

Microhabitat Preference and Vertical Use of Space by Patas Monkeys (*Erythrocebus patas*) in Relation to Predation Risk and Habitat Structure

Karin L. Enstam Lynne A. Isbell

Department of Anthropology, University of California at Davis, Davis, Calif., USA

Key Words

Antipredator behavior · *Erythrocebus patas* · Geographic information system · Habitat use · Habitat structure · Patas monkey · Predation risk · Predator detection · Ranging behavior

Abstract

Habitat structure can be important in determining habitat preference of animals because it is often closely linked to factors that affect survival and reproduction, such as food availability and predation risk. Here we examine the ways in which microhabitat structure and predation risk affect the habitat preference of wild patas monkeys (*Erythrocebus patas*). Patas monkeys in Kenya are typically restricted to *Acacia drepanolobium* habitat, but within our study group's home range, there are two distinct microhabitats, one with taller trees ('tall microhabitat') and one with apparently perennially shorter trees ('short microhabitat'). Examination of ranging behavior indicates that the patas monkeys preferred the tall microhabitat. In the tall microhabitat, focal animals climbed into trees that were significantly taller than average, indicating that they preferred tall trees. Female patas monkeys spent more time scanning from tall trees than from short trees and detected predators only from taller than average trees, based on alarm call data. Their use of tall trees may have decreased their predation risk by increasing their ability to detect predators. We found no evidence of increased food availability or reduced predator presence in the tall microhabitat that could contribute to the monkeys' preference for the tall microhabitat.

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Karin L. Enstam, Department of Anthropology/
Linguistics, Sonoma State University
1801 East Cotati Avenue, Rohnert Park, CA 94928 (USA)
Tel. +1 707 664 2944, Fax +1 707 664 3920
E-Mail karin.enstam@sonoma.edu

Introduction

Habitat preference has been shown to depend on a number of different variables, including distribution of water [Altmann and Altmann, 1970], availability of resources [Gautier-Hion et al., 1981; Kaplin, 2001] and reduced predation risk or increased potential for predator avoidance [Gautier-Hion et al., 1981; Cowlshaw, 1997a; Treves, 1997]. Habitats may vary in predation risk as a result of differences in predator species, predator density and habitat structure [Crook and Gartlan, 1966; Stanford, 1995; Hill and Dunbar, 1998; Hill and Lee, 1998]. Aspects of habitat structure that appear to affect predation risk include availability of and distance to refuges such as cliffs, burrows, trees and protective cover, and height and density of obstructive cover such as tall grass [Cowlshaw, 1997a, b; Hill and Dunbar, 1998]. Specifically, prey animals may prefer habitats that provide more refuges [Stacey, 1986; Dunbar, 1996; Cowlshaw, 1997b], increase protective cover [Treves, 1997] or increase predator visibility [Rasmussen, 1983; Dunbar, 1996; Cowlshaw, 1997a].

The ability to detect predators enables prey to take evasive action earlier, thus increasing their chances of escape [Pulliam, 1973; Bertram, 1978; van Schaik et al., 1983]. For terrestrial prey animals, the ability to detect predators can be improved by using areas with reduced ground cover, which increases their own detection ability while simultaneously decreasing the ability of predators to conceal themselves [Altmann and Altmann, 1970; Rasmussen, 1983; Isbell, 1994]. Animals that are not restricted to the ground can also increase their ability to see farther by increasing their height above the ground [van Schaik et al., 1983]. Arboreal animals such as primates take advantage of the increased visibility afforded by tall trees and cliffs to scan for conspecifics and predators [Altmann and Altmann, 1970; Baldehou and Henzi, 1992; Hamilton and Bulger, 1992].

Previous studies of primate habitat preference have examined avoidance of broadly different habitat types [Cowlshaw, 1997a; Chism and Rowell, 1988] or modifications in habitat use after environmental factors, such as fires, which dramatically changed the landscape [Rasmussen, 1983; Enstam and Isbell, in preparation]. Here we examine microhabitat preference of patas monkeys (*Erythrocebus patas*) in relation to microhabitat structure and predation risk by comparing their use of two *Acacia drepanolobium* microhabitats that differ in structure. We investigate the degree of use of both microhabitats and examine the vertical use of space to gain a better understanding of the aspects of habitat structure that affect habitat preference and perceived risk of predation in patas monkeys.

