

# Predation on Primates: Ecological Patterns and Evolutionary Consequences

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It has long been thought that predation has had important ecological and evolutionary effects on primates as prey. Predation has been theorized to have been a major selective force in the evolution of hominids.<sup>1</sup> In modern primates, behaviors such as active defense, concealment, vigilance, flight, and alarm calls have been attributed to the selective pressures of predation, as has group living itself. It is clear that primates, like other animals, have evolved ways to minimize their risk of predation. However, the extent to which they have been able to do so, given other constraints of living such as their own need to acquire food, has not yet been resolved. Perhaps most hotly debated is whether predation has been the primary selective force favoring the evolution of group living in primates. Part of the difficulty in resolving the debate lies in a paucity of direct evidence of predation. This is regrettable yet understandable since primatologists, by definition, focus on the study of primates, not predators of primates (unless these are also primates). Systematic direct evidence of the effects of predation can best be obtained by studying predators that are as habituated to observers as are their primate prey. Until this is done, we must continue to rely on opportunistic accounts of predation and predation attempts, and on systematically obtained indirect evidence. Such data reveal several interesting patterns: 1) although smaller primates may have greater predation rates than larger primates, even the largest primates are not invulnerable to predation; 2) the use by primates of unfamiliar areas can result in higher predation rates, which might be one pressure favoring philopatry, or site fidelity; 3) arboreal primates are at greater risk of predation when they are more exposed (at forest edges and tops of canopies) than in more concealed locations; 4) predation by mammalian carnivores may often be episodic; and 5) terrestrial primates may not experience greater predation than arboreal primates.

Predation on primates has long occupied a place in the minds of naturalists. Early in this century, Fitzsimons<sup>2</sup> described the behavior of vervet monkeys (*Cercopithecus aethiops*) in the presence of leopards (*Panthera pardus*):

When a leopard is discovered by a troop of Vervet Monkeys they invariably

desert the locality, for they are well aware that otherwise it is but a matter of time for the whole of the troop to disappear one by one into the capacious stomach of their arch-enemy, which never neglects an opportunity of reducing their numbers and thus fulfilling its mission in life.

With the application of systematic science to natural history, we now know that vervets are less likely to leave the area when they see a leopard than to flee up the nearest tree and give alarm calls specific to leopards and other terrestrial carnivores.<sup>3,4</sup> Flight and alarm-calling are just two of the many behaviors that primates have at their disposal to avoid predation. In 1987, Cheney and Wrangham<sup>5</sup> provided an exemplary review of pre-

dition on primates. Since then, our knowledge of this subject has steadily increased. In this review, I will not try to cover again all of the information provided by Cheney and Wrangham, which I recommend as companion reading. Instead, I will attempt to bring together recent data and ideas about predation on primates in the light of previous information.

The kinds of anti-predator strategies available to primates depend, in part, on their body sizes relative to those of their predators.<sup>5</sup> Small primates can conceal themselves; larger primates may mob predators, with or without physical contact. All primates except the largest, *Gorilla gorilla*, sleep off the ground in nests, holes, or trees, or on cliffs. Sleeping in trees and other shelters, which undoubtedly reduces the risk of predation from strictly terrestrial predators, probably evolved to serve this purpose. Direct observations of avoidance, escape, and defensive behaviors by primates in the presence of predators suggest that predation has been an important selective force in the behavioral evolution of primates (reviewed in Cheney and Wrangham<sup>5</sup>; see also Table 1). Primates are not exceptional in this; such behaviors are common in most, if not all, animals.

## PREDATION AND THE EVOLUTION OF GROUP LIVING IN PRIMATES

Primates are among the most social orders of animals: at least 73% of species (94 of 129) are known to travel with one or more adult conspecifics.<sup>6</sup> Until recently, it was assumed that predation was the major selective force favoring group living in primates.<sup>7</sup> The assumption was that living in groups reduces the risk of predation by increasing vigilance and

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Key words: episodic predation, philopatry, resource competition, group living, predation rate

**TABLE 1. Suggested Behavioral, Morphological, and Social Adaptations to Predation and the Consequences of Predation on Demography and Habitat Use (From Cheney and Wrangham<sup>5</sup> and References in This Review)**

