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# 1 • An introduction to predator sensitive foraging

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Studies of predator sensitive foraging in nonhuman primates are in their infancy. Predator sensitive foraging (or threat sensitive foraging, Helfman 1989) represents the strategies that animals employ to balance the need to eat against the need to avoid being eaten. For decades, these trade-offs have been investigated, in both natural and laboratory settings, by dozens of scientists working with a wide array of invertebrate, piscine, avian, and mammalian species. Ecologists working with nonprimate taxa have developed theoretical models of considerable sophistication and have generated elegant data to test those models. However, only recently have primatologists begun to turn their attention to this area of research.

The fact that studies of primates lag behind those of other taxa is due, in part, to the difficulties of observing predation on primates or even evaluating the extent to which predation imposes selective pressures on primate populations. Furthermore, field research imposes additional challenges in controlling certain variables so as to isolate and assess the effects of others. However, primate research reveals complex interactions among variables and may therefore provide a more realistic portrait of animal ecology than do oversimplified laboratory experiments. Furthermore, given the diversity in primate morphology, social structure, and habitats, this taxon represents an important opportunity to test theoretical models. It is also valuable to study the principles of predator sensitive foraging in a group of animals that rely heavily upon learning and are remarkably flexible in their behavior, as these factors may lead to further diversity and specificity in foraging strategies. Altogether, primatology has the potential to make a significant contribution to this field of research.

This volume brings together primary data from a variety of primate species living in both natural habitats and experimental settings. The objectives are (a) to demonstrate that predator sensitive foraging is relevant to a wide array of primates, of various body sizes and group sizes, and living in different habitats; (b) to explore the variables that play a role in predator sensitive foraging decisions; and (c) to engender discussion about these data, including their strengths and weaknesses, in hopes that such discussion might lead to further research. Thus, in some ways this volume represents a work in progress as we hope it will result in greater interest and further investigation into this topic.

This introductory chapter serves several purposes. First, it discusses some of the variables that affect an individual's vulnerability to predation. These variables give rise to a 'perceived' level of risk that should, in turn, influence foraging decisions as animals make adaptive compromises between avoiding predators and meeting nutrient requirements. Second, this chapter also reviews some of the relevant ecological literature. Information about primates is not included here; instead, I have left it to the authors of each chapter to review the studies that pertain directly to their subject species and/or the theoretical issues at hand. Neither does this chapter provide an exhaustive review of the nonprimate literature, as there are literally hundreds of published studies and a complete listing would be far beyond the scope of this volume. Instead, I make reference to just a few of the key articles; should the reader wish to delve deeper into this literature, this chapter provides a starting point. Finally, this introduction summarizes the contents of the volume and the contribution that each chapter makes to the overall theme.

## Vulnerability, perceived risk and foraging decisions

Vulnerability is used here as a qualitative measure of the probability that an individual will be the victim of a predator at any given moment. Through experience and/or genetic inheritance, an individual animal's behavior reflects an apparent 'perceived' risk. In particular, an individual's foraging decisions are expected to vary with its vulnerability (cf., Krebs 1980, Mangel and Clark 1986, McFarland 1977, Sih 1980; see Lima and Dill 1990 for a recent review). That is, individuals who perceive themselves to be more susceptible to predation would be expected to take fewer risks when foraging, even at the cost of reduced access to important resources, while those who perceive themselves to be less susceptible exploit riskier settings in order to increase nutrient intake.

These consequent differences in foraging success are expected to have fitness ramifications (cf., Wilson 1975).

An individual's level of vulnerability depends upon a number of variables. For heuristic purposes, I have chosen to sort these variables into three categories: biological, social, and environmental. Similarly, I have organized the volume around these categories. Some chapters might arguably fit into more than one section of the volume. For example, a study that compares two species may explore the biological differences between them, the habitat preferences of each one, and individual foraging decisions based upon social rank. I have placed each chapter where the research gives greatest emphasis. Primates show considerable flexibility in their responses to selective pressures, and readers are encouraged to show similar flexibility in their use of this volume's organization.

