

BEHAVIOUR DILEMMA: ROLE OF PREDATION RISK IN ANIMAL DECISION-MAKING WHEN FORAGING

Conscience Oriade Ogunleye

A.P. Leventis Ornithological Research Institute, University of Jos, Department of Zoology and Biological Conservation, Nigeria

Corresponding Author Email Address: conscience19944@gmail.com

ABSTRACT

Predation has long been thought to have had a significant selective role in the evolution of a number of animal morphological and behavioural traits. Although predation's significance in evolutionary time is obvious, growing evidence indicates that animals possess the ability to assess and behaviourally control their risk of being preyed upon in ecological time. An animal might not get a meal one day and be hungry, or it might not find a mate and have little success reproducing, but over the course of a lifetime, these shortfalls may not have much of an impact on fitness. However, few failures are as cruel as failing to escape a predator because getting killed significantly reduces future fitness. Therefore, this review focuses on how animals' foraging decisions are impacted by the risk of predation. This review explores and brings together findings from a wide range of studies to show how predation risk influences foraging behaviour across different species and ecological contexts. Foragers can lower their individual risk of predation in the presence of predation hazards by implementing a variety of antipredatory behavioural strategies, such as becoming more vigilant, joining a larger group, changing their food choices, mobbing predators, finding sanctuary, or fleeing totally.

Keywords: Predation Risk, Predators, Foraging, Antipredatory Tactics.

INTRODUCTION

Predators not only kill prey, but they also influence a variety of behaviour such as habitat selection (Brown 1999; Morris 2001), alertness, and aggression (Brown 1999; Altendorf *et al.*, 2001; Dall *et al.*, 2001), patch utilisation (Brown & Kotler 2004; Orrock *et al.*, 2004), and nest-site selection (Forstmeier & Weiss 2004), as well as altering offspring development rates (Coslovsky & Richner 2011) and generating indirect mortality (McCauley *et al.*, 2011). Such effects are especially intriguing when modelling prey foraging games (Brown 1999; Brown & Kotler 2004), as prey normally maximise foraging by collecting more resources from "safe" covered patches (those where predators are less likely to be met) than from "risky" open patches.

The diets and foraging habits of woodland animals are significantly influenced by risk and reward (Halliday & Morris 2013). Animals are often forced to adapt to the trade-off between risking their safety for a reward, usually food (Makin *et al.*, 2012). Animals must balance the need to forage with exposure to predators, which is challenging (Laundré *et al.*, 2010). As food consumption and growth enable investment in reproduction, successful foraging impacts the likelihood of survival of the individual organism and its reproductive potential. Actively foraging animals may incur an increased risk of predation, because foraging activities can increase their exposure time and conspicuousness to predators

and compromise their vigilance, and predators may preferentially target foragers that are less wary and more vulnerable (Krause & Godin, 1996; Lima, 1998). Natural selection should therefore favour individuals who can reliably assess the local danger of predation and weigh the benefits of foraging against the risk of predation in a way that maximises fitness (Lima, 1998).

Behavioural decisions of animals foraging under the risk of predation

Foragers can lower their individual risk of predation in the face of predation hazard by engaging in a variety of antipredatory behavioural strategies, including becoming more vigilant, joining larger groups, altering their food source, finding safety, mobbing predators or fleeing (Stankowich & Blumstein, 2005). Choice of a feeding site, latency time to resume feeding and giving-up density (GUD) are some other decisions a foraging animal makes when responding to the risk of predation. Because antipredatory tactics are inherently costly in terms of energy expenditure and lost opportunities (including reduced foraging opportunities; Lima, 1998), the intensity of an individual's antipredatory response to a threat of predation should be graded and proportional to the perceived magnitude of threat, as proposed by the threat-sensitive predator avoidance hypothesis (Helfman, 1989).