| Characteristic  | Supporting Evidence | Examples   | Comments  |
|---|---------------------|--|---|
| <b>Suggested Adaptations to Predation:</b>              |                     |  |   |
| Aggressive defense                                      | Direct observation  | Howlers, capuchins, <sup>78</sup> red colobus, macaques, baboons, gorillas | Observations of mobbing   |
| Sex differences in aggressive defense                   | Direct observation  | Red colobus, patas, baboons, howlers, capuchins                            | Males can be more involved in defense than females  |
| Concealment   | Direct observation  | Tamarins, many other species   |   |
| Flight  | Direct observation  | Squirrel monkeys, galagos, vervets, patas, many other species              |   |
| Alarm calls   | Direct observation  | Guenons, ring-tailed lemurs, callitrichids                                 | Specific to predator species  |
| Reaction to alarm calls                                 | Direct observation  | Vervets  | Appropriate to predator species   |
| Philopatry (site fidelity)                              | Inferred            | Vervets  | Higher predation in unfamiliar areas  |
| Sleeping in trees or above-ground shelters              | Inferred            | All but gorillas   |   |
| Sexual dimorphism in canine size                        | Inferred            | Baboons  | Males often involved in active defense more than females  |
| Sexual dimorphism in body size                          | Inferred            | Baboons  | Same as above   |
| Vigilance   | Inferred            | Vervets, capuchins, squirrel monkeys <sup>79</sup>                         | Per capita vigilance lower in larger groups; vigilance greater in unhabituated groups   |
| Greater height in trees                                 | Inferred            | Long-tailed macaques, capuchins  | Smaller groups higher in trees  |
| Central spatial position in group                       | Inferred            | Baboons, wedge-capped capuchins  | High-ranking animals more central (possible alternative explanation: better-quality food in central areas)                                      |
| Polyspecific associations                               | Inferred            | Guenons, squirrel monkeys, capuchins                                       | Partitioning of "vigilance" to different forest strata; per capita vigilance lower in polyspecific associations <sup>80</sup>                   |
| Nocturnal living in smaller primates                    | Suggested           | Galagos  | Small species may be hard to detect at night  |
| Birth synchrony within groups                           | Suggested           | Squirrel monkeys <sup>79</sup>   | Selective disadvantage of asynchrony not yet shown  |
| <b>Group Size Effects:</b>                              |                     |  |   |
| Larger groups   | Inferred            | Long-tailed macaques, vervets  | Overall vigilance increases in larger groups; larger groups react more quickly to human presence; smaller groups on islands with less predation |
| Group living  | Inferred            | Many species   | Very large primates and nocturnal primates are solitary; see comments for larger groups   |
| All-male bands vs. solitary males                       | Inferred            | Patas vs. other guenons  | Solitary males often in arboreal habitats (assumes terrestriality to be high-risk)  |
| Multiple males in female groups                         | Inferred            | Vervets, red colobus, baboons  | High-risk and terrestrial species often multi-male (see above)  |
| Smaller groups (including monogamy and solitary living) | Suggested           | Gibbons, Mentawai langur   | Smaller groups less likely to be detected?  |

(Continued on next page)

TABLE 1. *Continued*

| Characteristic  | Supporting Evidence | Examples                          | Comments   |
|---|---------------------|-----------------------------------|--|
| <b>Suggested Patterns of Predation:</b>               |                     |                                   |  |
| Human presence reduces predation                      | Inferred            | Vervets                           | Predation negatively correlated with spatial and temporal variation in human presence                    |
| Males at greater risk                                 | Inferred            | Species with male dispersal       | Sex ratio often skewed toward adult females; males have higher mortality than females                    |
| Predation limits populations                          | Inferred            | Red colobus                       | Predation high with no evidence of food competition  |
| Smaller primates at greater risk                      | Inferred            | Many strepsirhines, callitrichids | Smaller primates may be vulnerable to greater numbers of predators and cannot actively defend themselves |
| Correlated with number of estrous females of predator | Inferred            | Red colobus                       | Male chimpanzees provide meat to estrous females   |
| Terrestrial primates at greater risk                  | Suggested           | Baboons, vervets, patas           | Evidence not convincing  |

flight distance and by decreasing the probability that any particular individual would be killed during a predation event. Alexander suggested that only this reduction in the risk of predation could outweigh the inevitably higher costs of food competition resulting from living in close proximity to conspecifics.<sup>7</sup>

A number of studies have provided evidence that intragroup competition increases as group size increases.<sup>8-12</sup> There is also evidence that groups provide an advantage in avoiding or minimizing predation. Among wedge-capped capuchins (*Cebus olivaceus*) and vervets, for example, large groups show higher levels of vigilance than do small groups.<sup>13,14</sup> Among long-tailed macaques (*Macaca fascicularis*), large groups detect human potential predators earlier than do small ones. The large groups also spend more time low in the canopy where, presumably, they are at greater risk from terrestrial predators than they would be at higher levels.<sup>15</sup> However, it is not yet clear whether the avoidance of predation is a primary cause or a secondary consequence of living in groups (see Box 1).

Wrangham challenged the notion that predation avoidance is the sole factor favoring group living, arguing that although living in groups necessarily increases competition for food within the group (intragroup competition), this cost is outweighed, not primarily by decreased predation, but by greater advantages in competition

against solitary individuals and smaller groups for food (intergroup competition).<sup>16</sup> Predation avoidance and intergroup competition are not the only explanations for the evolution of group living—for example, improved foraging efficiency could also favor group living.<sup>17,18</sup> Nevertheless, Wrangham's seminal paper polarized the views of some primatologists as they attempted to exclude either predation avoidance or intergroup competition as the primary selective force favoring group living.

In one such attempt, van Schaik<sup>19</sup> suggested that the two selective pressures predict different birth rates in groups of different sizes. He argued that if predation is the primary selective force favoring group living, then birth rate, measured by numbers of infants per adult female, should decrease as group size increases, because food intake decreases with group size. On the other hand, Schaik contended, if intergroup competition is the primary selective force favoring group living, birth rate should first increase as group size increases and then decrease when the group becomes very large because intragroup competition for food eventually outweighs the advantage of being in the largest groups. Using a sample of 14 species, most with single-male, multi-female grouping patterns, he found that the pattern of birth rates fit closely with his prediction derived from the predation hypothesis. However, much rests on

whether the underlying assumptions are reasonable. For instance, social instability or high rates of infanticide in large single-male, multi-female groups might cause the same pattern predicted by the predation hypothesis.<sup>11,20</sup> Two long-term studies of species with multi-male, multi-female grouping patterns found that female reproductive success increased with group size, a result that is consistent with the intergroup competition hypothesis.<sup>21,22</sup>

Isbell et al.<sup>23</sup> suggested that in vervets the behavior of juveniles could be used to distinguish between the effects of predation avoidance and intergroup competition in maintaining groups as cohesive units. We consistently observed that vervet groups declining in size persisted as separate units as long as there were at least two adults in each group. Almost immediately after losing its penultimate adult, however, each group fused with a neighboring one. The number of juveniles did not appear to influence the timing of group fusions. Juveniles are active participants in predator detection, but not in aggressive intergroup encounters. This suggests that minimum group size in vervets is a limitation set by successful intergroup competition rather than by predator detection or avoidance (see Box 1).

