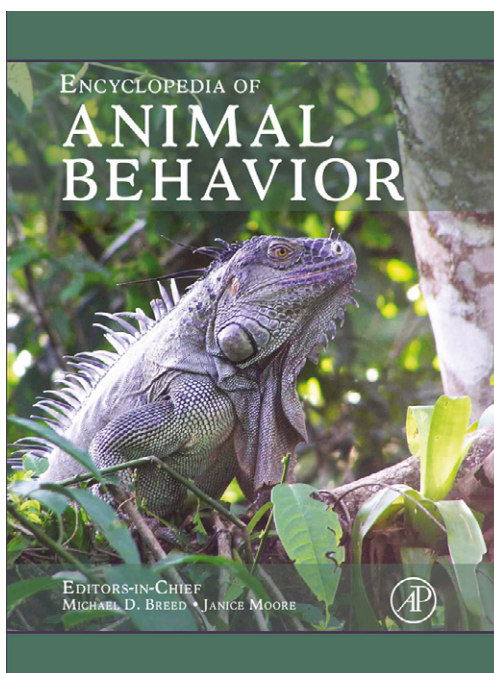


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Risk Allocation in Anti-Predator Behavior

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Introduction

Antipredator behaviors (e.g., flushing, refuge use, avoidance of risky habitat) allow animals to reduce the risk of being captured by predators, providing a net benefit in terms of survival. However, antipredator behavior can be costly: direct energy expenditure and loss of opportunities for acquiring food, mates, nest sites, etc. Prey should weigh the risk of predation against various potential fitness benefits when choosing how much effort to invest in a given behavior and, in some contexts, combine different behaviors to reduce risk. For example, if body mass (as a result of a recent meal) or the distance to the nearest refuge increases, more time would be invested in monitoring the environment for predators or moving closer to cover to reduce exposure, which may decrease risk but reduce access to food-rich patches.

The relationship between predation risk and prey behavior has been widely studied. Most of these studies deal with snapshots of how predation risk influences short-term changes in prey behavior. However, the perception of risk at a given point in time is also likely to be affected by the previous experiences of the animal (e.g., number of times it had been exposed to a predator). For instance, imagine two individuals defending a territory in different locations: one with raptors flying around regularly during most of the day and one without raptors. The individual with high predator exposure may not be able to cope with its energetic needs or find a mate if, after detecting the predator, it always reacts with the safest antipredator response (e.g., seeking cover). Thus, the individual with high predator exposure may be forced to hide for just very brief periods of time or allow closer predator approaches, flushing only when the risk is extremely high. On the other hand, the individual with low predator exposure may allocate more time and energy to antipredator behavior if a predator happens to show up. The reason is because a superfluous escape from a long distance or a prolonged time hiding in the bushes would likely not increase starvation risk or decrease mating opportunities, given the availability of time with low risk that had been allocated to resource acquisition.

The importance of the risk history had been greatly overlooked until the formulation of the risk allocation hypothesis by Steven Lima and Peter Bednekoff in 1999. This hypothesis is based on the fact that the risk of predation experienced by an animal is not fixed in time,

and it generates temporal variation in risk. Based on the risk history, the risk allocation hypothesis intends to establish how the animal allocates effort optimally between resource exploitation and behaviors that reduce risk. While it is clear that prey should allocate greater antipredator effort to high-risk situations than to low-risk situations, the risk allocation hypothesis stresses that the actual antipredator effort allocated to each situation will depend on the relative proportion, duration, and intensity of high- and low-risk situations experienced by the animal in the past.

When high-risk situations are brief and infrequent, the risk allocation hypothesis predicts that animals should allocate their greatest antipredator effort to the pulses of high risk, since they can easily compensate for time lost by maximizing resource acquisition in the prolonged low-risk periods. On the other hand, when high-risk situations are frequent and/or lengthy, animals are forced to reduce allocation of antipredator effort in each high-risk situation (e.g., hiding for a shorter period of time), and to further reduce antipredator investment in the few available low-risk situations (e.g., reduce scanning behavior to the minimum while foraging) to gather enough resources. Additionally, as the relative degree of risk in high-risk situations increases, animals are expected to allocate relatively more antipredator effort to high-risk situations and less to low-risk situations.