## Biological variables

By biological variables, I refer to characteristics of the species that are largely, or perhaps completely, under genetic control. For example, an individual's vulnerability might be influenced by body size which should, in turn, determine the risks it takes while foraging . (For a recent review, see Lima and Dill 1990.) From this hypothesis, we would predict that members of a larger species would be safer than members of a similar but smaller species in the same environment. Furthermore, within a single species, we would expect adults to be safer than juveniles or infants, and – for sexually dimorphic species – males should be safer than females. Again, those that are less vulnerable may exhibit riskier foraging behavior if there is incentive to do so. Body size has proven to play a large role in foraging decisions for various fish (Bishop and Brown 1992, Helfman 1989, Johnsson 1993, Werner *et al*. 1983), aquatic insects (Sih 1982), gastropods (Rochette and Himmelman 1996), crustaceans (Stein and Magnuson 1976, Wahle 1992), rodents (Brown *et al*. 1988, Kotler 1984), and ungulates (Berger and Cunningham 1988, and see Kie 1999 for a review). In at least some cases (e.g., Werner *et al*. 1983), the fact that smaller animals adjusted foraging location and/or time in order to reduce predator exposure was shown to have feeding consequences that could impact fitness. Thus, the predator sensitive decisions that individuals make can represent adaptive compromises between opposing selective pressures.

Apart from body size, some species are better equipped than

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others to detect, flee from, or repel predators. For example, among rodent species, the type of habitat commonly used (e.g., habitats that offer heavy vs. light cover) varies with the volume of the auditory bulla (which probably influences these animals' ability to hear predators) and mode of locomotion (which affects the ability to escape from predators) (Brown *et al.* 1988, Kotler 1984). Stream insects differ in their predator sensitivity based upon the presence or absence of protective equipment (Kohler and McPeek 1989). Thus, the genetic endowment of each species will impact the extent to which their foraging is predator sensitive.

Taking a different (though still biological) approach, those individuals whose fitness is most heavily dependent upon nutrient intake might be expected to take the greatest risks to enhance access to resources. Thus, for many taxa, females are expected to maximize foraging effort even at the cost of greater exposure to predators. Abrahams and Dill (1989) showed that, for guppies, males needed significantly more incentive than females to forage in a risky area. Thus, the sex of an individual can impose conflicting needs. Females of many species are smaller than males, and therefore are more vulnerable, but their fitness demands may encourage them to take greater risks in order to maximize access to resources.

Following this logic, an individual's vulnerability may play a lesser role in foraging decisions than its energetic needs. For example, hungrier animals are expected to take greater risks than those that are well fed. Hunger was shown to be negatively correlated with predator sensitivity in fish (Dill and Fraser 1984, Godin and Sproul 1988, Gotceitas and Godin 1991; see also Giles 1983), aquatic insects (Kohler and McPeek 1989), and gastropods (McKillup and McKillup 1994). A few researchers have attempted to quantify the effect of hunger on predator sensitivity. Kennedy *et al.* (1994) have shown that, for bullies, the nutrient reward would have to be increased 28-fold to overcome the threat of a predator (see also Abrahams and Dill 1989). Thus, predators represent considerable disincentive to feed in richer patches, but eventually an individual's energetic state may drive it to take this risk.

Taken together, we can see that an individual's foraging decisions will depend upon biological factors that may be fixed throughout its lifetime (such as auditory equipment), factors that change relatively slowly (such as body size), and factors that may change over a relatively short period of time (such as hunger level). These biological variables will influence both vulnerability and incentive to feed, two states that often generate opposing needs for the individual. How the individual balances these needs, and the resulting patterns of behavior, are the subjects of recent primate research.