On an ecological time scale, the influences of predation and food competition may, in fact, be nearly inextricable. For example, declining food resources caused large groups of

## The Evolution of Group Size and the Evolution of Group Living

What selective forces are responsible for the evolution and maintenance of group living in animals? Tests of hypotheses addressing this question have examined the advantages and disadvantages of modern variation in group size, and therefore address the evolutionary maintenance of group size and, by extension, group living. There are two ways in which these are risky tests of the conditions favoring the initial evolution of group living.

First, the selective factors that maintain a trait are not necessarily the ones that were responsible for its origination.<sup>18,74</sup> For example, there is evidence that, in several primate species, individuals in large groups benefit in both intergroup competition and predator avoidance. However, this evidence does not necessarily identify either benefit as the primary selective force on group size or group living. Even negative evidence for one selective force need not eliminate it as the initial cause: the conditions that existed at the time the adaptation (group living) first arose may not be the same as the conditions under which current selective factors are being tested.<sup>74</sup> Such historical effects may include changes in predation risk, food abundance, or food distribution. They may also include group size itself.

This leads to the second point. Group living evolved when the first individuals of an evolutionary lineage ceased to live alone, probably through mothers' tolerance of their daughters. In any case, the initial transition was almost certainly from living solitarily to living in groups of two. However, most tests of the advantages of group living are not directed at this threshold of sociality. The selective forces that first favored living in pairs over living alone need not have been the same selective forces that now favor a group of twenty over a group of ten. Most social primates live in groups far above this threshold, only rarely providing opportunities to examine behaviors at minimal group size, and even then, under extreme and possibly anomalous conditions.<sup>23</sup> Better tests might be carried out among primates in which group sizes are characteristically small, such as callitrichids and many prosimians. Thus far, such tests are lacking. The fission-fusion societies of chimpanzees may provide some insight here. Fusion among chimps is often associated with intergroup conflict.<sup>75,76</sup> However, mass attacks on predators are also observed.<sup>35</sup> We may still be left with multiple supportable hypotheses.

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vervets to supplant small ones, and all groups moved into areas where they became more vulnerable to predation.<sup>24</sup> Similarly, a change in predation rate can affect food competition. If predation increases to a level that lowers prey population size it could increase the availability of food for those remaining and, presumably, decrease food competition. On the other hand, a decrease in predation and the subsequent increase in the prey population could increase food competition within it.

As another example of the codependence of predation and food competition, vigilance is often inversely related to time spent foraging.<sup>14,25</sup> For individuals in smaller groups, greater demands on their time for vigilance

could reduce their food intake and, therefore, their reproductive success relative to that of individuals in larger groups (see also Janson<sup>26</sup>). In groups of all sizes, decreased food availability could increase time members spend foraging and decrease their vigilance, leading to an increase in predation on them. Even within groups, individuals may face different trade-offs between vigilance and food intake. In a study of brown capuchins (*Cebus apella*), for example, dominant adults foraged in the most productive areas, while subordinate adults foraged in sub-optimal areas both for food intake and vigilance. Juveniles, on the other hand foraged in suboptimal areas where they also spent less time in vigilance.<sup>25,27</sup>

Figure 1 suggests that group living could have evolved by predation alone (pathway 1), resource competition alone (pathway 2), or through a combination of predation and resource competition (pathway 3). Given the interactive effects of predation and food competition, debate about their relative influences on group living should continue to flourish until more data have become available and additional creative tests have been developed, if not for even longer (see Box 1). Most valuable will be investigations that dispassionately consider multiple causation.<sup>18</sup>

## DIFFICULTIES IN DOCUMENTING PREDATION ON PRIMATES

No tests of the effects of predation and food competition have directly measured the intensity of predation. It has been relatively easy to document the advantages of large groups in intergroup competition in various species.<sup>18,21-24,28</sup> It has been more difficult to document predation. There are several reasons for this.

First, predation rates are often very low. Based on extrapolation from suspected numbers of predations, Cheney and Wrangham<sup>5</sup> estimated that the median yearly predation rate in 24 populations of primates was about 3% (range, 0-15%). Second, even when predation rates are high, individual events often happen so quickly that there is little chance of observing them. For example, in a recent account of lion predation on a savannah baboon (*Papio cynocephalus anubis*), the entire episode took only one minute.<sup>29</sup> Third, many predators, such as barn owls (*Tyto alba*)<sup>30</sup> and leopards,<sup>31</sup> hunt at night when observers are not usually present. Fourth, observers may, in fact, inhibit the hunting activities of predators. In the first six months of a recent study of vervet monkeys, Isbell and Young<sup>32</sup> found that leopard predation on vervets was significantly lower when observers were present in the study area than when they were absent. As the study progressed, this difference disappeared. Observations of one leopard increased, suggesting that it was becoming habituated to the observers and less wary of hunting vervets while observers were in the area. Nonethe-

