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Comparison of Responses to Alarm Calls by Patas (*Erythrocebus patas*) and Vervet (*Cercopithecus aethiops*) Monkeys in Relation to Habitat Structure

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ABSTRACT We studied responses to alarm calls of sympatric patas (*Erythrocebus patas*) and vervet (*Cercopithecus aethiops*) monkeys in relation to habitat structure, with the intention of understanding the relationship between the environment and predator avoidance. Patas and vervet monkeys are phylogenetically closely related and overlap in body size. However, while patas monkeys are restricted to nonriverine habitats at our study site, vervets use both nonriverine and riverine habitats, allowing us to "vary" habitat structure while controlling for effects of group size, composition, and phylogeny. Patas monkeys in the nonriverine habitat responded to mammalian predator alarm calls with a greater variety of responses than did vervets in the riverine habitat, but not when compared with vervets in the nonriverine habitat. Ecological measurements confirm subjective assessments that trees in the riverine habitat are significantly taller and occur at lower densities than trees in the nonriverine habitat. Despite the lower density of trees in the riverine habitat, locomotor behavior of focal animals indicates that canopy cover is significantly greater in the riverine than the nonriverine habitat. Differences in responses to alarm calls by the same groups of vervets in different habitat types, and convergence of vervets with patas in the same habitat type, suggest that habitat type can be a significant source of variation in antipredator behavior of primates. Am J Phys Anthropol 119:3–14, 2002.

Despite the fact that attempted and successful predation on primates is rarely observed (Cheney and Wrangham, 1987; Isbell, 1990, 1994; for exceptions, see Busse, 1980; Gautier-Hion et al., 1983; Struhsaker and Leakey, 1990; Sherman, 1991; Baldellou and Henzi, 1992; Peetz et al., 1992; Condit and Smith, 1994; Julliot, 1994; Stanford, 1998; Mitani et al., 2001), several studies suggest that the risk of predation influences many aspects of primate behavior. Indeed, increased predation risk has been associated with larger group sizes (Crook and Gartlan, 1966; van Schaik and van Noordwijk, 1985; Hill and Lee, 1998), greater group cohesion (Rasmussen, 1983; Boinski, 1987; Stanford, 1995; Boinski et al., 2000; but see Treves, 1999; Isbell and Enstam, 2002), higher frequency of polyspecific associations (Struhsaker, 1981, 2000; Peres, 1993), increased rates of vigilance (Caine and Marra, 1988; Cords, 1990; Bshary and Noë, 1997; Cowlishaw, 1997a; but see Chapman and Chapman, 1996; Treves, 1997, 1999), variation in the timing of births (Jolly, 1972; Chism et al., 1983), cryptic behavior at sleeping sites (Hall, 1965; Chism et al., 1983; Caine, 1990; Heymann, 1995; Boinski et al., 2000), reduced inter- and intragroup calling behavior (van Schaik and van Noordwijk, 1985), and decreased foraging time (Stacey, 1986).

In addition, several studies have shown that primates are sensitive to the structure of their environment when under risk of predation, and will alter their behavior to reduce that risk. For example, risk of predation has been linked to changes in ranging behavior (Rasmussen, 1983; Stacey, 1986; Cowlishaw, 1997b; Boinski et al., 2000), increased time spent on or near refuges (Stacey, 1986; Cowlishaw, 1997a), changes in habitat use (Bshary and Noë, 1997; Treves, 1997), increased height above the ground in the presence of terrestrial predators (de Ruiter, 1986; Boesch, 1994; Wright, 1998), decreased height above the ground in the presence of avian predators (Wright, 1998; Boinski et al., 2000), and increased levels of vigilance away from refuges

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(Cowlishaw, 1997a, 1998). Habitat structure also affects the antipredator behavior of primates under immediate threat of attack by predators. Red colobus monkeys (*Procolobus badius*) use different tactics to escape chimpanzees (*Pan troglodytes*), depending on the structure of the immediate environment (Boesch, 1994; Stanford, 1995; Noë and Bshary, 1997). In Gombe National Park, Tanzania, red colobus are much more aggressive toward chimpanzees than are red colobus in Taï National Park, Côte d'Ivoire. This difference in antipredator behavior is apparently due to differences in tree height and canopy cover between the two sites: taller trees with overlapping canopies at Taï allow red colobus to escape chimpanzees by moving higher into the canopy, but shorter trees with less overlapping canopies at Gombe require red colobus to react aggressively toward chimpanzees because they cannot escape by seeking refuge in tall trees (Boesch, 1994; Stanford, 1995). Similarly, red colobus in Kibale Forest, Uganda, have acted aggressively toward humans in low-stature, but not high-stature, forest (Skorupa, 1988; L.A. Isbell, personal observation).

Studies of vervet monkey (*Cercopithecus aethiops*) responses to alarm calls have revealed that vervets respond differently (and appropriately) to acoustically different alarm calls that refer to predators with different hunting strategies (Struhsaker, 1967a; Seyfarth et al., 1980a,b; Cheney and Seyfarth, 1990), indicating that vervets are sensitive to both the hunting strategies of different predators and the structure of their immediate surroundings (i.e., whether they are in bushes, in trees, or on the ground at the time of the alarm call). For example, when vervets on the ground hear a "leopard" alarm call, they climb trees, but when they hear an "eagle" alarm call, they look up and run into bushes (Seyfarth et al., 1980a,b).

