6. Are there viable strategies to reduce the effects of within-group competition, and if so, what are their effects on group size?

7. For species with mixed diets (e.g., insects and tree fruits), what are the interactive and independent effects of patch depletion and search field overlap on travel costs?

8. How are the ecological constraints model's predictions affected by individual differences in competitive abilities (e.g., costs and benefits of traveling for lactating adult females vs. adult males)?

9. How does variation in perceived predation risk affect animals' decisions to be in groups of different sizes?
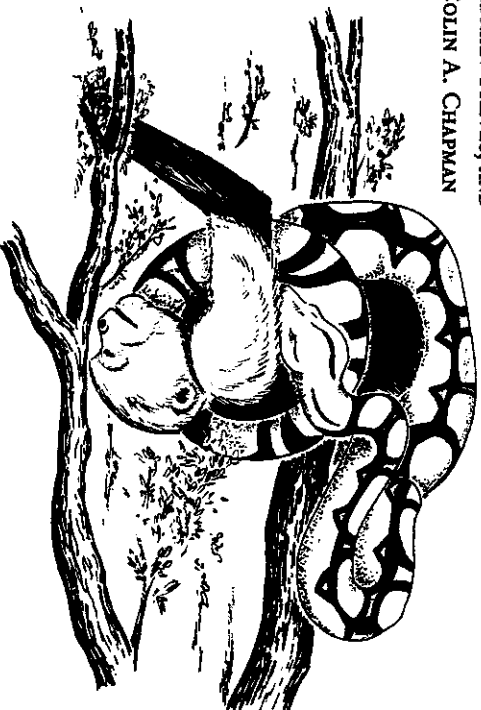
Acknowledgments

A Critical Evaluation of the Influence of Predators on Primates: Effects on Group Travel

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A troop of Costa Rican squirrel monkeys (*Saimiri oerstedii*) is in a patch of early second-growth forest, eating fruits of *Cecropia* (Moraceae) and *Piper* (Piperaceae) and the occasional caterpillar. The sudden onset of raucous and frenetic alarm calls disturbs the tranquil scene, yanking the observer's attention to a voracious-looking crested eagle (*Morphnus guianensis*) perched 4 meters above the ground in what had been the center of the troop's dispersion. Adult females and immatures immediately coalesce into a writhing ball of more than forty squirrel monkeys within the protective confines of a dense vine tangle. Meanwhile, twenty foolishly valiant adult and subadult males are mobbing the raptor, literally throwing themselves at the bird. The squirrel monkeys slide off the raptor and thump to the ground below without ruffling a feather, much less the predator's composure. After several minutes of barrage by the small-bodied squirrel monkeys, the crested eagle spreads its wings and launches into a flight that skims the shrubby growth. It makes

a brief dip to grab a young adult male with its talons, and is last seen landing with its prey in the canopy of a distant tree. The remaining troop members are immobilized for nearly 15 minutes, so still and quiet that they become almost invisible. Then, ever so quietly and slowly, they creep to the ground, following the lead of four adult males. The troop walks single-file into the grass, and continues walking on the ground for more than a kilometer, until it reaches the portion of its range with the densest and lowest ground cover, too impenetrable for the human observer to follow. The troop remains in this thicket for the next 3 days (S. Boinski, pers. obs.).

There is good evidence that even some of the largest species in the primate order have strategies designed to decrease the risk of predation. For example, Tutin, McGrew, and Baldwin (1981, 1983) report a complex of antipredator behaviors used by savanna-dwelling chimpanzees (*Pan troglodytes*) at Mt. Assirik, Senegal, a habitat containing abundant predators, including leopards, lions, spotted hyenas, and wild dogs. Chimpanzees, when moving long distances, congregate in large parties and move in a rapid, directed fashion, while remaining unusually silent. These traveling parties are also described as being intensely alert when moving through open areas, frequently standing bipedally to scan their surroundings.

These and many other anecdotes imply that groups, and the individuals within groups, behave so as to limit predation risk. Moreover, predation has traditionally received the widest attention as a factor making group living advantageous for primates (van Schaik 1983). A group-living animal is thought to obtain antipredation benefits in the form of (1) decreased individual vulnerability (the more group members, the smaller the likelihood that any single individual will be killed during a predator attack), (2) increased effectiveness in detecting and deterring potential predators, (3) increased opportunities to confuse the predator, and (4) greater information on the presence of predators from alarm calls emitted by other group members (Hamilton 1971; Pulliam 1973; Powell 1974; Bertram 1978; van Schaik 1983; Terborgh and Janson 1986). Nevertheless, predation risk as an influence on primate behavior in general, and group movement in particular, remains controversial. Quantitative and particularly experimental documentation are scanty. Correspondingly, Janson (1992) notes that theoretical models and indirect tests provide the bulk of the evidence indicating that predation avoidance is a beneficial consequence of primate grouping.

In this chapter we consider the proposition that group movement is influenced by the risk of predation, both in the absence of attack and subsequent to an attack, presumably a period of more certain and elevated risk. The focus of our inquiry is a set of traits thought to affect predation risk—group travel, spatial structure, and habitat use—and the arsenal of presumptive predator avoidance, detection, and deterrence techniques. We critically examine the methods currently employed to evaluate the effects of predation on primate sociality. Then we propose specific methodological approaches useful in future research on predation and group movement. Last, potential interactions between predators and the many components of group movement in primates are considered in detail. We do not consider how group movement is influenced by primates when they themselves act as predators of vertebrates (Stanford 1995b; Rose 1997).

Evidence that Predation Is a Finite Risk to Primates

Views on the impact of predation on primate behavior within the discipline of primatology have swung like a pendulum. Early field-workers presumed that susceptibility to predation was a stringent constraint on the behavior and morphology of primates, although predation attempts on primates were rarely documented in these early studies (Carpenter 1934; Chance 1955; DeVore and Hall 1965; Nishida 1968). By the 1970s the dearth of predation data had become so conspicuous that a groundswell of researchers expressed doubts as to its significance (Aldrich-Blake 1970; Rodman 1973b). Most of the classic edited volumes in primatology from this period did not even include a predation entry in the index (e.g., DeVore 1965; Jay 1968). This skepticism continued into the early 1980s. Wrangham (1979, 1980), Fittinghoff and Lindberg (1980), and Collins (1984) all concluded that predation on primates was so seldom observed that its impact as a selective pressure was best considered weak. Yet Stuart Altmann (1974) countered that predation's biological importance cannot be evaluated on the basis of frequency of occurrence. He noted that although births, like deaths, are only rarely observed among wild primates, they represent a biological event of immense consequence.

By the mid-1980s, however, a substantial number of publications reporting successful and unsuccessful predation attempts on primates were collated by Anderson (1986) and Cheney and Wrangham (1986). Sufficient data had accrued to allow preliminary quantitative analyses relating interspecific differences in predation rate to group size, body size, arboreal versus terrestrial habits, and diurnal

nal versus nocturnal activity (Anderson 1986; Cheney and Wrangham 1986; Isbell 1994). In general, higher predation rates were significantly predicted by smaller body and group sizes, but terrestrial primates did not have higher rates of predation per capita than arboreal primates. These studies relied on small sample sizes, explained little variance, and sometimes produced conflicting results (Boinski and Chapman 1995). Nevertheless, predation could no longer be easily dismissed as a negligible ecological factor on the basis of rarity. Despite these advances, primatology has remained locked in a tradition of "bean counting" predation events. What is really needed to evaluate the impact of predation are data that compare victims with survivors and track behavioral and genotypic changes over time.