Choice of Feeding Site

The perceived danger of predation definitely influences foraging behaviour; numerous research have shown that feeding sites are chosen based on a trade-off between foraging efficiency and the requirement to limit predation risk (Quinn *et al.*, 2012). The choice of a feeding location that borders an area of protective (escape) cover has been linked to escape subcomponents of risk. Schneider (1984) discovered that white-throated sparrows *Zonotrichia albicollis*, feed as close to cover as possible unless food is substantially depleted close to cover or more dominant individuals force them away from cover. Similar findings were made in a research on willow tits (Ekman, 1987). Contrary to these findings, Lima *et al.* (1987) discovered that some finches (Emberizidae) frequently feed well outside of cover. According to observations and experimental findings, these finches view cover as a source of both safety and threats, and their behaviour reflects a trade-off between the perceived risks of feeding too close to cover versus that of feeding too far away.

Carey (1985) and Underwood (1982) discovered that yellow-bellied marmots *Marmota flaviventris*, and African antelopes avoid cover that may disguise and/or contain predators; for these species, cover is not a sanctuary, but merely a source of risk. Lima *et al.* (1985) discovered that black-capped chickadees *Parus atricapillus*, and gray squirrels occasionally bring food items to protective cover to consume. Their proclivity to carry objects to cover increases with

both a reduction in the distance to cover and an increase in the size of the food item (Phelps & Roberts, 1989). This behaviour is consistent with an energy-predation risk trade-off in which time spent susceptible to attack (i.e., away from protective cover) is the most important component of risk under behavioural control.

Vigilance

Prey animals use a variety of behaviours to assess the amount of threat around them. Because vigilance is displayed when animals visually monitor their surroundings, it is a simple activity to document (Caro, 1987). Many animals exhibit this anti-predatory behaviour to secure their safety and their progeny if they have any (Caro, 1987). The two sides of the essential trade-off/balancing act that many animals face are vigilance and foraging. Prey must decide on an appropriate degree of alertness that allows them to feed effectively while being wary of their surroundings and probable predators (Brown *et al.*, 1999). Several studies have found a negative relationship between vigilance and flock size. Individuals in bigger groups tend to devote more time to feeding and less time to vigilance (Avilés & Bednekoff, 2007; Boukhriess *et al.*, 2007). The "group size effect" refers to this inverse association (Robinette & James, 2001). The group size effect is explained by three ideas: the "many eyes" hypothesis proposes that as the number of flock members increases, more eyes are able to detect predators, allowing individuals to relax their own vigilance (Pulliam, 1973; Boukhriess *et al.*, 2007). Individuals reduce their vigilance with an increase in group size, according to the "dilution effect," because the individual probability of predation decreases (Hamilton, 1971). According to the "scramble competition" concept, when members in a larger group compete for a limited number of resources, individual vigilance declines (Beauchamp, 2001, 2003; Boukhriess *et al.*, 2007; Rieucan & Giraldeau, 2009). Additional variables may also impact vigilance, including nearest neighbor distance or group density (Pöysä, 1994; Proctor *et al.*, 2003; Fernández-Juricic *et al.*, 2007), age (Boukhriess *et al.*, 2007), sex (Reboreda & Fernandez, 1997), ambient temperature (Boysen *et al.*, 2001), distance to a refuge (Lima, 1987; Lazarus & Symonds, 1992), visual blockage (Lima & Zollner, 1996), flock shape (Treves, 2000; Dias, 2006), individual location within a flock (Lazarus, 2003; Beauchamp, 2005; Randler, 2005; Dias, 2006), human presence (Manor & Saltz, 2003), time of day (Elgar, 1989; Randler, 2005), and season (Tebbhich *et al.*, 2004; Pechacek, 2006).

Depending on feeding habits, certain animals may have more opportunity to remain watchful. Birds frequently interrupt feeding and lift their heads to scan their surroundings (Bednekoff & Lima, 2002; Beauchamp, 2003; Randler, 2005). Certain herbivores may have additional possibilities for vigilance since they can examine their environment while feeding. While grazing, American bison (*Bison bison*) and elk (*Cervus canadensis*) can be attentive, keeping their heads up and monitoring their surroundings (Fortin *et al.*, 2004). Other species, on the other hand, will feed with their heads down, which is clearly a far more dangerous position with minimal opportunity for monitoring (other than using sound-based or olfactory cues).