While the mechanisms of the risk allocation hypothesis may seem intuitive, some of its implications may not. The risk allocation hypothesis predicts that animals living in an area with high predator abundance should be less wary to predator approaches than animals living in an area where predators are less abundant. Moreover, the behavioral responses predicted by risk allocation can be confused with those predicted by other mechanisms, such as habituation.

Experimental Evidence Behind the Risk Allocation Hypothesis

Since the formulation of the risk allocation hypothesis, a number of studies have tested its predictions, with mixed results. Most of these studies created experimental scenarios in the laboratory using mostly aquatic animals (snails, crayfish, fish, tadpoles) in which the addition of predator cues and/or alarm olfactory cues from conspecifics causes changes in the frequency (e.g., number of

times animals are exposed to predators) and/or intensity (e.g., degree of severity) of risk. Several studies have found a clear relationship between the risk history and the animal response to a given situation of risk, with lower antipredator responses (usually measured as the use of refugia or reductions in activity levels) after a history of frequent high-risk situations. Specifically, studies on cichlid fish by Maud Ferrari, Grant Brown, Patricia Foam, and others provide consistent support for the risk allocation hypothesis and highlight the predicted interaction between frequency and intensity of risk (see earlier). However, several other studies did not find clear evidence supporting the influence of the frequency of risk on prey antipredator responses.

These contradictory results were found even in closely related species, like in the studies conducted by Keith Pecor and Brian Hazlett on crayfishes, in which the behavior of *Oreonectes virilis* matched the predictions of the risk allocation hypothesis, but the behavior of the closely related *O. rusticus* did not support the hypothesis. In a recent comparative study, Kate Boersma and collaborators suggest that different species of North Pacific flatfish may diverge in how they adjust to the risk allocation model depending on species-specific factors, such as the species ability to perceive risk changes, their preferred habitat (shallow and turbid waters that protect from most predator vs. deep and clear waters with higher predation risk), and their relative ability to avoid predation as a result of predator gape size. These species-specific factors could make some experimental designs unsuitable to detect patterns of risk allocation, as each species may have different risk thresholds before they start limiting antipredator responses. For instance, under a scenario with low frequency of high-risk events, small increases in the frequency of risky events may not elicit a reduction in antipredator behavior, since animals still have prolonged periods of safety to exploit resources. However, as the frequency of risky events continues to increase, it may reach a threshold that would start causing the reduction in antipredator effort predicted by the risk allocation hypothesis. Differences in this threshold among species may cause interspecific variation in risk allocation behavior. While this concept of risk threshold has only been suggested in the flatfish study, it could be present even between populations or individuals.

Risk thresholds may also explain the lack of support to the risk allocation hypothesis in other experimental studies. Usually, lab experiments include only two frequency of risky scenarios (low and high), assuming that at least one will fall above the risk threshold; however, the specific threshold level is largely unknown for the model species. Moreover, the physiology of the model species may affect the need to engage in foraging efforts. Josh Van Buskirk and collaborators, as well as Keith Pecor and Brian Hazlett suggested that given the low temporal

scale of many risk allocation experiments, some animals may not require foraging at all over the entire duration of the experiment, and thus invest nearly all their effort in antipredator behavior (e.g., animals are not sensitive to frequency of risk). Although this shortcoming could be solved by modifying food-deprivation schedules, the ability of prey to detect changes in predation risk is an implicit assumption of the risk allocation hypothesis.

Field Evidence Supporting the Risk Allocation Hypothesis

Some patterns observed under field conditions may actually be the result of risk allocation. For instance, the reduction in antipredator responses to humans in areas with a high rate of human visitation has been found in many vertebrate taxa, with habituation to humans usually proposed as the mechanism underlying this pattern. However, it is unclear whether habituation and/or risk allocation are involved. Humans do not directly prey on wildlife in many areas but nonetheless they are perceived as predators, causing antipredator responses similar to those elicited by real predators. Under the risk allocation hypothesis, this scenario of frequent high-risk situations (e.g., high frequency of human approaches) should result in a reduction in antipredator responses to each risky situation as compared to scenarios with less frequency of high-risk situations. This prediction has been tested by Iñaki Rodríguez-Prieto and collaborators using blackbird *Turdus merula* flight responses in urban parks. This study clearly differentiated for the first time the effects of risk allocation from those of habituation, finding that habituation complements risk allocation to produce the pattern of reduced antipredator responses in areas with a high frequency of human visitation. In this study, animals experienced different risk histories by park-specific daily patterns of human visitation. While the history of risk was naturally produced by human visitors, the tests on blackbird flight responses were performed by both human observers and novel predators (e.g., radiocontrolled vehicle) to help differentiate habituation from risk allocation.