Materials and Methods

Study Site and Animals

The study was conducted between October 1997 and 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 and supports populations of several known and potential predators of patas monkeys, including lions (*Panthera leo*), leopards (*P. pardus*), cheetahs (*Acinonyx jubatus*), black-backed jackals (*Canis mesomelas*), domestic dogs (*C. familiaris*), African wildcats (*Felis lybica*) and martial eagles (*Polemaetus bellicosus*).

The historic home range of the patas group is approximately 4,000 ha [Isbell, unpubl. data]. Within the study group's home range *A. drepanolobium* comprises over 97% of the woody species [Enstam and Isbell, 2002]. However, there are two distinct types of *A. drepanolobium* habitat (hereafter referred to as 'microhabitats'), that with taller trees (hereafter referred to as 'tall microhabitat') and that with apparently perennially shorter trees (hereafter referred to as 'short microhabitat').

One group of patas monkeys was monitored regularly from August 1992 to July 2002. Our study group was a single-male, multi-female group for most of the year, like patas monkeys studied elsewhere [Hall, 1965; Struhsaker and Gartlan, 1970; Gartlan, 1974; Harding and Olson, 1986; Chism and Rowell, 1988; Nakagawa, 1999], 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 by 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 and 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]. All 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.

Data Collection and Analysis

Habitat Structure. Tree and grass height were measured in 5 paired transects in the tall and short microhabitats. Paired transects were randomly selected and set up on days when the study group was not in the area. A stake forming the beginning of a paired transect was placed on the boundary between the short and tall microhabitats, and remained fixed until the pair of transects was completed. Transects extended into each microhabitat perpendicular to the boundary. The boundary between the tall and short microhabitats was abrupt and easily determined by sight. Subsequent analyses of the tree nearest the boundary in each microhabitat in each paired transect show that trees at the edge of the tall microhabitat were significantly taller than those at the edge of the short microhabitat (Wilcoxon signed-rank test: $z = 15$, $p = 0.05$, $n_{s/r} = 5$). Three of the paired transects were 400 m in length (200 m in each direction), and two were 300 m in length (150 m in each direction), for a total of 900 m in each microhabitat. All transects were 5 m wide. Tree and grass height were also measured in 22 additional transects throughout the tall microhabitat in the study group's home range. These 22 transects were laid down at points randomly selected from Garmin GPS II Plus (Global Positioning System) readings of the study group's movements.

Trees between 0.5 and 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 the 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 (Wilcoxon signed-rank test: $z = 1.42$, $p = 0.16$, $n = 16$). Because the average tree height in the tall microhabitat was 2.6 ± 0.14 m [Enstam and Isbell, 2002], all trees ≥ 3.0 m in height were considered 'tall trees' and all trees < 3.0 m were considered 'short trees' in analyses. We converted tree density in the transects to number of trees per hectare by multiplying the number of trees in the 200-meter transects by 10 and the number of trees in the 150-meter transects by 13.34 (each 200-meter transect had an area of 1,000 m²; $1,000 \text{ m}^2 \times 10 = 1 \text{ ha}$; each 150-meter transect had an area of 750 m²; $750 \text{ m}^2 \times 13.34 = 1 \text{ ha}$). Grass height was measured to the nearest centimeter using a meter stick at 5-meter intervals within the transects. Grass height throughout the study group's home range was 43.15 ± 19.2 cm (range 0–86 cm) after the El Niño weather event (October–December 1997) and remained tall during the 2-year study while eventually turning brown.

Activity Budgets. During 572 h of observation on the patas group between November 1997 and September 1999, K.L.E. collected point samples on activity budgets of all adult males and females in the patas group during focal samples [Martin and Bateson, 1993]. Fo-

Table 1. Operational definitions of activities recorded during focal samples

Feed	Ingestion of food
Forage	Searching for and manipulating food with hands or mouth before ingestion
Move	Any form of locomotion (e.g. walking, running, climbing); type of locomotion was specified
Groom	Inspection of another animal's fur and skin or having one's own fur and skin inspected by another animal
Rest	Inactivity; may have eyes open or closed
Bipedal scan	Staring intently into the distance while moving head from side to side and standing on hind legs on the ground
Arboreal scan	Staring intently into the distance while moving head from side to side in a tree
Social	Any interactions between the focal and at least one other animal, excluding grooming

'Feed' and 'forage' were combined during analyses of vertical use of space.