Although vigilance is vital in detecting prospective predators, prey can also perceive and respond to cues directly from the predator using visual, auditory, and olfactory cues. Fox squirrels (*Sciurus niger*) may immediately respond to olfactory cues of a predator, whereas thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) respond to visual cues, such as a plastic owl put

in their habitat (Thorson *et al.*, 1998). Finally, prey's capacity to perceive and respond to indications from a possible predator, even if it involves investing more energy, boosts their chances of survival significantly.

Latency Time to Resume Foraging

When a predator is nearby, many foraging birds take cover instantly. Often, they lose sight of the predator, even if it is lying in ambush close by. However, the birds must eventually resume feeding. The restart of feeding after a period of food deprivation may also be affected by predation risk. Once within a refuge, an individual must make a decision about when to resume foraging and other activities (Lima & Dill, 1990; Lima, 1998). The period an individual spends before returning to a food patch it temporarily quit is known as 'latency time to resume foraging'. An individual forager's assessment of the ambient threat of predation outside the refuge, which is generally variable and uncertain, the availability of food outside the refuge compared to inside, and its current energetic state should all play a role in the latency time to emerge and resume activity (McNamara & Houston, 1990; Sih, 1992, 1997). De Laet (1985), Hegner (1985), and Hogstad (1988) observed that dominant great tits (*Parus major*), blue tits (*Parus caeruleus*), and willow tits (*Parus montanus*) often delay the resumption of feeding until inferior individuals, who may be more energetically stressed, do.

The farther the distance between an exploited open-habitat food patch and a refuge, the greater the danger of predation for a forager (Lima & Dill, 1990; Stankowich & Blumstein, 2005), and hence the larger the latency period. Turney and Godin (2014) experimentally tested the threat-sensitive avoidance hypothesis by providing wild passerine birds supplemental food (on a raised feeding platform) at either 1 or 4 m from the edge of forest cover (potential refuge), in either the presence or absence of a nearby simulated predation threat (a sharp-shinned hawk *Accipiter striatus* model). They found that wild passerine birds responded to an apparent threat of predation in a graded manner, with stronger latencies to re-emergence from refuge in the presence of a visible hawk mount and at increasing distance of the food patch from forest cover. Such a graded antipredation response shows that, in the face of increasing predation risk, avoiding exposure while feeding in open habitats by seeking refuge beneath forest cover was detrimental for the birds, at least in terms of missed foraging opportunities (Turney & Godin, 2014). Everything else being equal, a recent encounter with a predator in open habitat, on the other hand, should enhance an animal's latency to emerge from sanctuary and resume activity (Lima & Dill, 1990; Sih, 1992, 1997).

Mobbing Predators

The threat of predation is a powerful selection force that can alter avian social and communicative behaviour. Individuals in many species alert the predator to surrounding prospective prey, frequently by loud vocalisations that both conspecifics and heterospecifics respond to (Templeton & Greene, 2007; Wheatcroft & Price, 2013).

Mobbing is characterised as prey movements towards a predator that include both assaults with stereotyped behaviour and readily localisable cries that swiftly bring a throng of both conspecific and heterospecific prey against the predator (Curio, 1978; Hurd, 1996; Randler & Vollmer, 2013). Harvey & Greenwood (1978) consider mobbing of predators by potential prey species as an anti-predator

strategy. Individuals engaging in mobbing typically make clearly detectable noises when near the predator, which is occasionally physically repelled.

