are more tolerant). The body size effect was unexpected since prior work indicated that larger birds were more likely to be disturbed by humans [42<sup>\*</sup>]. This suggests that larger species are more prone to prosper around humans. Moreover, body size was the strongest predictor of survival in the cities in another study of 68 urbanized species: larger birds survive better than smaller birds [43]. Generalizations like these are important because many management decisions are species-specific [44].

FID can also be used as a non-invasive index of hunting pressure. For example, FID of Sooty-headed Bulbuls (*Pycnonotus aurigaster*) increased significantly as hunting pressure increased [45]. Similarly, hunted populations of impala (*Aepyceros melampus*) and greater kudu (*Tragelaphus strepsiceros*) fled approaching humans at substantially greater distances than non-hunted conspecifics [46]. FID has also been used to study the response of fish on and off marine protected areas to determine their response to spear guns, and in one case suggests that animals off protected areas might be exposed to spear fishing [47].

Escape behavior may shed light on why and how some animals are more likely than others to be hit by vehicles [48]. To avoid collision, an animal must detect a vehicle, assess time to impact, and move out of the way [49]. For this reason, studies of alert distance and FID have provided key insights into vulnerability to vehicle collision. Some species are unable to track increases of velocity above a certain threshold, and therefore fail to escape [50,51].

Researchers also have used FID to investigate the effect sound pollution on antipredator ability: intra-specific and inter-specific communications are important sources of information for predation risk assessment [52,53]. For

Table 1

**Recent work has contributed to emergence of several generalizations about escape behavior. These are shown with suggestions for advances for each. FID, flight initiation distance.**

Generalization	Research needs
Theory successfully predicts FID and applies to more scenarios than previously considered.	Measurement of fitness costs.
Escape behavior is sensitive to both costs and benefits of fleeing, but the importance of these costs varies by taxa.	Modeling joint effects of cost factors. A systematic investigation by taxa.
Escape behavior is part of a syndrome of escape traits that in some cases illustrates compensatory responses.	Hypothesis-driven studies.
Escape behavior is sometimes, but not always, individually repeatable.	What drives personality variation in escape behavior?
Isolation on islands affects escape behavior.	Does island tameness occur in other taxa? Effects of isolation time. Empirical investigation of the mechanism behind sex-specific variation of escape response along latitudinal gradients.
Escape behavior varies geographically.	Why does the relationship between FID and population trend vary among geographical regions?
Escape behavior can be used to inform wildlife management.	More multi-species studies to permit generalizations to inform wildlife managers. How do we understand 'filtering processes' that prevent us from studying escape behavior in species that do not coexist with humans?

example, house sparrows (*Passer domesticus*) exposed to traffic noise while in their nests flushed earlier than non-disturbed individuals, suggesting compensation for reduced ability to assess risk [54].

## Conclusion

We believe that the economic study of escape behavior illustrates tremendous successes in the scientific method [2]. Models have been developed and predictions evaluated. These results have generated model refinement and more empirical studies. Both comparative analyses and meta-analyses have helped identify relatively important factors influencing escape and large-scale evolutionary patterns. And the results have been used to inform wildlife conservation and management. All this began with a simple, elegant, and very timely model [1\*,55].

Our review has been selective. We have not discussed the FEAR [6,56\*,57,58\*,59,60] and DREAD [61\*] hypotheses, for which there seem to be compelling support. We have not discussed additional insights about how life history traits influence escape behavior. Nonetheless, our selective review has illustrated how the integrative study of escape behavior has been remarkably productive. For the topics we focused on, we summarize some generalizations in Table 1 and suggest unanswered questions. We hope that this will help guide future studies of escape behavior.

## Conflicts of interests

The authors declare that there is no conflict of interest.

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