Preface

The impact of predation on the morphology, behavior, and ecology of animals has long been recognized by the primatologist community (Altmann, 1956; Burtt, 1981; Curio, 1976; Hamilton, 1971; Kruuk, 1972). Recent thorough reviews of adaptations of birds and mammals to predation have emphasized the complex role that predation threat has played in modifying proximate behaviors such as habitat choice to avoid predator detection, degree and type of vigilance, and group size and defense, as well as ultimate factors including the evolution of warning systems, coloration, and locomotor patterns (Thompson et al., 1980; Sih, 1987; Lima & Dill, 1990; Curio, 1993; Caro, 2005).

From the late 1960s, primatologists have adopted similar techniques to analyze the impacts of predation on the social systems of monkeys and apes (Crook & Gartlan, 1966; Eisenberg et al., 1972; Goss-Custard et al., 1972; Clutton-Brock, 1974; van Schaik & van Hooff, 1983). The fact that actual predation was witnessed but rarely fueled a debate regarding whether predation or food acquisition played a more important role in primate evolution (Wrangham, 1980; van Schaik, 1983; Anderson, 1986; Janson, 1987; Wrangham, 1987; Rodman, 1988; Janson, 1998). More recent studies are more subtle in their design, and have worked from a hypothetical framework that an animal's being eaten is more costly than its missing a meal; they have thus attempted to quantify how animals perceive and act upon predation risk rather than the act of predation itself (Cords, 1990; Boesch, 1994; Isbell, 1994; Cowlishaw, 1997; Hill & Dunbar, 1998; Cowlishaw, 1998). Other investigations have been founded on how primate cognitive abilities and complex social learning aid them in avoiding predators (Seyfarth et al., 1980; Bshary and Noë , 1997; Zuberbühler et al. , 1999; Zuberbühler, 2000; Shultz et al., 2004). These, and a multitude of other studies, are beginning to elucidate our understanding of the impact of predation on primate evolution. Or are they?

We have conducted research on nocturnal primates for more than ten years. Immersed as we have been in the literature of nocturnal primatology we recognize a spectrum of diversity amongst the nocturnal primates in their social organization, cognitive behavior, and ecology (Charles-Dominique, 1978; Bearder, 1999; Müller and Thalmann, 2000). Our studies on tarsiers and lorises showed that these species were highly social and that resource distribution was not

sufficient to explain why they defied the supposed "stricture" of being solitary (Gursky, 2005a; Nekaris, 2006). Furthermore, our animals defied another supposed "rule" — namely, that all nocturnal primates should avoid predators by crypsis (Charles-Dominique, 1977). Even recent reviews of primate social organization and predation theory included one-sentence write-offs, excluding nocturnal primates from discussions of primate social evolution on the basis that crypsis is their only mechanism of predator avoidance (Kappeler, 1997; Stanford, 2002).

An analysis of the mammalian literature shows this type of generalization to be crude at best. Small mammals are known to have extraordinarily high rates of predation, and a plethora of studies of rodents, insectivores, and lagomorphs, among others, have shown that predation is a viable and powerful ecological force (Lima & Dill, 1990; Caro, 2005). Furthermore, although researchers have long considered it critical to include prosimian studies in a general theoretical framework concerning the evolution of the order Primates (Charles-Dominique & Martin, 1970; Cartmill, 1972; Oxnard et al., 1990), a pervading view contends that prosimians are too far removed from humans for the former's behavior to shed any light on the patterns of behavior seen in anthropoids (Kappeler & van Schaik, 2002; Stanford, 2002).

Such notions are perhaps fueled by a paucity of predation research on prosimians in general. This lack of literature may relate to the fact that the study of nocturnal primates is still in the descriptive rather than the theoretical phase; with so many species still being described, data collection on endangered species may begin with recording basic parameters of the diet and home range of these animals (Bearder, 1999). Furthermore, any study of nocturnal and cathemeral primates that goes beyond collecting radio-tracking fixes has proved to be a challenge; much more difficult has been the actual observation of predation events (Sterling et al., 2000). However, an excellent review by Goodman et al. demonstrates the dramatic effect predation can have on lemurs, and it remains the most highly quoted resource on lemur predation, despite that it was published in 1993. Studies of referential signaling aid in dispelling the view that prosimians are primitive and not worthy of comparison with monkeys and apes (Oda, 1998; Fichtel & Kappeler, 2002). A handful of studies further reveal that prosimians are not always cryptic and may engage in social displays toward predators (Sauther, 1989; Schülke, 2001; Bearder et al., 2002; Gursky, 2005b).