We are not going to attempt quantitative analyses incorporating the more recent predation data (see our concerns expressed below regarding currently attempting cross-species analyses). Instead, readers are encouraged to examine documented cases of successful predation reported in the literature (tables 3.1 and 3.2). Mammals, birds, and reptiles are the major primate predators. Only in Africa are primates a significant predator of other primates. Both terrestrial and arboreal primates are taken by every type of predator, although there seems to be a tendency toward greater vulnerability of arboreal primates to raptors and terrestrial primates to mammalian carnivores. It is also evident that for most genera the cumulative total of the published number of successful predation events in our tally remains relatively small (mode = 1), and reporting and/or actual predation is highly skewed (mean = 32.6, median = 6, SD = 122, skew = 5). Even if this figure were doubled to compensate for an incomplete literature search or incomplete reporting of observed predation events, the cumulative total of documented predation events would be minuscule compared with the cumulative number of hours invested by field-workers in observation of primates. For example, for squirrel monkeys observed at two sites, the rates were 0.0016 and 0.0024 predation deaths per hour of observation respectively (Mitchell, Boinski, and van Schaik 1991).

Quantitative Analyses Based on Multiple Species

There is great temptation to incorporate every scrap of predation data, such as those presented in table 3.2, into a single analytic model. However, many difficulties arise in testing predictions concerning the evolutionary, ecological, and behavioral consequences

Table 3.2 Types of predators reported to kill primates and their wild primate prey by genus and region

Region	Class	Predator type	Primate genera observed as prey or found in the remains of kills	References[a]
Asia				
	Reptiles	Snakes	*Macaca, Semnopithecus*	1, 2, 43
		Crocodiles	*Homo, Macaca*	3, 4
	Birds	Hawks, eagles	*Macaca*	5
	Mammals	Carnivores	*Homo, Hylobates, Loris, Macaca, Nycticebus, Pongo, Semnopithecus*	1, 2, 6–9
		Primates*	*Nycticebus*	10
Africa				
	Reptiles	Snakes	*Cercopithecus, Hapalemur, Microcebus, Papio*	1, 11, 12
		Crocodiles	*Homo, Papio*	12, 13
	Birds	Hawks, eagles	*Avahi, Cercopithecus, Cheirogaleus, Colobus, Eulemur, Homo, Lemur, Lepilemur, Lophocebus, Microcebus, Mirza, Papio, Procolobus, Propithecus*	11, 12, 14–16
		Owls	*Lepilemur, Microcebus*	11
	Mammals	Carnivores	*Cercopithecus, Colobus, Eulemur, Gorilla, Homo, Lemur, Microcebus, Pan, Papio, Procolobus, Propithecus*	11, 12, 17–22
		Primates	*Cercopithecus, Colobus, Galago, Homo, Lophocebus, Microcebus, Papio, Perodicticus, Procolobus*	1, 12, 23–28
Americas				
	Reptiles	Snakes	*Cebus, Saguinus*	29, 30
	Birds	Hawks, eagles	*Alouatta, Ateles, Callithrix, Cebus, Chiropotes, Saguinus, Saimiri, Pithecia*	31–36
	Mammals	Carnivores	*Alouatta, Aotus, Ateles, Homo, Saguinus, Saimiri*	37–41
		Primates	*Callicebus*	42

Note: Primate predators are restricted to nonhuman primates because humans probably hunt most primates. Attacks on humans are restricted to those that involve predation (i.e., no elephant trampling or snakebites).

[a] 1, Cheney and Wrangham 1986; 2, Rajpurohit and Sommer 1991; 3, Galdikas and Yeager 1984; 4, M. Leighton, pers. comm.; 5, Rodman 1988; 6, Rijksen 1978; 7, Stanford, 1989; 8, Seidensticker 1983; 9, Sunquist 1981; 10, Utami and van Hooff 1997; 11, Goodman, O'Connor, and Langrand 1993; 12, Cowlishaw 1994; 13, *Uganda News* 1997; 14, Boshoff et al. 1991; 15, Struhsaker and Leakey 1990; 16, Steyn 1982; 17, Boesch 1991a; 18, Fay et al. 1995; 19, Cheney, Lee, and Seyfarth 1981; 20, Busse 1980; 21, Struhsaker 1975; 22, Treves and Naughton-Treves 1999; 23, Hladik, Charles-Dominique, and Petter 1980; 24, Butynski 1982b; 25, Wrangham and Riss 1990; 26, Hausfater 1976; 27, Uehara et al. 1992; 28, Treves and Naughton-Treves 1999; 29, Chapman 1986; 30, Heymann 1987; 31, Izor 1985; 32, Mitchell, Boinski, and van Schaik 1991; 33, Juillot 1994; 34, Ferrari and Lopes-Ferrari 1990; 35, Goldizen 1986; 36, Stafford and Ferreira 1995; 37, Peetz, Norconk, and Kinzey 1992; 38, Emmons 1987; 39, Galef, Mittermeier, and Bailey 1976; 40, Schaller 1983; 41, Hill and Hurtado 1995; 42, Freese and Oppenheimer 1981; 43, Shine, Harlow, Keogh, and Boeadi 1998; 44, Wright and Martin 1995; 45, Maisels et al. 1994; 46, Stanford et al. 1994; 47, Goodall 1986.

Table 3.2 Reported killings of primates

Taxonomic group	Genus	Number of kills	References[a]
Family Cheirogaleidae	Microcebus	7	11
	Cheirogaleus	3	44
	Eulemur	2	11
Family Lepilemuridae	Lemur	1	11
	Hapalemur	1	11
	Mirza	1	11
	Lepilemur	1	11
Family Indridae	Avahi	1	11
	Propithecus	6	11
Family Lorisidae	Galago	5	1, 24
	Nycticebus	7	10
Subfamily Atelinae	Alouatta	6	31, 37
	Ateles	1	33
Subfamily Callitrichinae	Callithrix	2	34, 36
	Saguinus	11	1, 30
Subfamily Cebinae	Cebus	7	1, 29
	Saimiri	12	32
Subfamily Cercopithecinae	Cercopithecus	33	1, 15, 19, 26, 45
	Macaca	18	3, 6, 43
	Papio	59	12, 14, 20
Subfamily Colobinae	Colobus	1	15
	Procolobus	629	21, 25, 27, 46, 47
	Semnopithecus	14	2, 43
	Trachypithecus	1	7
Family Hominidae	Pan	3	17
	Pongo	9	6
	Homo	33	22, 41

Note: This table is a selected review of reported killings of primates. Caution should be used when interpreting these values since, as noted in the text, reporting is biased to certain taxa, the number of hours of observations on different taxa vary greatly, and many reports stem from observations of primates killing other primates. To exclude the possibility of including observations of scavenging events, this listing does not include observations of remains of prey found in feces or at nest sites, or of prey being consumed by predators unless the freshly killed body was seen.