Among primates, many biological variables come into play. Morphological differences among species may influence responses to predators and the ability to flee once detected, which may in turn influence foraging decisions. In this volume, Bearder *et al.* examine calling and travel patterns in Mysore slender lorises and southern lesser galagos, and how these species foraged under varying conditions of moonlight. Their results show strong differences in antipredator behaviors. When the rapidly leaping galagos detected potential predators, they frequently responded by mobbing and giving loud alarm calls. In contrast, lorises, lacking the ability to leap to safety, used no mobbing calls. However, contrary to common belief, galagos were generally more cryptic than lorises. Galagos usually reduced their travel and remained silent during periods without any moonlight, largely because small carnivores represented a significant risk when the subjects crossed the ground between trees. Despite their slower pace, lorises were actually less vulnerable than the galagos, perhaps because they made less frequent use of the ground. Similarly, their rates of travel and contact calling were independent of moonlight. The disparity in activity patterns probably reflects each species' attempt to balance selective pressures, pressures that are, in part, mediated by biological characteristics.

Sympatric species may employ different foraging strategies based upon their vulnerability. Prescott and Buchanan-Smith explore how risk taking varies among closely related tamarin species that are sympatric in the wild. They found that, in an experimental setting, saddle-backed tamarins were more willing than red-bellied tamarins to forage low in their enclosure when food rewards were held constant. This probably represents some intrinsic difference as it is similar to their foraging patterns in the wild. However, red-bellied tamarins were more predator sensitive than saddle-backed tamarins in so far as the red-bellied were quicker than the saddle-backed to take a greater risk (feed at a low box) if the reward was large, rather than stay at a safer site (feed at a high box) if the reward was small. Therefore the red-bellied were quicker to take the greater risk and therefore got the bigger food reward. It is sometimes difficult to discern the mechanisms by which different species express predator sensitivity, but perhaps selection has

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shaped primate populations so that divergent strategies allow coexistence of multiple species.

Within some species, individuals demonstrate differential ability to detect food and predators. In this volume, Caine describes research showing that, among Geoffroy's marmosets, those with trichromatic vision were better able to find food items when color was an available cue, but suffered some disadvantages that dichromats did not face when targets were color camouflaged. The author speculates that this polymorphism may contribute to cooperative foraging and predator detection in callitrichids.

In most primate species, females are constantly accompanied by their dependent offspring, and thus mothers are especially vulnerable, because they are encumbered and because their infants are often targeted by predators. Sterck's study of Thomas langurs indicates that this heightened vulnerability can lead to differential foraging strategies. The results clearly demonstrate that subjects only made use of the ground while foraging, and otherwise avoided what they may have perceived as a risky area. However, females with small infants were significantly less likely to forage on the ground than were those with larger or no infants. Thus, despite their greater energetic requirements, mothers may have to make foraging compromises in order to increase the safety of their dependent offspring.

## Social variables

A variety of social variables should influence an individual's vulnerability to predation and therefore foraging decisions. (For a recent review, see Lima and Dill 1990.) One of the most important is group size. Members of larger groups are expected to be safer than those in smaller groups (cf., Alexander 1974, van Schaik 1983; see also Caraco *et al*. 1980, Jarman 1974), because of group vigilance (Elgar 1989, Pulliam 1973, Triesman 1975), dilution effects (Hamilton 1971), and the increased probability of successful mobbing (e.g., Altmann 1956, Curio 1978). Therefore, it might be expected that group size would influence predator related foraging decisions: members of larger groups, because of lower vulnerability, are able to exploit resources that are located in risky areas which members of smaller groups must avoid. However, a recent review of the literature has turned up few studies that address this issue directly (though see Clutton-Brock *et al*. 1999, Molvar and Bowyer 1994).