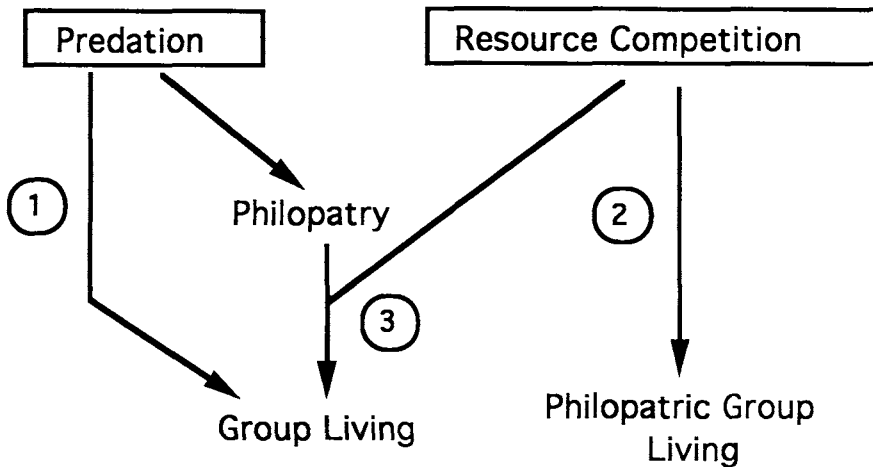


Figure 1. Possible routes to group living in primates. Pathway 1: Predation favors group living as a direct result of the benefits it provides in reducing the risks of predation. Female philopatry (i.e., site fidelity) is not required.<sup>7,19</sup> Pathway 2: Resource competition favors the evolution of groups in defense of resources; members gain inclusive fitness benefits by forming groups with relatives.<sup>16</sup> Pathway 3: Predation favors the evolution and maintenance of female philopatry (site fidelity). Resource competition combines with philopatry when the advantages of cooperative defense favor the evolution of groups. This combination results in the formation of kin groups because relatives live closer to each other than to nonrelatives.

less, no direct observations of predation were ever witnessed during the study, even though the annual rate of predation in 1987 was estimated to be at least 45%, which is an exceptionally high rate even for this population.<sup>33</sup>

A final reason for the lack of documentation of predation on primates is that such studies are likely to involve great investment of time and energy in return for relatively few data points because predators eat other animals besides primates. Primatologists are understandably more eager to con-

duct studies that guarantee higher productivity.

#### PATTERNS OF PREDATION ON PRIMATES

Given these problems, it is not surprising that there has been heavy reliance on indirect evidence and opportunistic reports of predation events and attempts. As the data have trickled in, however, interesting patterns have begun to emerge.

1) Large primates should be inherently less vulnerable to predation than

smaller primates, if for no other reason than that fewer species are likely to prey on them. It has also been suggested that large groups are less subject to predation than are small ones, which will be less effective in detecting or repelling predators. Unfortunately, mean feeding group size and adult body size covary across species.<sup>34</sup> Therefore, analyses that compare estimated predation rates across species cannot reliably separate the effects of body size and group size. Cheney and Wrangham<sup>5</sup> showed that estimated predation rates tend to decline with increasing body size among smaller primates (they excluded apes from their analysis). Reanalysis of their data in conjunction with data on body size and mean group size<sup>34</sup> indicates that body size and (log) group size are equally good predictors of estimated predation rate (see Fig. 2).

Great apes have large bodies and smaller than average group sizes. Although pongids are not invulnerable to predation,<sup>35,36</sup> their predation rates are apparently quite low (<5% per year). This may indicate that the effects of body size on predation rate may be stronger than the effects of group size, if such comparisons across species are legitimate. An attempt to find an association between group size and estimated predation rate across groups within a population of vervets failed to find a significant effect<sup>32</sup> (Fig. 3b). The fact that even larger primates, including chimpanzees,<sup>35,36</sup> are sub-

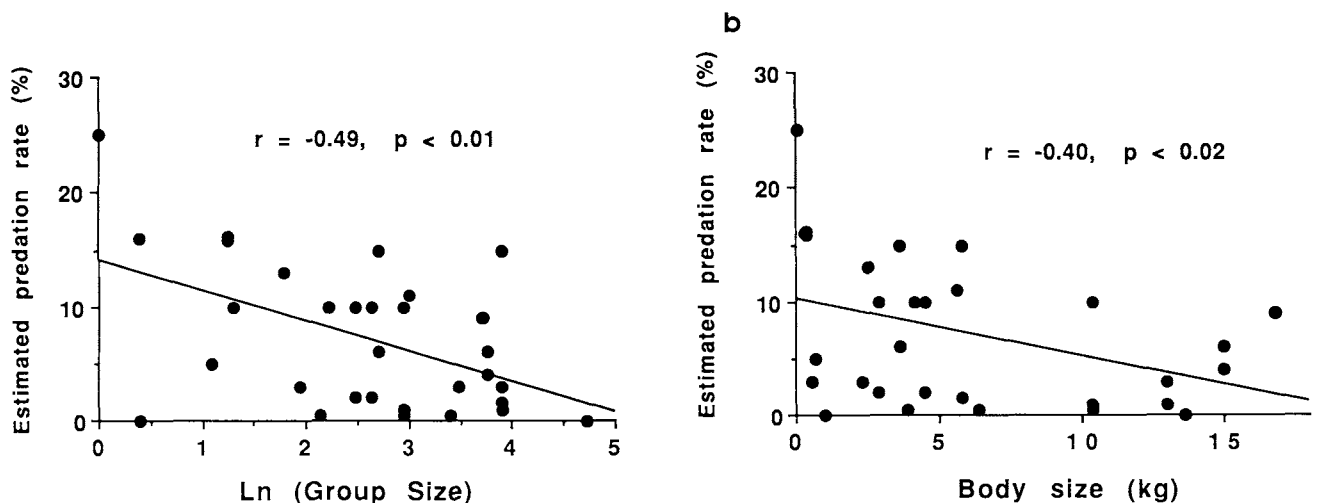


Figure 2. The relationship between estimated predation rate and group size (a) and body size (b), among smaller primate species (excluding apes). From data in Cheney and Wrangham,<sup>5</sup> Goodman et al.,<sup>30</sup> and Clutton-Brock and Harvey.<sup>34</sup>