[a]As given in Table 3.1.

of predation when using between-species comparisons. Foremost among these difficulties is that inferential data structure our current knowledge of how predation shaped or is shaping primate behavior (i.e., predator risk is inferred from logical deductions by human observers regarding how predators and prey should behave). A second difficulty is that a panoply of parameters potentially contribute to the influence of predation risk on group movement. It is desirable in comparative studies to statistically control the interaction be-

tween variables, in effect statistically removing the effects of various parameters when considering the effect of a single variable. An obviously desirable control, for example, would be removal of the effect of body size when considering the relationship between predation risk and terrestriality. At the present time, however, such controlled comparisons are limited given the relatively restricted number of primate species for which data are available. As a consequence, the amount of variance explained in comparative analyses is low, usually less than 15% (Isbell 1994; Boinski and Chapman 1995). Third, when attempting to extract comparable predation data from many primate species, one is limited to extremely crude estimators of predation pressure, such as predation events per unit time. The following are some of the more obvious factors that also reduce the utility of comparative analyses on the influence of predation.

1. Published reports of the effects of predation are often based on disappearance data, not events (e.g., Boinski 1987a; Isbell 1990; Peetz, Norconk, and Kinzey 1992; Boinski and Chapman 1995). Disappearance can result from a variety of causes (e.g., mortality due to disease, dispersal), of which predation is only one. Thus, disappearance data should be used with caution and only when the researcher has a detailed understanding of the pattern and rate of dispersal in the species.

2. Reporting of predation events is biased to the spectacular. Little incentive exists for publishing a report stating that in 2,000 hours of observation no predation attempts were observed. Yet this is exactly the data needed for an accurate representation of predation pressure.

3. The present predation rate in any population may not reflect the former predation regime that selected the current antipredation behavior (Cheney and Wrangham 1986; Byers 1997).

4. The appropriate taxonomic level at which to conduct comparative analyses may not be obvious. Species are not independent events, but are nested within phylogenies. There are statistical procedures that can be used to deal with such difficulties (Cheverud, Dow, and Leutenegger 1985; Martins and Hansen 1996).

5. Group size counts for a primate species in comparative data sets are usually based on many groups of widely varying sizes, but predation rates come from only one or a few groups (Boinski and Chapman 1995).

6. If the relationships between predation rate and group size are simply compared across species, we ignore species and individual differences in the costs of group living. For example, some folivorous primates are thought to experience reduced between- and within-group feeding competition compared with many frugivorous

primates (Isbell 1991). Furthermore, males and females may experience different costs associated with group membership (Chapman 1990a; Chapman, Wrangham, and Chapman 1988; Chapman 1995; Treves 1998).

7. Observed predation rates may seriously underestimate actual rates because the presence of the observer deters many predators. The impact of this effect is extremely difficult to quantify and no doubt varies among predator species and sites according to the degree of local development, size and type of research station, and human activity in the area. Anecdotal data could be useful in evaluating to what degree observers deter predators. Thus, field-workers might consider recording information on relevant observations (e.g., the number of predators seen avoiding the observer, the number of times a group mobs a predator even when the identity of the predator is unknown). For example, more than half of the fifty successful and unsuccessful predation attempts reported for Costa Rican squirrel monkeys occurred when the observer was still and obscured by foliage or an umbrella (Boinski 1987a).

8. 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, through increased mortality rates due to predation. In Stanford's (1995b) study of chimpanzee predation on red colobus (*Procolobus badius*), colobus troops within the core of the chimpanzee hunting area averaged 46% smaller than troops on the periphery of the chimpanzee range, where hunting pressure on red colobus troops seemed much reduced.

9. Tremendous variation exists across sites in the densities of alternative mammalian prey species available to predators. This fact suggests that the predation rate for any single species is dependent on the current availability of other potential prey in its community (Wright, Gompper, and DeLeon 1994).

10. Different predators within a primate community present different risks and may evoke widely divergent antipredator responses. For example, large mammalian carnivores and raptors are characterized by markedly different senses to detect prey, morphological adaptations to pursue and capture prey, times of hunting activity (cats are usually nocturnal and raptors diurnal), and microhabitats searched for prey (van Schaik and Kappeler 1996). Primates often distinguish between aerial and terrestrial predators in their alarm calling and evasive responses (Struhsaker 1967a; Cheney and Seyfarth 1990; Macedonia and Evans 1993; Wright 1998).

11. Individual variation in response to predation risk and attack is evident even within a primate species. Scanning patterns vary within groups by age, sex, and dominance rank (Rose and Fedigan 1995; Gould, Fedigan, and Rose 1997; Treves 1997a,b, 1998). On the other hand, group behavior can mask diverse antipredator responses among the troop members. Group movement decisions in

the troops of some, but not all, primate species are determined by one or a few group members (Boinski 1996; Boinski, chap. 15, this volume). Plausibly, the antipredator tactics of subordinate individuals may be compromised by the actions of leaders.

12. Predation risk to infants probably does not have the same influence on individual and group decisions with regard to group movement as would, say, risk to an old male past his prime. Similarly, predation risk to infants in a species with a very long interbirth interval (e.g., black-handed spider monkey *Ateles geoffroyi*, 34 months: Chapman and Chapman 1990) may not have the same impact as predation risk to infants in a species with a short interbirth interval (e.g., spectral tarsier, *Tarsius spectrum*, 152 days: Harvey, Martin, and Clutton-Brock 1986).

13. Many fishes (Christenson and Persson 1993) and birds (Lima and Valone 1991) rely upon structurally complex microhabitats as refuges from predators. Casual inspection of the physical environments used by primates also suggests that habitats are selected to decrease the likelihood of predator detection or attack. Cords (1990b) found that increasing density of foliage was associated with decreased vigilance in redtail monkeys (*Cercopithecus ascanius*) and blue monkeys (*C. mitis*). This finding suggests that individual movement patterns and microsite preferences may influence investment in self-protection.

14. Circumstantial data, unlike metric measures such as distances, rates, and group size, are difficult to incorporate into quantitative models of predation pressure. Yet the anecdotal literature on predation on primates is often sufficiently rich to provide convincing evidence for the importance of predation to specific taxa.

15. Researchers have warned that the rate and pattern of predation observed by field-workers is that occurring despite the array of antipredation behaviors primates exhibit (Boesch 1991a; Cowlishaw 1994; Dunbar 1997). In effect, the actual predation rate is not a reflection of the total risk to which group members are exposed, but the net predation risk after all precautions have been taken.

16. The relationship between predation rate and the antipredator behavior expressed by primate groups is unlikely to be linear (Sih 1987; Lima 1993). Although a sudden increase in predation pressure is predicted to instigate a surge in antipredator behavior, a decrease or even absence of predators in a community is unlikely to extinguish antipredator behaviors, especially if these behaviors are not costly in terms of time and energy. The degree to which the relationship between predation rate and the antipredator behavior is linear could be assessed, but only under situations in which the majority of predator attempts are known.

A review of the above list suggests that caution should be used when evaluating the influence of predation using comparative data that contrast many divergent taxonomic groups. Comparisons of a

simple index of predation risk and primate behavioral patterns are unlikely to be robust.