cal samples were initially 30 min long with point samples taken every minute but were changed after 5 months to 20-min focal samples with point samples taken every 5 min to increase the probability that the data points would be independent. The sampling regimes did not differ statistically (Wilcoxon signed-rank test: $z = 3$; $p > 0.10$; $n_{s/r} = 6$). K.L.E. randomly sampled all adults without replacement. Data collected during focal samples included substrate (ground or tree) and activities. Activities recorded during focal samples included 'feed', 'forage', 'move', 'groom', 'rest', 'bipedal scan', 'arboreal scan' and 'social' (table 1). For each focal sample, we calculated the percentage of time spent in arboreal scanning and feeding/foraging to minimize potential problems of dependence of sample points. Focal samples for the same individual were then combined for an average percentage of time spent in arboreal scanning and feeding/foraging per individual (focal samples for the same individual were always separated by more than 24 h). Only focal samples that had matching ecological samples (see below) were used in analyses.

Ecological Samples. While K.L.E. conducted focal samples, her field assistant, Rashid Mohammed (R.M.), conducted simultaneous 'ecological samples' on the same animal. To maximize interobserver reliability, K.L.E. and R.M. synchronized their watches at the beginning of each observation day so as to record behavioral and ecological data simultaneously. To further test for interobserver reliability, we analyzed the substrate data collected by both observers in a random sample of 710 sample points from 8 focal animals. Substrate data were the same in 704 of 710 (99%) sample points (range per focal animal: 95–100%). Included in ecological samples were data on substrate (ground or tree) and habitat. When the focal animal was in a tree, R.M. recorded tree species, tree height and height of the focal animal. The accuracy of the estimates of height was confirmed by comparing the estimates of a subset of trees with measurements of the same trees using a tangent height gauge. There was no difference between estimated heights and heights measured with the tangent height gauge (see above). When the focal animal was on the ground, R.M. recorded grass height.

Analyses of the height of trees in which focal animals were found and the height of animals in these trees were taken from these ecological samples. We calculated the average height of all trees that each focal animal used, and the focal animal's average height in those trees per sample to determine vertical use of space and to avoid potential problems of dependence of data points. Average tree height and average focal animal height per focal sample were then averaged for each focal animal to provide 2 numbers per animal (average tree height used by the focal animal and average height of the focal animal in trees). The averages for all focal animals were then compared to the average height of trees in the 22 tran-

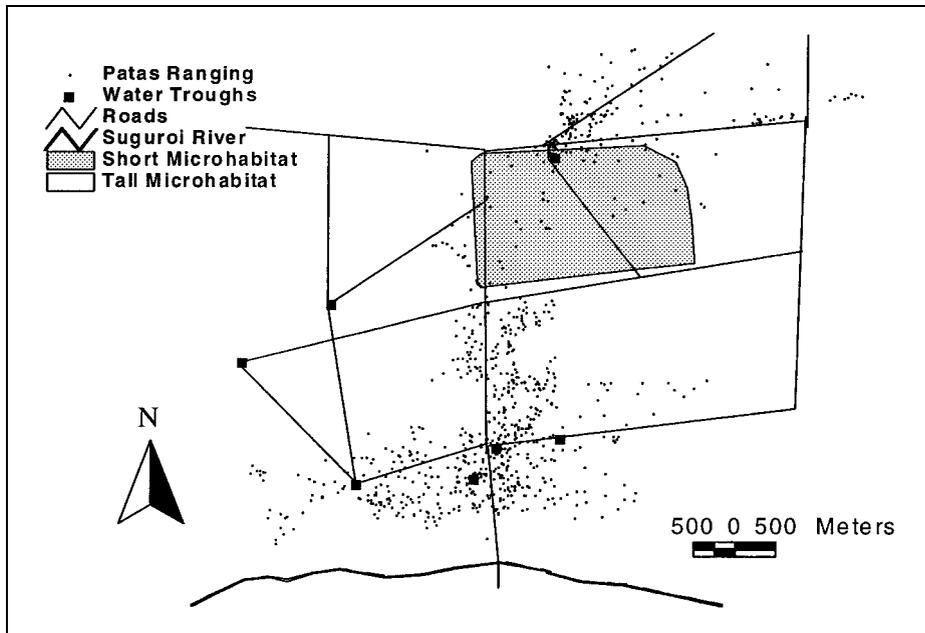


Fig. 1. Map of the study group's ranging. Points show the study group's position at 30-min intervals on all observation days.

sects measured throughout the tall microhabitat of the patas monkey home range. Analyses of behavior and vertical use of space were restricted to the tall microhabitat because the small number of data points in the short microhabitat ($n = 2$ focal samples) precluded statistical analysis. We assumed that tree height and height in a tree on one day did not influence a focal animal's subsequent use of trees because focal samples for the same individual were always separated by at least 24 h. Dependence of the data was minimized by using the individual as the unit of analysis for all behavioral and vertical use of space analyses.