This paper examines the antipredator responses of the same groups of vervet monkeys to naturally occurring alarm calls in two different habitat types, and compares them to the responses of broadly sympatric patas monkeys (*Erythrocebus patas*). Patas and vervet monkeys present an excellent opportunity to conduct a comparative study of the relationship between ecology and antipredator behavior because they are more closely related to each other than either is to other cercopithecines (Groves, 1989, 2000; Disotell, 1996, 2000), and aside from adult males, they overlap in body size (Haltenorth and Diller, 1980), making them (theoretically) vulnerable to predation by the same species of predators. Their vulnerability to the same predators is potentially greater at our study site because they share the same ecosystem, and therefore, the same community of predators. Within this ecosystem, however, there are two habitat types, riverine and nonriverine. The structure of the two habitat types differs quantitatively in several ways that may affect predation risk, including tree height, tree density, and degree of canopy cover. While vervets use both habitat types, patas use only the nonriverine habitat, providing an opportunity to compare the effect of habitat type on 1) the same groups of vervets as they use two different habitats, and 2) vervets and patas as they use the same habitat type.

MATERIALS AND METHODS

Study site and animals

The study was conducted between October 1997–September 1999 at Segera Ranch (36° 50′ E, 0° 15′ N; elevation, 1,800 m) on the Laikipia Plateau in central Kenya. Segera is a privately owned conservation area and cattle ranch of 17,000 ha, with stable populations of at least 30 species of large mammals (for detailed description, see Isbell et al., 1998a). The ranch is also home to several known and potential predators of vervet and patas monkeys, including lions (*Panthera leo*), leopards (*P. pardus*), cheetahs (*Acinonyx jubatus*), black-backed jackals (*Canis mesomelas*), domestic dogs (*C. familiaris*), servals (*Felis serval*), African wildcats (*F. lybica*), and martial eagles (*Polemaetus bellicosus*).

There are two habitat types at the study site: riverine woodland dominated by *Acacia xanthophloea* (fever trees), here called riverine habitat, and more open woodland dominated by *A. drepanolobium* (whistling thorn acacias) in areas away from rivers, here called nonriverine habitat. Patas are found only in nonriverine habitat, but vervets use both riverine and nonriverine habitats, sleeping in riverine habitat at night but foraging in both riverine and nonriverine habitats during the day.

One group of patas monkeys and 1–2 groups of vervet monkeys were observed regularly from August 1992–September 1999 (in June 1999, the two vervet groups fused into one group). Patas monkeys form single-male, multi-female groups for most of the year (Hall, 1965; Struhsaker and Gartlan, 1970; Gartlan, 1974; Harding and Olson, 1986; Chism and Rowell, 1988; Nakagawa, 1989), with multi-male influxes sometimes occurring during the breeding season (Chism and Rowell, 1986; Harding and Olson, 1986; Cords, 1987; Ohsawa et al., 1993; Carlson and Isbell, 2002). Females are philopatric, whereas males disperse at sexual maturity and live either as extragroup males or as residents of female groups (Chism et al., 1984; Chism and Rowell, 1986; Cords, 1987; Enstam et al., 2002). Between October 1997–September 1999, the period of intensive sampling for this study, the patas group declined in size from 51 to 20 individuals; much of the decline was associated with illness following unusually heavy El Niño rains (Isbell and Young, in preparation). Adult patas monkeys were identified by natural markings, and immatures by dye marks (black Nyanzol D powder, Belmar, Inc.) sprayed onto the pelage with a syringe.

The home ranges of the vervet study groups were about 4 km from the home range of the patas. Like female patas monkeys, female vervets remain in

TABLE 1. Operational definitions of antipredator response categories[1]

Active defense	A single animal chasing or hitting a mammalian predator
Alarm call	Emitting a vocalization in presence of a predator (often given in conjunction with "arboreal scan")
Arboreal scan	Gazing into distance while moving head from side to side while in a tree (may or may not be accompanied by "alarm call")
Bipedal scan	Gazing into distance while moving head from side to side while standing on hind legs while on the ground
Climb tree	Starting on ground, moving up trunk of a tree
Descend	Starting in tree, moving down trunk to ground
None	No change in behavior during alarm call
Run away	Rapid terrestrial locomotion (with only two feet on ground at any given time) in opposite direction that alarm call is directed

[1] One or several of response categories listed above made up the response during each alarm call (see text).

their natal groups throughout life (Cheney and Seyfarth, 1989). Unlike patas monkeys, however, vervet groups typically include multiple adult males year-round (Struhsaker, 1967b; Cheney and Seyfarth, 1987; Melnick and Pearl, 1987; Isbell et al., 1990, 1998b; Baldellou and Henzi, 1992), and males disperse to other (usually neighboring) groups when they reach sexual maturity (Cheney and Seyfarth, 1983; Isbell et al., in press). During the period of intensive sampling for this study, the two vervet groups declined in size from 30 to 9 and 10 to 5 individuals, respectively, and eventually fused into one group; the decline was largely a result of suspected and confirmed predation (Isbell and Enstam, 2002). The home ranges of the two vervet groups were adjacent to one another, and intergroup encounters occurred along their shared boundary (L.A. Isbell, unpublished data; K.L. Enstam, personal observation). All vervets were individually identified by natural markings and physical characteristics.

Data collection

Predator presence. Between November 1997–August 1999, all potential predators of primates that were seen directly or indirectly (e.g., tracks, reliable reports from cattle herders) were noted, along with the number of individuals and their location within the home range of each study group. Predator presence was estimated from these data.

Alarm calling behavior. Alarm calls have been documented by all observers on the long-term project since it began in 1992. Data collected during alarm calls included identity of caller(s) when known, type of alarm call and its duration, and stimulus that elicited the alarm call, when known.