In addition to the above cited works, our colleagues regaled us with tales of lemurs, bushbabies, and lorises that demonstrate how these animals employ numerous tactics against predators beyond crypsis. Their observations showed that strategies of nocturnal and cathemeral primates they studied were not unlike antipredator strategies exhibited by the better-studied diurnal primates — conclusions that contradict the popular view (Stanford, 2002). The anecdotal nature of many of these observations, however, suggested that an outlet was needed to report them; thus the idea for this volume was formed.

The original goal of this volume was to synthesize current research on the anti-predator behavior of nocturnal and cathemeral primates. We quickly realized, however, that although we could, in this volume, emphasize these less-studied

species, we would fall into the same trap as previous researchers if we did not consider primates as an order. Thus, the seventeen chapters in this volume consider anti-predator strategies exhibited across primates including: crypsis, alarm calling (referential or otherwise), mobbing behavior, production of toxins, group cohesion, behavioral modification due to environmental factors (habitat choice, sleeping site choice, visibility, moonlight), and vigilance, among others. This volume is organized into three sections: predation theory, anti-predator strategies of nocturnal and cathemeral primates, and anti-predator strategies of diurnal primates. Although we have divided it in this manner, we hope the reader can see the common theoretical and behavioral threads that unite these primate studies as emphasized here.

The two chapters of Section One bring together an immense volume of literature and observations on two important areas of primate predation studies. Zuberbühler fuels a discussion on the effect of predation on primate cognitive evolution with examples from long-term research by himself and colleagues at the Taï forest in West Africa. The studies at the site benefited from complementary observations of the predators themselves — a component often lacking in primate fieldwork. Zuberbühler's comprehensive experience of this ecological system leads him to the controversial conclusion that at Taï, predation does not drive traditionally recognized traits such as group size, body size, life history etc. Rather, it has selected for the evolution of sophisticated cognitive processes, including semantic predator-specific calls, amongst the sympatric primates. This straying from typical predation theory is also emphasized by Hart in her biogeographical analysis of primate predation. Hart's comprehensive dataset of inferred and observed instances of predation on primates allowed her to search for regional patterns to predation. Although primates in some regions (the Neotropics and Madagascar) seem to be more heavily preyed upon than in others (Africa and Asia), Hart found the overall scarcity of data a limiting factor in interpreting them. She did uncover, however, that primates of all body sizes, activity cycles, and ecological niches as determined by strata were preyed upon. This study reminds us that the range of primates from small-bodied nocturnal primates to large-bodied apes cannot be removed from our consideration of predation theory.

Section Two on cathemeral and nocturnal primates contains two major areas: reviews from long-term studies of multiple species, and specific field studies of one or more species. Dollar et al., in line with Zuberbühler, contribute the first research project directly aimed at analyzing the foraging strategies of the largest Malagasy predator — the fossa. Their research shows, contradictorily to the findings of Hart, that although the fossa is capable of taking many species, the taxon most likely to fall victim to it is *Lepilemur*, possibly due to that primate's predictable pattern of sleeping in tree holes, slow locomotion, and solitary lifestyle. Indeed, in her contribution Nash sheds further light on factors that might influence the desirability of *Lepilemur* as a prey item. *Lepilemur* at Nash's study site did not significantly moderate its behavior in relation to different quantities of moonlight, as did many nocturnal mammals. Although they did reduce their time in the highest part of the canopy during moonlit times, perhaps as a device to avoid aerial

predators, in general, Nash proposes, their nutrient-poor diet does not allow for much behavioral flexibility.

Karpanty & Wright, Scheumann et al., and Colquhoun present informative reviews on lemur predation that link to other theoretical perspectives in this volume. Karpanty & Wright synthesize an enormous dataset on lemur predation collected over nineteen years in Ranomafana National Park. *Ad libitum* observations, combined with playback experiments, analyses of predator scats, and systematic fieldwork, aided in formulating a picture of the impact of predation on the rainforest primate community. Although some lemurs relied on the traditional pattern of crypsis, others were highly vocal. Furthermore, they found that both activity pattern and body size *did* have an effect on predation, again in contradiction to Hart. Scheumann et al. review the scanty body of studies on lemur predation and examine their own long-term studies in northwestern Madagascar. They find that, as in the Taï forest, predation clearly has had an impact on cognitive evolution in lemurs, with numerous lemurs using predator-specific referential signals that appear to be socially learned. Body size not only seems to relate to predation risk, but also seems to influence what types of predator strategies lemurs use to combat potential predators. Colquhoun reviews the anti-predator strategies of cathemeral primates, which, due to their potential for activity in the day or night, may need a defense system against a greater array of predators. He suggests that in these small, group-living primates crypsis may play a role; however, cathemerality is not fully understood amongst most of the larger-bodied taxa. For the better-studied *Eulemur*, all of which are sexually dichromatic, he puts forth the interesting hypothesis that this coloration may be a form of polymorphic strategy to counter apostatic predation. All three of these studies are excellent illustrations for revaluating the "crypsis only" view.