Alarm Calls. Alarm calls were documented by all observers from 1992 to 2002. Data collected during alarm calls included date and time of the alarm call, identity of the caller(s) when known, the type of alarm call and its duration, and the stimulus that elicited the alarm call, when known. Here we concentrate on the vertical use of space during mammalian predator alarm calls because the majority of patas monkey alarm calls (72%) were directed at mammalian predators [Enstam and Isbell, 2002]. Only alarm calls given by focal animals during simultaneous ecological and focal samples are used in analyses.

Ranging Behavior. Data on ranging behavior were collected every 30 min using a GPS every observation day between June 5, 1998, and September 6, 1999 ($n = 91$ days). During this time, K.L.E. collected 826 GPS coordinates of the group's location (fig. 1). K.L.E. took GPS coordinates when she was in the center of the group, defined as the location at which K.L.E. could locate at least half of the group's adult females in positions to the north, south, east and west of herself. Although the study group was most often located when they were on or near roads and tracks, this sampling artifact is unlikely to affect the microhabitat preference results because we routinely drove on *all* roads and tracks in the patas monkey home range when searching for the group. There is no reason to suspect that we would have been less likely to detect the group from roads or tracks in the short microhabitat, if they had been there.

To examine microhabitat preference, we determined the relative time the patas monkeys spent in each microhabitat (tall or short) by counting the number of days in which all ranging points for those days were within the tall and short microhabitats and compared these to the expected number of days in each microhabitat based on the relative size of the microhabitats used by the patas monkeys during the study period ('all points'). We excluded from analysis those days in which the patas monkeys spent time in both microhabitats ($n = 11$). Because an individual's location at any one time is not independent of its earlier location, we minimized dependence of data by using only the GPS coordinates taken at the middle of each observation day ('daily mid-point') or the group's overall daily position for each observation day, which we calculated from the average of all GPS points collected each day ('daily centered point'). Both approaches thus yielded 1 GPS point per observation day. For these two approaches, only nonconsecutive days consisting of 3 or more hours of observation ($n = 69$ days) were included in analyses to further ensure independence of data points. We determined the area used by the patas monkeys during the study period by drawing a grid of 500×500 m squares over the map of all patas monkey GPS points. Only squares that the patas monkeys entered during GPS data collection were included in analyses. This yielded the most conservative estimate of the size of the tall microhabitat within the study group's home range.

We used a similar method to rule out the possibility that the study group's preference for the tall microhabitat was due to the fact that patas monkeys often drank from water troughs, the majority of which (6 out of 7) were in the tall microhabitat (fig. 1). We drew a circle (600 m in circumference) around the water trough that was located at the northern edge of the tall microhabitat. This circle included some tall microhabitat, about 125 m from the water trough at the closest point. We marked this area and rotated the circle so that the area of the tall microhabitat fell within the short microhabitat, thereby ensuring that we compared samples of the same size and distance from the water trough. To make our comparison as conservative as possible, we chose the area of the small microhabitat with the most ranging points.

We also investigated the likelihood that the patas group would remain in either the short or the tall microhabitat by analyzing the direction of movement of the patas group between successive GPS readings (30 min apart) within 300 m of the short/tall microhabitat boundary ($n = 69$ GPS points). Since the patas group moved an average of 301.1 m/30 min (range: 137.8–400.5 m/30 min), when they were within 300 m of the boundary between the two microhabitats, they had the potential to be in the other microhabitat 30 min later. To balance microhabitat representation and maximize the area included in the analysis, we superimposed 4 plots, centered on the northern, southern, eastern and western boundaries between the two microhabitats extending 300 m into each microhabitat. Superimposed plots were truncated 300 m from the edge of the short microhabitat to ensure that the same amount of tall and short microhabitats were included in analyses, giving the study group an equal chance of moving between microhabitats between successive GPS readings.