The primary advantage of mobbing is to cooperatively chase the predator away ('move-on hypothesis,' Curio, 1978; Flassekamp, 1994; Pavey & Smyth, 1998), albeit this tactic is not without danger (Dugatkin & Godin, 1992; Sordahl, 1990). Mobbing may have consequences for participants, such as an increased risk of mortality and injury, energy expenses, missed foraging and mating chances, and the possibility of exploitation by conspecifics, because animals are unable to secure their partners or defend their food supplies when mobbing (Dugatkin & Godin, 1992). According to a majority of research, animals modify the strength of their mobbing behaviour based on the perceived risk associated with either predator dangerousness or local predation pressure (Graw & Manser, 2007; Kaplan *et al.*, 2009; Koboroff, 2004; Koboroff *et al.*, 2013). Predator dangerousness, or the rate at which predators kill prey, varies widely among predator species, whereas predatory pressure is mostly determined by the abundance of a local predator species. Although research on mobbing has only evaluated prey reactions to predators and nonpredatory species, mobbing is assumed to have a positive correlation with predator dangerousness (Koboroff, 2004; Lind *et al.*, 2005). Lind *et al.* (2005), for example, demonstrated that great tits, *Parus major*, do not approach and mob European robins, *Erithacus rubecula*, a nonpredatory species, but do approach and mob Eurasian pygmy owls, *Glaucidium passerinum*, a predator that is especially deadly to great tits. Inoffensive species, such as the European robin, may be distinguished acoustically from predatory species.

Field observations and research have shown that prey often alter their vocalisations in response to approaching predators—either by changing the type of call or the frequency with which it is given (Naguib *et al.*, 1999; Manser, 2001; Graw & Manser, 2007). In meerkats (*Suricata suricatta*), mobbing calls vary depending on the predator's type and the level of threat it poses, prompting conspecifics to adjust their predator inspection behaviour accordingly (Manser *et al.*, 2001). Similarly, jays modify their responses based on the predator's behaviour (Griesser, 2008). When confronted by an active or hunting predator, jays seek immediate cover; however, when faced with a stationary or perched predator, they approach and swoop over it while producing a range of mobbing calls. These calls often prompt a rapid retreat by the predator (Griesser & Ekman, 2005).

Fleeing from Predators

Since escaping entails costs (energy expenditure and missed chance to participate in other activities like foraging), the decision should be based on the animal's risk assessment (Ydenberg & Dill, 1986). The danger in a predator-prey interaction is determined, among other factors, by how long it takes the prey to reach safety once it begins to flee distance (Ydenberg & Dill, 1986). For foraging animals, this implies that decisions about where and how to feed involve balancing food intake against the distance and speed required to escape to cover. The distance at which an animal begins to flee from an oncoming predator is known as the flight initiation distance (FID) (Ydenberg & Dill, 1986). FID is a good statistic for quantifying an individual's fearfulness in a given situation. Dill & Houtman (1989) demonstrated that the FID of grey squirrels attacked by a remote-control predator increases with increasing distance to safety (the nearest tree). *Melanochromis*

chipokae, a rock-dwelling African cichlid fish, produced a similar result. When a predator approaches, fish farther away from safety (rocks) begin their flight back to the rocks sooner than those closer to the rocks. FID and speed appear to be set in such a way that a fish arrives at the rocks a consistent amount of time before the predator; the fish appears to maintain a constant "margin of safety" (Dill, 1990). McLean & Godin (1989) observe comparable behaviour in banded killifish, but not in more strongly armoured (and hence less susceptible) sticklebacks (*Gasterosteus* and *Pungitius* spp.). Field observations suggest a relationship between FID and the proximity of cover or predators. In brook trout (*Salvelinus fontinalis*), Grant and Noakes (1987) found that FID decreases as cover density increases—indicating an inverse relationship with distance to the nearest refuge. Similarly, in white-tailed deer (*Odocoileus virginianus*), the likelihood of fleeing from a human detected at a distance is influenced by habitat type. Deer are more likely to flee in forested areas than in open grasslands, possibly because forests are perceived as more threatening environments (LaGory, 1987). Okafor *et al.* (2025) found that the number of individuals approaching birds significantly affected their risk assessment and escape behaviour, as they initiated flight earlier when approached by multiple individuals. The higher FIDs of birds on water and ground habitats indicate that individuals in more exposed environments are more vigilant and perceive greater predation risk due to increased visibility compared to those in tree or shrub habitats. The shorter flight distances observed during three-person approaches when birds were oriented backwards suggest that individuals are less able to detect threats approaching from behind, which increases their vulnerability to rearward predation (Okafor *et al.*, 2025). This highlights a potential trade-off between foraging and safety, as birds concentrating on feeding may pay less attention to their surroundings and thus delay threat detection.