Responses to alarm calls by primates were recorded by K.L.E. between October 1997–September 1999. If K.L.E. was conducting a focal sample on one animal at the start of its or another's alarm call, she continued to follow that focal animal for the duration of the alarm call, recording substrate (tree or ground) and habitat type (riverine or nonriverine) of the focal animal at the start of the alarm call, and its response to others' alarm calls. If K.L.E. was not conducting a focal sample at the start of an alarm call, she scanned the group from left to right, and recorded the identities of as many individuals as possible within 15 sec, their substrates and habitat types at the start of the alarm call, and their responses. The possibility that scans underestimated subtle responses (e.g., freezing or hiding; Wahome et al., 1993) was examined with focal data. No responses by focal animals involved such subtle behaviors. It is unlikely, therefore, that group scans were biased toward obvious responses. Responses included "active defense," "alarm call," "arboreal scan," "bipedal scan," "climb tree," "descend," "none," "run away," and combinations of these. Operational definitions of these response categories are listed in Table 1.

Alarm calls were considered separate bouts if they were separated by 15 min with no calling (Cheney and Seyfarth, 1981). In cases when different species of predators were confirmed for alarm calls separated by less than 15 min, the two alarm calls were counted as different bouts. This happened only once for each study species. Rates of alarm calls are based on data collected by K.L.E. between October 1997–September 1999 during 572 hr of observation on the patas and 561 hr of observation on the vervets. Alarm calls directed at humans, nonpredators, and vehicles were excluded from analyses.

Tree height, density, and cover. The heights of all trees greater than 0.5 m were recorded in 25 $\times$ 5 m transects ($n = 24$ transects in the patas home range, all in nonriverine habitat; $n = 26$ transects in the vervet home range, 10 in riverine habitat, 16 in nonriverine habitat). Transects were laid down at points randomly selected from Garmin GPS II Plus (Global Positioning System) readings of group movements, so that ecological data were collected only from areas that the study groups had been observed in. Trees between 0.5–2.0 m were measured using a meter stick, whereas the heights of trees taller than 2.0 m were estimated by eye to the nearest meter. The accuracy of estimates of tree heights was confirmed by measuring a subset of the same trees with a tangent height gauge. There was no significant difference between measurements by eye and tangent height gauge (paired *t*-test: $P > 0.8$, df = 30).

We converted tree density in the transects to number of trees per hectare by multiplying number of trees in each transect by 80 (each transect had an area of 125 m^2; 125 m^2 $\times$ 80 = 1 ha). We defined extent of canopy cover by the locomotor behavior of focal animals moving between trees. Continuous canopy cover was scored when animals either leaped or climbed directly between trees without descending; discontinuous cover was scored when animals descended one tree, and then traveled on the ground before climbing a second tree. Behavioral measures were used instead of more conventional measures because we wanted to determine which habitat affords greater opportunities to remain in trees in the event of a predator attack. Locomotor data are based on 71 focal hr on the vervets (60.3 hr in riverine habitat, 10.7 hr in nonriverine habitat) and 101 focal hr on the patas in nonriverine habitat, and were extracted from data on activity budgets of adult males and females collected by K.L.E. from March 1998–September 1999. We included data only for which habitat type was specified.

Data Analysis

Responses to alarm calls by patas and vervets were often composed of several discrete behaviors (Table 1). For 24 alarm calls, the response of only one individual was recorded because K.L.E. was recording its behavior as part of a focal sample, and in 23 cases, the responses of multiple individuals were recorded because K.L.E. was not conducting a focal sample. In 39 cases, the alarm call occurred too quickly to allow K.L.E. to record the responses of individuals, and the general response of the "group" was recorded instead.

When the responses of multiple individuals were recorded, each response was counted only once for a particular alarm call when multiple animals responded identically, in order to minimize dependence of data points. Thus, if four vervets responded to a "leopard" alarm call by climbing trees, that response ("climb tree") was counted only once in analyses, not four times. When the responses of multiple individuals were different, each different response was counted one time in analyses. Multiple responses were included in analyses when the responses differed because we are examining responses to alarm calls, not the alarm calls themselves, and excluding responses from our analyses could bias the data. When responses of the "group" were used in analyses, each response type was counted only once, since multiple animals were responding in the same way. Responses to both known alarm call types (e.g., "leopard" alarm call) in the presence or absence of stimuli, and unspecified alarm call types with observed stimuli, were used in analyses. Responses to unspecified alarm call types in the absence of stimuli were excluded from analyses. To minimize possible bias due to differences in interobserver reliability, only responses recorded by K.L.E. were included in analyses, except where noted.

Contingency tables were collapsed into 2×2 tables for statistical analyses because the number of responses in some response categories was limited. Previous studies indicate that monkeys utilize trees as refuges during alarm calls at mammalian predators (e.g., Cheney and Seyfarth, 1981, 1990; Stelzner and Strier, 1981; Bailey, 1993; Condit and Smith, 1994). The response "arboreal scanning" (which also included animals that were alarm-calling while scanning) was thus considered the standard response for animals in trees. All other response types were combined under the category "other responses." The same reasoning led us to label the responses "climb tree and scan" as the standard response for animals on the ground, with all other responses being combined under the category "other responses." Two-tailed tests were used in all cases. All data were imported from Excel (Microsoft, version 9.0) into JMP (SAS Institute, version 3.2) for analysis.

RESULTS

Predator presence

Between October 1997–September 1999, we found tracks or dung, received reliable reports from cattle herders ("indirect observations"), and directly observed ("direct observations") 10 known or potential predator species in the vervet home ranges and 8 known or potential predator species in the patas home range (Table 2). Known predators are species that have been observed preying upon, attempting to prey upon, or eating patas or vervet monkeys. Potential predators are those species that are capable of killing patas- and vervet-size prey. Baboons are included in Table 2 because baboons have preyed or attempted to prey upon vervets at other sites (Struhsaker, 1967c; Altmann and Altmann, 1970; Hausfater, 1976; Seyfarth, et. al., 1980b; Cheney and Seyfarth, 1981), and since adult female vervet and patas monkeys overlap in body size (Haltenorth and Diller, 1980), we consider baboons potential predators of immature patas monkeys as well. In addition, the behavior of immature patas monkeys in the presence of baboons (e.g., running away, watching them intently from a distance) suggests that they were fearful of baboons (K.L. Enstam, personal observation). All species listed in Table 2 were present in both study species' home ranges, except where noted, indicating that the same guild of predators was present for both vervets and patas monkeys. Although leopards or their signs were not seen in the patas home range during this 2-year study, they had been observed there before and after K.L.E.'s tenure (L.A. Isbell, unpublished data).

