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Effects of Habitat Structure on Perceived Risk of Predation and Anti-Predator Behavior of Vervet (*Cercopithecus aethiops*) and Patas (*Erythrocebus patas*) Monkeys

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Introduction

This chapter summarizes the ways in which habitat structure affects perceived risk of predation and responses to predators (i.e., anti-predator behavior) by cercopithecines (Superfamily: Cercopithecoidea), with specific reference to vervet (*Cercopithecus aethiops*) and patas (*Erythrocebus patas*) monkeys. Predation has long been thought to be an important selective pressure on primate behavior and sociality (e.g., Altmann, 1974; Busse, 1977; Struhsaker, 1981; van Schaik, 1983; Cheney & Wrangham, 1987; Cords, 1987; Isbell, 1991, 1994; Miller, 2002). Among Old World monkeys, predation has been argued to have favored traits such as large group size (e.g., van Schaik, 1983), multi-male groups (e.g., Henzi, 1988; van Schaik & Hörstermann, 1994), sexual dimorphism in canine size (e.g., Harvey & Kavanagh, 1978; Plavcan & van Schaik, 1994), and polyspecific associations (e.g., Gautier-Hion et al., 1983; Cords, 1987; Struhsaker, 1981, 2000), although others maintain that these traits have been selected for by feeding competition (Wrangham, 1980, 1983; Janson & Goldsmith, 1995), sexual selection (Andelman, 1986; Ridley, 1986; Altmann, 1990; Mitani et al., 1996), or, most recently, infanticide (van Schaik & Kappeler, 1997; Isbell et al., 2002).

Cercopithecines have a wide array of known and potential predators (Table 15.1) that differ greatly in hunting style (e.g., Kruuk & Turner, 1967; Boesch, 1994; Shultz, 2001). Thus, it is not surprising that they display a variety of behaviors in response to the threat of predation, including alarm calls (Seyfarth et al., 1980; Cheney & Wrangham, 1987; Cheney & Seyfarth, 1990; Isbell, 1994; Zuberbühler et al., 1999; Zuberbühler, 2001), cryptic behavior (i.e., silence: Hall, 1965; Tilson, 1977; Chism et al., 1983; Chism & Rowell, 1988; Wahome et al., 1993; Boesch, 1994; Isbell, 1994), and the formation of

TABLE 15.1. Confirmed and potential predators of cercopithecines^a (data on guenons adapted from Enstam & Isbell, 2007 in *Primates in Perspective* by Bearder et al., copyright Oxford Univ. Press, Ltd. Reprinted with permission of Oxford Univ. Press, Inc.). Absence of data (blank spaces) indicates that data are unavailable; ^a“Confirmed” predators include species that have been observed preying on a particular cercopithecoid species, whether the attack was successful or not. Confirmed predators also include species that have left remains of monkeys in their nests or dung; ^b“Potential” predators are species researchers listed as possible predators, but have not been observed attacking, or attempting to attack the species in question. In general, potential predators are those that co-occur with monkeys and are known to take prey of equal or greater size than that species, even if they have not been observed preying on that species.

Species	Confirmed ^a	Potential ^b	Sources
GUENONS			
<i>Cercopithecus aethiops</i>	leopard, martial eagle, python, yellow baboon, black eagles	lion, spotted hyena, African wild cat, serval, black-backed jackal, cheetah, caracal	Haufstater, 1975; Haltnorth & Diller 1980; Isbell Seyfarth et al., 1980; Boshoff et al., 1991; Gevaerts, 1992; Enstam, 2002
<i>C. ascanius</i>	crowned eagle, chimpanzee		Cords, 1987, 1990, 2002a; Skorupa, 1989; Struhsaker & Leakey, 1990; Wrangham & Riss, 1990; Gevaerts, 1992; Colyn, 1994; Mitani & Watts, 1999; Mitani et al., 2001; Sanders et al., 2003
<i>C. campbelli</i>	leopard, crowned eagle, chimpanzee		Hoppe-Dominik, 1984; Oates et al., 1990; Shultz, 2001; Zuberbühler, 2001; Zuberbühler & Jenny, 2002; Shultz et al., 2004
<i>C. cephus</i>	crowned eagle, human	python, golden cat, leopard	Gautier-Hion & Gautier, 1976; Gautier-Hion et al., 1983; Gautier-Hion & Tutin, 1988
<i>C. diana</i>	chimpanzee, human, leopard, crowned eagle		Hoppe-Dominik, 1984; Boesch & Boesch, 1989; Oates et al., 1990; Zuberbühler et al., 1997; Zuberbühler et al., 1999; Shultz, 2001; Zuberbühler & Jenny, 2002; Shultz et al., 2004
<i>C. lhoesti</i>	crowned eagle	leopard, golden cat, python	Haltnorth & Diller, 1980; Skorupa, 1989; Struhsaker & Leakey, 1990; Gevaerts, 1992; Colyn, 1994; Mitani et al., 2001 Sanders et al., 2003
<i>C. mitis</i>	crowned eagle chimpanzee, human		Napier, 1981; Skorupa, 1989; Struhsaker & Leakey, 1990; Wrangham & Riss, 1990; Gevaerts, 1992; Mitani & Watts, 1999; Struhsaker, 2000
<i>C. neglectus</i>	crowned eagle	leopard, golden cat, python	Gautier-Hion & Gautier, 1976 Haltnorth and Diller, 1980; Gevaerts, 1992; Wahome et al., 1993; Colyn, 1994

TABLE 15.1. (Continued).

Species	Confirmed ^a	Potential ^b	Sources
GUENONS			
<i>C. nictitans</i>	crowned eagle, human	python, golden cat, leopard	Gautier-Hion & Gautier, 1976; Gautier-Hion et al., 1983 Gautier-Hion & Tutin, 1988; Gevaerts; 1992; Zuberbühler & Jenny, 2002
<i>C. petaurista</i>	leopard, crowned eagle chimpanzee		Hoppe-Dominik, 1984; Zuberbühler & Jenny, 2002; Shultz et al., 2004
<i>C. pogonias</i>	crowned eagle, human	python, golden cat, leopard	Gautier-Hion & Gautier, 1976; Gautier-Hion et al., 1983; Gautier-Hion & Tutin, 1988
<i>C. wolfi</i>	crowned eagle	leopard	Zeeve, 1991; Gevaerts, 1992; Colyn, 1994
<i>Erythrocebus patas</i>	black-backed jackal, domestic dog	leopard, serval, caracal, African wild cat, lion, spotted hyena, martial eagle, chimpanzee, wild dog, baboon	Haltnorth & Diller, 1980; Chism et al., 1983; Chism & Rowell, 1988; Isbell & Enstam, 2002; Isbell, in prep; Isbell, unpubl. data
<i>Miopithecus talapoin</i>		leopard, golden cat, genet Nile monitor, crowned eagle	Gautier-Hion, 1971; Gautier-Hion & Gautier, 1976; Haltnorth & Diller, 1980
MANGABEYS			
<i>Cercocebus torquatus</i>	leopard, crowned eagle, chimpanzee		Hoppe-Dominik, 1984; Zuberbühler & Jenny, 2002
<i>Lophocebus albigena</i>	crowned eagle		Gautier-Hion & Tutin, 1988; Colyn, 1994; Skorupa, 1989; Struhsaker & Leakey, 1990; Mitani et al., 2001; Olupot & Waser, 2001; Sanders et al., 2003 Horn, 1987 Colyn, 1994
<i>L. aterrimus</i>	crowned eagle, human		
MACAQUES			
<i>Macaca fascicularis</i>		monitor lizard, reticulated python, clouded leopard, golden cat, tiger	Napier & Napier, 1967; Fittinghoff & Lindburg, 1980; van Schaik & van Noordwijk, 1985
<i>M. mulatta</i>	tiger, unidentified raptor	jackal, leopard, tiger	Lindburg, 1977; Edgaonkar & Chellam, 2002
<i>M. radiata</i>	leopard	tiger, domestic dog, hyena, wild dog, python	Fa, 1989; Ramakrishnan et al., 1999; Ramakrishnan & Coss, 2000; Edgaonkar & Chellam, 2002

TABLE 15.1. (Continued).

Species	Confirmed ^a	Potential ^b	Sources
BABOONS			
<i>Papio anubis</i>	crowned eagle, chimpanzee, leopard		Kruuk & Turner, 1967; Goodall, 1986; Mitani et al., 2001; Sanders et al., 2003
<i>P. cynocephalus</i>	lion, leopard, hyena		Altmann, 1980; Rasmussen, 1983; Condit & Smith, 1994
<i>P. ursinus</i>	lion, leopard, crocodile, black eagle	python, hyena, wild dog	Busse, 1980; Boshoff et al., 1991; Cheney et al., 2004
<i>P. hamadryas</i>	dog, leopard	Verreaux's eagle, lion, leopard, cheetah, wolf, hyena, jackal, crocodile	Kummer, 1968; Nagel, 1973; Haltnorth & Diller, 1980; Sigg, 1980; Biquand et al., 1992; Zinner & Pelaez, 1999; Swedell, 2006

polyspecific associations (Struhsaker, 1981; Gautier-Hion et al., 1983; Cheney & Wrangham, 1987; Cords, 1987; Struhsaker & Leakey, 1990; Isbell, 1994; Bshary & Noë, 1997; Noë & Bshary, 1997; Chapman & Chapman, 2000; Enstam & Isbell, 2007). Although cercopithecines sometimes harass, mob, attack and drive off, or kill predators (e.g., Altmann & Altmann, 1970; Lindburg, 1977; Gautier-Hion & Tutin, 1988; Boesch, 1994; Cowlshaw, 1994; Stanford, 1995, 1998; Iwamoto et al., 1996; Boesch & Boesch-Achermann, 2000), the majority of recorded responses involve fleeing from predators (e.g., Seyfarth et al., 1980; van Schaik et al., 1983; Cheney & Seyfarth, 1990; Isbell, 1994; Iwamoto, 1993; Boesch, 1994; Bshary & Noë, 1997; Boesch & Boesch-Achermann, 2000; Ramakrishnan & Coss, 2000; Bshary, 2001; Enstam & Isbell, 2002), often after an alarm call has been given.

Early warning of predator presence is apparently so vital for effective escape that a number of cercopithecine species respond to alarm calls given by sympatric (primate and non-primate) prey species (e.g., Gautier-Hion et al., 1983; Seyfarth & Cheney, 1990; Ramakrishnan & Coss, 2000; McGraw & Bshary, 2002). Furthermore, research on the responses of cercopithecines to alarm calls indicates that the “correct” response depends on both predator hunting style (e.g., Seyfarth et al., 1980; Cheney & Seyfarth, 1990; Zuberbühler, 2001; Bshary, 2001; Shultz et al., 2004) and habitat structure (e.g., Boesch, 1994; Stanford, 1995; Noë & Bshary, 1997; Enstam & Isbell, 2002).