Adaptive Story Telling: The Difficulty of Providing Functional Interpretations

A significant proportion of the antipredator behaviors ascribed to specific primate populations are probably best regarded as plausible, yet unsubstantiated, adaptive hypotheses. Quantitative data supporting claims of the functional significance of particular behaviors are frequently not provided, and alternative hypotheses are not considered. Two aspects of primate lifestyles often assumed to be under stringent antipredator selection, activity schedules and sleeping site selection, are prime examples of such conflicting scenarios. In regard to activity schedules, Moynihan (1976) claims that most primates have become diurnally active so as to be able to sleep in comparative safety at night. Similarly, Wright (1989) argues that by being nocturnal, the owl monkey (*Aotus trivirgatus*) avoids predation from a multitude of diurnal raptors. Yet, the anomalous extended bouts of foraging activity observed in Paraguay during bright daylight by owl monkeys are explained as a response to intense nocturnal predation pressure by great horned owls combined with the local extinction of many diurnal raptors (Wright 1994). Garcia and Braza (1987) argue instead that the frequently cold temperate-latitude nights in Paraguay provide a better explanation for the activity cycle shift in this population. The second example concerns sleeping site selection. Following the logic of many previous researchers, van Schaik, van Amerongen, and van Noordwijk (1996) concluded that persistent selection of sleeping sites on river banks by long-tailed macaques (*Macaca fascicularis*) is consistent with a functional hypothesis of predator avoidance. Nevertheless, the authors also clearly warn readers that their field data are unable to exclude the alternative explanations that these macaques are merely avoiding mosquitoes or conspecific troops.

Predation and behavioral data from many primate populations come from sites where predator populations have been reduced (Bishop et al. 1981; Seidensticker 1983; Rajpurohit and Sommer 1991). Attempts have been made to exploit these populations at artificially reduced predation risk as "natural" experiments. Yet too many alternative interpretations remain in these situations to allow robust conclusions to be drawn. A good illustration is Goodman's (1994) proposal that a large Malagasy eagle of the genus *Aquila* went extinct sometime between 500 and 4,000 years ago. He reasons

that the stereotyped, strong antipredator response of large Lemuridae is a relic response to this raptor because extant raptors pose little threat to adults and subadults. As Csermely (1996) has pointed out, however, there are several problems with this argument, and multiple alternative hypotheses cannot be excluded. First, *Aquila* are not forest-hunting eagles presently, so the forest-living *Lemur* and *Propithecus* considered by Goodman may never have faced predation from this extinct raptor. Second, the argument that present-day antipredator responses are too strong and stereotyped is unjustified. Third, occasional predation by the small extant raptors may be sufficient to maintain the antipredator response described by Goodman. Fourth, the antipredator response of (putatively immune) adults could be designed to help immatures to recognize danger, as they are not immune to extant raptors.

Even the presence or absence of significant predation risk is a contested premise of some predation scenarios. Most notably, Southeast Asia is the focus of conflicting accounts of predation risk from raptors and felids. In regard to raptors, Southeast Asia is described by some as devoid of monkey-killing raptors (Bennett and Davies 1994), although the Philippine monkey eagle is reported to be an efficient hunter of primates (Kennedy 1977). Rodman (1988) recounts the case of a raptor killing a long-tailed macaque and uses this occurrence and others to dispute the long-standing contention about felid predators put forth by van Schaik and van Noordwijk (1985). The latter authors suggest that the Simeulue Islands lack felid predators and thus propose a direct comparison of group size with that at Ketambe, a Sumatran site with a full complement of predators. Unfortunately, the monkeys watched by van Schaik and van Noordwijk on Simeulue were not habituated, while the Ketambe macaques had been studied for 6 years. In this situation, censuses of subgroups might be expected to vary simply because of differences in observer avoidance by the two study populations. Food abundance, habitat differences, trail cutting, and temporal differences also were uncontrolled. Finally, Rodman also notes that raptors may have been present on Simeulue, so the absence of felids does not mean the absence of predators.

Recommended Strategies: Hypothesis Testing through Experimentation and Detailed Field Observations

In the previous sections we have outlined the obstacles to obtaining useful comparative data on the influence of predation on group movement and other aspects of social behavior and the difficulty of

testing alternative adaptive scenarios. What can be done? Isbell (1994) advocated a quest for better data on predation rates, in the form of studying predators or conducting experiments. Both approaches should certainly be explored. Since researchers interested in the influence of predation on primate group movement are not likely to launch detailed studies of the predators themselves, we focus on the second approach: conducting experiments.

While providing useful observations, studies that draw conclusions about predation in a post hoc manner (Boinski 1987a; Chapman 1986) seldom allow for alternative hypotheses to be distinguished. For more powerful studies, explicit hypotheses should be laid out prior to the collection of data. We emphasize two useful methodologies: field experiments and detailed field observations, both of which must be finely tailored to the study species' apparent antipredator adaptations. We illustrate the utility of this approach with a number of examples in table 3.3. The hypothesis that sleeping site selection is made so as to maximize concealment and minimize accessibility to predators, for example, has at least two possible approaches. Not only can observations of the vegetation surrounding the selected site versus alternative sites be compared quantitatively, but the availability and the structure of sleeping sites can also be altered in a manipulative protocol.

The value of field experiments is well illustrated by studies of vervet monkeys (*Chlorocebus aethiops*). Building on the original field observations by Struhsaker (1967a,b) of predator avoidance by vervets, Cheney and Seyfarth published a now classic series of field experiments examining the production of alarm calls in response to perceived predators as well as responses to playbacks of those calls (Cheney and Seyfarth 1981, 1985, 1990). Field experiments on other primate systems using stuffed predator models (Kortlandt 1963; van Schaik and van Noordwijk 1989; van Schaik and Mitrasetia 1990; Macedonia and Young 1991) and sound playbacks of alarm or predator calls (van Schaik and van Noordwijk 1989; van Schaik and Mitrasetia 1990; Chapman and Chapman 1996; Treves 1997a [thesis]) have also yielded persuasive corroboration of antipredator hypotheses based solely on field observations.

Precise sampling and quantification of individual and group-level behavior can provide powerful tests of hypotheses regarding the effects of predation on travel routes and the spacing, activity, and positioning of individuals within groups (Janson 1990a,b; Cords

1990b; Rose and Fedigan 1995; Hall and Fedigan 1997; Cowlishaw 1994, 1997; Treves 1997a). The field situation that Rose and Fedigan (1995) exploited for their observational study of the function of vigilance in white-faced capuchins (*Cebus capucinus*) was particularly propitious. Four capuchin troops at the Costa Rican study site were well habituated and individually recognized, thus allowing four replicate tests of the research questions, among which were, first, are males more vigilant than females? and second, does the number of adult males in a group affect individual investment in vigilance? These questions were formulated after years of previous fieldwork at this site. Not only did males in all four groups invest more time in vigilance than females, but the overall mean rate of vigilance in each group was negatively related to the number of males and independent of group size.