Ultimate strategies for avoiding predation are explored by Crompton & Sellers Hagey et al., and Nekaris et al. Crompton & Sellers consider the function of the unique locomotor pattern exhibited by many nocturnal primates: vertical clinging and leaping. By showing that galagos, tarsiers, and some lemurs are capable of leaping far beyond their average distance, they suggest that, from an energetic perspective, the most likely selective factor influencing this ability would be confounding, avoiding, or escaping from a predator. Hagey et al. present long-awaited data on the function and composition of the brachial gland of *Nycticebus.* Their study confirms that small levels of toxic compounds are indeed present in the gland, possibly having evolved as a complex chemical signal to conspecifics and as a toxin for immobilizing prey. The ecological ramifications of chemical communication are presented by Nekaris et al. Novel field data on West African pottos and Sri Lankan slender lorises are compared to revaluate the role that crypsis supposedly plays in the anti-predator strategies of these primates. Although the authors report that lorises engaged in noisy displays and were faster and more vocal than the relatively cryptic pottos, they also describe the prevalence of olfactory communication in all taxa. Comparing their work with the mammalian literature in general, they stress the olfactory capabilities of predators and warn against dismissing olfactory communication as cryptic.

Bearder & Gursky both present data from long-term field studies on strategies that nocturnal primates employ to cope with danger. Both papers reinforce elements presented by Scheumann et al. and by Zuberbühler in that both find evidence for referential signaling. In his paper on calling patterns in two species of galagos, Bearder not only describes, for the first time, the large array of alarm calls emitted by these species, but also contextualizes them. Not only are the calls acoustically distinct, based on the level of fear or arousal of the emitter, they also vary in speed and intensity. Although calls may not have predator-specific contexts, they were situation-specific and were uttered according to the level of danger. Similarly, Gursky discovered that tarsiers incorporate a wide range of tactics to cope with potential predators. Systematic presentation of avian and terrestrial predator models allowed for detailed observations on how spectral tarsiers react in the presence of a potential predator. Not surprisingly, although some predators elicited cryptic responses from them, tarsiers also vocalized, banded together and mobbed predators, again contradicting the view of the cryptic prosimians.

The studies of diurnal primates have been grouped together in Section Three, but certain themes continue throughout these studies. Long-term studies of *Lemur catta* allow for a review by Gould & Sauther supplemented with novel data. These data emphasize that ring-tailed lemurs, like other well-studied diurnal primates, form larger groups and increase vigilance in areas of vulnerability and during vulnerable times of the year (during and after weaning). Referential signaling is also evident, reinforcing the postulation of Scheumann et al. that this cognitive system is characteristic of lemurs. In line with Dollar et al., Gil da Costa approached the predator and prey relationship between harpy eagles and howler monkeys. In a unique situation whereby harpy eagles were released into an area from which they had been extirpated, Gil da Costa was able to analyze both the eagles' and the monkeys' tactics. Whereas monkeys immediately adopted strategies such as group repositioning and vigilance, the eagles too adopted their own mechanisms, learning situations where stealth or attack would improve their capture rate. This study shows how quickly primates and prey can adapt in only one generation.

Long-term field studies on estimating predation risk are presented by Enstam and by Hill & Weingrill. Enstam reviews the impact on predation risk on cercopithecines and illustrates the importance of the study of multiple aspects of habitat structure rather than ecosystem type alone in order to estimate risk. She demonstrates through her own studies of vervet and patas monkeys that even with a highly flexible suite of anti-predator strategies, these primates still can suffer high predation pressure. We have stressed throughout this review that studies of predation on nocturnal primates are in their infancy. In their chapter Hill & Weingrill reiterate this point for diurnal primates and provide elegant guidelines for the measurement of predation risk in terrestrial environments. By focusing on their work with chacma baboons, they show how baboons respond behaviorally to habitat-specific levels of predation risk, even in environments where predators are scarce. These results suggest a deeper ultimate impact of predation on the primate behavior.