Difficulties in Documenting Predation in Cercopithecines

Challenges to the importance of predation in shaping primate traits and behaviors come from several fronts. First, while some anti-predator behaviors, such as alarm calls, mobbing, and evasive maneuvers, are relatively easy for observers to document, it is considerably more difficult to document predator-directed

vigilance (Janson, 2000). Among both cercopithecines and colobines, vigilance has been shown to increase with increasing predation risk, regardless of whether this increased risk is due to social factors (e.g., group size: Isbell & Young 1993; Hill & Cowlshaw, 2002; Shultz et al., 2004; position within the group: Steenbeek et al., 1999; nearest neighbor distances: Cowlshaw, 1998; Treves, 1998; Hill & Cowlshaw, 2002; Stanford, 2002; absence of neighbors: Steenbeek et al., 1999, but see Cords, 1990) or ecological factors (e.g., exposure to predators: Cords, 1990; Steenbeek et al., 1999; Sterk, 2002; Shultz et al., 2004; visibility: Cowlshaw, 1998; proximity to refuges: Cowlshaw, 1997a,b, 1998; Hill and Cowlshaw, 2002; unfamiliar habitat: Isbell et al., 1991, 1993). Further complications with documenting predator-directed vigilance arise because in some cercopithecines and colobines a large proportion of time dedicated to scanning is in fact directed at detecting potential competitors, infanticidal males, or mates (e.g., Keverne et al., 1978; Baldellou & Henzi, 1992; Cowlshaw, 1998; Steenbeek et al., 1999; Treves, 1999), rather than predators.

Second, traits (such a large group size; Hill & Weingrill, 2006; this volume) that may increase predator avoidance capability may also increase a group's ability to compete with other groups for food, while also increasing intragroup competition for food. This means that it can be difficult to separate the relative influences of predation and feeding competition on primate traits and behaviors (but see Cowlshaw, 1997a).

Finally, predation on cercopithecines is often difficult to observe (Cheney & Wrangham, 1987; Isbell, 1990; but see Busse, 1980; Gautier-Hion et al., 1983; Struhsaker & Leakey, 1990; Baldellou & Henzi, 1992; Condit & Smith, 1994; Stanford, 1998; Mitani et al., 2001, for observations of predation on specific cercopithecine species), so accurate predation rates are difficult to obtain. The result is that arguments that maintain predation has favored traits such as large group size and sexual dimorphism are largely based on the finding that these traits tend to vary with gross habitat type. Among cercopithecines, terrestrial monkeys tend to be larger, with larger group sizes, multiple males, and greater sexual dimorphism in canine and body size (Crook & Gartlan, 1966; Clutton-Brock & Harvey, 1977; Dunbar, 1988; but see Cheney & Wrangham, 1987; Isbell, 1994, for an alternative view), and terrestrial monkeys are often assumed to be (e.g., Dunbar, 1988; Plavcan & van Schaik, 1994), and in some habitats are (e.g., Shultz, 2004; but see Olupot & Waser, 2001; Zuberbühler & Jenny, 2002, for an alternative view) at greater risk of predation than their arboreal counterparts.

Predation Risk vs. Predation Rate

Given all of this, gaining an accurate picture of predation pressure on cercopithecines is difficult. There are two ways to measure the level of predation pressure on a population: predation rate and predation risk. Predation *rate* refers to the annual mortality rate within a population that is due to predation and represents the level of successful attacks after the prey have employed their anti-predator strategies (Hill & Dunbar, 1998). Predation *risk*, on the other hand, refers to the

animals' perceptions of the likelihood of attack (regardless of whether it is successful or not) or their perceived danger in a habitat or area, based on the animals' behavior, as inferred by researchers (Hill & Dunbar, 1998; Hill & Lee, 1998; Stanford, 1998). Predation risk may be thought of as the probability of an individual or group encountering a predator, and it is this risk of predation on which animals base their anti-predator strategies (Hill & Dunbar, 1998; but see Vermeij, 1982, for an alternative view).

For primates in particular, both predation rate and predation risk can be difficult variables to measure. Accurate predation rates for many primate populations are difficult to obtain (Janson, 2000) because predators are rarely habituated to observers, and predation tends to occur when observers are absent (Isbell & Young, 1993; Stanford, 1995). Observers may return to their study groups to find animals missing, but with little or no direct evidence of their fate. Thus, researchers must estimate predation rates and do so using a variety of methods (see "How estimated" in Table 15.2), which may account for much of the variation in estimated predation rates presented in Table 15.2. The few studies in which predation by mammals on cercopithecines and colobines have been accurately estimated are those in which predators are habituated to human presence (e.g., Wrangham & Riss, 1990; Stanford et al., 1994; Stanford, 1995, 1998). These studies indicate that predation rates on Old World monkeys can be as high as 35% per year (Wrangham & Riss, 1990; Stanford et al., 1994).

When predators are not habituated and predation events are not directly observed, estimates of predation rates are determined by indirect methods including: (1) counting animals as victims of predation if they disappeared in apparently healthy condition within a short time (e.g., days) of the observer's last observation (Cheney et al., 1988; Isbell, 1990); (2) counting primate remains found under raptor nests (e.g., Struhsaker & Leakey, 1990; Shultz et al., 2004) or in the dung of mammalian predators (e.g., Karanth & Sunquist, 1995; Boesch & Boesch-Achermann, 2000; Bagchi et al., 2003); (3) counting unexplained disappearances as deaths based on the known mortality rate (i.e., known number of deaths per population size; Alberts & Altmann, 1995); and (4) locating collars from radio-collared individuals in the presence or absence of primate remains (Olupot & Waser, 2001). Estimates of predation rates of cercopithecines based on circumstantial evidence vary widely, from less than 1% to as much as 35% per year (Cheney & Wrangham, 1987; Table 15.2). Under certain circumstances, predation rates can be extremely high. For example, Isbell (1990) estimated the predation rate on Amboseli vervets (*C. aethiops*) in 1987 was at least 45% due to increased leopard (*Panthera pardus*) predation. Indeed, predation can greatly impact the size and structure of cercopithecoid populations (Stanford, 1998) and may lead, at least temporarily, to reduced group sizes (Isbell, 1990; Stanford, 1995, 1996; Isbell & Enstam, unpubl. data), lower population densities (Stanford, 1996, 1998), skewed adult sex ratios (Struhsaker & Leakey, 1990), more males per group (Stanford, 1998), or the elimination of groups altogether (Isbell, 1990; Stanford, 1998).

TABLE 1.5.2. Estimated predation rates of cercopithecines. ^a Unless noted otherwise under "How estimated"; ^b The authors of the original study did not distinguish between species; ^c multiple percentages are given in parentheses indicate the respective predation rates of the specified predators in the "Predators Responsible" column.

Species	Estimated Annual Predation Rate ^a	Predator(s) Responsible	Site	Reference	How Estimated
GUENONS					
<i>Cercopithecus aethiops</i>	45% (1987)	leopard(primarily)	Amboseli NP, Kenya	Isbell, 1990	Overall percent of all adult females that died/disappeared
	11% (1977–1986)	leopard, pythons, martial eagles	Amboseli NP, Kenya	Isbell, 1990	Overall percent of all adult females that died/disappeared
	56% (1992–2001)	leopard, martial eagle	Segera Ranch, Kenya	Isbell & Enstam, 2002	Overall percent of all adult Female that died/disappeared
<i>C. diana</i>	7% (1.5%, 5.5% ^c)	leopard, crowned eagle	Tai forest, Cote d'Ivoire	Shultz et al., 2004	# individuals removed per km ² by each predator species
	0.5–1%	chimp	Tai forest, Cote d'Ivoire	Boesch & Boesch-Achermann, 2000	
<i>C. campbelli/petaurista</i> ^b	9.50% (1.5%, 7.75%, 0.25%)	leopard, crowned eagle, chimp	Tai forest, Cote d'Ivoire	Shultz et al., 2004	# individuals removed per km ² by each predator species
<i>C. petaurista</i>	0.30%	crowned eagle	Forest, Cote d'Ivoire	Boesch & Boesch-Achermann, 2000	minimum % killed/year (separated by male & female, I
<i>C. mitis</i>	0.58% (1/86–1/88)	crowned eagle	Kibale NP, Uganda	Struhsaker & Leakey, 1990	added the numbers of each sex & divided by the minimum # of kills for each sex)

<i>C. mona</i>	0.30%	chimp	Tai Forest, Cote d'Ivoire	Boesch & Boesch-Acherermann, 2000	minimum % killed/year (separated by male & female, I added the numbers of each sex & divided by the minimum # of kills for each sex)
<i>C. ascanius</i>	0.16% (1/86-1/88)	crowned eagle	Kibale NP, Uganda	Struhsaker & Leakey, 1990	
<i>Erythrocebus patus</i>	34% (1992-2001)	leopard, cheetah	Segera Ranch, Kenya	Isbell & Enstam, 2002	Overall percent of all adult females that died/disappeared
MANGABEYS					
<i>Cercocebus atys</i>	0.40%	chimp	Tai Forest, Coted'Ivoire	Boesch & Boesch-Acherermann, 2000	Minimum % killed/year (separated by male & female, I added the numbers of each sex & divided by the minimum # of kills for each sex)
<i>Lophocebus albigena</i>	2.78% (1/86-1/88)	crowned eagle	Kibale NP, Uganda	Struhsaker & Leakey, 1990	
BABOONS					
<i>Papio ursinus</i>	8% (9/77-2/80)	leopard, lion	Moremi, Botswana	Busse, 1980	

Predation risk may be even more difficult to measure. Frequency of attempted predation, both successful and unsuccessful, can provide a reasonable estimate (Hill & Lee, 1998), but observers rarely witness predation attempts, successful or not. Estimating the risk of predation for cercopithecines and colobines is complicated because a number of factors may influence predation risk, including predator species (Isbell, 1990) and density (Stanford, 1995), prey preferences of individual predators (Kruuk, 1986; Kruuk & Turner, 1967; Isbell, 1990; Boesch, 1994; Cowlshaw, 1994; Stanford et al., 1994; Stanford, 1996), prey body weight or age (Struhsaker & Leakey, 1990; Boesch, 1994; Isbell, 1994; Stanford et al., 1994; Hill & Dunbar, 1998; Mitani & Watts, 1999), prey group size (Crook & Gartlan, 1966; Clutton-Brock & Harvey, 1977; van Schaik & van Noordwijk, 1985; but see also Isbell, 1994), proximity to humans (Isbell & Young, 1993), and habitat structure (Crook & Gartlan, 1966).

Importance of Habitat Structure

Aspects of habitat structure that may affect predation risk of cercopithecines include access to refuges (Stacey, 1986; Cowlshaw, 1997b; Hill & Weingrill, 2006; this volume), tree height (Boesch, 1994), and degree of obstructive cover (Altmann & Altmann, 1970; Rasmussen, 1983; Cowlshaw, 1994, 1997a; Hill & Weingrill, 2006; this volume). It has been assumed that predation risk is greater in savannahs than in rainforests because savannahs provide fewer refuges (e.g., trees) from predators (Crook & Gartlan 1966; Clutton-Brock & Harvey 1977; Dunbar 1988). Although this assumption is now being challenged (Isbell, 1994; Olupot & Waser, 2001), even within the same broad type of habitat (e.g., "savannah," "woodland," "rainforest") more subtle differences in structure may also influence primates' perceived risk of predation. For example, in savannahs few trees and short grass may actually lower predation risk because such habitats provide terrestrial stealth predators with little cover from which to hunt (Isbell, 1994; FitzGibbon & Lazarus, 1995). In contrast, savannah areas with more trees and tall grass may be riskier because terrestrial predators are provided with more cover for ambushes (Kruuk & Turner, 1967; Altmann & Altmann, 1970; Rasmussen, 1983; Isbell, 1994). This means that terrestrial cercopithecines may sometimes be at greater risk of predation from terrestrial predators, at least during the day, when they are on the ground nearer trees than when they are farther away. Subtle differences in habitat structure of forests can have similar effects on predation risk. For example, reduced canopy cover or tree height can increase risk of predation on red colobus monkeys (*Procolobus badius*) by chimpanzees (*Pan troglodytes*) (Boesch, 1994; Stanford, 1995).