Antipredator behavior

Alarm calls. Fifty-seven alarm call bouts were given by the patas during 572 hr of observation, of which 41 (72%) were toward mammalian predators (7.2 alarm calls at mammalian predators per 100 hr of observation). Twenty-nine alarm call bouts were given by vervets during 562 hr of observation, of which 25 (86%) were given toward mammalian predators. The rate of alarm calls for vervets was 5.2 alarm calls at mammalian predators per 100 hr of

TABLE 2. Known and potential predators between November 1997–August 1999 (after Isbell and Enstam, 2002)[1]

Predator species	Vervet home ranges		Patas home range	
	Direct observations	Indirect observations	Direct observations	Indirect observations
African wildcat (*F. libyca*)	1	0	10	0
Baboons (*P. anubis*)[2]	8	0	28	0
Black-backed jackal (*C. mesomelas*)[3]	3	0	93	1
Caracal (*F. caracal*)	0	0	2	0
Cheetah (*A. jubatus*)	4	1	3	0
Domestic dog (*C. familaris*)[3]	2	0	27	0
Leopard (*P. pardus*)[2]	3	5	0	0
Lion (*P. leo*)	1	3	4	18
Martial eagle (*P. bellicosus*)[2]	2	0	2	0
Serval (*F. serval*)	2	0	0	0
Spotted hyena (*Crocuta crocuta*)	0	4	0	3
Total	26	13	169	22

[1] See text for definitions of direct and indirect observations of predators.
[2] Confirmed predator of vervets at this (martial eagle) or another (baboon: Struhsaker, 1967c; Altmann and Altmann, 1970; Hausfater, 1976; Seyfarth et al., 1980b; Cheney and Seyfarth, 1981; leopard: Struhsaker, 1967c; Seyfarth et al., 1980b; martial eagle: Struhsaker, 1967c; Seyfarth et al., 1980b) site.
[3] Confirmed predator of patas at this (black-backed jackal) or another (domestic dogs: Chism and Rowell, 1988) site.

TABLE 3. Number of alarm call bouts given and predators seen during alarm call bouts for each category of predator between October 1997–September 1999 (excluding humans, nonpredator species, and vehicles)

Alarm calls and predator sightings	Study groups	Mammalian predators	Avian predators	Reptilian predators	Unspecified[3]	Total	Observation hours	Calls per 100 hr
Alarm call bouts	Vervets[1]	25	1	2	1	29	562	5.2
	Riverine	22	1	2	1	26	398	6.5
	Nonriverine	3	0	0	0	3	164	1.8
	Patas	41[2]	3	7	6	57	572	10.0
Predator sightings	Vervets[1]	9	0	4	0	13	562	
	Riverine	2	0	2	0	4	398	
	Nonriverine	7	0	0	0	3	164	
	Patas	34	3	6	0	43	572	

[1] For vervets, alarm call bouts and predator sightings are also given by habitat type.
[2] For patas, alarm calls at mammalian predators include all confirmed mammalian predator alarm call types as well as unspecified alarm call types where the stimulus of the alarm call was a mammalian predator. Includes "chutter," "nyow," and "cough" alarm calls (see text).
[3] Unspecified alarm calls include alarm calls for which the observer did not indicate the alarm call type and the predator was not seen by an observer.

observation, slightly more than half the rate of alarm calls at mammalian predators given by patas monkeys (Table 3). Looking at vervet leopard alarm calls by habitat type, 22 of 25 (88%) were given in the riverine habitat, at a rate of 6.5 leopard alarm calls per 100 hr of observation in the riverine habitat. Vervets gave significantly more leopard alarm calls in the riverine habitat than in the nonriverine habitat ($\chi^2 = 6.3$: $P < 0.012$, df = 1). We were able to identify the stimulus (i.e., the predator) of patas mammalian predator alarm calls (34 of 41; 83%) more often than vervet leopard alarm calls (9 of 25; 36%) ($\chi^2 = 17.7$: $P < 0.0001$, df = 1). Habitat type affected our ability to locate the stimulus of vervet leopard alarm calls. We were able to identify the stimulus of leopard alarms less often in the riverine (2 of 22; 9%) than in the nonriverine (3 of 3; 100%) habitat (Fisher's exact test, two-tailed: $P = 0.004$; df = 1; Table 3). We concentrate on the responses of vervets and patas to mammalian predator alarm calls, since the majority of alarm calls were of this type (Table 3).

Patas monkeys gave acoustically distinct alarm calls for different types of predators (Table 4; for further qualitative descriptions of patas monkey alarm calls, see Hall, 1965; Olson and Chism, 1981; Chism and Rowell, 1988). In most cases, these alarm calls seemed to converge acoustically with vervet alarm calls. Like adult male vervet monkeys (Seyfarth et al., 1980b) and some forest geunons (e.g., Diana monkeys (*Cercopithecus diana*): Zuberbühler et al., 1997; Campbell's monkeys (*Cercopithecus campbelli*): Zuberbühler, 2001), adult male patas monkeys have a mammalian predator alarm call that is acoustically distinct from the calls given by adult females, juveniles, and infants. This two-note alarm call ("bark grunt") appears to be equivalent to the male vervet leopard alarm call, although it is a deeper vocalization.