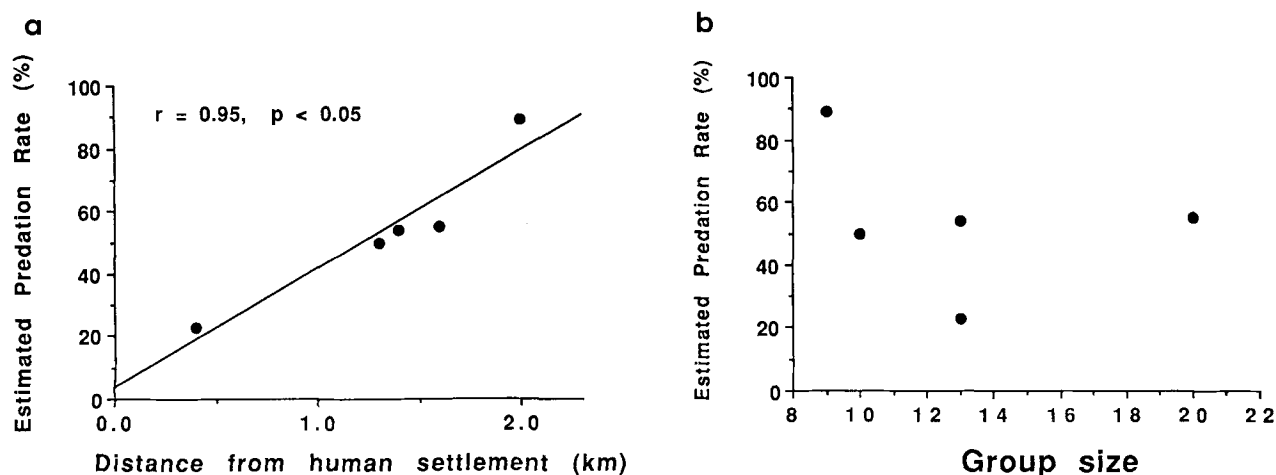


Figure 3. The relationship between estimated predation rate and distance to human habitation (a) and group size (b) across five groups of vervet monkeys in Amboseli, Kenya.<sup>32</sup>

ject to predation adds credence to the notion that predation could have been a strong selective force on early hominids.<sup>1</sup>

2) It has long been hypothesized that animals are more vulnerable to predation when they are in unfamiliar areas.<sup>37,38</sup> Support for this notion has now been obtained from vervets. As a result of natural habitat change in Amboseli National Park, Kenya, entire vervet groups gradually shifted their home ranges into areas they had not previously inhabited.<sup>24</sup> Some of these groups eventually became so small that the remaining members abandoned their home ranges and immigrated into groups with different ranges.<sup>39</sup> In both situations, vervets began using areas that were unfamiliar to them. During this time, many vervets disappeared, most often as a result of leopard predation.<sup>33</sup> Whether they moved as entire groups or as immigrants into established groups, predation increased when they spent time in unfamiliar areas. Immigrants were most vulnerable during the first six months after joining new groups. Thereafter, their vulnerability declined to a level comparable to that of the residents of the groups they had joined. This suggests that experienced animals did not pass on sufficient knowledge of the area to naive animals to provide them with equal protection from predators. Animals may be required to learn this information through their own experience.

Familiarity with an area may mean knowing the locations of shelters and the patterns of individual predators, such as their favored ambush sites. The safest way for an animal to gain this knowledge is to remain in the home range where it was born. Many

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animals, including solitary ones, apparently follow this rule. They are spatially philopatric, remaining in their home ranges throughout their lives.<sup>40</sup> (This differs from the behavior of remaining in one's natal group, which may or may not include spatial philopatry.<sup>24</sup>) Predation may have favored the evolution of spatial philopatry; it may also contribute to its maintenance. Spatial philopatry is considered an important step in the evolution of group living because, in

many species, groups are composed of related females.<sup>40</sup> This is particularly true among Old World primates. Thus, once grouping became advantageous, predation may have contributed to the evolution of kin-groups (pathway 3 in Fig. 1).

3) It appears that arboreal primates are more vulnerable to predation when they are at forest edges, in open forest, or on top of the canopy, where the sparseness of vegetation makes them more visible and more accessible than when they are in dense forest.<sup>41-44</sup> Primates that commonly use such areas—for example, black and white colobus (*Colobus guereza*)—may therefore be particularly vulnerable.<sup>45,46</sup>

4) Predation, at least by mammals, may often be episodic. Condit and Smith reported that disappearances of baboons at the Tana River Reserve, Kenya, which they attributed to lion (*Panthera leo*) predation, were episodic.<sup>29</sup> Busse observed leopards hunting roosting baboons in the Moremi Wildlife Reserve, Botswana, five times within a three-month period but only once in the 27 months of observation outside that time.<sup>31</sup> Leopards were also implicated in an abrupt increase in disappearances of vervets in Amboseli National Park, Kenya. During one 30-day period within 526 days of observation, 14 vervets disappeared. This rate was more than seven times greater than the rate during the previous six months.<sup>32</sup> One possible

### Predation Risk, Predation Rate, and the Effectiveness of Anti-predator Traits

One measure of the effectiveness of anti-predator traits would be the demonstration that individuals, populations, or species that share a particular trait are subject to a lower rate of predation than are individuals, populations, or species that do not exhibit this trait. However, of all the traits listed in Table 1, the only ones that have been statistically related to variation in estimated predation rates are body size and group size (across species; see Fig. 2),<sup>5</sup> human presence<sup>32</sup> (Fig. 3a), and movement into unfamiliar areas<sup>24</sup> or groups<sup>39</sup> (among groups within a population). Attempts to find such direct patterns have failed for a number of traits, including group size<sup>32</sup> (intraspecific; Fig. 3b), terrestriality,<sup>5</sup> and birth synchrony.<sup>79</sup> These failures may sometimes, but not always, be a result of the rarity of predation events.