Such subtleties suggest that it is no longer useful to identify predation risk simply by ecosystem type. Rather, looking more carefully at habitat structure within ecosystems may reveal more meaningful patterns. To illustrate the importance of habitat structure on the perceived risk of predation and anti-predator behavior of cercopithecines I focus now on the relationship between the structure

of open *Acacia* woodland habitat and the behavior of two cercopithecine primates, vervet and patas (*Erythrocebus patas*) monkeys. Although the data presented below have been presented separately elsewhere (Enstam, 2002; Enstam & Isbell, 2002, 2004), I combine them here to illustrate the importance of examining *multiple* aspects of habitat structure (e.g., tree height, canopy cover, and ground cover) for their potential effects on anti-predator behavior and perceived risk of predation.

Methods

The Study Species and the Study Site

I studied one group of patas monkeys and two groups of vervet monkeys between October 1997 and September 1999 on Segera Ranch in central Kenya. During the study period the patas group declined in size from 51 to 20 individuals. Much the decline was associated with illness following unusually heavy El Niño rains (Isbell & Young, in preparation). The two vervet groups also declined during the study, from 30 to 9 and 10 to 5 individuals, respectively, and in June 1999 these two groups fused into one. The decline in the vervet group sizes was largely the result of suspected and confirmed predation (Isbell & Enstam, 2002). A detailed description of the data collection methods and statistical results are provided in Enstam (2002) and Enstam & Isbell (2002, 2004).

Patas monkeys are highly terrestrial primates that live in grassland and open woodland habitat below the Sahara Desert from northwest Senegal through Sudan to eastern Ethiopia, northern Uganda, central Kenya, and northern Tanzania (Isbell, submitted) and they possess a number of anatomical adaptations for cursorial locomotion, including long limbs (Hurov, 1987; Strasser, 1992; Gebo & Sargis, 1994) and digitigrade feet (Meldrum, 1991; Gebo & Sargis, 1994). The home range of the patas study group was about 4 km from the home range of the vervet study groups. Vervets are also highly terrestrial, although they spend more time in trees than do patas monkeys (Chism & Rowell, 1988) and do not possess the extreme cursorial adaptations of patas monkeys (Strasser, 1992; Gebo & Sargis, 1994). Vervet monkeys occupy savannah woodland habitats and are patchily distributed along waterways throughout the woodlands of sub-Saharan Africa (Wolfheim, 1983; Isbell & Enstam, submitted).

Vervet and patas monkeys are ideal subjects upon which to pursue a study of the effects of habitat structure on perceived risk of predation. First, they are closely related, thereby minimizing confounding factors resulting from different phylogenetic histories. This provides a clearer picture of the effects of ecology on their behavior. Indeed, recent studies suggest that vervets and patas are more closely related to one another than either is to any other cercopithecine (Groves, 1989, 2000; Disotell, 1996, 2000). Second, except for adult males, patas and vervets overlap in body size (adult female vervets—weight: 2.5–5.3 kg; length, excluding tail: 40–61 cm; adult female patas—weight: 4–7.5 kg; length,

TABLE 15.2. Signs of potential predators from November 1997– August 1999 in the home ranges of the study groups of vervet and patas monkeys (from Isbell & Enstam, 2002, reprinted with permission of Cambridge Univ. Press).^a “Direct observations” indicate sightings made by observers. “Indirect observations” indicate sightings based on tracks, dung, and reliable cattle herders; ^b confirmed predator of vervets at Segera Ranch (martial eagle) or another site (baboon: Struhsaker, 1967c; Altmann & Altmann, 1970; Hausfater, 1976; Seyfarth et al., 1980b; Cheney & Sayfarth, 1981; leopard: Struhsaker, 1967c; Seyfarth et al., 1980b, martial eagle: Struhsaker, 1967c; Seyfarth et al., 1980b); ^c confirmed predator of patas at Segera Ranch (black-backed jackal) or another site (domestic dogs: Chism & Rowell, 1988); ^d numbers indicate the number of individual direct and indirect observations of predators. A “zero” indicates no observations during the study period.

Predator Species	Vervet Home Ranges		Patas Home Range	
	Direct obs. ^a	Indirect obs. ^a	Direct obs.	Indirect obs.
African wildcat (<i>Felis libyca</i>)	1 ^d	0	10	0
Baboons (<i>Papio anubis</i>) ^b	8	0	28	0
Black-backed jackal (<i>Canis mesomelas</i>) ^c	3	0	93	1
Caracal (<i>F. caracal</i>)	0	0	2	0
Cheetah (<i>Acinonyx jubatus</i>)	4	1	3	0
Domestic dog (<i>C. familiaris</i>) ^c	2	0	27	0
Leopard (<i>Panthera pardus</i>) ^b	3	5	0	0
Lion (<i>P. leo</i>)	1	3	4	18
Martial eagle (<i>Polemaetus bellicosus</i>) ^b	2	0	2	0
Serval (<i>F. serval</i>)	2	0	0	0
Spotted hyena (<i>Crocuta crocuta</i>)	0	4	0	3
Total	26	13	169	22

excluding tail: 50–60 cm; Haltenorth & Diller, 1980), and are thus (theoretically) vulnerable to predation from the same predators, reducing the likelihood that differences in anti-predator behavior are related to inherent differences in vulnerability. Third, at the Segera Ranch study site in Laikipia, Kenya, they share the same ecosystem (*Acacia* woodland) and, therefore, the same community of predators (Enstam & Isbell, 2002; Isbell & Enstam, 2002; Table 15.2), again reducing the chances that observed differences in behavior are due to differences in the predators that each study group encounters.

Habitat Structure of the Study Site

Although vervet and patas monkeys occupy the same ecosystem (i.e., open *Acacia* woodland), there are two habitat types at the Segera Ranch study site. While patas are found only in non-riverine habitat, vervets use both riverine and non-riverine habitats, sleeping in riverine habitat at night but foraging in both riverine and non-riverine habitats during the day. These two habitats differ in several aspects of habitat structure, including tree height and canopy cover, which appear to affect the animals' perceived risk of predation as well as their responses to both

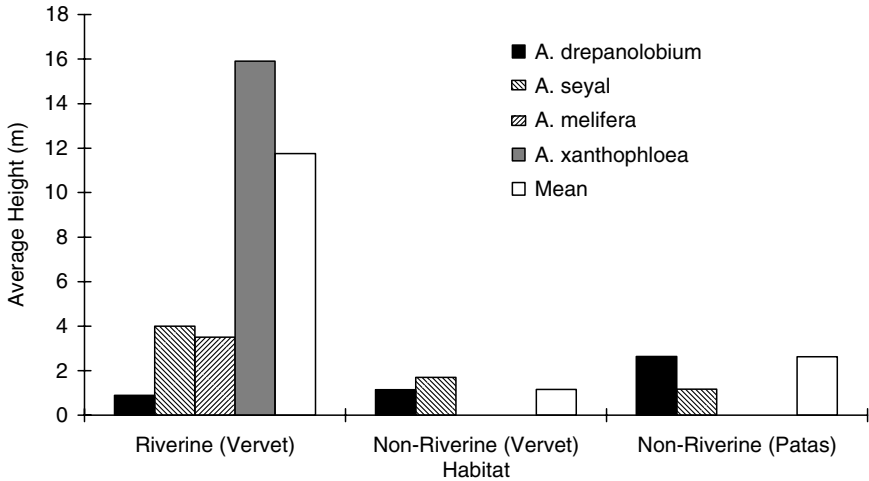


FIGURE 15.1. The height (in meters) of all trees in the riverine and non-riverine habitats. *Acacia melifera* did not occur in any transects in the patas home range, and *Acacia xanthophloea* did not occur in any transects in the non-riverine habitat (from Enstam & Isbell, 2002, reprinted with permission of Wiley-Liss)

nocturnal and diurnal predators. Areas along the river (i.e., riverine habitat) are dominated by *A. xanthophloea* (fever trees), while areas away from rivers (i.e., non-riverine habitat) are dominated by *A. drepanolobium* (whistling thorn acacias) (Enstam & Isbell, 2002). In addition to differing in species composition, the riverine and non-riverine habitats differ in structure since *A. xanthophloea* and *A. drepanolobium* differ in size and structure. Specifically, the average height (Figure 15.1) and degree of canopy cover of trees in the riverine habitat are significantly greater than those in the non-riverine habitat (Enstam & Isbell, 2002).

In addition, within the non-riverine habitat, there are two microhabitats that differ most obviously in height. I use the term “microhabitat” to refer to areas within the same general habitat type (i.e., non-riverine) that differ in key structural features, such as tree height (see Enstam & Isbell, 2004). Average tree height in the tall microhabitat was significantly taller than average tree height in the short microhabitat (Enstam & Isbell, 2004).

Results

Sleeping Site Choice

For cercopithecines and colobines at risk of predation by nocturnal predators, sleeping site selection may be an important anti-predator strategy and sleeping sites that afford as much security from terrestrial predators as possible should be preferred (Anderson, 1984). Some research on sleeping site selection has shown that distribution and availability of food (e.g., chacma baboons (*P. ursinus*), cf.

Hamilton, 1982; bonnet macaques (*M. radiata*), cf. Rahaman & Parthasarathy, 1969; black and white colobus (*Colobus guereza*), cf. von Hippel, 1998) presence of water (e.g., rhesus macaques (*M. mulatta*), cf. Lindburg, 1971), or conspecific groups (black and white colobus, cf. von Hippel, 1998) can influence the location of sleeping sites; but other research has indicated that selection of sleeping sites may also afford anti-predator benefits. For example, bonnet macaques and black and white colobus both prefer to sleep high up in tall trees with few or no low branches, apparently because such trees reduce access by terrestrial predators (von Hippel, 1998; Ramakrishnan & Coss, 2001). Safe, elevated sleeping sites are so important for some cercopithecines that, in some cases, their social systems have adapted to take advantage of the best possible sleeping sites. The fission-fusion social system of hamadryas baboons (*Papio hamadryas*), for example, which occupy the highlands of Ethiopia, Somalia, and Saudi Arabia, is apparently designed for life in an environment with few trees and low food abundance. In this species, multiple one-male units converge together at night in the form of a troop at one of the few safe sleeping sites in their habitat: sheer cliff faces (Kummer, 1968, 1995; Swedell, 2006).