All data were imported from Excel (Microsoft, version 9.0, 1985–1999) into JMP (SAS Institute, version 3.2, 1989–1997) for analysis. When the data were normally distributed, we employed parametric statistical tests. Otherwise, we employed nonparametric tests. Statistical significance was set at $\alpha = 0.05$. All tests are two-tailed unless noted.

Results

Microhabitat Structure and Preference

During the 2-year intensive behavioral study, the patas monkeys used 2,851 ha of their entire home range (approx. 4,000 ha). The tall microhabitat comprised approximately 80% (2,284 ha) of the home range that was used by the group during this study, while the short microhabitat comprised approximately 20% (567 ha; fig. 1). The average height of trees in the tall microhabitat paired transects was $2.2 \pm$

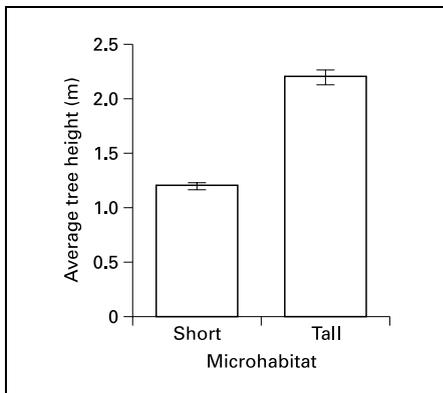


Fig. 2. Average tree height in the short and tall *A. drepanolobium* microhabitat paired transects. Bars represent 1 standard error. Trees in the short microhabitat were significantly shorter than trees in the tall microhabitat (paired t test: $t = 7.66$; $p = 0.0016$; $d.f. = 4$).

0.07 m (range: 0.5–7.0 m). There was no statistical difference in tree height between the tall paired transects and the transects collected throughout the rest of the patas monkey home range (all tall microhabitat: 2.6 ± 0.14 m; range = 0.5–6.0 m; $n = 22$ transects in tall microhabitat [Enstam and Isbell, 2002]; Mann-Whitney U test: $z = 0.97$; $p = 0.33$). The majority (83%) of trees in transects in the tall microhabitat was between 0.5 and 4.0 m in height [Enstam and Isbell, 2002; Young et al., 1997]. In contrast, the average height of trees in the short microhabitat was 1.2 ± 0.03 m (range: 0.4–6.0 m). The boundary between the short and tall microhabitats was abrupt, as evidenced by the difference in tree heights in the 5 paired transects (fig. 2). Although tree height differed significantly in the two microhabitats, tree density and grass height did not [tree density: short microhabitat, 1,342.8 trees/ha (range: 960.0–1,770.0 \pm 152.3 trees/ha), tall microhabitat, 1,075.6 trees/ha (range: 547.0–1,660.0 \pm 193.0 trees/ha), paired t test: $t = 1.14$; $p = 0.318$; $d.f. = 4$]; grass height: short microhabitat, 46.5 ± 2.0 cm (range: 0.0–99.0 cm), tall microhabitat, 41.6 ± 1.8 cm (range: 8.0–100.0 cm), paired t test: $t = 1.37$; $p = 0.24$; $d.f. = 4$].

The patas monkeys spent more days than expected in the tall microhabitat and fewer days than expected in the short microhabitat based on the relative size of each microhabitat (tall microhabitat: 2,066 ha, short microhabitat: 484 ha) regardless of the method used (all points method: $n = 75$ days in the tall microhabitat, $n = 4$ days in the short microhabitat; $\chi^2 = 8.92$; $p < 0.01$; $d.f. = 1$, fig. 1; mid-point method: $n = 65$ days in tall microhabitat, $n = 4$ days in short microhabitat; $\chi^2 = 6.98$; $p < 0.01$; $d.f. = 1$; centered-point method: $n = 63$ days in tall microhabitat, $n = 6$ days in short microhabitat; $\chi^2 = 4.11$; $p = 0.04$; $d.f. = 1$). Analysis of the group's ranging behavior around the one water trough in the short microhabitat shows that, controlling for distance from the trough, the patas monkeys spent more time in the tall microhabitat than in the short microhabitat (Fisher's exact probability test: $p < 0.03$). The patas monkeys were also more likely to remain in the tall microhabitat than in the short microhabitat between successive 30-min intervals when they were within 300 m of the boundary between the microhabitats ($\chi^2 = 4.3$; $p < 0.04$; $d.f. = 1$).