Adult female, juvenile, and infant patas gave three acoustically different alarm calls to mammalian predators. First, they emitted the "nyow" call, a high-pitched, staccato call which during this study was only given in the presence of baboons and domestic dogs, but has been emitted in the presence of large carnivores (e.g., lions) (L.A. Isbell, unpublished data). This call is acoustically similar to the female vervet leopard alarm call. Second, they gave

TABLE 4. Alarm call types and known and potential predator species that elicited alarm calls between October 1997–September 1999

Vervet monkeys	Patas monkeys
No equivalent heard at this study site.	"Cough" alarm[1]
	Given by adult females, juveniles, and infants
	Jackals
	Wildcats
Small mammalian predator alarm[2]	Loud chutter
Not heard at this study site.	Given by adult females, juveniles, and infants
	Baboons
	Domestic dogs
	Jackals
	Wildcats
	Unidentified felid spp.
Female leopard alarm[3]	"Nyow" alarm[4]
Given by adult females and juveniles	Given by adult females and juveniles
Leopard	Baboons (with loud chutter)
Cheetah	Domestic dogs (with loud chutter)
Serval	Lion
Monitor lizard (juvenile only)	
Male leopard alarm[3]	Bark grunt
Given by adult and subadult males	Given by adult males
Leopard	Baboons (with loud chutter)
Cheetah	Jackals (with loud chutter)
Serval	
Snake alarm[3]	Quiet chutter
Given by adult males, adult female, and juveniles	Given by adult females, juveniles, and infants
Puff adder	Egyptian cobra
Unidentified snake spp.	Puff adder
Monitor lizard	Unidentified snake spp.
Eagle alarm[3]	Gecker[5]
Given by adult males, adult females, and juveniles	Given by adult females
Martial eagle	Brown snake eagle
African hawk-eagle (juvenile only)	Unidentified raptor spp.

[1] Given to minor mammalian predators that were within 50 m of the group, or discovered within the group.
[2] Follows classification of Struhsaker (1967a).
[3] Follows classification of Seyfarth et al. (1980a,b).
[4] Terminology of Struhsaker (1967a).
[5] Follows description by Olson and Chism (1981).

"loud chutter" alarm calls to smaller mammalian predators, such as jackals and domestic dogs. This call, which is softer than the "nyow" call, may be the equivalent of the small mammalian predator alarm call of vervets described by Struhsaker (1967a) but not heard during the course of this study. Finally, patas emitted a "cough" alarm call when a smaller mammalian predator (e.g., jackal or wildcat) was detected near (<50 m) or within the group. This call was softer than the "loud chutter" and evoked a response of active defense (i.e., chasing or hitting the predator) on three separate occasions.

Adult female, juvenile, and infant patas monkeys gave a "quiet chutter" alarm call in the presence of snakes, a call which is similar to the vervets' snake alarm call. Only adult females were heard to give a "gecker" alarm call in the presence of raptors (see also Olson and Chism, 1981). For six alarm calls, the observer did not specify the call type.

Like other cercopithecines, some vocalizations that patas give in response to predators are also given under other circumstances. For example, like the long-distance calls of male Diana monkeys (Zuberbühler et al., 1997) and the leopard alarm calls of male vervets (Cheney and Seyfarth, 1990) at our study site, the "bark grunt" was emitted by resident adult male patas when they detected extragroup males. "Chutters" were also used by patas in a wide variety of situations, including inter- and intragroup interactions. Acoustic analyses of patas vocalizations are required to determine if vocalizations used under different circumstances that sound similar to human observers are in fact vocalizations with different acoustic properties (Zuberbühler et al., 1997). Such analyses are beyond the scope of this study. We conservatively included "chutters," "geckers," and "bark grunts" in our analyses only if they were directed at known or potential predators or if the responses to these vocalizations were typical of those directed at predators.

The alarm calls of vervet monkeys were described in detail elsewhere (Struhsaker, 1967a; Seyfarth et al., 1980a,b; Cheney and Seyfarth, 1990). Vervets at this site were similar to vervets in Amboseli in that they gave acoustically distinct alarm calls to mammalian ("leopard alarm calls," Seyfarth et al., 1980a,b), avian ("eagle alarm calls," Seyfarth et al., 1980a,b), and reptilian ("snake alarm calls," Seyfarth et al., 1980a,b) predators (Table 4). One alarm call could not be categorized.

TABLE 5. Responses of patas and vervet monkeys, excluding infants, to mammalian predator alarm calls[1]

	Vervets					
	Riverine habitat		Nonriverine habitat		Patas, nonriverine habitat	
Response	In tree	On ground	In tree	On ground	In tree	On ground
Arboreal scan[2]	36	0	3	0	13	0
Alarm call only	0	0	0	0	0	0
Climb tree	0	0	2	0	3	0
None	4	0	0	0	2	5
Descend, run	0	0	2	0	5	2
Run away	0	0	0	1	0	7
Bipedal scan	0	0	0	1	0	10
Climb and scan	0	3	0	1	0	6
Active defense	0	0	0	0	0	1
Total	40	3	7	3	23	31

[1] Each response was counted only once in analyses, regardless of number of animals displaying that response.
[2] Includes arboreal scanning only and alarm calling while arboreal scanning.

Responses to alarm calls at mammalian predators in different habitats: when animals were in trees initially. In the nonriverine habitat, patas monkeys had 54 different reactions to 30 mammalian predator alarm calls (n = 23 for animals in trees, n = 31 for animals on the ground), and vervets had 10 responses to two mammalian predator alarm calls (n = 7 for animals in trees, n = 3 for animals on the ground; Table 5). In the riverine habitat, vervets reacted to 18 mammalian alarm calls. These 18 alarm calls yielded 43 responses (n = 40 for animals in trees, n = 3 for animals on the ground). In the nonriverine habitat, both patas and vervet monkeys left the trees during mammalian predator alarm calls. In contrast, vervets in trees in the riverine habitat never descended during mammalian predator alarm calls.

