

Forum

Flush early and avoid the rush: a general rule of antipredator behavior?

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Well-understood subjects should lead to the development of general hypotheses, rules, and ultimately, laws. Unlike the fields of physics, which has many laws (e.g., gravity, thermodynamics, etc.), ecology, which has a series of biogeographic rules (e.g., Allen's, Bergmann's, Cope's, Gloger's, Rapoport's rules), and evolution, which has a grand theory (evolution by natural selection), behavioral ecology lacks such generalizations. There is a great deal of controversy about whether fields other than physics can or should have laws, and this has led to a spirited debate in the ecological literature (e.g., Lawton 1999; Mitchell 2000; Murray 2000; Jørgensen 2002; Colyvan and Ginzburg 2003; Lange 2005). I would like to acknowledge this controversy but note (that with some exceptions) behavioral ecologists often focus on documenting and understanding behavioral variation rather than summarizing it into formal hypotheses or rules. Some notable exceptions may include Hamilton's rule (Hamilton 1964a, 1964b) and Trivers' various hypotheses (Trivers 1971, 1974; Trivers and Willard 1973). I also acknowledge that some may consider these too restrictive and not having the precise predictive ability of what we would want a generalization to contain. Indeed, one might argue that a lesson from behavioral ecology is that all individuals face trade-offs, but this itself does not allow us to predict behavior in the way that a formal rule would. Rules, however specific, allow us to predict behavior.

In this forum piece, I would like to propose a hypothesis that, with time, may rise to a rule. The hypothesis is that "animals will flee approaching predators soon after they detect and identify them as a threat to reduce or minimize ongoing attentional costs of monitoring the approaching predators." The implication of this "flush early and avoid the rush hypothesis" is that species that first detect threats at a greater distance (e.g., because of body size, eye size, habitat visibility, etc.) will be more distracted by approaching threats than those who are unable to detect them until they are closer. This differential distraction has implications for coexistence with both predators and humans. I pose this hypothesis in the spirit that by trying to make broad generalizations, and testing them, the field of behavioral ecology will advance well beyond the great conceptual advances made in the 1970s and 1980s (Birkhead and Monaghan 2010). Advances will range from identifying the conditions (i.e., state space, species, etc.) under which broad generalizations are possible, to perhaps generating truly universal rules.

Animals may perceive humans as predators (Frid and Dill 2002), and this simple observation has allowed the systematic study of antipredator behavior across many taxa. When a human walks toward an animal, species that use flight to escape their predators will inevitably move away. This response is called "flight initiation distance" or, in the wildlife manage-

ment literature, "flush distance" (Stankowich and Blumstein 2005). In many cases, prior to flight, the prey will orient or otherwise look at the approaching threat. This response is called "alert distance" (Blumstein et al. 2005). The distance from which a human begins approaching an individual is called "starting distance" (Blumstein 2003). In many cases, starting distance is used as a proxy for alert distance because it is often difficult to accurately identify when an animal becomes alert to an approaching threat. Indeed in some cases, animals may flush as soon as they become aware of an approaching threat (e.g., Stankowich and Coss 2006). The field will advance as we apply more sensitive assays to identify detection (e.g., cardiac or other "cryptic" autonomic nervous system responses—Blumstein and Bouskila 1996), so that we can better study the decision to flee.

Flight initiation distance has been extensively reviewed (Stankowich and Blumstein 2005) and modeled (Ydenberg and Dill 1986; Blumstein 2003; Cooper and Frederick 2007). Studying factors that influence both flight initiation distance and alert distance has led to both theoretical and applied insights. Although animals may dynamically modify their alert and flight initiation distances to manage their response to threats, there is a species-specific component to these antipredator responses as well (Blumstein et al. 2003), and it is possible to study the evolution of both alert distance and flight initiation distance (Blumstein et al. 2005; Blumstein 2006).

A general observation that emerges from studies of birds, mammals, and some lizards is that there is a statistical relationship between the distance the human starts walking toward the animal and both the alert distance and the flight initiation distance (Blumstein 2003; Blumstein et al. 2005; Cooper 2005; Stankowich and Coss 2006; Cooper et al. 2009) and that there is a statistical relationship between the alert distance and the flight initiation distance (Cárdenas et al. 2005). The relationship between starting distance and flight initiation distance is not always present (Cooper 2005), may in some circumstances be an artifact (Cooper 2008), and may be modified by other risk factors (Cooper et al. 2009), but it is nevertheless very common. The relationship between alert distance (which can't always be properly measured, and thus starting distance is sometimes used as a proxy) and flight initiation distance seems more robust.