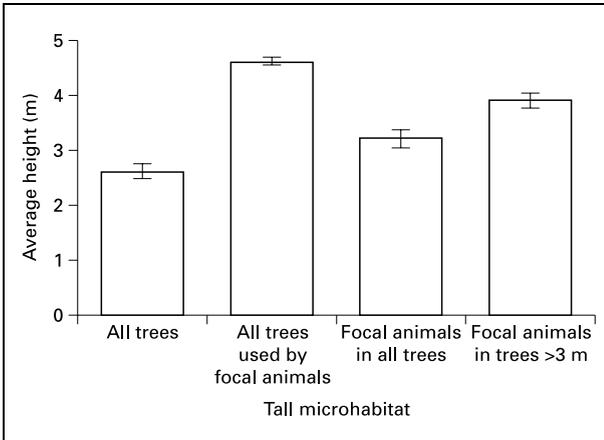


Fig. 3. Average height of trees [Enstam and Isbell, 2002], trees into which focal animals climbed, focal animals in all trees they climbed and focal animals in trees >3.0 m tall in the microhabitat. Bars represent 1 standard error.

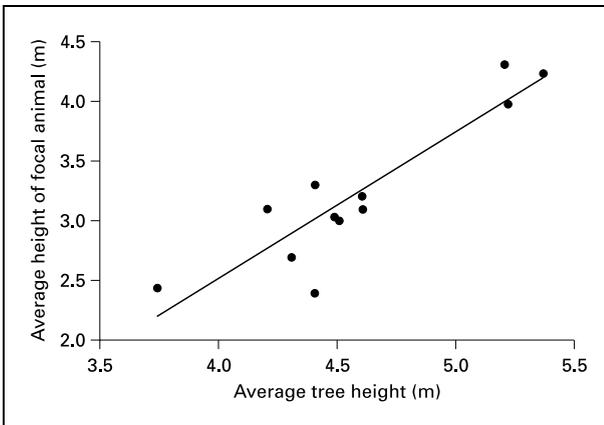


Fig. 4. Correlation between average tree height and average height where the focal animal was found in the tall microhabitat.

Vertical Use of Space, Scanning, Feeding and Foraging and Alarm Calling Behavior

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. Focal animals climbed into trees that were significantly taller than the average tree height (Mann-Whitney U test: $z = 4.73$; $p < 0.001$; fig. 3), indicating that they preferentially used tall trees. In all trees used by focal animals in the tall microhabitat, the average height of focal animals was 3.2 ± 0.16 m (range: 1.8–4.5 m). In only tall trees (>3 m), focal

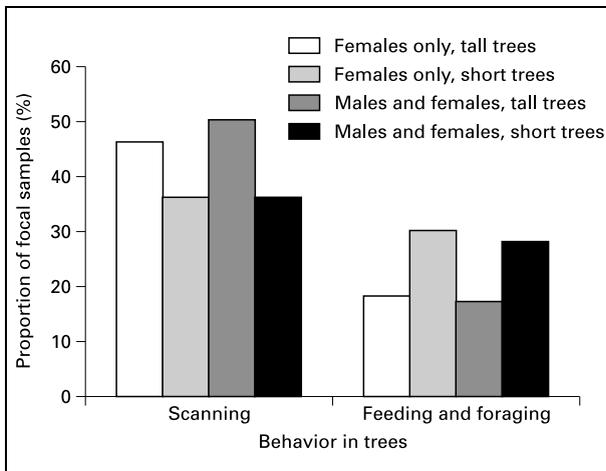


Fig. 5. Scanning and feeding/foraging behavior of adult male and female patas monkeys in short (<3.0 m in height) and tall (>3.0 m in height) trees. Patas monkeys spent a greater proportion of time during focal samples scanning from tall trees and feeding and foraging in short trees.

animals were found higher than average tree height ($\bar{x} = 3.9 \pm 0.13$ m, range: 3.1–5 m; Mann-Whitney U test: $z = 3.36$; $p = 0.0008$; fig. 3). Height of focal animals was correlated with tree height in the tall microhabitat (Pearson's product-moment correlation test: $r^2 = 0.82$; $p < 0.0001$; d.f. = 10; fig. 4), suggesting that the animals climbed as high into trees as the trees would allow.