Although closely related, patas and vervet monkeys display strikingly different sleeping site preferences and behaviors, which appear to be due in large part to differences in habitat structure, and studies of patas monkey sleeping site habits suggest that their dispersed sleeping patterns in both time and space may be an adaptation to avoid predation by nocturnal predators where only small trees exist (Chism et al., 1983). Vervets do not require such adaptations because they rely on much taller sleeping trees, which may reduce the risk of predation from terrestrial predators (see Anderson, 1984). For example, at night, patas scatter over a wide area and sleep singly in trees (Hall, 1965; Chism et al., 1983; Enstam, pers. obs.), whereas entire groups of vervets often sleep in the same tree (Struhsaker, 1967; Enstam, pers. obs.). Moreover, patas rarely sleep in the same trees on consecutive nights (Chism et al., 1983; Enstam, pers. obs.), whereas vervets frequently sleep in the same trees on multiple consecutive nights (Struhsaker, 1967, Enstam, pers. obs.). Also, unlike vervet monkeys (and other cercopithecoids), who typically give birth at night, patas monkeys typically give birth during the day, which may further reduce predation at night (Chism et al., 1983).

Diurnal Anti-Predator Behavior

Like sleeping site behavior, the diurnal behavior of vervet and patas monkeys in the presence of predators can be strikingly different and, I argue, is attributable to differences in habitat structure. In open woodland habitat trees are valuable refuges from terrestrial predators once primates get into them (Stacey, 1986; Cowlshaw, 1997b), but they vary in structure and height. Thus, some trees may be more effective refuges than others. Taller trees with overlapping canopies are expected to be more effective as refuges than shorter trees with little overlapping canopies because the former enable primates to get both up and away from terrestrial predators. Likewise, taller trees with thinner, more dense, and more vertical

TABLE 15.3. Responses of patas and vervet monkeys, excluding infants, to mammalian predator alarm calls (from Enstam & Isbell, 2002, reprinted with permission of Wiley-Liss). Each response was counted only once in analyses, regardless of the number of animals displaying that response; ^aincludes arboreal scanning only and alarm calling while scanning arboreally; ^bnumbers indicate the number of observations of the different types of anti-predator responses. A “zero” indicates the behavior was not observed; “N/A” indicates that the behavioral response is not applicable for the specific substrate.

Response	Vervets				Patas	
	Riverine habitat		Non-riverine habitat		Non-riverine habitat	
	In tree	On ground	In tree	On ground	In tree	On ground
Arboreal scan ^a	36 ^b	N/A	3	N/A	3	N/A
AC only	0	0	0	0	0	0
Climb tree	N/A	0	N/A	2	N/A	3
None	4	0	0	0	2	5
Descend, run	0	N/A	2	N/A	7	N/A
Run away	N/A	0	N/A	1	N/A	7
Bipedal scan	N/A	0	N/A	1	N/A	10
Climb & scan	N/A	3	N/A	1	N/A	6
Active defense	0	0	0	0	0	1
Total	40	0	5	5	22	32

branches might be expected to be more effective as refuges than smaller trees with thicker, less dense, and more horizontal branches because the latter may be more accessible to mammalian predators that can climb trees. In Amboseli National Park, Kenya, for example, leopards were found more often in umbrella trees (*Acacia tortilis*), which are shorter with thicker and less angled branches than fever trees (*A. xanthophloea*), the other available tree species (Isbell, pers. comm.).

At the Segera Ranch site, the same vervet study group used both the riverine and non-riverine habitats. Since the habitats differ in key structural features, I was able to examine how differences in tree height and canopy cover between the two *Acacia* woodland habitats affect the responses of vervet monkeys to alarm calls at mammalian predators and to compare their responses to those of the patas study group. Earlier studies of vervet responses to “leopard” alarm calls at Amboseli showed that vervets respond by climbing into tall trees, or remaining in them and not descending (Seyfarth et al., 1980). My research at the Segera Ranch study site supported these results, as the vervets responded as “typical vervets” to mammalian predator alarm calls (Enstam & Isbell, 2002; Table 15.3). Such behavior is a good strategy to avoid attack by terrestrial predators in riverine habitat, where trees are quite tall (11.8 m, on average at the Segera Ranch study site) (Enstam & Isbell, 2002).

Patas monkeys, on the other hand, respond quite differently to mammalian predators. While their primary response is to scan the environment (apparently in an attempt to locate the stimulus of the alarm call), their secondary response differs depending on the substrate they are occupying at the time of the alarm call. If they are in trees at the time of a mammalian predator alarm call, patas monkeys will descend the tree they are in and run away. Although this behavior is not

part of the “typical” vervet repertoire in riverine habitat, when they were in the non-riverine habitat arboreal vervet monkeys were observed to descend and run away during a mammalian predator alarm call (Table 15.3). Similarly, while patas monkeys on the ground at the time of a mammalian predator alarm call will climb trees and scan the environment, just as vervets do (Table 15.3), they will also engage in behavior not seen in the typical vervet anti-predator repertoire. Specifically, patas monkeys will scan bipedally from the ground, run away (past the nearest trees without climbing them), or engage in “active defense” by attacking the predator if it is close to the group (Enstam & Isbell, 2002; Table 15.3).

Even though some behaviors exhibited by patas monkeys are not displayed by vervets in their “typical” (riverine) habitat does not mean that the vervets’ anti-predator response repertoire is inflexible. Just as vervets (and patas) respond differently to different *types* of alarm calls (denoting different predators with different hunting techniques: Seyfarth et al., 1980; Enstam, pers. obs.), vervets also alter their repertoire of responses depending on habitat type. In the non-riverine habitat, vervets respond with patas-like behaviors, including descending trees, bipedally scanning, and running away from predators, rather than climbing the nearest tree (Enstam & Isbell, 2002; Table 15.3).

Height is not the only aspect of tree structure that may play a role in affecting perceived risk of predation and responses to predators. Tree density is significantly higher in the non-riverine habitat of both the vervet home ranges (Figure 15.2), but degree of canopy cover is lower. Degree of canopy cover is often an important measure for determining abundance of food resources (e.g., Chapman et al., 1994; Pruettz & Isbell, 2000; Wiczowski, 2004), but it may also be important in terms of providing viable escape routes for monkeys under

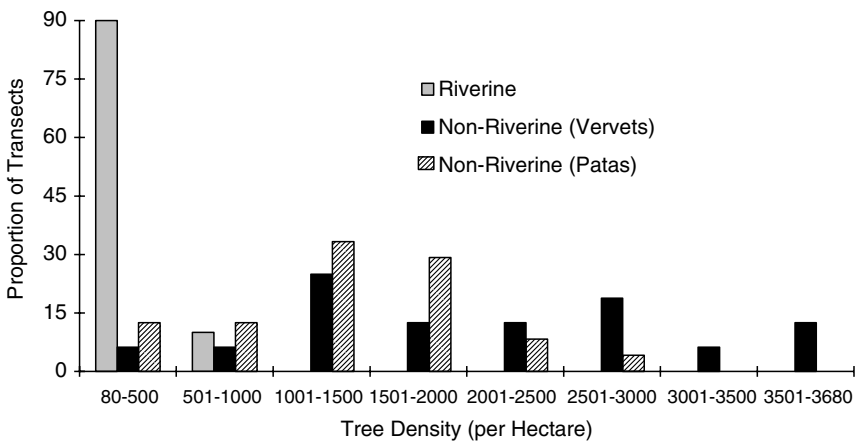


FIGURE 15.2. Tree density (in hectares) of riverine and non-riverine habitats. The non-riverine habitat has greater variation in tree density and greater average tree density (from Enstam & Isbell, 2002, reprinted with permission of Wiley-Liss)

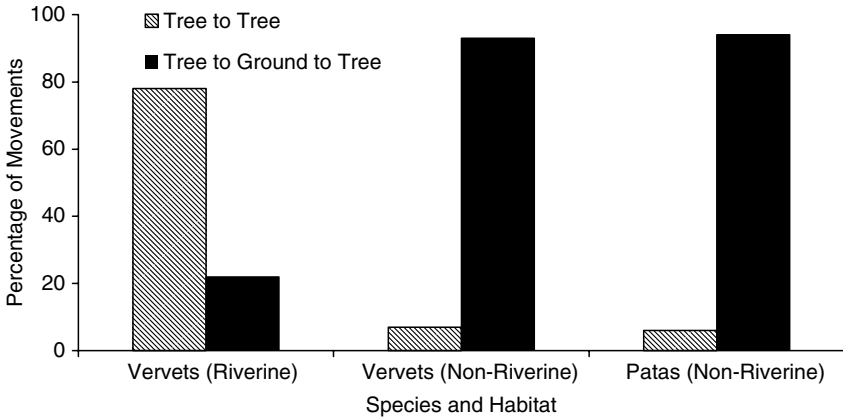


FIGURE 15.3. Percentage of movements between trees in which the focal animal remained arboreal (tree to tree movements) or descended one tree before climbing the next tree (tree to ground to tree movements) (from Enstam & Isbell, 2002, reprinted with permission of Wiley-Liss)

threat of predation. Because I was interested in discovering which habitat afforded greater opportunities to remain arboreal during a predator attack, I used a behavioral measure of canopy cover, namely, movements between trees by focal animals (Enstam & Isbell, 2002). Analysis of movements between trees indicates that the riverine habitat has more continuous canopy cover than the non-riverine habitat, because vervets in the former habitat were able to move between trees without descending significantly more often than the same group of vervets in the non-riverine habitat (Enstam & Isbell, 2002; Figure 15.3). This change in vervet behavior indicates that, at least to the monkeys, the non-riverine habitat has a more discontinuous canopy, and the results agree with data obtained from ecological measurements of average maximum crown diameter (Pruetz, 1999), which show that the canopy of the riverine habitat overlaps more extensively than the non-riverine habitat. When not under the threat of predation, vervets in the riverine habitat were able to remain arboreal significantly more often than vervets or patas in the non-riverine habitat. In the presence of mammalian predators this, in combination with the presence of appreciably taller trees, is especially significant because it means that vervets can increase their distance from predators both *vertically* (by climbing or remaining in tall trees) and *horizontally* (by moving between trees without descending) (see also Enstam & Isbell, 2002).

Such a strategy is unavailable in the non-riverine habitat because there the trees are short with discontinuous canopy cover, which makes them ineffective means by which an animal can increase vertical and horizontal distance from predators while remaining arboreal, particularly if those predators can climb trees (see also Enstam & Isbell, 2002). Monkeys may be able to avoid predation by mammalian predators that cannot effectively climb tall trees, such as cheetah (*Acinonyx*

jubatus), if they can simply get high into tall trees before being attacked. “Tall” is the operative word, however, since lions (*P. leo*) are large enough to presumably push a small tree over or swat a monkey out of a short *Acacia drepanolobium* by standing bipedally. But vervets and patas do fall prey to mammalian predators, such as leopard, which can climb trees, and when under threat of predation by leopard, climbing a tree (even a tall tree) may not be sufficient. Under such circumstances, horizontal arboreal flight would be the best option, and this option is only available in the riverine habitat where canopy cover is relatively continuous.

Given the differences in tree structure between the two habitats it is not surprising that vervets adopt different anti-predator strategies in the non-riverine habitat; strategies that are comparable to those of patas monkeys. In a habitat filled with relatively short trees with little continuous canopy cover, the best anti-predator strategy appears to be to increase horizontal distance between oneself and one’s predator as quickly as possible by running in the opposite direction of the predator, even if that means descending a tree one is occupying during the alarm call. This is exactly what both vervet and patas monkeys do in the non-riverine habitat.