Group size may affect feeding patterns through the medium of shared antipredator vigilance. There is considerable evidence that members of smaller groups must devote more time to vigilance, usually measured by rates of scanning, while those in larger groups share the burden and thereby reduce individual load (see Elgar 1989, Lima 1995 and Treves 2000 for reviews). Since scanning probably reduces feeding time and/or efficiency (Lendrem 1983, 1984), group size should be positively correlated with individual food intake (Dehn 1990, Lima 1995, Quenette 1990, Roberts 1996). Thus, for species in which increasing group size is an effective antipredator mechanism (i.e., as opposed to species that practice cryptic behavior such as traveling and foraging solitarily) members of larger groups should achieve a predator related foraging advantage by greater access to certain resources and/or by greater foraging efficiency.[1] Members of smaller groups are expected to exhibit risk minimizing behavior which may reduce individual feeding success. In the long run, however, each individual must balance the selective pressures of its social environment in order to maximize its fitness.

In addition to group size, group composition might also be expected to affect individual vulnerability, and therefore foraging decisions. For example, if adult males played a protective role, then members of groups with a greater number of adult or subadult males (or other sentinels) might be expected to exhibit riskier behavior, especially if it afforded them greater access to important resources (e.g., in birds: Yasukawa *et al.* 1992; in viverrids: Clutton-Brock *et al.* 1999, Rasa 1986; see also Bednekoff 1997 and Lima and Dill 1990).

Cohesion and centrality are additional social variables often thought to correlate with vulnerability. Due to increased vigilance and a dilution effect, individuals with near neighbors are thought to be safer than those at a distance from conspecifics (or other potential prey items). Similarly, those in the center of the group are expected to be targeted by predators less frequently than those on

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[1] From a different perspective, group foraging may instead have a negative impact on feeding success. It is often suggested that optimal group size represents a trade-off between the threat of predation and the cost of intragroup feeding competition (cf., van Schaik 1983, Dunbar 1988). Therefore, for some populations, members of large groups, not small groups, may be making the adaptive compromises as they endure higher rates of feeding competition, and therefore lower food intake, in exchange for safety. However, this model swings away from our focus on predator sensitive foraging and therefore will not be discussed further here.

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the periphery (e.g., in ungulates: Berger and Cunningham 1988). Of course, individual spacing and location within the group are generally more labile characteristics than are group size or composition; they can be adjusted as demanded by changing levels of risk or hunger. Thus, modifying its position may be one mechanism by which an individual can reduce its vulnerability (e.g., in ungulates: Green 1992). However, feeding in proximity to conspecifics may reduce foraging success (e.g., in birds: Cresswell 1998; in ungulates: Lipetz and Bekoff 1982), and animals must therefore balance risk against nutritional needs, which is the essence of predator sensitive foraging.

Finally, social rank has been shown to affect predator sensitive foraging (e.g., in fish: Gotceitas and Godin 1991) but the interactions among variables can be complex. For example, higher ranking individuals may be larger, thus less vulnerable, and therefore willing to take risks (e.g., in fish: Johnsson 1993). Alternatively, those of lower rank may have poor access to food, and thus be driven by hunger to take more risks (e.g., in fish: Metcalfe 1986; in birds: Ekman and Askenmo 1984). Furthermore, higher ranking individuals can probably maintain choice locations within the group and therefore have greater options when it comes to developing a foraging strategy.

Although many primatologists have explored the effects of group size on feeding behaviors, few have specifically addressed predator sensitive foraging (see individual chapters for references). In this volume, Miller tests the hypothesis that membership in a larger group bestows a foraging advantage through the medium of reduced vulnerability to predators. This study of wedge-capped capuchins demonstrates that, during certain months of the year, females living in a larger group foraged and traveled on the ground three times as frequently as did those in a smaller group, and collected twice as much food from this substrate. Females in the smaller group, who restricted their foraging to arboreal locations, experienced significantly lower levels of food intake for several months of the year. Thus, among capuchins, predator sensitive foraging may have significant fitness ramifications.

Lending further support to the model that group size affects predator sensitive foraging, the chapter by Sauther explores the behavior of two troops of ring-tailed lemurs. Sauther's data show that members of a small group avoided foraging on the ground when predator pressure was high, and that this pattern resulted in reduced leaf and fruit intake. The small group was also more likely to form mixed-species associations with sifakas, especially while feeding and most frequently when infants were present. In contrast, the large group was more willing to enter new regions of the forest, which was associated with increases in both fruit feeding and predator encounters. Thus, Sauther's work confirms that predator sensitivity entails trade-offs between safety and foraging success, and that primates alter their behavior in ways that balance these variables, within the context of their social environments.