Giving-Up Density (GUD)

If the value of food patches varies, an increase in predation risk may cause foragers to be more selective in their judgments about where to forage and for how long (Gilliam & Fraser, 1987). A food patch's giving-up density is the amount of food that remains in the patch after the animal has stopped foraging in it (Brown, 1988). It can frequently reveal more about the forager than just the amount of food consumed/harvested (Brown, 1988). In general, a forager's GUD should correspond to the harvest rate that balances foraging metabolic costs, predation risk, and the rate of lost chances that the forager experiences by remaining in a particular patch (Brown, 1988). This concept emphasises the idea that foragers will have a higher GUD when they engage in activities like hypervigilance. In other words, because of the fear of predation, they are more inclined to abandon foraging in a particular patch. A higher GUD suggests that the food patch is of little benefit to the forager in comparison to the costs of foraging there (Druce *et al.*, 2009). For example, klipspringers (*Oreotragus*, a small African antelope) have high GUDs near human-placed drainage lines and low GUDs near rocks, implying that klipspringers perceive greater predation risk when they are farther from the protective influence of the rocks (Druce *et al.*, 2009). Similarly, white-tailed deer (*Odocoileus virginianus*) exhibit higher GUDs in areas with deep snow, where the risk of sinking increases. The deep snow makes the habitat appear more dangerous, as it hampers their mobility and reduces their ability to escape predators (Rieucou *et al.*, 2009).

Abdulwahab *et al.* (2019) conducted a field experiment to measure

giving up density with the aim of investigating how predation risk is perceived by granivorous bird species with respect to different habitat and microhabitat types, time of day and food types in Amurum Forest Reserve, Nigeria. They recorded higher food remnants in the open than in cover microhabitats, as birds exploited food patches in the cover more and stated that the reason for this outcome could be that predation is highly probable in the open than in cover, and that vegetation provides safety from predators (Lomas *et al.*, 2014). Using GUD as a tool, one may assess the relative risk of predation in a specific region.

Conclusion

Predation risk plays a major role in shaping animal behaviour. It affects where animals go, how they find food, and how they stay safe. This review shows that fear of predators is not just a reaction to danger; it is a key part of how animals make decisions in their daily lives. Almost all animals are likely to be prey for another species at some stage in life. Predators are therefore powerful drivers of evolution, shaping not only physical defenses such as spines, shells, and armor (Lima & Dill, 1990), but also the ways animals behave. This review highlights that the chance of being preyed upon directly influences how animals behave in their environment, both in space and time.

However, important gaps still exist in our understanding. Much of what we know comes from studies on a few animal groups, mostly in temperate regions. Tropical ecosystems, especially in Africa, are underrepresented, even though they are rich in species and have complex food webs. We need more research from these areas to understand how different species respond to predation in diverse habitats.

Also, many studies view predation risk as something fixed, when in fact it changes with time of day, habitat type, and human activity. New tools such as GPS tracking, motion-sensitive cameras, and remote sensors now allow us to study animal behaviour in much greater detail. These tools can help us understand how animals adjust their actions in real time as risk changes.

Finally, while we know a lot about how individuals respond to fear, we still know little about how these responses affect entire populations and ecosystems. Small changes in animal behaviour, such as feeding less or moving differently, can lead to larger effects on plant growth, species interactions, and ecosystem balance.

In places like Africa, where both biodiversity and human pressure are high, it is vital to understand how animals respond to fear. By studying this more closely, we can improve how we protect wildlife and manage natural areas in a changing world.

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Data Availability Statement

This review article does not contain any original data. No datasets were generated or analysed during the preparation of this manuscript.

Conflicts of Interest

The author declares no conflicts of interest.

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