

Predation on Primates: Where Are We and What's Next?

In a recent review of predation on primates, Lynne Isbell and co-contributors¹ present a timely update on our current understanding of the influence of predation on primate grouping and behavior. Isbell notes that the risk of predation has traditionally been viewed as a major selective force favoring group living and specific anti-predator behavior in primates, but she also discusses alternate hypotheses for some of these traits. Although Isbell provides a list of selected anecdotal evidence of anti-predator behaviors, these are passed over briefly; instead, more emphasis is placed on comparisons across species and tests of specific hypotheses within species. In this commentary, we would like to reverse the priority and show that: 1) the anecdotal literature is sufficiently rich in some cases to provide convincing evidence for the importance of predation to individual primate species; and 2) many difficulties arise in testing predictions concerning the evolutionary consequences of predation, especially when using comparisons across species.

We also wish to reinforce one of her major themes. If we are to understand ecological and evolutionary consequences of predation for primates, "more studies of the interactions between predators and their primate prey are greatly needed."¹

Isbell tabulated a long list of behavioral and morphological characteristics of primates suggested to represent anti-predation adaptations. This list, however, does not illustrate the rich and pervasive circumstantial evidence for the potential importance of predation as a selective factor structuring the activities and biology of primates. Tamarins (*Saguinus* and *Leontopithecus*) provide a good exam-

ple. Predation risk on tamarins has been documented to be high.² Not only do tamarins allocate much time to scanning and vigilance,^{3,4} but reactivity to perceived threats or even unexpected stimuli is strong and occurs with only slight provocation.⁵ Individuals avoid being spatially separate

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from a group by even short distances.⁶ The intragroup vocal behavior of tamarin species features a variety of contact calls and alarm calls, which are produced at high rates. As a result, group members are in near constant auditory contact, especially when visual contact is not possible.^{7,8} Even the acoustic structure of several tamarin vocalizations is thought to minimize information available to potential predators regarding the location of the caller.⁸ A suite of adaptations suggests that their susceptibility to predation at night is strong. Tamarins retire before dusk, use sleeping holes, and often closely monitor the near vicinity of the sleeping hole for up to an hour before

entering.^{3,4} Many species of tamarins are commonly found only in mixed-species groups, a situation Peres³ has shown benefits individuals in terms of increased overall vigilance offered by larger groups. Indeed, Caine⁶ argues that the intense cooperation and tolerance exhibited by tamarin groups is best explained as an anti-predation adaptation. All of these behaviors appear to serve the function of decreasing the risk of predation. However, incorporating these diverse behaviors in comparative models to predict social structure or group size has proven difficult.

APPLYING THE COMPARATIVE METHOD TO QUANTIFY THE EVOLUTIONARY CONSEQUENCES OF PREDATION

Larger primates are commonly viewed as inherently less vulnerable to predation than smaller primates, and primates in large groups are suggested to be less vulnerable to predation than those in small groups. Isbell¹ correctly points out that the independent and interactive effects of body size and group size on predation risk are difficult to separate since the two variables covary strongly. On the basis of the predation rate data of Cheney and Wrangham^{9,10} and Goodman et al.,¹¹ she demonstrates that both increased group size and increased body size are negatively related to predation rate. Although these results are significant, it is useful to note that only a very small amount of the variation in predation rate can be explained by either of these two variables.

Primates live in a diversity of habitats and are exposed to a diversity of predators. One might expect to be able to increase the predictive power of the relationships between body size or

group size and predation rate, if one analyzed only species exposed to particular types of predators under similar settings. For example, it has often been suggested that terrestrial primates experience intensified risk of predation because they are potentially threatened by mammalian and avian predators^{12,13} or that nocturnal primates can more easily avoid predators in the dark.^{13,14} However, we repeated Isbell's comparative analyses of predation rates for select subsets of species (terrestrial, arboreal, diurnal) and found that the amount of variance in predation rates explained by group size or body size did not change markedly.

The difficulty of predicting predation rate based on body size is illustrated by Struhsaker and Leakey's¹⁵ study of crowned hawk eagle predation on primates. For red colobus, the eagles selected young and juveniles, the smallest members of the group, but for the four other common diurnal monkeys in the area they selected adult males, the largest members of the group.

Results from any of these comparative analyses must be considered to be tentative, since a) the estimated predation risk is often based on disappearance data, not observed predations, b) species are represented more than once in these data sets; we do not know the appropriate level (group, species, genera, etc.) to conduct the analyses, and c) present predation rate may not reflect how predation acted in the past as a selection pressure.¹⁰ Such data analyses do illustrate that our current knowledge of how predation shaped or is shaping primate social lives is based largely on inferential data.