Deconstruction of Predation Risk

The space-specific risk of predation for baboons results from the fact that the baboons' predators tend to concentrate their hunting to particular habitats within the home range. For example, leopards stalk from cover and are seldom seen in areas of low open grassland. The baboon's problem then is to avoid areas of high risk and yet still get at areas with concentrated resources. (S. A. Altmann 1974, 245)

A successful predation episode reflects a dynamic sequence of events involving both predator and prey, and prey greatly benefit from obstructing this interaction whenever and however possible (Lima and Dill 1990; Endler 1991). Also, survivors presumably benefit by observing and learning from successful and unsuccessful predation attempts. From the perspective of the predator, a predation episode can be summarized as prey location, pursuit, attack, and retention (Kerfoot and Sih 1987). Two basic counterstrategies are available to prey: avoidance and deterrence (van Schaik and van Hooff 1983, 1996; Pulliam and Caraco 1984; Sih 1987; Brodie, Formanowicz, and Brodie 1991). In the course of predator avoidance, prey employ concealment, crypticity, and avoidance of habitats with predators to reduce the opportunities for prey detection. In contrast, deterrence by prey attempts to foil pursuit, attack, and retention by a predator once the prey has been detected. Of course, some behaviors, such as selection of propitious travel routes, might under most circumstances be best described as predator avoidance measures, but switch into predation deterrence in the aftermath of a predator attack.

Table 3.3 (continued)

Formal hypothesis	Quantification	Specific predictions	Observational tests	Experiments
		(1) Groups that vary in size, group spread, biomass, movement speed, loud call production, and arboreality will differ in detectability.	Observers should have more difficulty finding groups with low detectability. Predator encounter rates should be lower also.[b]	(a) Naive observer[c] searches for groups; records species, traces (sound, sight, smell), height, size, spread.
Group movement produces audible and visible signs that may increase detection by predators.	Measure the sensory traces produced by groups varying in size, movement speed, cohesion, and arboreality. Sensory traces may be visual, auditory, or olfactory (e.g., feces).	(2) Conspicuousness will be reduced by behavioral tactics and timing. Such reductions should be associated with predator encounter or dangerous times of day.	The timing of conspicuous displays will coincide with periods of predator inactivity or will profit from concealment and synchrony, or will be followed by rapid movement.	(b) Measure conspicuous activity (signaling, playing, moving) before and after predator playbacks or real attempts.
		(3) Running water, dense vegetation, and windy habitats will provide more background "noise" and reduce the conspicuousness of primate groups.	Groups in these habitats will be noisier, more colorful, use more elaborate visual displays, and move less cohesively.	(c) Within habitats, species differing in conspicuousness will respond differently to predator or alarm call.

[a]Note that type ≠ species, i.e., the same predator may use different hunting styles in different contexts.

[b]Accurate determination of predator encounter rates requires habituation of predators and prey.

[c]Must be absolutely unfamiliar with ranges, habitat features, etc.

Discussion of the evolutionary impact of predation can be framed in terms of costs and benefits (Ydenberg and Dill 1986; Smith and Winterhalder 1992). A primary trade-off in behavioral options confronting the typical prospective prey item, such as a primate, is thought to exist between minimizing predation risk and maximizing foraging success (Schoener 1971; Stephens and Krebs 1986; Ferguson, Bergerud, and Ferguson 1988; Kennedy et al. 1994). Although the cost-benefit ratio to be optimized can be described tidily as a trade-off between two endpoints on a continuum, this does not mean that the underlying decision-making process is likely to be simple. Instead, predation risk is probably incorporated into each step of a cascade of hierarchical decisions that precede a foraging decision, including when, where, and what food to search for, and how to search for, capture, and process it (Lima and Dill 1990). Travel figures significantly in the resolution of the predation-foraging trade-off. Nonforaging factors that can engender group movement are probably weighted by predation risk, including de-fense of food resources and mates and travel to safe sleeping sites.

A still more realistic perspective is that multiple factors, not just predation risk versus foraging success, contribute to movement de-cisions. The travel pattern of a small troop of a given primate spe-cies might be predicted to differ from that of a large troop given varying predation risk and anticipated foraging success (see Chap-man and Chapman, chap. 2, this volume). Further complexity is added when additional factors are incorporated into the algorithm, such as the probability of both attack and escape in alternative hab-itats (Lima 1992), the availability of effective predator detection and deterrence (Cheney and Seyfarth 1981), and pregnancy-enhanced vulnerability to predation (Berger 1991). Despite the probable mul-tifactorial nature underlying most travel decisions, simple cost-benefit models do work. Trade-offs between foraging success and predation risk, for example, are documented in the movements of social groups of baboons (Papio cynocephalus) (Cowlishaw 1997) and mountain sheep (Ovis dalli) (Berger 1991; Frid 1997).

Do primates overestimate predation risk? Clearly the primary effect of predation on primate groups is not the absolute mortality inflicted. The successful predation of a primate is at best an uncom-mon event (see table 3.1; Anderson 1986; Cheney and Wrangham 1986). About the only situation for which all the information needed to determine the optimal solution is available is theoretical models presented in academic texts (Stephen and Krebs 1986;

Smith and Winterhalder 1992). In the daily reality faced by primate troops, the quality of data on predation risk probably ranges from moderately to grossly inaccurate. Obtaining accurate information would also be expensive; "testing the waters" by having one or a few troop members act as scouts to ascertain the presence or absence of predators in alternative foraging areas would probably be quite hazardous, at least for the scouts. In fact there is negligible evidence that primates expend much effort beyond vigilance in updating knowledge of predation risk. Optimization models suggest that in situations of imperfect knowledge, if the total cost of overestimating predation risk is less than the cost of underestimating predation risk, overestimation should be the favored strategy (Bouskila and Blumstein 1992; Abrams 1994); mortality rates are likely to be higher in primates who underestimate than in those who overestimate. Accurate estimates, even if sought, would be difficult to garner because predation risk is a phenomenon resulting from the complex behavioral interactions of predator and prey (Lima and Dill 1990; Abrams 1994).

Features of Group Travel Suggested to Reduce Susceptibility to Predation

In this section we survey the many components of group travel that may be manipulated by primates to reduce predation risk. They vary widely in both the number of primate species in which they are evident and the extent to which their purported antipredation function has been critically evaluated. This discussion highlights parameters and concepts meriting careful examination in future research. Our intent is not to exhaustively review the literature, but to indicate the manifold predator avoidance and predation deterrence tactics available to primates.

At the outset we admit that setting firm limits on the influence of predation on primate social behavior is difficult. Although it is often suggested as an ultimate factor making group living advantageous, little evidence suggests that predation directly affects the internal social structure of primate groups (van Schaik 1983; Terborgh 1983; Terborgh and Janson 1986; Treves and Chapman 1996; but see Stanford 1998). Predation rate does not broadly predict interspecific differences in social relationships, such as dominance and affiliation, or sex differences in dispersal patterns (Cheney and Wrangham 1986). With reference to group movement issues, predation risk is also unlikely to be a factor of broad influence on territo-

lity (see Peres, chap. 5, this volume) or other situations of intertroop aggression (see Boinski, chap. 15, this volume). Yet these exclusions must be qualified because in specific instances predation might well be a contributing factor in territorial behavior or intertroop aggression, as when the resources being defended are safe sleeping sites or refuges.

For ease of presentation, the following list of antipredation behaviors is divided into spatial and social tactics. These categories are not mutually exclusive. Spatial tactics encompass those behaviors that result in changes in the position of animals in three-dimensional space. Social tactics are frequency-dependent behavioral adaptations whose expression by an individual hinges on the behavioral responses of other group members. As in mate selection or foraging behavior (Hinde 1983), the expression of individual behavioral strategies to reduce predation risk may well be affected by kin selection and reciprocal altruism (Trivers 1971; Seyfarth and Cheney 1984).