Partly in response to these failures, it has been recommended that we make a distinction between inherent predation risk and realized predation rate.<sup>51</sup> For example, it is possible that the failure to find that terrestrial primates experience higher predation rates than do arboreal primates may be because terrestrial primates have evolved adaptations to deal with their inherently greater predation risk. In this context, presumed predation risk may be an appropriate correlate of past selective pressure, whereas realized pre-

dition rate may be a better measure of present selective pressure.

Another use of the concept of risk is that it allows researchers to examine anti-predator traits even in populations in which predation events are rarely documented. For example, the increased presence of predators or predator surrogates (models or humans), which is presumed to be an appropriate measure of predation risk, has been correlated with many of the traits in Table 1. This assumes, of course, that researchers' abilities to recognize risk are realistic. This may not always be the case, as shown, for example, by the assertion that distance from trees is positively associated with predation risk (see text).

Vermeij<sup>77</sup> has suggested that neither presumed predation risk nor realized predation rate is the best evolutionary measure of anti-predator adaptation. If all predation attempts are successful (or if all are unsuccessful), there can be no selection for anti-predator traits, regardless of the rate of predation. He suggests instead that the failure rate of predation attempts is the most appropriate measure. An example of this might be the difference in the abilities of primate groups of different sizes to detect predators.<sup>13,15</sup>

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explanation of episodic predation is that the ranging patterns of individual predators encompass more area than the home range of any particular primate group; another is that individual predators prefer a particular prey species. Leopards are especially known for having individual preferences.<sup>33,35,47-49</sup> In contrast, there is little evidence that predation by raptors or reptiles is episodic, perhaps because mammalian predators can consume more primates within a shorter time than can raptors, snakes, or crocodiles.

5) The more terrestrial primates, especially those in eastern and southern Africa, may not be subject to greater risk or higher rates of predation than are arboreal primates (see Box 2). Primates, such as baboons and vervets, spend more time on the ground than arboreal primates. They are exposed not only to raptors and snakes, as are arboreal primates, but also to terrestrial carnivores<sup>50</sup> such as lions, leopards, cheetahs (*Acinonyx jubatus*), and jackals (*Canis* spp.). In addition, they are often farther away from the safety of trees than are arboreal primates.<sup>51</sup> Therefore, it has long been assumed that, in comparison to arboreal primates, these frequent ground dwellers

are more vulnerable to predation. Surprisingly, this assumption has been subjected to little scrutiny. In a survey of field workers, however, Cheney and Wrangham<sup>5</sup> provided the first indication that terrestrial primates may not have higher estimated predation rates than arboreal primates.

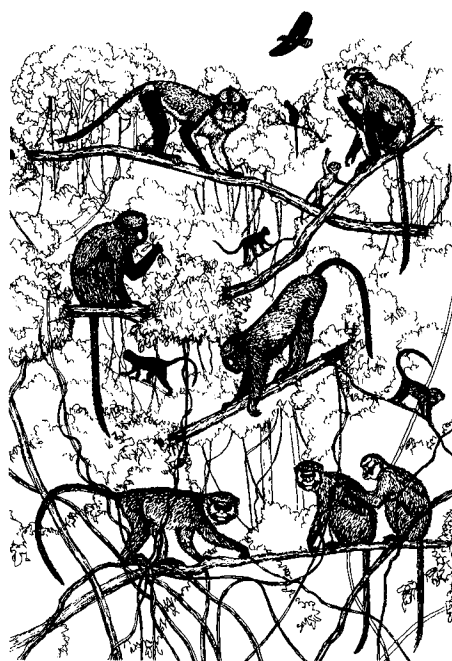
Terrestrial carnivores commonly have access to high densities of alternative prey.<sup>52</sup> No primates were killed during a study of lions lasting more than three years in Serengeti National Park, Tanzania. In addition, primates (six baboons) accounted for less than 1% of the diet of lions in Lake Manyara National Park, Tanzania, during two years of observation.<sup>48</sup> All terrestrial mammalian predators probably are opportunistic to some extent, and will not avoid killing a primate if success is likely. However, savannah primates are eaten so rarely compared to other animals that they are often either left off lists of the prey of terrestrial mammals or listed as "other prey." Only leopards appear to be frequent terrestrial predators of savannah primates in eastern and southern Africa. Of the five large terrestrial carnivores in South Africa—leopards, lions, hyenas (*Crocuta crocuta*),

cheetahs, and wild dogs (*Lycaon pictus*)—only leopards ate terrestrial primates as a substantial part (10%) of their diet.<sup>53</sup> Leopards can also be serious predators of arboreal primates. In Tai National Park, Ivory Coast, arboreal primates represented 24% of the prey items in the scats of leopards.<sup>49</sup> In the Ituri Forest, arboreal primates are also a major component of the diet of leopards (J. Hart and T. Hart, personal communication).