These data on the same group of vervet monkeys indicate a number of important aspects about the effects of habitat structure on vervet anti-predator behavior that may also apply to other cercopithecine species. First, as with many other cercopithecine (and, indeed, primate) behaviors, the response of vervets to the threat of predation from terrestrial predators does not appear to be hard-wired, but rather is flexible and sensitive, both to the hunting strategy of the specific type of predator (Seyfarth et al., 1980), and the height and canopy cover of trees in the immediate habitat (Enstam & Isbell, 2002). While vervets in riverine habitat responded to mammalian predator alarm calls as “typical” vervets, when they were in the non-riverine habitat their responses were more similar to the responses of patas monkeys in the same habitat. In fact, in the non-riverine habitat, vervets responded to mammalian predator alarm calls with behaviors that were observed in patas in that habitat, but not in the same group of vervets in the riverine habitat. The change in the anti-predator behavior of the same group of vervet monkeys is apparently related to the limited number of refuges (i.e., tall trees with overlapping canopy) from large mammalian predators that exist in the *A. drepanolobium* habitat.

Even within the same habitat type, small differences in habitat structure can lead animals to prefer one microhabitat instead of another. The patas study group rarely entered the riverine habitat, using the non-riverine habitat almost exclusively (Enstam, pers. obs.; see also Chism & Rowell, 1988). But the non-riverine habitat is not uniform in structure. Rather, there is a very distinct and abrupt difference within the non-riverine habitat in tree height. During my two-year study the patas study group used 2,851 ha of their approximately 4,000-ha home range. Within these 2,851 ha the microhabitat with tall *A. drepanolobium* trees (hereafter called “tall microhabitat”) comprised approximately 80% (2284 ha), while the microhabitat with apparently perennially short *A. drepanolobium* trees (hereafter called “short microhabitat”) comprised approximately 20% (567 ha). A comparison of the number of observation days the patas group spent in each

microhabitat relative to its size indicated that the patas group preferred the tall microhabitat, spending more days there than expected (Enstam & Isbell, 2004).

But what led the patas group to prefer the tall microhabitat? Among cercopithecines, habitat preference may be related to differences in resource availability (Clutton-Brock, 1975; Gautier-Hion et al., 1981; Harrison, 1983; Olupot et al., 1997) or predation risk and avoidance (Treves, 1997; Hill & Weingrill, 2006; this volume), or monkeys may attempt to trade off these variables by preferring microhabitats that provide either more resources but with greater risk of predation or greater safety with fewer resources (Cowlshaw, 1997a).

The patas monkeys appeared to prefer the tall microhabitat for the greater number of taller than average trees found there. In the tall microhabitat, focal animals were found in trees that were, on average 4.6 ± 0.16 m (range: 3.1–5.7 m) in height, and they climbed into trees that were significantly taller than the average height of trees in the non-riverine habitat (Enstam & Isbell, 2004; Figure 15.4). Moreover, when focal animals were in trees taller than average tree height (> 3 m), they were found high up in the trees, at higher-than-average tree height (Enstam & Isbell, 2004; Figure 15.4). Finally, height of focal animals was correlated with tree height in the tall microhabitat (Figure 15.5), suggesting that the animals climbed as high into trees as the trees would allow (Enstam & Isbell, 2004).

Patas monkeys at the Segera study site obtain the majority of their food (83%) from *A. drepanolobium* trees (Isbell, 1998), with swollen thorns making up the main part of their diet (Isbell, 1998; Pruettz & Isbell, 2000). However, swollen thorns do not appear to be less available to patas monkeys in the short

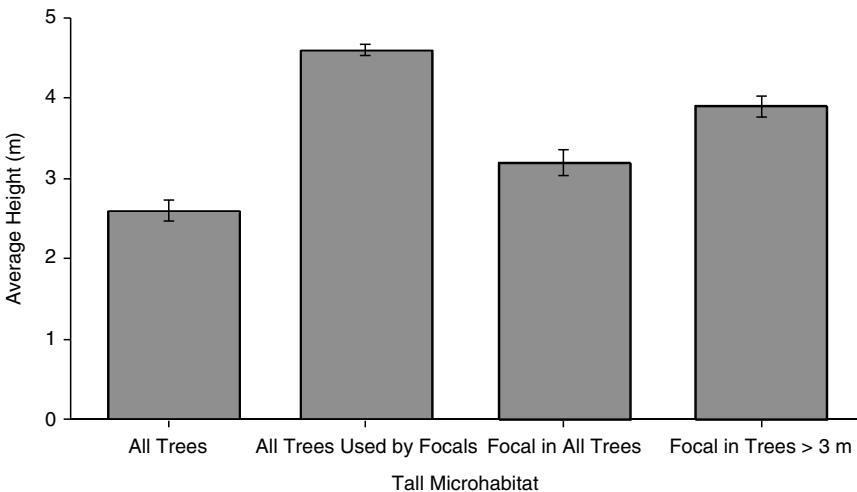


FIGURE 15.4. Average height of (a) trees (see Enstam & Isbell, 2002), (b) trees into which focal animals climbed, (c) focal animals in all trees they climbed, and (d) focal animals in trees > 3.0 m tall in the microhabitat. Bars represent one standard error (from Enstam & Isbell, 2004, reprinted with permission of Karger)

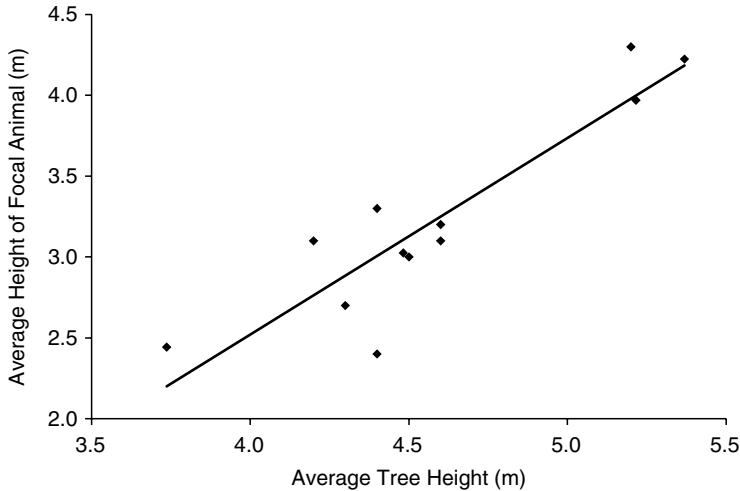


FIGURE 15.5. Correlation between average tree height and average focal animal height in the tall microhabitat (from Enstam & Isbell, 2004, reprinted with permission of Karger)

microhabitat. First, the density of *A. drepanolobium* trees did not differ between the short and tall microhabitats (Enstam & Isbell, 2004). Second, swollen thorns are found on all *A. drepanolobium* trees, regardless of height (Isbell, 1998). Third, patas monkeys typically feed on only 1–2 swollen thorns per tree due to the fact that the ants (*Crematogaster spp.*) that live on the *A. drepanolobium* trees defend the trees by biting intruders (Isbell, 1998; Isbell et al., 1998; Madden and Young, 1992; Young et al., 1997). Thus, both short and tall trees provide patas monkeys with as many swollen thorns as the monkeys can tolerate taking. Finally, the monkeys seem to prefer feeding in short trees (average feeding height for swollen thorns: 75 cm) (Pruetz, 1999), perhaps because feeding from the ground reduces the harassment by the ants that live on the trees.

Instead, it appears that patas preferred the tall microhabitat for its predation avoidance benefits. Focal animals spent more time scanning from taller than average trees (> 3 m), and spent less time feeding and foraging there. Scanning from tall trees was also useful in detecting predators. In six focal samples for which the height of the focal animal was recorded while it gave an alarm call, patas monkeys were in trees that were significantly taller than average tree height, and they were significantly higher in these trees than the average tree height would have allowed (Enstam & Isbell, 2004). In five of the six cases, the focal animals were within a half-meter from the top of the tree while giving an alarm call (Enstam & Isbell, 2004).

Although access to resources is important, these results suggest that the microhabitat preference of patas monkeys at Segera Ranch is based more on predator detection, and the group minimized their use of a microhabitat within their home range despite the potential opportunity to feed longer or more efficiently on

short trees that predominate there. As stated earlier in this chapter, the majority of responses by cercopithecoids to predator presence involves fleeing (e.g., Seyfarth et al., 1980; van Schaik et al., 1983; Cheney & Seyfarth, 1990; Isbell, 1994; Iwamoto, 1993; Boesch, 1994; Bshary & Noë, 1997; Boesch & Boesch-Achermann, 2000; Ramakrishnan and Coss, 2000; Bshary, 2001; Enstam and Isbell, 2002), and the effectiveness of that flight may be greatly enhanced by early detection. It is in the tall, rather than the short, microhabitat that patas monkeys gain a predator detection advantage based on their ability to scan from taller than average trees (Enstam & Isbell, 2004).

Trees are only one aspect of habitat structure that affects predation risk, however. Ground cover is also important to consider because ground cover affects the visibility of both predators and prey. Prey species that rely heavily on concealment to avoid being detected by predators often use protective cover to avoid detection (e.g., Lloyd et al., 2000; Fisher & Goldizen, 2001). On the other hand, species like diurnal cercopithecines that are unable to hide from predators rely on detecting the predator before being detected themselves. Cercopithecines may use a number of different strategies to increase their ability to detect predators, including living in (larger) groups, forming mixed-species associations, and using areas with reduced ground cover (e.g., Struhsaker, 1981; Rasmussen, 1983). Areas with reduced ground cover also provide the additional benefit of reducing hunting success in many mammalian predators that rely on cover to get as close to their prey as possible before attacking (e.g., Schaller, 1972; Eaton, 1974; van Orsdol, 1984; Bothma et al., 1994; Caro, 1994; Cowlshaw, 1994).

Because both vervet and patas monkeys are highly terrestrial (Chism & Rowell, 1998; Enstam & Isbell, 2002; Isbell, submitted), effects of ground cover may be a significant aspect of habitat structure affecting their perceived risk of predation and anti-predator behavior. After a wildfire burned the ground cover of a significant portion of the home range of a vervet study group, the vervets ranged significantly farther from the core of their home range along the river, moving into the burned area, where they had never been observed to go before the fire occurred (Enstam, 2002). Three lines of evidence indicate that the vervets entered the burned area because they perceived a lower risk of predation there. First, the wildfire significantly reduced grass cover and enabled the vervets to see significantly farther while on the ground in the burned area, potentially increasing their ability to detect predators at a greater distance (Enstam, 2002). Second, the burned area was safer because it contained fewer mammalian predators and poisonous reptiles for vervet monkeys to encounter (Enstam, 2002). Finally, female vervets scanned bipedally less often in the burned area than in the unburned areas (Enstam, 2002). Among cercopithecines, rates of scanning have been correlated with predation risk (e.g., Cowlshaw, 1998), so the reduced rate of scanning in vervets suggests that they felt less threatened in the burned area (Enstam, 2002).