Spatial Tactics

Familiarity. Perhaps the most prominent commonality evident in primate group movement is the existence of core areas, heavily used portions of the home range. Great advantages appear to follow from using familiar habitat for which the best, most often updated information on the whereabouts of potential predators is available (Lima and Dill 1990; van Schaik, van Amerongen, and van Noordwijk 1996; Isbell and van Vuren 1996). There is some evidence that mortality increases when primate groups are forced out of familiar ranging areas (Isbell 1990; Isbell, Cheney, and Seyfarth 1990; Peetz, Norconk, and Kinzey 1992). An alternative interpretation is that familiarity with the distribution of food sources is the primary advantage responsible for the existence of core areas (Waser 1977a; Chapman 1990b; Newton 1992).

It is also interesting to note that no nomadic groups of nonhuman primates exist comparable to the nomadic human (*Homo sapiens*) pastoralists described by McCabe (chap. 22, this volume). The most wide-ranging nonhuman primates, including solitary gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) (Watts 1994; van Schaik and van Hooff 1996), bachelor herds of langurs (*Semnopithecus entellus*) (Vogel and Loch 1984), and, possibly, seasonal range shifts in gorillas (Vedder 1984), have annual ranges of probably less than 40 km² Yet the annual range of Turkana pasto-

ralists in northwestern Kenya can exceed 2,400 km² (McCabe, chap. 22, this volume).

Travel Route Selection. Numerous researchers working with terrestrial primates note that travel routes appear to minimize exposure to "risky" habitats, those with high-density vegetation offering cover for predators, such as lions and leopards (Rasmussen 1983; Isbell 1994; Cowlishaw 1997). For forest primates there is evidence of at least transitory avoidance of, and precautions to carefully inspect, areas in which a predation attempt has occurred (Boinski 1989). A typical example is the behavior of a moustached tamarin (*Saguinus mystax*) group after the successful predation of a group member on a fallen tree trunk (Heymann 1987). The site was part of a traditional, frequently used travel route, but 8 days passed without the group coming near the predation site. For an additional 4 days the group cautiously approached the tree trunk in a markedly excited manner while emitting alarm calls at a high rate, and still did not venture across the tree trunk.

Sleeping Site Selection. Circumstantial evidence suggests that sleeping site preferences in at least some primates may be an adaptation to reduce predation risk. First, arboreal sleeping sites, nest holes, steep cliffs, or other sites limiting access by terrestrial predators are typical sleeping sites for primates, even large terrestrial species (Gautier-Hion 1973; Anderson 1984; Chapman 1989b; Chapman, Chapman, and McLaughlan 1989; Ferrari and Lopes-Ferrari 1990). Second, in those species switching between a number of alternative sites, effort is apparently expended to avoid signaling the location of that evening's sleeping site to predators (Tutin, McGrew, and Baldwin 1981; Heymann 1995). Third, primates spend a large portion of their lives at sleeping sites (tamarins often spend more than 60%: Heymann 1995); therefore circumspect selection of a sleeping site to reduce vulnerability to predators would appear to be important.

Caution should be used, however, when considering the argument that sleeping site selection by primate groups reflects strategies to reduce predation risk. First, aside from baboons (Hamilton, Buskirk, and Buskirk 1975; Busse 1980; Hamilton 1982), there are not many records of predation attempts at sleeping sites (Galef, Mittermeier, and Bailey 1976; Wright, Heckscher, and Durham 1997). This is what would be expected if primates were successful

at choosing nonrisky sleeping sites. It would also be expected because most researchers do not watch their study groups at night. This fact results in there being few studies of predation at sleeping sites; and thus limits our ability to consider whether sleeping site selection is influenced by predation risk. Second, both repeated and nonrepeated use of sleeping sites (e.g., consistently using one or a few sleeping locations versus using many different locations) are argued to be strategies to elude predators. Repeated use of the same sleeping site is often presumed to result from the specific location being particularly effective in deterring surprise attacks or permitting rapid escape (Wright 1981; Snowdon and Soini 1988). On the other hand, changing sites frequently is said to make location of the group more difficult for the local predators (Ferrari and Lopes-Ferrari 1990; Wright 1998).

Whether or not sleeping sites that curtail or minimize exposure to predators are a limited commodity to primate troops has two important implications. First, the distribution of species locally and regionally might depend on secure sleeping sites or other environmental features that allow predator avoidance (Anderson 1984; Lima 1993). Dietz, Peres, and Pinder (1997) suggest that golden lion tamarins (*Leontopithecus rosalia*) are limited to primary forest and prevented from exploiting secondary forest because of the dearth of suitable tree cavities for sleeping sites in the latter habitat. Second, if sleeping sites are merely rare within a troop's ranging area, their distribution may well constrain the troop's ranging behavior (Sigg and Stolba 1981; Chapman 1989b; Chapman, Chapman, and McLaughlan 1989) If a troop uses one of only a few sites each night, the likelihood of troop movement to a specific foraging area decreases as distance from the refuge(s) increases (Hamilton and Watt 1970; Schoener 1971; Chapman, Chapman, and McLaughlan 1989). In at least some primate species, sleeping sites appear to be limited in number, and troops select those sites closest to their current feeding area, thereby minimizing travel costs (spider monkeys, *Ateles geoffroyi*: Chapman 1989b; Chapman, Chapman, and McLaughlan 1989; Chapman 1990a; baboons: Rasmussen 1979). In other primates, however, sleeping sites appear not to affect travel distances or routes significantly (wedge-capped capuchin, *Cebus olivaceus*: Robinson 1986).

Height Above Ground. In most forests exploited by primates, predation risk from terrestrial canids, felids, and snakes is argued to

spend significant portions of the day still in nest holes or other concealed refuges (Terborgh 1983).

Escape Responses. Changes in the demeanor of a troop's movement after a predator attack are often striking. Dramatic increases and decreases in the apparency of group members to the predator can occur, and both are described as antipredation responses (Goeldi's marmoset, *Callimico goeldi*: Pook and Pook 1979; golden lion tamarin; common marmoset, *Callithrix jacchus*: Stafford and Ferreira 1995; tamarins, *Saguinus* spp.: Heymann 1990b; blue monkey: Cords 1987; redtail monkey: Cords 1987, Treves 1997a). For example, after the successful predation of a troop member by a raptor, the five surviving members of a tamarin (*Saguinus nigricollis*) troop clung motionless to tree trunks for 37 minutes, and once the troop started moving, they traveled slowly and close to the ground (Izawa 1978). Similarly, one of the common reactions by female and young de Brazza's monkeys to a dangerous situation is complete immobilization and absolute silence (Gautier-Hion 1973; Wahome, Rowell, and Tsingalia 1993). This "freezing" can be maintained for periods exceeding 10 minutes (Gautier-Hion 1973). In contrast, when a primate troop flees from a predator as soon as it is detected, great commotion may occur; red colobus monkeys respond to predators by extremely rapid locomotion characterized by a high frequency of leaping and vertical bounding (Gebo et al. 1994; Chapman and Chapman 1996).