The volume is concluded with a review by Treves & Palmqvist. When we were organizing this volume, our colleagues asked us if we would include humans. The scope of understanding the development of *Homo* as a predator would require a volume in its own right. However, Treves & Palmqvist attempt to reconstruct the interactions of hominins prior to *Homo ergaster*, particularly with respect to them as prey to mammalian carnivores. By reconstructing the hunting habits and the diets of paleocarnivores, Treves & Palmqvist suggest that strong group cohesion, vigilance, and last but not least, extreme crypsis, would have characterized early hominin anti-predator strategies.

Many of the contributors to this volume stress how the study of predation, in whichever form it takes, is still at an early stage. A number of the authors outline areas of further study or present compelling hypotheses worthy of additional testing. Although this book focuses mainly on prosimians, we hope that the unifying themes running through all the essays will aid the reader in considering predation theory in a broader light. These studies show that species, regardless of their activity rhythm, body size, or brain size, do not engage in uniform or predictable strategies. At the very least we hope that this volume will dispel a myth as well as encourage a new spectrum of research on primate anti-predator strategies.

References

Altmann, S.A. (1956). Avian mobbing behavior and predator recognition. *Condor*, 58: 241–253.

Anderson, C.M. (1986). Predation and primate evolution. *Primates*, 27: 15–39.

Bearder, S.K. (1999). Physical and social diversity among nocturnal primates: A new view based on long term research. *Primates*, 40(1): 267–282.

Bearder, S.K., Nekaris, K.A.I., and Buzzell, C.A. (2002). Dangers in the night: Are some nocturnal primates afraid of the dark? In E. Miller (Ed.), *Eat or be eaten: Predator sensitive foraging in primates* (pp. 21–40). Cambridge: Cambridge Univ. Press.

Boesch, C. (1994). Chimpanzee-red colobus monkeys: A predator-prey system. *Animal Behaviour*, 47: 1135–1148.

Bshary, R., and Noë, R. (1997). Anti-predation behaviour of red colobus monkeys in the presence of chimpanzees. *Behavioral Ecology and Sociobiology*, 41: 321–333.

Burtt, E.H. (1981). The adaptiveness of animal colors. *BioScience*, 31: 721–729.

Caro, T. (2005). *Antipredator defenses in birds and mammals.* Chicago: Univ. of Chicago Press.

Cartmill, M. (1972). Arboreal adaptations and the origin of the order Primates. In R. Tuttle (Ed.), *The functional and evolutionary biology of the primates* (pp.97–122). Chicago: Aldine Atherton.

Charles-Dominique, P. (1977). *Ecology and behaviour of nocturnal primates*. London: Duckworth Press.

Charles-Dominique, P. (1978). Solitary and gregarious prosimians: Evolution of social structures in primates. In D.J. Chivers and K.A. Joysey (Eds.), *Recent advances in primatology*, *Vol.3* (pp. 139–149). London: Academic Press, London.

Charles-Dominique, P. and Martin, R.D. (1970). Evolution of lorises and lemurs. *Nature*, 227: 257–260.

Clutton-Brock, T.H. (1974). Primate social organization and ecology. *Nature*, 250: 539–542.

Cords, M. (1990). Vigilance and mixed-species association of some East African forest monkeys. *Behavioral ecology and sociobiology*, 26: 297–300.

Cowlishaw, G.C. (1997). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, 53: 667–686.

Cowlishaw, G.C. (1998). The role of vigilance in the survival and reproductive strategies of desert baboons. *Behaviour*, 135: 431–452.

Crook, J.H., and Gartlan, J.S. (1966). Evolution of primate societies. *Nature*, 210: 1200–1203.

Curio, E. (1993). Proximate and developmental aspects of anti-predator behavior. *Advanced study of behavior*, 22: 135–238.

Curio, E. (1976). *The ethology of predation.* New York: Springer-Verlag.

Eisenberg, J.E., Mukenhirn, N.A., and Rudran, R. (1972). The relation between ecology and social structure in primates. *Science*, 176: 863–874.

Fichtel, C., and Kappeler, P.M. (2002). Anti-predator behavior of group-living Malagasy primates: Mixed evidence of a referential alarm call system. *Behavioural Ecology and Sociobiology*, 51: 262–275.

Goodman, S.M, O'Connor, S., and Langrand, O. (1993). A review of predation on lemurs: Implications for the evolution of social behavior in small, nocturnal primates. In P.M. Kappeler and J.U. Ganzhorn (Eds.), *Lemur social systems and their ecological basis* (pp. 51–66). New York: Plenum Press.