Conclusions

Predation has been argued to have exerted strong selection pressures on primates, favoring a number of behavioral and morphological traits (e.g., Busse, 1977; Harvey & Kavanagh, 1978; Struhsaker, 1981; Gautier-Hion et al., 1983; Terborgh & Janson, 1986; Cords, 1987; Cheney & Wrangham, 1987; Henzi, 1988; van Schaik, 1983; Isbell et al., 1990; Isbell, 1994; van Schaik & Hörstermann, 1994; Plavcan & van Schaik, 1994; Struhsaker, 2000). Cercopithecines, like other primates, display a variety of behaviors in response to the threat of predation, including alarm calls and the formation of polyspecific associations. These responses are not always successful, however, and many cercopithecines, including vervet and patas monkeys, can suffer relatively high mortality due to predation (Isbell, 1990;



FIGURE 15.6. Evidence of suspected predation attempt on an adult female patas monkey. Note the healed wounds that resemble scratches on her right hip (photo: K.L. Enstam)

Chism et al., 1984; Isbell & Enstam, 2002; Table 15.2). Despite these sometimes high mortality rates, not all predation attempts are successful (Figure 15.6). It is possible that primates can extract themselves from death by responding appropriately based on both the hunting strategy of the predator and the structure of habitat they are in when the predator attacks. Vervet and patas monkeys exemplify the ability of cercopithecines to respond to predation risk with flexibility, altering their behavior when changes in risk occur. Predation risk and predation rate can be difficult variables to quantify. Since predation risk depends greatly on habitat structure, studies of the effects of *multiple aspects* of habitat structure on primate behavior (e.g., Boesch, 1994; Stanford, 1995; Cowlshaw, 1997a,b; Enstam & Isbell, 2002, 2004) promise to help primate behavioral ecologists gain a better understanding of the variables that affect predation risk, and ultimately, predation rate.

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References

- Alberts, S.C., and Altmann, J. (1995). Balancing costs and opportunities: Dispersal in male baboons. *Amer. Nat.*, 145: 279–306.
- Altman, J. (1980). *Baboon mothers and infants*. Cambridge, MA: Harvard Univ. Press.
- Altmann, J. (1990). Primate males go where the females are. *Animal Behav.*, 34: 193–194.
- Altmann, S.A. (1974). Baboons, space, time, and energy. *Amer. Zool.*, 14: 221–248.
- Altmann, S.A. and Altmann, J. (1970). *Baboon ecology*. Chicago: Univ. of Chicago Press.
- Andelman, S.J. (1986). Ecological and social determinants of Cercopithecine mating patterns. In D.I. Rubenstein and R.W. Wrangham (Eds.), *Ecological aspects of social evolution* (pp. 201–216). Princeton, NJ: Princeton Univ. Press.
- Anderson, J.R. (1984). Ethology and ecology of sleep in monkeys and apes. *Adv. Stud. Behav.*, 14: 165–229.
- Bagchi, S., Goyal, S.P., Sankar, K. (2003). Prey abundance and prey selection by tigers (*Panthera tigris*) in a semi-arid, dry deciduous forest in western India. *Jour. Zool., Lond.*, 260: 285–290.
- Baldellou, M., and Henzi, S.P. (1992). Vigilance, predator detection and the presence of supernumary males in vervet monkey troops. *Animal Behav.*, 43: 451–461.
- Biquand, S., Biquand-Guyot, V., Boug, A., and Gautier, J.-P. (1992). The distribution of *Papio hamadryas* in Saudi Arabia: Ecological correlates and human influence. *Inter. Jour. Primatol.*, 13: 223–243.

- Boesch, C. (1994). Chimpanzee-red colobus monkeys: A predator-prey system. *Animal Behav.*, 47: 1135–1148.
- Boesch, C., and Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *Amer. Jour. Phys. Anthropol.*, 78: 547–573.
- Boesch, C., and Boesch-Achermann, H. (2000). *The chimpanzees of the Tai forest: Behavioural ecology and evolution*. Oxford: Oxford Univ. Press.
- Boshoff, A.F., Palmer, N.G., Avery, G., Davies, R.A.G., and Jarvis, M.J.F. (1991). Biogeographical and topographical variation in the prey of the black eagle in the Cape Province, South Africa. *Ostrich*, 62: 59–72.
- Bothma, J. du P., van Rooyen, N., Theron, G.K., and leRiche, E.A.N. (1994). Quantifying woody plants as hunting cover for southern Kalahari leopards. *Jour. Arid Environ.*, 26: 273–280.
- Bshary, R. (2001). Diana monkeys, *Cercopithecus diana*, adjust their anti-predator response behaviour to human hunting strategies. *Behav. Ecol. Sociobiol.*, 50: 251–256.
- Bshary R., and Noë R. (1997). Red colobus and Diana monkeys provide mutual protection against predators. *Animal Behav.*, 54: 1461–1474.
- Busse, C.D. (1977). Chimpanzee predation as a possible factor in the evolution of red colobus monkey social organization. *Evolution*, 31: 907–111.
- Busse, C.D. (1980). Leopard and lion predation upon chacma baboons living in the Moremi Wildlife Reserve. *Bots. Notes Rec.*, 12: 15–21.
- Caro, T.M. (1994). *Cheetahs of the Serengeti plains: Group living in an asocial species*. Chicago: Univ. of Chicago Press.
- Chapman, C.A., and Chapman, L.J. (2000). Interdemic variation in mixed-species association patterns: Common diurnal primates of Kibale National Park, Uganda. *Behav. Ecol. Sociobiol.*, 47: 129–139.
- Chapman, C.A., Wrangham, R., and Chapman, L.J. (1994). Indices of habitat-wide fruit abundance in tropical forests. *Biotropica*, 26: 160–171.
- Cheney, D.L., and Seyfarth, R.M. (1981). Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour*, 76: 25–61.
- Cheney, D.L., and Seyfarth, R.M. (1990). *How monkeys see the world: Inside the mind of another species*. Chicago: Univ. of Chicago Press.
- Cheney, D.L., and Wrangham, R.W. (1987). Predation. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, and T.T. Struhsaker (Eds.), *Primate societies* (pp. 227–239). Chicago: Univ. of Chicago Press.
- Cheney, D.L., Seyfarth, R.M., Andelman, S.J., and Lee, P.C. (1988). Reproductive success in vervet monkeys. In T.H. Clutton-Brock (Ed.), *Reproductive success* (pp. 384–402). Chicago: Univ. of Chicago Press.
- Cheney, D.L., Seyfarth, R.M., Fischer, J., Beehner, J., Bergman, T., Johnson, S.E., Kitchen, D. M., Palobmit, R.A., Rendall, D., and Silk, J.B. (2004). Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. *Inter. Jour. Primatol.*, 25: 401–428.
- Chism, J. and Rowell, T.E. (1988). The natural history of patas monkeys. In A. Gautier-Hion, F. Bourliere, J.-P. Gautier, and J. Kingdon (Eds.), *A primate radiation: Evolutionary biology of the African guenons* (pp. 412–438). Cambridge: Cambridge Univ. Press
- Chism, J., Olson, D.K., and Rowell, T.E. (1983). Diurnal births and perinatal behavior among wild patas monkeys: Evidence of an adaptive pattern. *Inter. Jour. Primatol.*, 4: 167–184.

- Chism J., Rowell T.E., and Olson D. (1984). Life history patterns of female patas monkeys. In M.F. Small (ed.), *Female primates: Studies by women Primatologists* (pp. 175–190). New York: Alan R. Liss, Inc.
- Clutton-Brock, T.H. (1975). Ranging behaviour of red colobus (*Colobus badius tephrosceles*) in the Gombe National Park. *Animal Behav.*, 23: 706–722.
- Clutton-Brock, T.H. and Harvey, P.H. (1977). Primate ecology and social organization. *Jour. Zool. Soc. London*, 183: 1–39.
- Condit, V.K., and Smith, E.O. (1994). Predation on a yellow baboon (*Papio cynocephalus cynocephalus*) by a lioness in the Tana River National Primate Reserve, Kenya. *Amer. Jour. Primatol.*, 33: 57–64.
- Colyn, M. (1994). Données pondérales sur les primates Cercopithecidae d’Afrique Central (Bassin du Zaïre/Congo). *Mammalia*, 58: 483–487.
- Cords, M. (1987). *Mixed-species association of Cercopithecus monkeys in the Kakamega forest, Kenya*. Berkeley: Univ. of California Publications in Zoology.
- Cords, M. (1990). Vigilance and mixed-species association of some East African forest monkeys. *Behav. Ecol. Sociobiol.*, 26: 297–300.
- Cords, M. (2002). Foraging and safety in adult female blue monkeys in the Kakamega forest, Kenya. In L.E. Miller (Ed.), *Eat or be eaten: Predator sensitive foraging among primates* (pp. 205–221). Cambridge: Cambridge Univ. Press.
- Cowlishaw, G. (1994). Vulnerability to predation in baboon populations. *Behaviour*, 131: 293–304.
- Cowlishaw, G. (1997a). Trade-offs between foraging and predation risks determine habitat use in a desert baboon population. *Animal Behav.*, 53: 667–686.
- Cowlishaw, G. (1997b). Refuge use and predation risk in a desert baboon population. *Animal Behav.*, 54: 241–253.
- Cowlishaw, G. (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.
- Disotell, T.R. (1996). The phylogeny of Old World monkeys. *Evol. Anth.*, 5: 18–24.
- Disotell, T.R. (2000). The molecular systematics of the Cercopithecidae. In P.F. Whitehead and C.J. Jolly (Eds.), *Old World monkeys* (pp. 29–56). Cambridge: Cambridge Univ. Press.
- Dunbar, R.I.M. (1988). *Primate social systems*. London: Croom Helm.
- Eaton, R.L. (1974). *The cheetah: The biology, ecology and behavior of an endangered species*. Malabar, FL: R.E. Krieger Publishing Co.
- Edgaonkar, A., and Chellam, R. (2002). Food habit of the leopard, *Panthera pardus*, in the Sanjay Gandhi National Park, Maharashtra, India. *Mammalia*, 66: 353–360.
- Enstam, K.L. (2002). Behavioral ecology of perceived risk of predation in sympatric patas (*Erythrocebus patas*) and vervet (*Cercopithecus aethiops*) monkeys in Laikipia, Kenya. Doctoral dissertation. University of California, Davis.
- Enstam, K.L., and Isbell, L.A. (2002). Comparison of responses to alarm calls by patas (*Erythrocebus patas*) and vervet (*Cercopithecus aethiops*) monkeys in relation to habitat structure. *Am. Jour. Phys. Anth.*, 119: 3–14.
- Enstam, K.L., and Isbell, L.A. (2004). Microhabitat preference and vertical use of space by patas monkeys (*Erythrocebus patas*) in relation to predation risk and habitat structure. *Folia Primatol.*, 75: 70–84.
- Enstam, K.L., and Isbell, L.A. (2007). The guenons (Genus: *Cercopithecus*) and their allies: Behavioral ecology of polyspecific associations. In C.J. Campbell,