Indeed this observation extends beyond vertebrates. While recently studying a terrestrial hermit crab (*Coenobita clypeatus*), I noticed that the distance a hermit crab first responded to an approaching human was highly correlated with the distance at which it withdrew into its shell and hid ($r = 0.916$, $P < 0.0001$, $n = 60$). This hiding initiation distance (Chan et al. 2010) is an analog to flight initiation distance in a species that hides, rather than flees, from approaching humans.

This general relationship—seen in birds, mammals, lizards, and now an invertebrate—is not simply driven by the fact that animals that are first approached at a very close distance must orient and flush at a closer distance than those who are first approached at a farther distance. Indeed, the range of starting distances in well-studied species is broad (Blumstein et al. 2005). And, even if one starts approaching an animal from a relatively close distance, they often fail to respond for a while. If anything, there may be a bias in the other direction in that

animals first approached at longer distances may not be able to detect the approaching threat. I have previously referred to this as a zone of awareness; a region beyond which dynamic risk assessment is occurring (Blumstein 2003). However, if the data were comprised of distances so great that animals could not detect an approaching threat, then we would expect that once the human was within its detection distance it would orient and flush and there would be little variation to explain. Yet, there is substantial variation to explain.

Thus, for many vertebrates and at least one invertebrate, there is a general relationship between the starting distance or the alert distance and flight initiation distance. This alone is a generalization, but we may also ask why it is present.

Cooper (2005) suggested that when predators continue to approach a prey, the prey assesses this ongoing approach as indicative of it being detected and under attack. Thus, simply because the approach continues, prey can acquire information about the predator's intentions and thus threat. He contrasted this to differential threats imposed by different predator behavior (e.g., fast or slow approaches) and developed a methodology that may (in some cases) be used to identify how important predator behavior (as opposed to prey risk assessment) may influence escape decisions.

Stankowich and Coss (2006) suggested that male deer (*Odocoileus hemionus columbianus*) were more likely to flee at greater distances when the approaching human pretended to be disinterested by looking away from them compared with approaches where they looked directly at them. They interpreted this finding as a way to avoid confrontation before the prey detected the predator—an important component of antipredator behavior (Sansom et al. 2009).

Stankowich and Coss (2006) also found quadratic relationships between flight initiation distance and starting distance and between starting distance and alert distance. These relationships suggest that deer could be approached closer at the largest starting distances and alert distances. This pattern might be explained by the fact that ongoing monitoring was imperfect and that animals that were first approached from beyond their zone of awareness missed the opportunity to detect the threat because they were focusing their predator-detection attention elsewhere.

Drawing from this, I suggest that the mechanism underlying this common relationship is that ongoing monitoring requires attention. Attention is viewed as a finite entity and individuals must allocate their finite attention to various tasks (Bushnell 1998; Dukas 2004; Washburn and Tagliabue 2006). While foraging or relaxing, once a threat is detected, some ongoing monitoring is required. This may reduce foraging success or simply be disturbing. Thus, it is better to “flush early and avoid the rush” than to continue its current activity and have to allocate attention to ongoing monitoring.

This attentional hypothesis has predictive power. Animals generally may attempt to reduce attention costs so that they can focus on a task at hand or divide their attention in ways to optimize the chance of detecting another threat. To test this attentional hypothesis, distractors (such as sounds, flashing lights, other threats located at different locations, etc.) can be used while approaching animals (e.g., see Chan et al. 2010). If, by distracting prey flight behavior is modified, then attentional processes are important in explaining antipredator behavior (e.g., Blumstein 1998; Dukas 2004). Predator-prey interactions may also be viewed as a game between predators and prey (Caro 2005), and an alternative hypothesis is that flight initiation dynamics are explained by detection signaling to the predator. The pattern of responses may be similar (i.e., communicate to the predator by becoming alert or moving away as soon as it is detected). However, under a detection-signaling hypothesis, flight dynamics

should not be influenced by the addition of attentional distractors. I expect that as the effect of attention on flight behavior is studied in more species, we will commonly see that attention influences flight behavior.

Developing hypotheses with predictive power and plausible mechanisms are essential to both explain diversity and to apply these findings. Individual-based models of behavior (Grimm and Railsback 2005) must be based on empirical rules and (ideally) a sound mechanistic understanding (e.g., Blumstein and Fernández-Juricic 2010). I suggest that the attentional basis of flush early and avoid the rush is one and that with more effort we can identify others. Such efforts will be rewarded if we then can better understand and explain the diversity of behavior.

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