Vervets in trees in the riverine habitat displayed a significantly smaller range of reactions to mammalian predators than did patas monkeys ($\chi^2 = 8.2$: $P < 0.005$, df = 1) or vervet monkeys (Fisher's exact test, two-tailed: $P = 0.011$; df = 1) in trees in the nonriverine habitat. When vervets were in trees in the nonriverine habitat, however, their range of responses was not significantly different from the range of responses of arboreal patas monkeys in trees (Fisher's exact test, two-tailed: $P = 0.67$; df = 1).

Responses to alarm calls at mammalian predators in different habitats: when animals were on the ground initially. In the nonriverine habitat, patas and vervet monkeys on the ground responded to mammalian predator alarm calls more often by remaining on the ground (e.g., scanning bipedally or running away) than by climbing trees. Vervets on the ground in the riverine habitat, on the other hand, always responded to mammalian predator alarm calls by climbing *A. xanthophloea* trees. Vervets on the ground in the riverine habitat responded to mammalian predator alarm calls with a narrower range of behaviors (n = 3) than did patas monkeys (n = 31) in the nonriverine habitat (Fisher's exact test, two-tailed : $P = 0.014$; df = 1; Table 5). Vervets climbed *A. xanthophloea* trees more often than expected, given the proportion of *A. xanthophloea* trees in the riverine habitat (Kolmogorov-Smirnov goodness of fit test: D = 0.65; $P < 0.01$; df =1).

In contrast, the range of responses of vervet monkeys on the ground in the nonriverine habitat (n = 3) did not differ significantly from that of patas (Fisher's exact test, two-tailed: $P = 0.51$; df = 1). Small sample sizes precluded statistical analysis of the responses of vervets when they were on the ground at the beginning of the alarm call in the nonriverine (n = 3) and riverine (n = 3) habitats.

Although patas and vervets converged to a large extent in their responses to alarm calls at mammalian predators while in the same habitat type, only patas engaged in active defense (Table 5). Active defense was observed in patas five times during the course of the 2-year study. Three of the 5 observations of active defense occurred during "cough" alarm calls (see Table 4). Active defense was displayed by adult male, adult female, and juvenile patas monkeys. An adult male lunged at a black-backed jackal that was running through the center of the group and chased a wildcat out of the group as juveniles alarm-called at it. An adult female chased a caracal away from the group. Finally, a juvenile hit a wildcat on the rump as it ran out from under a bush, and another chased a wildcat for about 10 m. In addition, although we did not observe interactions between patas and large predators (i.e., lion, leopard, and cheetah), prior to this intensive behavioral study the group followed and alarm-called at a leopard as it moved away from them (L.A. Isbell, unpublished data).

Habitat structure

Tree height. The 22 transects in the patas home range (all nonriverine) contained 404 trees with an average height of 2.6 ± 0.14 m (range, 0.5–6.0 m; Fig. 1). Eighty-three percent of trees were between 0.5–4.0 m in height (see also Young et al., 1997). *Acacia drepanolobium* comprised 98.5% of the trees in the patas home range (Fig. 2). The 16 transects in the nonriverine habitat of the vervet home ranges

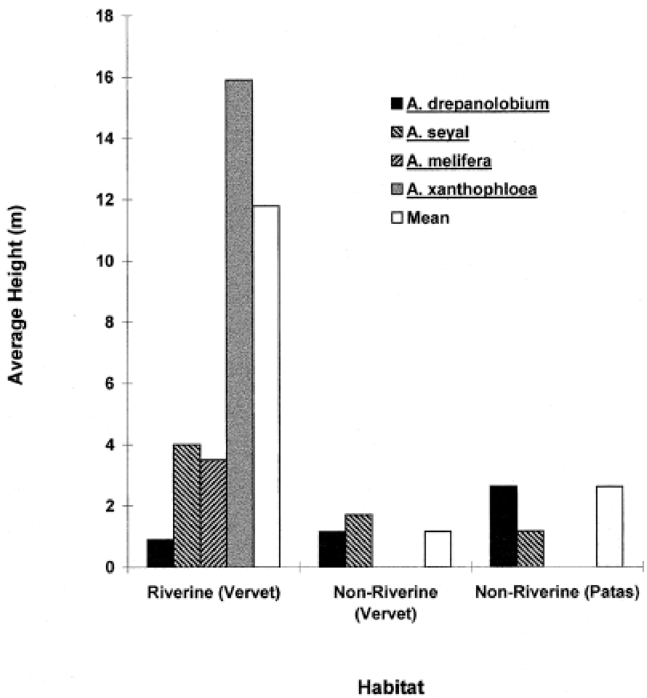

Fig. 1. Height (in meters) of all trees in riverine and nonriverine habitats. *Acacia melifera* did not occur in any transects in the patas home range, and *Acacia xanthophloea* did not occur in any transects in the nonriverine habitat.