It is debatable how socially coordinated either rapid movements or cryptic evasions truly are. A more conservative interpretation is that these group responses are best explained as synchronous individual responses. The basis of these evasions in separate individual reactions is most obvious among smaller primates, in which the response to alarming stimuli is to either immediately drop to the ground or scatter in different directions to protected positions (Pook and Pook 1979; Heymann 1990b; Stafford and Ferreira 1995).

Social Tactics
Group Dispersion. In a famous simile Kummer (1967) likens group dispersion to an amoeba, constantly changing its shape in space. Group dispersion commonly refers both to the expanse and shape of the area encompassed by a group and to the density of group members within that area. The dispersion of a group reflects the

results of spacing decisions by individual group members. Usually dispersion is greatest in foraging contexts and clumped in nonforaging contexts (Stolz and Saayman 1970; Busse 1984; Boinski 1987b). This continuum is thought to result from a trade-off between foraging competition and predation risk. Individuals are predicted to distance themselves from others to enhance foraging efficiency, but at a cost of greater susceptibility to predation as the separation from neighbors increases (Janson 1990a). Near neighbors potentially offer antipredation advantages in the form of (1) increased probability of predator detection (Rodman 1973b; Struhsaker 1981; Gautier-Hion, Quris, and Gautier 1983; Boinski 1987a, 1989; van Schaik and van Noordwijk 1985, 1989; Cords 1990; Norconk 1990a,b; Terborgh 1990; Chapman and Chapman 1996), (2) greater confusion of a predator trying to focus on an individual prey (Morse 1977), (3) a decreased probability of each individual being captured by predators (Hamilton 1971), and (4) increased defense against predators (Struhsaker 1981; van Schaik and van Noordwijk 1985, 1989; Boinski 1987a; Gautier-Hion and Tutin 1988; van Schaik and Hörstermann 1994).

Three additional sets of observations reinforce the generalization that predation risk curtails the tolerable extent of group dispersion. First, groups often become most clumped and cohesive during those periods when the perceived predation risk is apparently greatest (Tutin, McGrew, and Baldwin 1983; Boinski 1987a) or subsequent to some predator attacks (van Schaik and Mitrasetia 1990). Baboons, for example, often cluster tightly when traveling through portions of their range where predators are often encountered (Altmann and Altmann 1970; Harding 1977).

Second, in many species, group members seldom wander far from the periphery of a troop. Field studies commonly report that group members avoid separation from the main body of the group. Anecdotal evidence suggests that the smaller the species, the shorter the tolerated distance from the group, a response consistent with the expectation that small body size is linked with enhanced susceptibility to predation. While the limit for a woolly monkey, 8.25 kg, is about 100 m (Peres 1993c, 1996b), that for adult brown capuchins (*Cebus apella*) and white-faced capuchins, approximately 3–4 kg, is much smaller, usually less than 50 m (Janson 1990a; Hall and Fedigan 1997). For Costa Rican and Peruvian squirrel monkeys (Boinski 1991; Boinski and Mitchell 1992) and golden lion tamarins (Boinski et al. 1994), all less than 1 kg, the

maximum dispersion of an individual from the main body of the troop seldom exceeds 10 m.

Third, the extreme of interanimal dispersion is seen in large-bodied taxa such as spider monkeys (6 kg) and chimpanzees (37 kg), whose fission-fusion social organization involves animals often traveling apart from others for long periods (Terborgh and Janson 1986; Chapman 1990a; Chapman, Wrangham, and Chapman 1995). Adults of both of these species spend their time in small subgroups that change size and composition frequently as animals join existing subgroups or as subgroups split. Thus, unlike most primate species, which have cohesive social groups, spider monkeys and chimpanzees are not always in the same group. Each individual has the option of associating with subgroups of different sizes and compositions, and individuals are frequently solitary. One inference here is that large body size affords a reduced susceptibility to predation that permits adjustment of group size to food patch size (see Chapman and Chapman, chap. 3, this volume), a strategy unavailable to smaller primate species. However, long-tailed macaques, baboons, and howler monkeys (*Alouatta palliata*) also form subgroups (Fittinghoff and Lindburg 1980; van Schaik et al. 1983; Anderson 1981, 1983; Chapman 1988a). Moreover, mothers with infants and juveniles would logically be suspected to face high levels of predation risk, yet they often travel alone in several species (Chapman, Wrangham, and Chapman 1995). These counterexamples suggest that the connection between the tendency of a species to form subgroups and that species' risk of predation warrants further study.

Position Within the Dispersion of a Troop. The configuration of troop members within a troop perimeter does not result in equal exposure to predation risk (Collins, Henzi, and Motro 1984; Ron 1996). In a stationary group, predation risk is often viewed to be greatest on the periphery of the group and to decrease toward the center; peripheral group members have the fewest neighbors to assist in the detection and deterrence of predators and will be the first to encounter approaching predators (DeVore 1965; Hamilton 1971; Vine 1971). Of course, primate troops are not perpetually stationary, but allocate a significant proportion of time to travel. Advantages of different positions vary in a moving troop in that there is a food depletion cost to troop members foraging in the wake of previous troop members (Whitten 1983; Watts 1985, 1992; Chapman

1988a; Janson 1990a,b; Hall and Fedigan 1997). Furthermore, it has been suggested that group members within the vanguard, or leading edge, of a moving group may incur enhanced predation risk compared with subsequent group members (Boinski, chap. 15, this volume). Not only will these individuals be the first to enter the capture radius of "sit and wait" predators (Rhine 1975), but the group benefits of vigilance will be reduced because these areas will have been less thoroughly scanned for predators (Hall and Fedigan 1997).

Vigilance. Visual scanning with the apparent goal of detecting potential predators is a behavior commonly described in primates (Cords 1990b; Janson 1990a; Treves 1997a, 1998). Furthermore, vigilance rates are often exploited by researchers as a measure of predation risk perceived by individual group members. The proportion of time individuals typically allocate to vigilance varies within and between species. In some primate species, adult males are most vigilant (e.g., Costa Rican squirrel monkey: Boinski 1987b), yet females predominate in others (e.g., *Lemur catta*: Gould 1996). Juveniles and immatures, although often the most susceptible to predation, typically exhibit negligible amounts of vigilance behavior (Janson and van Schaik 1988).

While vigilance appears to afford antipredation benefits, these benefits are usually argued to be costly in terms of the reduction of time available for foraging (Pulliam and Caraco 1984). An individual cannot efficiently search for food and concurrently to survey its surroundings in search of predators. Direct tests of this purported trade-off between feeding and vigilance in primates remain to be performed.

Vigilance must be documented carefully and interpreted cautiously, as both social and antipredator functions may underlie the expression of this behavior in some primate species. Much of the time allocated to vigilance by adult male Peruvian squirrel monkeys (Mitchell 1990), vervets (Baldellou and Henzi 1992), white-faced capuchins (Rose and Fedigan 1995), and red colobus and redtail monkeys (Treves 1997a) is aimed at conspecifics, not at potential predators.