In some cases, social variables are more important than biological factors in predator related behaviors. Overdorff *et al*. explore the extent to which body size and group size influence the risks that prosimians take when foraging. Their study compares the behaviors of three species: red-bellied lemurs that are small-bodied and live in small groups, rufus lemurs that are small-bodied but live in larger groups, and Milne Edward's sifakas that are larger-bodied and also live in larger groups. The data demonstrate that the variance in these species' use of exposed habitat and distance between nearest neighbors was more heavily dependent upon group size than body size.

It has often been suggested that primates form mixed-species aggregations in order to reduce predator vulnerability by increasing the overall size of the social unit. Increased troop size, however, is generally expected to result in higher foraging costs. In this volume, Garber and Bicca-Marques explore predator sensitive foraging in single- vs. mixed-species troops of tamarins. A review of the tamarin literature reveals no consistent differences in predation risk for members of single- vs. mixed-species troops. Moreover, data from their study of mixed-species troops show no signs of cooperative vigilance, or other indications that, as the number of animals present at a feeding site increased, individuals foraged in a less predator sensitive way. Tamarins have developed other antipredator strategies, such as avoiding use of the same travel routes on consecutive days, and having certain group members (such as adult males) serve as sentinels while others are feeding. However, based on time spent at feeding sites, there was no evidence that the animal that served as a sentinel had lower foraging success. Thus, new data constantly encourage us to reconsider our models.

Predation models suggest that primate groups should increase their cohesion (or reduce spread) in response to risk. However, in this volume, Isbell and Enstam present data that support a different model. They have compared the behavior of (a) vervets and patas monkeys living in the same ecosystem, under similar threat of predation but using two different habitats, and (b) the same group of vervets while using two different subhabitats. The results suggest that group spread was more highly correlated with resource dispersion than with predator pressure. Again, some primates demonstrate limited predator sensitivity, and force us to look for alternative explanations for their behavior.

Individual primates occupying risky positions within a social group may be forced to devote time and energy to antipredator behaviors; however, this does not always have an impact on feeding efficiency. Gleason and Norconk studied predator responses among white-faced sakis and found that alarm calling was more frequent among subjects that were at the periphery of the group, and less frequent among those in close proximity to conspecifics. However, the data revealed no association with foraging success. This chapter posits that more extreme antipredator behavior, such as prolonged mobbing or cryptic 'freezing,' must eventually reduce feeding time, but these data are currently unavailable. Studies such as these generate testable hypotheses and therefore contribute to our advancement of research.

## Environmental variables

An individual's risk will vary with the area in which it is foraging. It has generally been asserted that open areas leave animals more vulnerable than do areas with heavy cover (e.g., in rodents: Brown *et al.* 1988, Kotler 1984, though see Longland 1994; in birds: Suhonen 1993; in ungulates: Underwood 1982). Animals may opt for foraging substrates of lesser quality in order to increase cover and thereby reduce risk (e.g., in fish: Abrahams and Dill 1989, Gilliam and Fraser 1987, Holbrook and Schmitt 1988, Kennedy *et al.* 1994, Werner *et al.* 1983, though see Morin 1986), indicating that individuals must make adaptive compromises between the needs to maximize foraging success and minimize the threat of predation. However, other studies demonstrate that animals may increase vigilance in habitats with restricted visibility (e.g., in ungulates: Goldsmith 1990, Underwood 1982). These individuals are actually less vulnerable in open areas owing to their heightened ability to spot predators and thereby avoid attack. Thus, we may need to have detailed information on predator–prey interactions before we can make appropriate predictions about behavior under different habitat conditions.

Vulnerability varies not only with foraging location but also