Dunbar<sup>51</sup> argued that terrestrial primates, because they are often farther away from the safety of trees, are at greater risk of predation than are arboreal primates. This may be true, however, only in areas with long grass and few trees, where cover for predators is increased and primates' ability to see them is decreased. Areas with few trees and short grass are not likely to be particularly risky because they provide terrestrial predators with little cover from which to hunt<sup>54,55</sup> and allow primates to see and keep a safe distance from any predator attempting to hunt without cover. The riskiest areas for terrestrial primates may, in fact, be areas with numerous trees and bushes, because they provide terres-

### Polyspecific Associations: An Anti-predator Tactic?

Mixed-species groups, in which troops of different primate species regularly feed and travel together, for hours, days, or even weeks, are relatively common<sup>81</sup> especially among guenons of Africa<sup>80-83</sup> and small New World monkeys.<sup>81,84</sup> Such polyspecific associations should entail increased feeding competition in species with significant dietary overlap or, at best, be neutral in species with little overlap. Most ecologists, therefore, have postulated enhanced predator awareness as the main benefit of such associations. Associating species would, in theory, reap several benefits, including increased overall awareness through the presence of additional eyes and ears; increased individual foraging time through decreased need for vigilance per individual; and the possibility that predators will confront increased confusion when attacking a large group. Observations that could be used to test the theory that polyspecific



Three guenon species from Gabon that frequently forage together in mixed-species groups: top, the crowned guenon (*Cercopithecus pogonias*); middle, the spot-nosed guenon (*C. nictitans*); bottom, the moustached monkey (*C. cephus*). The crowned hawk eagle, a common predator on these monkeys, soars overhead.

associations are an effective antipredatory tactic, particularly for smaller species, have yielded interesting, but not definitive results. Cords<sup>80,83</sup> reported that all 21 observed predation attempts by eagles on mixed-species groups on guenons in East Africa were unsuccessful, but could not demonstrate differences in predators' success rates in single-species groups versus mixed groups. However, Gautier-Hion and colleagues<sup>82</sup> reported that three of the four successful predation attempts by the eagles on *Cercopithecus cephus* were on single-species groups, whereas only one attempt occurred when *C. cephus* was foraging with other guenons (see Fig.).

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trial predators with extensive cover for ambushes. Indeed, in the more open habitats terrestrial primates may be at greatest risk of predation nearest their sleeping trees. The areas around these trees often provide cover for predators, many of which hunt most actively during the hours when primates are either descending or ascending their sleeping trees.

The assumption that the risk of predation is greater for terrestrial primates than arboreal primates is further weakened by evidence that predation on arboreal primates can be severe. There are terrestrial animals

that are capable of killing arboreal primates, at least in the Old World where fossas (*Cryptoprocta ferox*)<sup>30</sup> and leopards occur. There are also avian predators that specialize in killing arboreal primates in Africa, the Neotropics, the Philippines, and Madagascar.<sup>30,45,56</sup> In two studies of crowned eagles (*Stephanoaetus coronatus*) in Kibale Forest, Uganda, monkeys accounted for 87% and 89% of prey items.<sup>45,46</sup> In Guyana, monkeys, almost entirely cebids, were the most common prey of harpy eagles (*Hapria harpyja*), constituting 36% of their diets.<sup>42</sup> The grey mouse lemur (*Microcebus murinus*)

represented 23% of the total biomass taken by barn owls during one year in Beza Mahafaly, Madagascar.<sup>30</sup> In contrast, no avian predators are known to specialize in killing terrestrial primates.

The vulnerability of arboreal primates may also be increased by the fact that they generally are smaller than terrestrial primates.<sup>34</sup> For example, small primates are prey for a greater number of avian predators than are large primates. At least five species of birds are confirmed or suspected predators of the 800 gm squirrel monkey (*Saimiri sciureus*) in Manu National Park, Peru, whereas only two species of birds are confirmed or suspected predators of the 3 kg capuchin monkey in the same forest.<sup>57,58</sup> The vulnerability of small arboreal primates is exacerbated by the fact that small predators occur at greater densities than do large predators (see Terborgh,<sup>57</sup> pp 194-195). On the other hand, large body size may be seen as an evolutionary response to greater predation risk that has resulted in lower predation rates<sup>34</sup> (see Box 3). Nonetheless, these numerous lines of evidence suggest that the actual intensity of predation on terrestrial primates may have been exaggerated and the intensity of predation on arboreal primates underestimated.

### PRIMATES AS PRIMATE PREDATORS

Only a few studies of predation on primates have been conducted on habituated predators. Not surprisingly, those predators are also primates. Chimpanzees (*Pan troglodytes*), not typically considered carnivores, nevertheless kill and eat animals, mostly other primates. Primates accounted for 62 to 100% of the observed vertebrate prey of chimpanzees at three study sites in West and East Africa.<sup>59-61</sup> Most of these (55 to 82%) were red colobus (*Colobus badius*). At Gombe National Park, Tanzania, at least 20% of the red colobus population was estimated to have died in one year as a result of chimpanzee predation.<sup>61</sup> The success of chimpanzees apparently increases with the number of males involved in hunting.

Stanford<sup>62</sup> has examined predation by chimpanzees from the perspective of the prey. Groups of red colobus in



## Sex Roles in Predator Defense and Vigilance

Based on observations that among savannah-dwelling primates males are more aggressive than females in defense against predators, one early hypothesis of primate social ecology suggested that such sex differences could account for multi-male primate groups in predator-rich habitats.<sup>50,85,86</sup> Alternatively, multi-male groups may occur when large female groups and close synchrony of female estrous cycles make it impossible for a single male to monopolize access to breeding females.<sup>51,87</sup> Observations from many species continue to show that predator defense is often principally performed by males, even when there is only one male in the group (see review by Cheney and Wrangham<sup>5</sup>).