- A. Fuentes, K.C. MacKinnon, M.A. Panger, and S.K. Bearder *Primates in perspective* (pp. 252–273). Oxford: Oxford Univ. Press.
- Fa, J.E. (1989). The genus *Macaca*: A review of taxonomy and evolution. *Mammal. Rev.*, 19: 45–81.
- Fisher, D.O., and Goldizen, A.W. (2001). Maternal care and infant behaviour of the bridled naitail wallaby (*Onychogalea fraenata*). *Jour. Zool.*, 255: 321–330.
- Fittinghoff, N.A., Jr., and Lindburg, D.G. (1980). Riverine refuging in East Bornean *Macaca fascicularis*. In D.G. Lindburg (Ed.), *The macaques: Studies in ecology, behavior and evolution* (pp.182–214). New York: van Nostrand Reinhold Company.
- FitzGibbon, C.D., and Lazarus, J. (1995). Antipredator behavior of Serengeti ungulates: Individual differences and population consequences. In A.R.E. Sinclair and P. Arcese (Eds.), *Serengeti II: Dynamics, management, and conservation of an ecosystem* (pp. 274–296). Chicago: Univ. of Chicago Press.
- Gautier-Hion, A. (1971). L'écologie du talapoin du Gabon. *Terre et Vie*, 25: 427–490.
- Gautier-Hion, A., and Gautier, J.-P. (1976). Croissance, maturité sociale et sexuelle, reproduction chez les Cercopithecines forestiers arboricoles. *Folia Primatol.*, 4: 103–118.
- Gautier-Hion, A., and Tutin, C.E.G. (1988). Simultaneous attack by adult males of a polyspecific troop of monkeys against a crowned hawk eagle. *Folia Primatol.*, 51: 149–151.
- Gautier-Hion, A., Gautier, J.-P., and Quris, R. (1981). Forest structure and fruit availability as complementary factors influencing habitat use by a troop of monkeys (*Cercopithecus cephus*). *Reveu d'Ecol.*, 35: 511–536.
- Gautier-Hion, A., Quris, R., and Gautier, J.-P. (1983). Monospecific vs. polyspecific life: A comparative study of foraging and antipredatory tactics in a community of *Cercopithecus* monkeys. *Behav. Ecol. Sociobiol.*, 12: 325–335.
- Gebo, D.L., and Sargis, E.J. (1994). Terrestrial adaptations in the postcranial skeletons of guenons. *Am. Jour. Phys. Anth.*, 93: 341–371.
- Gevaerts, H. (1992). Birth seasons of *Cercopithecus*, *Cercocebus* and *Colobus* in Zaire. *Folia Primatol.*, 59: 105–113.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Harvard Univ. Press.
- Groves, C.P. (1989). *A theory of human and primate evolution*. Oxford: Clarendon Press.
- Groves, C.P. (2000). The phylogeny of the Cercopithecoidea. In P.F. Whitehead and C.J. Jolly, (Eds.), *Old World monkeys* (pp. 77–98). Cambridge: Cambridge Univ. Press.
- Hall, K.R.L. (1965). Behaviour and ecology of the wild patas monkey, *Erythrocebus patas*, in Uganda. *Jour. Zool. Soc. London*, 148: 15–87.
- Haltenorth, T., and Diller, H. (1980). *A field guide to the mammals of Africa including Madagascar*. London: William Collins, Sons and Co.
- Hamilton, W.J., III. (1982). Baboon sleeping site preferences and relationships to primate grouping patterns. *Amer. Jour. Primatol.*, 2: 149–158.
- Harrison, M.J.S. (1983). Patterns of range use by the green monkey, *Cercopithecus sabaues*, at Mt. Assirik, Senegal. *Folia Primatol.*, 41: 157–179.
- Harvey, P., and Kavanagh, M. (1978). Sexual dimorphism in primate teeth. *Jour. Zool. Lond.*, 186: 475–485.
- Hausfater, G. (1976). Predatory behavior of yellow baboons. *Behaviour*, 61: 44–68.
- Henzi, S.P. (1988). Many males do not a multimale troop make. *Folia Primatol.*, 51: 165–168.
- Hill, R.A., and Cowlshaw, G. (2002). Foraging female baboons exhibit similar patterns of antipredator vigilance across two populations. In L.E. Miller (Ed.), *Eat or be eaten:*

- Predator sensitive foraging among primates* (pp. 187–204). Cambridge: Cambridge Univ. Press.
- Hill, R.A., and Dunbar, R.I.M. (1998). An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour*, 135: 411–430.
- Hill, R.A., and Lee, P.C. (1998). Predation risk as an influence on group size in cercopithecoid primates: Implications for social structure. *J. Zool. Soc. Lond.*, 245: 447–456.
- Hill, R.A., and Weingrill, T. (2006). Predation risk and habitat-specific activity patterns in chacma baboons (*Papio hamadryas ursinus*). In S. Gursky and K.A.I. Nekaris (Eds.), *Primates and their predators* (pp. 337–352). New York: Kluwer Academic Press.
- Hoppe-Dominik, B. (1984). Etude du spectre des proies de la panthère, *Panthera pardus*, dans le Parc National de Taï en Côte d'Ivoire. *Mammalia*, 48: 477–487.
- Horn, A.D. (1987). The socioecology of the black mangabey (*Cercocebus atteriums*) near Lake Tumba, Zaire. *Am. J. Primatol.* 12: 165–180.
- Hurvo, J.R. (1987). Terrestrial locomotion and back anatomy in vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*). *Am. J. Primatol.*, 13: 297–311.
- Isbell, L.A. (1990). Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park, Kenya. *Am. Jour. Primatol.* 21: 41–52.
- Isbell, L.A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behav. Ecol.*, 2: 143–155.
- Isbell, L.A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evol. Anth.*, 3: 61–71.
- Isbell, L.A. (1998). Diet for a small primate: Insectivory and gummivory in the (large) patas monkey (*Erythrocebus patas pyrrhonotus*). *Amer. Jour. Primatol.*, 45: 381–398.
- Isbell, L.A. (submitted). Species profile: Patas monkey (*Erythrocebus patas*). To appear In J. Kingdon, D. Happold, and T. Butynski (Eds.), *The mammals of Africa*. New York: Academic Press.
- Isbell, L.A., Cheney, D.L., and Seyfarth, R.M. (1990). Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. *Behav. Ecol. Sociobiol.*, 27: 351–358.
- Isbell, L.A., Cheney, D.L., and Seyfarth, R.M. (1991). Group fusions and minimum group sizes in vervet monkeys (*Cercopithecus aethiops*). *Amer. Jour. Primatol.*, 25: 57–65.
- Isbell, L.A., Cheney, D.L., and Seyfarth, R.M. (1993). Are immigrant vervet monkeys (*Cercopithecus aethiops*) at greater risk of mortality than residents? *Animal Behav.*, 45: 729–734.
- Isbell, L.A., Cheney, D.L., and Seyfarth, R.M. (2002). Why vervets (*Cercopithecus aethiops*) live in multimale groups. In M. Glenn and M. Cords (Eds.), *The Guenons: Diversity and adaptation African monkeys* (pp. 173–187). New York: Kluwer Academic/Plenum Publishers.
- Isbell, L.A., and Enstam, K.E. (2002). Predator-(in)sensitive foraging in sympatric female vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*): A test of ecological models of group dispersion. In L.E. Miller (Ed.), *Eat or be eaten: Predator sensitive foraging among primates* (pp. 154–168). Cambridge: Cambridge Univ. Press.
- Isbell, L.A., and Enstam, K.L. (submitted). Species profile: Vervet monkey (*Cercopithecus pygerythrus*). To appear In J. Kingdon, D. Happold, and T. Butynski (Eds.), *The mammals of Africa*. New York: Academic Press.
- Isbell, L.A., Pruetz, J., Lewis, M., and Young, T.P. (1998). Locomotor activity differences between sympatric vervet monkeys (*Cercopithecus aethiops*) and patas monkeys

- (*Erythrocebus patas*): Implications for the evolution of long hindlimb length in *Homo*. *Am. Jour. Phys. Anthropol.*, 105: 199–207.
- Isbell, L.A., and Young, T.P. (1993). Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Animal Behav.*, 45: 1233–1235.
- Iwamoto, T. (1993). The ecology of *Theropithecus gelada*. In N.G. Jablonski (Ed.), *Theropithecus: The rise and fall of a primate genus* (pp. 441–452). Cambridge: Cambridge Univ. Press.
- Iwamoto, T., Mori, A., Kawai, M., and Bekele, A. (1996). Anti-predator behavior of Gelada baboons. *Primates*, 37: 389–397.
- Janson, C.H. (2000). Primate socio-ecology: The end of a golden age. *Evol. Anth.*, 9: 73–86.
- Janson, C.H., and Goldsmith, M.L. 1995. Predicting group size in primates foraging costs and predation risks. *Behav. Ecol.*, 6: 326–336.
- Karanth, K.U., and Sunquist, M.E. (1995). Prey selection by tiger, leopard and dhole in tropical forests. *Jour. Animal Ecol.*, 64: 439–450.
- Keverne, E.B., Leonard, R.A., Scruton, D.M., and Young, S.K. (1978). Visual monitoring in social groups of talapoin monkeys (*Miopithecus talapoin*). *Animal Behav.*, 26: 933–944.
- Kruuk, H. (1986). Interactions between Felidae and their prey species: A review. In S.D. Miller and D. D. Everett (Eds.), *Cats of the world: Biology, conservation, and management* (pp. 343–374). Washington, DC: National Wildlife Federation.
- Kruuk, H., and Turner, M. (1967). Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. *Mammalia*, 31: 1–27.
- Kummer, H. (1968). *Social organization of hamadryas baboons*. Chicago: Univ. of Chicago Press.
- Kumer, H. (1995). *In quest of the sacred baboon: A scientist's journey*. Princeton, NJ: Princeton Univ. Press. N.J.
- Leutenegger, W., and Cheverud, J. (1982). Correlates of sexual dimorphism in primates: Ecological and size variables. *Inter. Jour. Primatol.*, 3: 387–403.
- Lindburg, D.G. (1971). The rhesus monkey in North India: An ecological and behavioral study. In L.A. Rosenblum (Ed.), *Primate behavior: Developments in field and laboratory research* (pp. 1–106). New York: Academic Press.
- Lindburg, D.G. (1977). Feeding behaviour and diet of rhesus monkeys (*Macaca mulatta*) in a Siwalik forest in North India. In T.H. Clutton-Brock (Ed.), *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys, and apes* (pp. 223–249). London: Academic Press, Inc.
- Lloyd, P., Plaganyi, E., Lepage, D., Little, R.M., and Crowe, T.M. (2000). Nest-site selection, egg pigmentation and clutch predation in the ground-nesting Namaqua Sandgrouse *Pterocles namaqua*. *Ibis*, 142: 123–131.
- Madden, D., and Young, T.P. (1992). Symbiotic ants as an alternative defense against giraffe herbivory in spinescent *Acacia drepanolobium*. *Oecologia*, 91: 235–238.
- McGraw, W.G., and Bshary, R. (2002). Association of terrestrial mangabeys (*Cercocebus atys*) with arboreal monkeys: Experimental evidence for the effects of reduced ground predator pressure on habitat use. *Inter. Jour. Primatol.*, 23: 311–325.
- Meldrum, D.J. (1991). Kinematics of the cercopithecine foot on arboreal and terrestrial substrates with implications for the interpretation of hominid terrestrial adaptations. *Amer. Jour. Phys. Anth.*, 84: 273–290.