In addition to these procedural problems with interpreting predation data, the low amount of variance that can be explained may be attributed to a number of factors:

1. Many of the populations for which estimated predation rates were obtained are from locations where predator populations have been reduced. For example, Kibale Forest and Kakamega Forest, which contribute 5 of the 30 data points, no longer have leopards (leop-

ards are just now recovering in Kibale Forest). Some of the populations are influenced by human encroachment into the forest (e.g., Hato Masaguaral, Abu), and some locations have undergone dramatic ecosystem changes (e.g., Amboseli).

2. Counts of groups of very different sizes are often averaged to obtain a mean group size to represent a population (e.g., red colobus group size range from 9 to 68, with a mean of 34),¹⁶ yet the predation rate for that population is typically estimated for only one or a few of these study groups.
3. When we simply analyze the relationship between group size and predation rate, we ignore differences in the costs of group living. However, previous research has suggested that intergroup feeding competition may be reduced for some folivores,¹⁷ that different levels of within-group food competition exist,¹⁸ and that males and females may experience different benefits of being group members.^{19,20}
4. On an evolutionary time scale, increased predation pressure may favor large groups, but on a shorter ecological time scale, high predation levels may decrease group size directly, simply through the death of animals. Isbell¹ illustrated this by presenting Stanford's²¹ study of chimpanzee predation on red colobus. Red colobus in the chimpanzee's core area had group sizes that averaged 46% smaller than groups on the periphery of the community's home range.
5. By using the number of predation events per unit time in between-species comparisons, we are ignoring potentially important data. Does predation on infants have the same impact as predation on young reproductive females? Similarly, does a predation event occurring in a species with a very long interbirth interval (e.g., *Ateles geoffroy*—870 days) have the same

impact as a predation event for a species with a short interbirth interval (e.g., *Tarsius spectrum*—152 days)?²²

6. Such analyses typically assume that the advantage of group size for reducing predation risk is constant across all types of predators. This is unlikely to be true when predators on primates include animals that attack rapidly (e.g., raptors, cheetah), sit-and-wait predators (e.g., snake), leopards that rely on concealment, and chimpanzees, who often announce their approach from a great distance but hunt cooperatively.

WHERE DO WE GO NEXT?

These examples demonstrate the difficulty of testing predictions concerning how predation pressure will influence primate group size. The question that we now need to answer is where do we go from here? Isbell¹ concludes by suggesting that future studies take either an experimental approach where the behavior of the predator (or predator model) can be controlled, or involve habituation and study the predators themselves (a quest for more precise data). We agree that these are two very profitable avenues for future research, but suggest that the experimental approach may prove more useful in distinguishing between alternative hypotheses. If predation by mammalian predators is episodic, as the data Isbell presents indicate, it will be difficult to obtain an adequate sample size of predation events on known groups to address specific hypotheses. In contrast, predictions concerning indices of perceived predation risk may permit tests of specific predictions. For example, vigilance has been demonstrated to entail a large, but variable, proportion of the time budgets of different species. Detailed studies of vigilance a) in groups of different sizes, b) of animals that typically occupy different spatial positions in the group,^{23,24} c) between species with different body sizes, and d) of species when in polyspecific associations and when alone, relative to the foraging success of an individual, may permit the examination of specific predictions.²⁵ Species that have

very synchronized birth peaks, which are associated with increased predator risk and a reduction in group dispersion, may be suitable for making predictions concerning changes in the nature and level of vigilance.²⁶ Similarly, the association between predation rate and different feeding rate may reflect perceived predator risk. Subsequent to gathering baseline data on such variables as vigilance and group spread, the group's perception of predation risk could be altered through playback experiments of predator calls, with the responses of the group monitored.

It is apparent that in our understanding of the broad patterns of the impact on group living among primates there remains a considerable gap between the rich descriptions of anti-predator behaviors and what can truly be demonstrated with respect to how predation affects social structure. The challenges of collecting accurate data on predation for cross-taxa comparisons are compounded by divergent predator communities, defensive strategies, and life histories. We suggest that a useful and complementary strategy to the comparative approach would be experimental studies designed in light of detailed knowledge of the natural history of the taxa. In any case, the potential evolutionary importance of predation pressure on primate sociality warrants much further field investigation.

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