Focal animals performed different activities in trees of different heights. Females spent more time scanning from tall trees (46% of their time) than from short trees (36% of their time; Wilcoxon signed-rank test: $z = 2.06$; $p = 0.04$; $n_{s/r} = 10$; fig. 5). The small sample size for male patas monkeys ($n = 2$) precluded independent analyses of male scanning behavior, but the inclusion of the males did not alter the results (scanning from tall trees, males and females = 50% of their time; scanning from short trees, males and females = 36% of their time; Wilcoxon signed-rank test: $z = 2.41$; $p = 0.02$; $n_{s/r} = 12$; fig. 5).

In contrast, females spent less time feeding and foraging in tall trees (18% of their time) than in short trees (30% of their time; Wilcoxon signed-rank test: $z = 2.27$; $p = 0.02$; $n_{s/r} = 10$; fig. 5). As with scanning behavior, the inclusion of adult males did not alter the results (feeding and foraging in tall trees, males and females = 17% of their time; feeding and foraging in short trees, males and females = 28% of their time; Wilcoxon signed-rank test: $z = 2.33$; $p = 0.02$; $n_{s/r} = 12$; fig. 5).

During concurrent focal and ecological samples between November 1997 and September 1999, focal animals gave 7 mammalian predator alarm calls. In all 7 cases, the focal animal was in a tree in the tall microhabitat while emitting the alarm call. Height was not recorded for 1 focal animal. In the 6 other cases, the average height of trees that monkeys were in when they gave a mammalian predator alarm call was 5 ± 0.45 m (range: 3.0–6.0 m), and the average height of

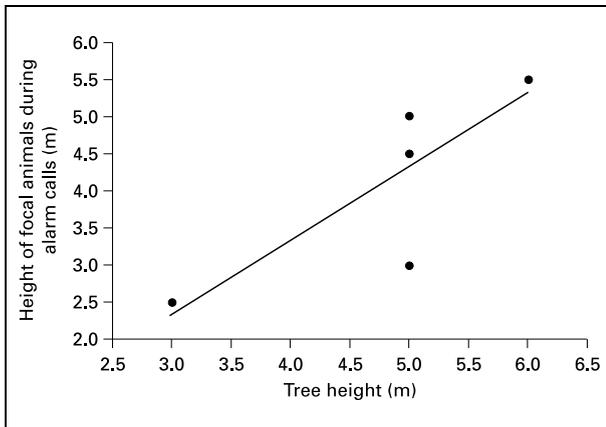


Fig. 6. Correlation between tree height and height where the focal animal was found. Five of 6 focal animals were within 0.5 m of the maximum tree height when giving an alarm call. The sixth individual was at 3 m in a 5-meter-tall tree. Note: only 5 points are visible because 2 individuals, WAR and SCO, were at 5.5 m in a 6-meter tree.

monkeys in these trees was 4.2 ± 0.63 m (range: 2.0–5.5 m). Patas monkeys gave these alarm calls from trees that were significantly taller than average tree height (Mann-Whitney U test: $z = 3.16$; $p < 0.002$). They were also significantly higher in these trees than the average tree height would have allowed (Mann-Whitney U test: $z = 2.02$; $p = 0.04$). The height of focal animals giving alarm calls was also correlated with tree height (Pearson's product-moment correlation test: $r^2 = 0.72$; $p = 0.03$; d.f. = 4; fig. 6), suggesting that focal animals took advantage of tall trees to detect predators. In 5 of 6 cases, the focal animal was within a half meter from the top of the tree while giving the alarm call (fig. 6). Tall trees were used more to detect predators than to escape from them. All focal animals were in the tree from which they uttered alarm calls for an average of 10.5 min (range: 2–25 min) before giving an alarm call, indicating that they were using the trees prior to detecting the predator, rather than climbing tall trees *after* detecting the predator from the ground.

One potential confounding factor was the presence of resident domestic dogs near the water trough on the northern edge of the short microhabitat (fig. 1). Domestic dogs are confirmed predators of patas monkeys [Chism and Rowell, 1988; Enstam and Isbell, 2002], and the study group always responded to their presence by alarm calling [Enstam and Isbell, 2002]. However, encounters between patas monkeys and dogs were not restricted to the short microhabitat; they also encountered domestic dogs in the tall microhabitat [Isbell, unpubl. data]. Moreover, the patas group often entered the short microhabitat, despite the presence of a known predator, to drink from a water trough at the northern edge of the short microhabitat (fig. 1). The group typically waited in trees near the water trough, scanning the area before approaching the water trough [Enstam, pers. observation]. Had the water trough not been there, the group might have avoided the short microhabitat to a greater extent, making our results even more striking.