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Recently, several authors have suggested that a special male role against predators could account for monogamy in territorial marmosets,<sup>51</sup> as well as multi-male group structures in species with small female groups, such as capuchin monkeys.<sup>72</sup> These recent twists on the original defense hypothesis are based on accumulating evidence that male primates are significantly more vigilant than females.<sup>72</sup> It has been experimentally established that male capuchins, at least, are more effective than females in detecting both aerial and ground predators. If females willingly mate with peripheral subordinate males that are more likely to detect predators, these males will then have an incentive to remain in a group despite strong competition from the dominant or resident male.

the core areas of the chimpanzee community home range averaged 46% smaller than groups at the periphery. Stanford attributed the smaller group sizes to selective hunting of immature red colobus and suggested that chimpanzee predation may limit red colobus population size below carrying capacity. Expected changes in the behavioral responses of red colobus in the presence of chimpanzees did not always occur. Groups became more cohesive and alarm calling occurred more frequently as chimpanzees approached, as expected. But even though the large group increased its height in the canopy when chimpanzees were present, the smaller group did not. Stanford suggested that behaviors such as early detection and flight, which are effective against ambush predators, may not be as effective against chimpanzees, which are social predators.

## Humans as Predators on Primates

One major primate predator of primates has thus far received little attention as an agent of evolutionary change in primates. Present-day humans have been documented as major predators of primates in West and Central Africa and in Amazonian South America.<sup>63,64</sup> Indeed, in one study of mammalian predators in neotropical countries,<sup>64</sup> human subsistence hunters killed more primates in more sites than did either pumas (*Felis concolor*) or jaguars (*Panthera onca*). Humans hunted primates in

three or four sites examined. In Ecuador, Venezuela, and Bolivia (same site in different years), primates accounted for 20 to 66% of the prey taken by humans. In contrast, pumas hunted primates in only one of four sites examined (Paraguay, 4% of prey items) and jaguars in only one of three sites examined (Peru, 5% of prey items). The greater presence of primates in human diets may, in part, reflect the greater ability of humans to hunt arboreal animals from a distance with weapons. Indeed, another study suggested that local Peruvian hunters

have been so successful at killing primates that the yields now appear to be unsustainable.<sup>65</sup>

Human and nonhuman primates have co-existed far longer in Africa and Asia than in the Neotropics and Madagascar. Although we do not yet have sufficient data to compare the rates of human predation on Old World and New World primates, it is possible that neotropical primates have had less time to evolve adaptations to avoid predation by humans and, hence, are more vulnerable to extinction as a result of hunting. This may have also been the case in Madagascar where, as recently as 2,000 years ago, at least 15 species of primates became extinct after the arrival of humans, who not only hunted them, but also changed their habitats by burning and cutting forest, and introducing domestic animals.<sup>66</sup> Differential responses by Old and New World primates to the threat posed by human predation have not yet been examined. This could be a fertile area for future collaborative research by cultural anthropologists, primatologists, and conservation biologists.

## CAN PREDATION REDUCE PRIMATE POPULATIONS BELOW CARRYING CAPACITY?

It has been difficult to determine whether predation or disease ever diminishes animal populations below the levels that can be supported by available food.<sup>67</sup> Several catastrophic die-offs of primate populations have been attributed to disease,<sup>68</sup> but there

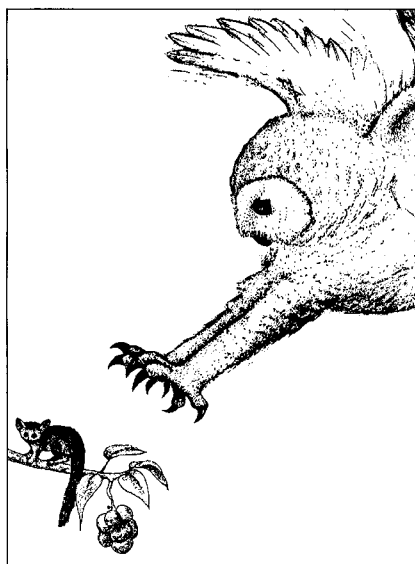


Figure 4. Mouse lemurs (*Microcebus murinus*) have been reported to suffer extremely high predation by the barn owl (*Tyto alba*) in southwestern Madagascar. Figure by Luci Betti.

is less evidence that predation has had negative effects on primate population size. A population of vervets may have been reduced below carrying capacity after it suffered a sudden short-term increase in predation.<sup>33</sup> However, there had also been a consistent, long-term decline in its food supply.<sup>24,69-71</sup> The predation rate within one year on a population of grey mouse lemurs at Beza Mahafaly, Madagascar, has been estimated at 25%,<sup>30</sup> among the highest for any primate species (Fig. 4).<sup>5</sup> Because its reproductive rates appear to be high, however, this population may not be limited by predation.<sup>30</sup> If there is any population that is limited by predation, it might be found where there is little evidence of food competition. For example, red colobus in Kibale Forest, Uganda, show no obvious behavioral expressions of food competition, leading to the suggestion that the size of this population may be constrained, at least in the short term, by something other than food, such as predation, disease, or social instability.<sup>11</sup> It is noteworthy that the only primate thus far thought to be limited by predation is another population of red colobus, in Gombe National Park, Tanzania.<sup>62</sup>

## CONCLUSION

Although ecological patterns of predation on primates are now beginning to emerge, our confidence in these patterns depends on the intensity of inquiry into the processes of predation. If we are to understand these processes, more studies of the interactions between predators and their primate prey are greatly needed. Most promising, perhaps, are experimental studies in which the behavior of the "predator" can be controlled. In the past, such studies have included observations of the responses of primates to models of predators,<sup>72,73</sup> and to previously recorded alarm calls.<sup>4</sup> It would be valuable to incorporate simulated attacks into experimental studies. Another useful approach would be for field biologists to organize and conduct collaborative studies in which the predators and the prey are habituated. Although habituation takes time, the benefits of habituation for observations of predator-prey interactions are unsurpassed. Until such

efforts are made, many of the outstanding questions in primate behavioral ecology will remain as hidden as a leopard in a bush.

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