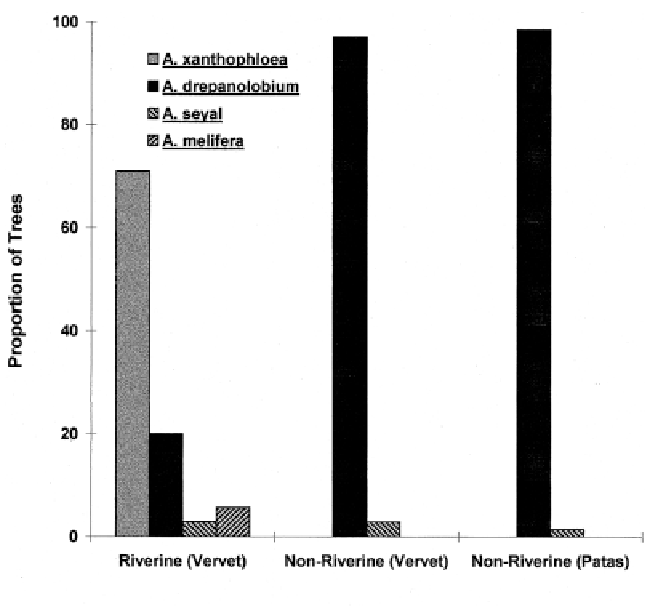

Fig. 2. Proportion of tree species in riverine and nonriverine habitats. Riverine habitat is composed primarily of *A. xanthophloea*. *Acacia drepanolobium* dominates nonriverine habitat.

contained 408 trees with an average height of 1.2 m (range, 0.5–4.0 m; Fig. 1). *Acacia drepanolobium* comprised 97.1% of the trees in transects in the nonriverine habitat of the vervet home ranges (Fig. 2). Within the nonriverine habitat, the trees in the patas home range were significantly taller than the

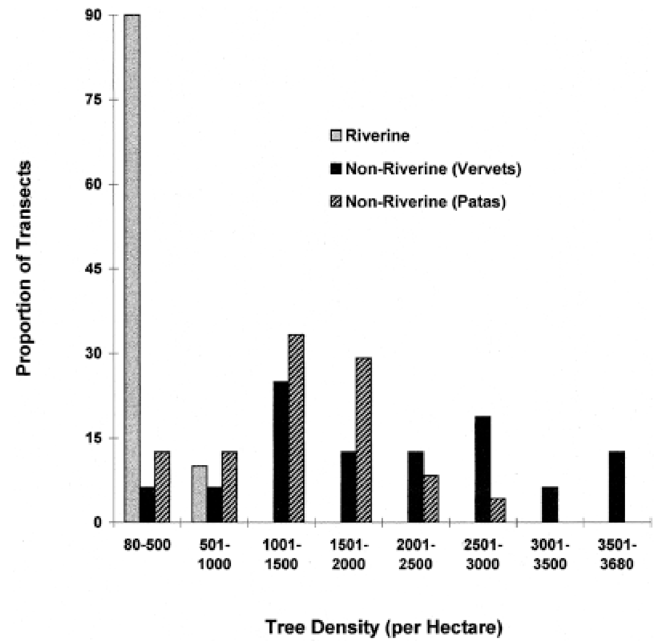

Fig. 3. Tree density (in hectares) of riverine and nonriverine habitats. Nonriverine habitat has greater variation in tree density, and greater average tree density.

trees in the vervet home ranges (t-test = 6.3; $P < 0.0001$, df = 36; see also Pruetz, 1999).

Including all tree species, the 10 transects along the river in the vervet home ranges contained 35 trees with an overall average height of 11.8 m (range, 0.5–20.0 m; Fig. 1; see also Pruetz, 1999). *Acacia xanthophloea* made up 71% of the trees in transects along the river in the vervet home ranges (Fig. 2) and had an average height of 15.9 ± 0.46 m (range, 1.0–20.0 m; n = 25; Fig. 1). Eighty percent of the *A. xanthophloea* in the riverine transects were between 15–20 m in height. Trees in the riverine habitat of the vervet home ranges were significantly taller than trees in the nonriverine habitat of the vervet (t-test = 14.2; $P < 0.0001$, df = 24; see also Pruetz, 1999) and patas (t-test = 14.2; $P < 0.0001$; df = 30) home ranges.

Tree density and canopy cover. The average density of trees in nonriverine transects was 1,347 trees per hectare in the patas home range (range, 240–2,720 trees per hectare), and 2,045 trees per hectare (range, 400–3,680 trees per hectare) in the vervet home ranges. The average density of trees in the riverine transects was 272 trees per hectare (range, 80–560 trees per hectare). The average density of trees in the riverine habitat was significantly less than in the nonriverine habitat of the vervet (t-test = 5.6, $P < 0.0001$, df = 24) or the patas (t-test = 5.1, $P < 0.0001$, df = 32; Fig. 3) home ranges (see also Young et al., 1997; Pruetz, 1999; Pruetz and Isbell, 2000).

Degree of canopy cover was estimated by percent of movements between trees that focal animals made without descending to the ground (see Mate-

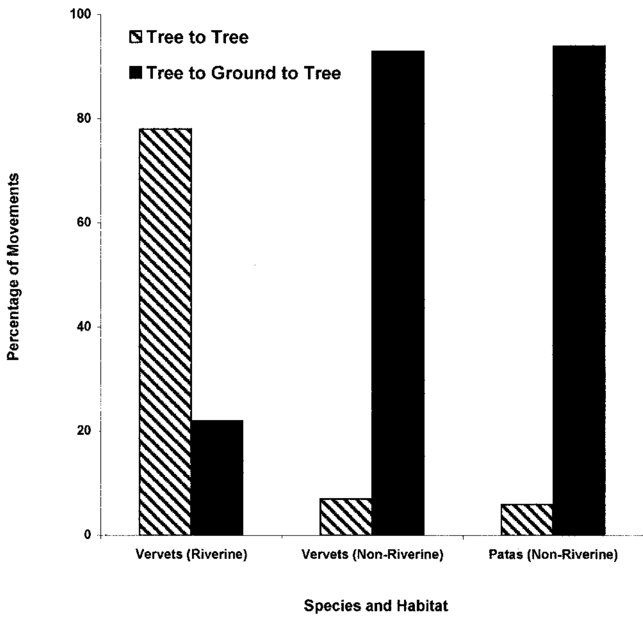

Fig. 4. Percentage of movements between trees in which focal animal remained arboreal (tree to tree movements) or descended one tree before climbing next tree (tree to ground to tree movements).

rials and Methods). Eighty-nine and 14 movements between trees were recorded for patas and vervet monkeys in the nonriverine habitat, respectively. Vervets in the riverine habitat moved between trees 63 times during focal samples. Movements by vervets between trees without descending were significantly greater in the riverine habitat (49 of 63) than in the nonriverine habitat (1 of 14) (Fisher's exact test, two-tailed: $P < 0.001$; df = 1; Fig. 4). The locomotor behavior of patas monkeys was not significantly different from the locomotor behavior of vervets in the nonriverine habitat (Fisher's exact test, two-tailed: $P = 1.00$), but was significantly different from the movements of vervets in the riverine habitat ($\chi^2 = 80.74$: $P < 0.001$; df = 1; Fig. 4).