Alarm Calls. Alarm calls may act to increase the cohesion of groups, warn predators away, and teach naive individuals about potential threats (Klump and Shalter 1984; Srivastava 1991; Ross

1993; Zuberbühler, Noë, and Seyfarth 1997). Variation in alarm call production by individual group members in at least some species is well predicted by inclusive fitness and reciprocal altruism (Sherman 1977; Owings and Leger 1980; Seyfarth and Cheney 1984). Alarm calls often appear extremely efficient, effective, and important in mobilizing appropriate antipredation responses among group members. Information on the source of the threat (i.e., what type of predator, aerial or terrestrial) can be conveyed by features of the vocalization's acoustic structure (Cheney and Seyfarth 1990; Macedonia and Evans 1993). Peres (1993a) credits the rapid response to alarm calls produced by moustached tamarin group members with foiling all nine predation attempts by raptors that he observed during the study.

Alarm calls are not produced automatically when an individual detects a predator, and recipients of the signal do not necessarily exhibit unvarying, automatic responses (Cheney and Seyfarth 1990). Solitary primates do not emit aerial predator alarm calls in response to frightening stimuli (S. Boinski, pers. obs; C. A. Chapman, pers. obs.), although solitary individuals of many species of primates and other social animals commonly produce terrestrial predator alarm vocalizations on encountering terrestrial stimuli perceived as threatening (Marler and Evans 1996; Boinski, Gross, and Davis in press). Responses to both aerial and terrestrial predator alarm calls by recipients in social groups may range from completely ignoring the vocalization, to looking about, to flight and evasion. Troop members appear to weight their response to the alarm calls produced by an individual by that individual's recent history of accuracy (Cheney and Seyfarth 1990) and the recent history of predator attacks (Heymann 1990b). Response to mistaken alarm calls can be costly in terms of lost foraging opportunities and risk of injury (Cheney and Seyfarth 1990; Macedonia and Young 1991; Peres 1993a). Production of alarm calls may also be costly, as some predators may target callers (Ivins and Smith 1983).

Mobbing and Other Forms of Active Predator Deterrence. Mobbing by primates usually entails vigorous vocal threats and displays by multiple group members at close proximity to a predator. It is sometimes accompanied by physical aggression, including punches, kicks, and bites (Teleki 1973; Kortlandt 1980; Ferrari and Lopes-

Ferrari 1990; Passamani 1995; Iwamoto et al. 1996) and blows with branches (Boinski 1988b; Chapman 1986) and stones (Hamilton, Buskirk, and Buskirk 1975). A poorly habituated white-faced capuchin once grabbed and threw a nearby Costa Rican squirrel monkey at a field-worker (Boinski 1988b). Chimpanzees (Haraiwa-Hasegawa et al. 1986) and baboons also chase predators away (Altmann and Altmann 1970; Baenninger et al. 1977; Iwamoto et al. 1996). Mobbing undoubtedly entails risk in the form of enhanced exposure to the predator and the possibility of injury. In many species adult males are the age-sex class most reliably participating in mobbing episodes; this pattern is suggested to represent kin selection, especially male parental investment in some taxa (Boinski and Mitchell 1994; van Schaik and van Noordwijk 1989b). Cowlishaw (1994) also notes that adult male baboons face lower risk during predator mobbing.

"Contact" Calls. The vocal repertoire of many primate species contains vocalizations commonly labeled "contact" or "separation" calls (Marler 1965; Byrne 1981; Caine and Stevens 1990; Hohmann 1991; Snowdon and Hodun 1981; Boinski et al. 1994; Peres 1996b). These vocalizations appear to permit the exchange of information among group members so as to facilitate group cohesion, especially in contexts where foliage or extensive interanimal distances impede visual contact among group members. Contact calls, unlike alarm calls, are often produced at high rates (Caine 1993). This is especially the case in those species in which group members forage while traveling, resulting in numerous opportunities for scattered individuals to stray and lose contact with the main body of the troop (Byrne 1981; Boinski 1991). For example, adult female squirrel monkeys in Costa Rica and Peru typically emit over a thousand contact calls a day (Boinski 1991; Boinski and Mitchell 1992, 1995, 1997). One probable consequence of the barrage of contact calls audible within a troop at any moment is that group members obtain reasonably accurate, continually updated information on the dispersion, rate of travel, and even activity of other group members (Boinski 1991; Boinski and Mitchell 1992, 1997). As such, contact calls may well be a crucial coordination mechanism allowing group members to disperse from one another sufficiently to accommodate foraging demands while retaining swift access to the other social antipredator tactics listed above.

Conclusion

Does predation have a pervasive effect on group movement? The answer is probably yes. But this answer is derived largely from indirect observations and circumstantial correlations. When studying any particular species, observers are invariably impressed by a varied arsenal of spatial and social strategies that appear to counter predation risk. Yet it is apparent that in our understanding of how predation risk influences group movement, there is a large gap between the rich descriptions of antipredator behaviors and what can truly be demonstrated. It is difficult to get beyond the presentation of evolutionary just-so stories to obtain adequate evolutionary and ecological data to distinguish between alternative hypotheses. As a result, we advocate species-level studies that test explicit hypotheses through both experiments and field observations as a useful and complementary strategy to the comparative approach.
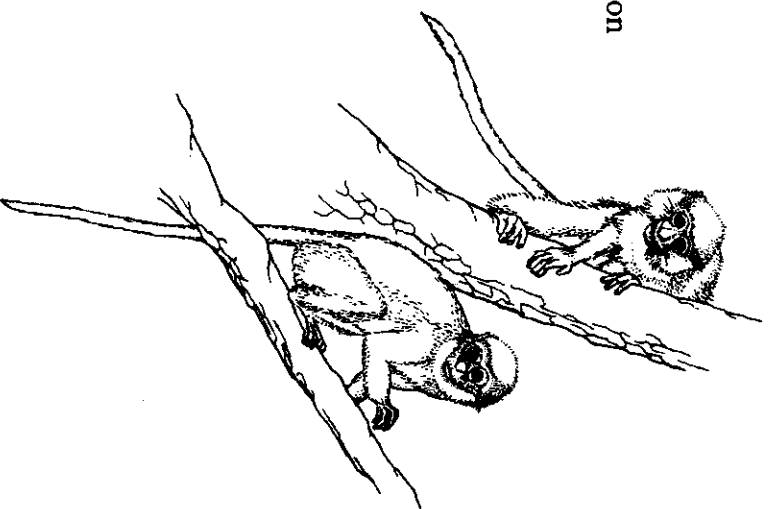
Mixed Species Association and Group Movement

MARINA CORDS

Most people who consider a "group" of primates probably imagine at least three individuals of the same species who are either physically or socially more cohesive with each other than they are with members of other groups. At any moment, most group-living primates belong to just one such group. There are, however, several primate species whose members belong to more than one group at a time. Their dual membership arises from the fact that their group of conspecifics associates with one or more groups of other species, so that each individual belongs to a smaller group of conspecifics as well as to a larger mixed-species group. (Mixed-species groups may also involve single members of one species associating with a group of heterospecifics—e.g., Fleury and Gautier-Hion 1997—but such associations will not be considered in this chapter.) While some of these mixed-species associations may result from brief chance encounters, others seem to occur too often, or last too long, to be explained as random events (Cords 1987, 1990a; Gautier-Hion 1988; Whitesides 1989; Buchanan-Smith 1990; Holenweg, Noë, and Schabel 1996). These latter associations appear instead

On the Move

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Travel in Groups

Edited by
Sue Boinski and Paul A. Garber

2000