That risk allocation is not predator specific is usually overlooked. For example, the risk history produced by frequent encounters with a snake species may lead to reduced prey responses not only to the snake but also to other types of predators, like raptors or mammals. Of course, the type of antipredator response may differ depending on the predator, but all antipredator responses are expected to be reduced as the frequency of high-risk situations from any predator increases.

While most of the known patterns of reduced antipredator responses in places with high density of predators come from areas with varying levels of human visitation, there are also some examples from areas with different

densities of real predators. A recent study by Scott Creel and others on elk antipredator behavior in relation to wolf presence has tested the prevalence of risk allocation in relation to other models by studying several prey populations experiencing temporally and spatially variable levels of actual predation risk. The findings provide support for the risk allocation hypothesis, with wintering elks reducing antipredator vigilance in areas where they were more frequently exposed to wolf predation. Because predation risk was produced by the main predators of elks, habituation of elks to wolves was not likely a problem in this study.

Risk allocation and habituation predictions are difficult to distinguish. If animals habituate to risk cues that are not coupled with potential predation, some experimental designs may not be able to tell apart behavioral responses produced by risk allocation from those produced by habituation, as acknowledged by Reehan Mirza and others. A strategy to avoid this problem may be to study scenarios with real predation where actual predators almost always pose a threat and actually attack and kill prey, and thus may preclude habituation. However, if researchers cannot perform the study with real predators, a potential solution may be to use at least two types of different predator cues, one for creating the risk history and the other for testing antipredator responses. For instance, if a scenario of frequent high-risk situations is created by the intermittent addition of predatory fish odor cues in the water, animals may become habituated to these cues and thus reduce their responses to further predatory fish cues just by a process of habituation, but not by risk allocation. However, once the risk history is established, another type of predator stimulus, like an overflying raptor silhouette, could be used to test if the antipredator responses follow risk allocation, since the potential habituation to the previously used odor cue can be ruled out as responsible for patterns of reduced responses to the raptor. Another strategy may be to take advantage of the different temporal scales in which habituation and risk allocation could be acting. A bird cannot be expected to habituate and dishabituate periodically in response to short-term changes in the frequency of risk. However, risk allocation can predict increases and reductions in antipredator responses to high-risk situations following changes in the frequency of these situations, for example, between consecutive and cyclical periods such as mornings and afternoons.

Broader Implications of Risk Allocation

Risk allocation can alter some paradigms commonly used in ecological models. For instance, most studies on the ecological impacts of predators assume that all the effects of predation increase with increasing exposure to predation risk. Scott Creel and collaborators suggest that while direct

mortality should increase with increasing attack ratios, the same does not apply to the costs of antipredator behavior since risk allocation suggests that the costs associated with antipredator behavior could be reduced or at least could remain relatively unchanged with increasing frequency of exposure to risk under the scenarios discussed earlier. Similarly, common ecological models assume that individual predators would suffer from reduced capture rates in areas with high density of competing predators since prey depletion and avoidance behavior may lead to a reduction in the per capita predator–prey encounter rate. However, Rodriguez-Prieto and collaborators suggested that the probability of prey being captured in any given predator–prey encounter would increase in areas with high density of predators, as animals would reduce their responses to predator approaches in those areas; hence increasing their vulnerability to predator attacks, which would potentially alter predator–prey dynamics.

The risk allocation hypothesis has opened new venues for behavioral research. While there have been some contradictory results, evidence is mounting in favor of risk allocation being an important force shaping the animal responses to temporal variation in predation risk. More research is needed, and there are some questions that seem particularly promising, for example, how and why different species (and probably different populations) vary in the thresholds at which they respond to predators, and how this variation affects predator–prey interactions.

See also: Ecology of Fear; Economic Escape; Predator Avoidance: Mechanisms; Trade-Offs in Anti-Predator Behavior; Vigilance and Models of Behavior.

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