DISCUSSION

Although vervets and patas converge in their responses to alarm calls in the same habitat, the differences in antipredator behavior of the same groups of vervets, and of vervets and patas in two different habitat types, are not likely due to differences in predator species. Almost all predator species were seen in the home ranges of both study species (Table 2). Although leopards were not observed in the patas home range during this intensive behavioral study, the patas have been exposed to them in the past, and leopards are suspected of preying on patas at another site in this region (Chism et al., 1983). Servals were not seen in the patas home range. They were replaced, however, by caracals, which are similar in body size and diet, but are found in drier (nonriverine) habitats (Haltenorth and Diller, 1977; Estes, 1991; Kingdon, 1997).

The differences in antipredator behavior both within the same groups of vervets and between vervets and patas appear instead to be a function of differences in habitat types. Although vervets responded to mammalian predator alarm calls with "typical" vervet behavior (i.e., climbing and remaining in trees) when they were in the riverine habitat (see also Seyfarth et al., 1980a,b; Cheney and Seyfarth, 1990), in the nonriverine habitat their responses were more similar to responses given by patas in the nonriverine habitat. In fact, in the nonriverine habitat, vervets responded to mammalian predator alarm calls with behaviors (i.e., bipedal scanning, running away, and descending trees) that were observed among patas in the nonriverine habitat, but never among vervets in the riverine habitat (Table 5). The differences in behavior by the same vervet groups in different habitat types, and the similarity between vervet and patas monkeys in the same habitat type, are associated with concomitant differences in habitat structure.

The structure of nonriverine and riverine habitats differs in two ways that affect the antipredator behavior of vervet monkeys: tree height and degree of canopy cover. The trees in the nonriverine habitat are nearly six times shorter than *A. xanthophloea* trees in the riverine habitat. None of the trees in the nonriverine transects exceeded 6 m, and the vast majority (83%) were less than 4 m in height. The difference in tree height (and the relatively unobstructed view of the nonriverine habitat from *A. xanthophloea* trees), rather than differences in predator presence, between the two habitats may also explain why rates of leopard alarm calling by vervets were significantly higher in the riverine habitat: vervets are simply better able to see approaching predators from *A. xanthophloea* trees. In fact, in 7 of 9 leopard alarm calls in which the stimulus was identified by observers, the stimulus was in nonriverine habitat, yet the alarm call originated from vervets in the riverine habitat. This explains why a higher number of mammalian predators were seen in the nonriverine habitat during mammalian predator alarm calls than there were alarm calls in the nonriverine habitat (Table 3). This high degree of visibility is not the case for a human observer on the ground in the riverine habitat, whose view is obstructed by the foliage of bushes and *A. drepanolobium* trees (K.L. Enstam, personal observation).

In addition, although tree density is higher in the nonriverine than riverine habitat, our behavioral measure of canopy cover (movements between trees) suggests that the canopy along rivers is more continuous than the canopy of the nonriverine habitat because it allowed for greater arboreal movement between trees. The results of the behavioral measure of canopy cover reported here agree with data derived from ecological measurements of average maximum crown diameter that show that the canopy of the riverine habitat overlaps more extensively than the nonriverine habitat (Pruetz, 1999). Because vervets had access to tall trees with overlapping canopy in the riverine habitat, they remained arboreal more often when they traveled between trees in this habitat, even in the absence of mammalian predators (Fig. 4). In the presence of mammalian predators, the structure of the riverine habitat enables vervets to increase their distance from predators, both vertically (by climbing, or remaining in, tall trees) and horizontally (by moving between trees without descending).

This strategy is not available to patas and vervet monkeys in the nonriverine habitat because short trees with discontinuous canopy cover are ineffective at increasing both vertical and horizontal distance from predators, especially those predators that can climb trees. Certainly, such qualities of trees would not deter leopards, which are adept at climbing trees, and lions, which are large enough that they could presumably push the tree over or swat a monkey out of a shorter *A. drepanolobium* by standing bipedally. Furthermore, the relative lack of canopy cover makes arboreal flight virtually impossible in the nonriverine habitat (see also Chism and Rowell, 1988). The best strategy for vervet and patas monkeys in a habitat filled with relatively short trees with little canopy cover appears to be to increase horizontal distance between oneself and the predator as quickly as possible. Our findings suggest that vervet antipredator behavior is flexible and linked closely to habitat structure (i.e., tree height and degree of canopy cover): in the presence of mammalian predators, vervets in the riverine habitat responded like vervets at other sites, whereas vervets in the nonriverine habitat responded more like patas monkeys.

Since the appropriate response for escaping a predator encountered in one type of habitat is not necessarily the most appropriate response if that same predator is encountered in a different habitat type, animals would run the risk of responding inappropriately (i.e., not escaping) if antipredator behavior was not flexible enough to adapt to variations in ecology. Our results indicate that behaviors related to escaping predators depend to a large extent on habitat type and structure. As such, antipredator behavior of a particular species may be of limited value if not studied in a microecological context.

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