- Miller, L.E. (2002). An introduction to predator sensitive foraging. In L.E. Miller (Ed.), *Eat or be eaten: Predator sensitive foraging among primates* (pp. 1–17). Cambridge: Cambridge Univ. Press.
- Mitani, J.C., and Watts, D.P. (1999). Demographic influences on the hunting behavior of chimpanzees. *Amer. Jour. Phys. Anth.*, 109: 439–454.
- Mitani, J.C., Gros-Louis, J., and Manson, J.H. (1996). Number of males in primate groups: comparative tests of competing hypotheses. *Amer. Jour. Primatol.*, 38: 315–332.
- Mitani, J.C., Sanders, W.J., Lwanga, J.S., and Windfelder, T.L. (2001). Predatory behavior of crowned hawk–eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behav. Ecol. Sociobiol.*, 49: 187–195.
- Nagel, U. (1973). A comparison of anubis baboons, hamadryas baboons, and their hybrids at a species border in Ethiopia. *Folia Primatol.*, 19: 104–165.
- Napier, P.H. (1981). *Catalogue of primates in the British Museum (Natural History), part 2: Family Cercopithecidae, Subfamily Cercopithecinae*. London: British Museum (Natural History).
- Napier, P.H. (1985). *Catalogue of primates in the British Museum (Natural History), part 3: Family Cercopithecidae, Subfamily Colobinae*. London: British Museum (Natural History).
- Napier, J.R., and Napier, P.H. (1967). *A handbook of living primates: Morphology, ecology and behaviour of nonhuman primates*. New York: Academic Press.
- Noë R., and Bshary R. (1997). The formation of red colobus–Diana monkey associations under predation pressure from chimpanzees. *Proc. Roy. Soc. Lond. B.*, 246: 253–259.
- Oates, J.F., Whitesides, G.H., Davies, A.G., Waterman, P.G., Green, S.M., Desilva, G., and Mole, S. (1990). Determinants of variation in tropical forest primate biomass: New evidence from West Africa. *Ecology*, 71: 328–343.
- Olupot, W., and Waser, P.M. (2001). Activity patterns, habitat use and mortality risks of mangabeys males living outside social groups. *Animal Behav.*, 61: 1227–1235.
- Olupot, W. Chapman, C.A., Waser, P.M., and Isabirye-Basuta, G. (1997). Mangabey (*Cercocebus albigena*) ranging patterns in relation to fruit availability and the risk of parasite infection in Kibale National Park, Uganda. *Amer. Jour. Primatol.*, 43: 65–78.
- Plavcan J.M., and van Schaik, C.P. (1994). Canine dimorphism. *Evol. Anth.*, 2: 208–214.
- Pruetz, J.D. (1999). Socioecology of adult female vervet (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) in Kenya: Food availability, feeding competition, and dominance relationships. Doctoral dissertation. University of Illinois at Urbana–Champaign.
- Pruetz, J.D., and Isbell, L.A. (2000). Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behav. Ecol. Sociobiol.*, 49: 38–47.
- Rahaman, H., and Parthasarathy, M.D. (1969). Studies on the social behaviour of bonnet monkeys. *Primates*, 10: 149–162.
- Ramakrishnan, U., and Coss, R.G. (2000). Recognition of heterospecific alarm vocalizations by bonnet macaques (*Macaca radiata*). *Jour. Comp. Psych.*, 114: 3–12.
- Ramakrishnan, U., and Coss, R.G. (2001). Strategies used by bonnet macaques (*Macaca radiata*) to reduce predation risk while sleeping. *Primates*, 42: 193–206.
- Rasmussen, D.R. (1983). Correlates of patterns of range use of a troop of yellow baboons (*Papio cynocephalus*). II. Spatial structure, cover density, food gathering, and individual behaviour patterns. *Animal Behav.*, 31: 834–856.
- Ridley, M. (1986). The number of males in a primate troop. *Animal Behav.*, 34: 1848–1858.

- Sanders, W.J., Trapani, J., and Mitanti, J.C. (2003). Taphonomic aspects of crowned hawk-eagle predation on monkeys. *J. Human Evol.*, 44: 87–105.
- Schaller, G.B. (1972). *The Serengeti lion: A study of predator-prey relations*. Chicago: Univ. of Chicago Press.
- Seyfarth, R.M., and Cheney, D.L. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behav.*, 40: 754–764.
- Seyfarth, R.M., Cheney, D.L., and Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behav.*, 28: 1070–1094.
- Shultz, S. (2001). Notes on interactions between monkeys and African crowned eagles in Tai National Park, Ivory Coast. *Folia Primatol.*, 72: 248–250.
- 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. *Proc. Roy. Soc. Lond. B.*, 271: 725–732.
- Sigg, H. (1980). Differentiation of female positions in hamadryas one-male units. *Zeit. für Tierpsychol.*, 53: 265–302.
- Skorupa, J.P. (1989). Crowned eagles *Stephanoaetus coronatus* in rainforest: Observations on breeding chronology and diet at a nest in Uganda. *Ibis*, 131: 294–298.
- Stacey, P.B. (1986). Group size and foraging efficiency in yellow baboons. *Behav. Ecol. Sociobiol.*, 18: 175–187.
- Stanford, C.B. (1995). The influence of chimpanzee predation on group size and anti-predator behaviour in red colobus monkeys. *Animal Behav.*, 49: 577–587.
- Stanford, C.B. (1996). The hunting ecology of wild chimpanzees: Implications for the behavioral ecology of Pliocene hominids. *Am. Anth.*, 98: 96–113
- Stanford, C.B. (1998). *Chimpanzee and red colobus: The ecology of predator and prey*. Cambridge, MA: Harvard Univ. Press.
- Stanford, C.B. (2002). Avoiding predators: Expectations and evidence in primate antipredator behavior. *Inter. Jour. Primatol.*, 23: 741–757.
- Stanford, C.B., Wallis, J., Matama, H., and Goodall, J. (1994). Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, Tanzania, 1982–1991. *Am. Jour. Phys. Anth.*, 94: 213–228.
- Steenbeek, R., Piek, R.C., van Buul, M., and van Hooff, J.A.R.A.M. (1999). Vigilance in wild Thomas' langurs (*Presbytis thomasi*): The importance of infanticide risk. *Behav. Ecol. Sociobiol.*, 45: 137–150.
- Sterk, E.H.M. (2002). Predator sensitive foraging in Thomas langurs. In L.E. Miller (Ed.), *Eat or be eaten: Predator sensitive foraging among primates* (pp. 74–91). Cambridge: Cambridge Univ. Press.
- Strasser, E. (1992). Hindlimb proportions, allometry, and biomechanics in Old World monkeys (Primates, Cercopithecidae). *Amer. Jour. Phys. Anth.*, 87: 187–214.
- Struhsaker, T.T. (1967). Behavior of vervet monkeys (*Cercopithecus aethiops*). *University of California Publications in Zoology*, 82: 1–74.
- Struhsaker, T.T. (1981). Polyspecific associations among tropical rain-forest primates. *Zeit. für Tierpsychol.*, 57: 268–304.
- Struhsaker, T.T. (2000). The effects of predation and habitat quality on the socioecology of African monkeys: Lessons from the islands of Bioko and Zanzibar. In P.F. Whitehead and C.J. Jolly (Eds.), *Old World monkeys* (pp. 393–430). Cambridge: Cambridge Univ. Press.
- Struhsaker, T.T., and Leakey, M. (1990). Prey selectivity by crowned hawk-eagles on monkeys in the Kibale forest, Uganda. *Behav. Ecol. Sociobiol.*, 26: 435–443.

- Swedell, L. (2006). *Strategies of sex and survival in hamadryas baboons: Through a female lens*. Upper Saddle River, NJ: Pearson/Prentice Hall.
- Terborgh, J., and Janson, C. H. (1986). The socioecology of primate groups. *Ann. Rev. Ecol. and System*, 17: 111–135.
- Tilson, R.L. (1977). Social organization of Simakobu monkeys (*Nasalis concolor*) in Siberut Island, Indonesia. *Jour. Mammal.*, 58: 202–212.
- Treves, A. (1997). Vigilance and use of micro-habitat in solitary rainforest animals. *Mammalia*, 61: 511–525.
- Treves, A. (1998). The influence of group size and near neighbors on vigilance in two species of arboreal primates. *Behaviour*, 135: 1–29.
- Treves, A. (1999). Within-group vigilance in red colobus and redtail monkeys. *Amer. Jour. Primatol.*, 48: 113–126.
- van Orsdol, K.G. (1984). Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *Afr. Jour. Ecol.*, 22: 79–99.
- van Schaik, C.P. (1983). Why are diurnal primates living in groups? *Behaviour*, 87: 120–144.
- van Schaik, C.P. and Hörstermann, M. (1994). Predation risk and the number of adult males in a primate group: a comparative test. *Behav. Ecol. Sociobiol.*, 35: 261–272.
- van Schaik, C.P., and Kappeler, P.M. (1997). Infanticide risk and the evolution of male-female association in primates. *Proc. Soc. Lond.*, 264: 1687–1694.
- van Schaik, C.P., and van Noordwijk, M.A. (1985). Evolutionary effects of the absence of felids on the social organization of macaques on the island of Simeulue (*Macaca fascicularis fusca*, Miller 1903). *Folia Primatol.*, 44: 138–147.
- Vermeij, G.J. (1982). Unsuccessful predation and evolution. *Amer. Nat.*, 120: 701–720.
- von Hippel, F.A. (1998). Use of sleeping trees by black and white colobus monkeys (*Colobus guereza*) in the Kakamega Forest, Kenya. *Amer. Jour. Primatol.* 45: 281–290.
- Wahome, J.M., Rowell, T.E., and Tsingalia, H.M. (1993). The natural history of de Brazza's monkey in Kenya. *Int. Jour. Primatol.*, 14: 445–466.
- Wieczkowski, J. (2004). Ecological correlates of abundance in the Tana mangabey (*Cercocebus galeritus*). *Amer. Jour. Primatol.*, 63: 125–138.
- Wolfheim, J.H. (1983). *Primates of the world: Distribution, abundance, and conservation*. Seattle: Univ. of Washington Press.
- Wrangham, R.W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75: 262–300.
- Wrangham, R.W. (1983). Ultimate factors determining social structure. In R.A. Hinde (Ed.), *Primate social relationships* (pp. 255–262). Oxford: Blackwell Scientific Publications.
- Wrangham, R.W., and Riss, E. (1990). Rates of predation on mammals by Gombe chimpanzees, 1972–1975. *Primates*, 31: 157–170.
- Young, T.P., Stubblefield, C., and Isbell L.A. (1997). Ants on swollen-thorn acacias: Species coexistence in a simple system. *Oecologia*, 109: 98–107.
- Zeeve, S.R. (1991). *Behavior and ecology of primates in the Lomako forest, Zaire*. Doctoral thesis. State University of New York, Stony Brook.
- Zinner, D., and Pelaez, F. (1999). Verreaux's eagles (*Aquila verreauxi*) as potential predators of hamadryas baboons (*Papio hamadryas hamadryas*) in Eritrea. *Amer. Jour. Primatol.*, 47: 61–66.

- Zuberbühler, K. (2001). Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*. *Behav. Ecol. Sociobiol.*, 50: 414–422.
- Zuberbühler, K., and Jenny, D. (2002). Leopard predation and primate evolution. *Jour. Human Evol.*, 43: 873–886.
- Zuberbühler, K., Jenny, D., and Bshary, R. (1999). The predator deterrence function of primate alarm calls. *Ethology*, 105: 477–490.
- Zuberbühler, K., Noë, R., and Seyfarth, R.M. (1997). Diana monkey long-distance calls: Messages for conspecifics and predators. *Animal Behav.*, 53: 589–604.