Goss-Custard, J.D., Dunbar, R.I.M., and Aldrich-Blake, F.P.G. (1972). Survival, mating, and rearing strategies in the evolution of primate social structures. *Folia Primatologica*, 17: 1–19.

Gursky, S. (2005a). Associations between adult spectral tarsiers. *American Journal of Physical Anthropology*, 128(1): 74–83.

Gursky, S. (2005b). Predator mobbing in spectral tarsiers. *International Journal of Primatology*, 26: 207–221.

Hamilton, W.D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, 31: 295–311.

Hill, R.A. and Dunbar, R.I.M. (1998). An evaluation of the roles of predation risk and predation rate as selective pressures on primate grouping behaviour. *Behaviour*, 135: 411–430.

Isbell, L.A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology*, 3: 61–71.

Janson, C.H. (1987). Food competition in brown capuchin monkeys (*Cebus apella*): Quantitative effects of group size and tree productivity. *Behaviour*, 105: 53–75.

Janson, C.H. (1998). Testing the predation hypothesis for vertebrate sociality: Prospects and pitfalls. *Behaviour*, 135: 289–410.

Lima, S.L., and Dill, L.M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68: 619–640.

Kappeler, P.M. (1997). Determinants of primate social organisation: Comparative evidence and new insights from Malagasy lemurs. *Biological Reviews of the Cambridge Philosophical Society*, 72: 111–151.

Kappeler, P.M., and van Schaik, C.P. (2002). Evolution of primate social systems. *International Journal of Primatology*, 23(4): 707–740.

Kruuk, H. (1972). *The spotted hyena: A study of predation and social behavior.* Chicago: Univ. of Chicago Press.

Müller, A.E., and Thalmann, U. (2000). Origin and evolution of primate social organisation: A reconstruction. *Biological Reviews of the Cambridge Philosophical Society*, 75: 405–435.

Nekaris, K.A.I. (2006). The social lives of Mysore slender lorises. *American Journal of Primatology*, 68: 1–12.

Oda, R. (1998). The response of Verreaux's sifakas to anti-predator alarm calls given by sympatric ring-tailed lemurs. *Folia Primatologica*, 69: 357–360.

Oxnard, C.E., Crompton, R.H., and Lieberman, S.S. (1990). *Animal lifestyles and anatomies*. Seattle: Univ. of Washington Press.

Rodman, P.S. (1988). Resources and group sizes of primates. In C.N. Slobodchikoss (Ed.), *The ecology of social behavior* (pp. 83–108). New York: Academic Press.

Sauther, M.L. (1989). Anti-predator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly Special Reserve, Madagascar. *International Journal of Primatology*, 10: 595–606.

van Schaik, C.P. (1983). Why are diurnal primates living in groups? *Behaviour*, 87: 120–144.

van Schaik, C.P., and van Hooff, J.A.R.A.M. (1983). On the ultimate causes of primates social systems. *Behaviour*, 85: 91–117.

Schülke, O. (2001). Social anti-predator behaviour in a nocturnal lemur. *Folia Primatologica*, 72: 332–334.

Sih, A. (1987). Predator and prey lifestyles: An evolutionary and ecological overview. In W.C. Kerfoot and A. Sih (Eds.), *Predation: Direct and indirect impacts on aquatic communities* (pp. 203–224). Hanover, NH: University Press of New England.

Seyfarth, R.M., Cheney, D.L., and Marler, P. (1980). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science*, 210: 801–803.

Shultz, S., Noë, R., McGraw, W.S., and Dunbar, R.I.M. (2004). A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proceedings of the Royal Society London. Series B*, 271: 725–732.

Stanford, C. (2002). Avoiding predators: Expectations and evidence in primate antipredator behavior. *International Journal of Primatology*, 23(4): 741–757.

Sterling, E.J., Nguyen N., and Fashing, P. (2000). Spatial patterning in nocturnal prosimians: A review of methods and relevance to studies of sociality. *American Journal of Primatology*, 51: 3–19.

Thompson, S.D., MacMillen, R.E., Burke, E.M., and Taylore, C.R. (1980). The energetic cost of bipedal hopping in small mammals. *Nature*, 287: 223–224.

Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75: 262–300.

Zuberbühler, K. (2000). Referential labeling in Diana monkeys. *Animal Behaviour*, 59: 917–927.

Zuberbühler, K., Jenny, D., and Bshary, R. (1999). The predator deterrence function of primate alarm calls. *Ethology*, 105: 477–490.

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