Discussion

Although patas monkeys in East Africa appear to prefer open acacia woodland to bushed woodland, open savannah and riverine woodland [Chism and Rowell, 1988], this is the first report of preferential use of taller microhabitats by patas monkeys. Their microhabitat preference does not appear to be related to differences in ground cover. Although differences in ground cover can affect the ranging behavior of some primates – e.g. baboons (*Papio cynocephalus*) [Rasmussen, 1983] or vervets (*Cercopithecus aethiops*) [Enstam and Isbell, in preparation] – grass height did not differ between the shorter and taller microhabitats in the patas monkey home range.

It is also unlikely that the study group avoided the short microhabitat because of reduced food availability. Patas monkeys at this site obtain the majority of their food (83%) from *A. drepanolobium* trees [Isbell, 1998], with swollen thorns forming the main component of their diet [Isbell, 1998; Pruettz and Isbell, 2000]. Swollen thorns do not appear to be less available to patas monkeys in the short microhabitat. First, the density of *A. drepanolobium* trees did not differ between the short and tall microhabitats. Second, swollen thorns are found on all *A. drepanolobium* trees regardless of height [Isbell, 1998]. Finally, and most importantly, patas monkeys typically feed on only 1–2 swollen thorns per tree because the ants (*Crematogaster* spp.) that live on *A. drepanolobium* trees defend them by biting intruders [Madden and Young, 1992; Young et al., 1997]. Short and tall trees thus provide the patas monkeys with equally as many swollen thorns as the monkeys can tolerate taking.

Previous research on the availability of *A. drepanolobium* gum (their other main food source [Isbell, 1998]) in the study group's home range indicates that gum sites are most abundant in trees greater than 2 m, although gum is nonetheless still available in trees from 0.5 to 2 m [Pruettz, 1999]. Although the tall microhabitat potentially contains more gum sites than the short microhabitat because it contains more tall trees (>3 m), both microhabitats may provide the patas monkeys with sufficient amounts of gum given their feeding behavior. Patas monkeys typically eat an average of only 2.1 food items per tree [Pruettz, 1999] approximately a third of which are gum sites [Isbell, 1998; Pruettz, 1999], and they do not eat gum from every tree, even when it is available [Enstam, pers. observation]. Thus, even though the tall microhabitat potentially contains more gum sites, it is unlikely that the patas monkeys feed on gum heavily enough to deplete the short microhabitat. As is the case with swollen thorns, both microhabitats likely provide ample gum sites for the patas monkeys.

Most importantly, however, patas monkeys spend more time feeding in short trees than in tall trees. Indeed, patas monkeys may even prefer to feed from short trees since they can feed on them from the ground. They spend most of their time feeding on *A. drepanolobium* while on the ground, choosing to feed on swollen thorns and exudate patches occurring at an average height of 75 and 90 cm, respectively [Pruettz, 1999].

Although patas monkeys must drink daily [Chism et al., 1984], their need for water does not explain their avoidance of the short microhabitat. The study group often drank from cattle troughs, especially in the dry season [Enstam, pers. observation], and their ranging does concentrate near these troughs (fig. 1). However,

analysis of the northernmost water trough, the only one on the boundary between the two microhabitats, shows that while the monkeys had the option of approaching the trough from within either the short or tall microhabitats, they spent significantly more time in the tall microhabitat near the trough.

Patas monkeys may have preferred the tall microhabitat for greater safety from predators, rather than advantages in food acquisition. The tall microhabitat may be safer in part because tall trees provide better vantage points from which to scan one's surroundings. Female patas monkeys use tall trees to scan their surroundings (fig. 5) and may scan for a variety of reasons. First, they may scan to keep other group members in view [Cowlshaw, 1998; Treves, 1999]. Second, they may scan for other groups, toward which they are invariably aggressive [Struhsaker and Gartlan, 1970; Chism et al., 1984; Chism and Rowell, 1988; Rowell, 1988]. We were unable to test whether females increase their conspecific detection rates from tall trees, however, because the density of patas monkeys at this site is extremely low [Enstam et al., 2002], and no intergroup encounters, or detection of conspecifics by females, occurred during the 2-year study. Certainly, male patas monkeys detect extragroup males from tall trees. Bark-grunts are associated with the presence of strange males [Hall, 1965; Napier, 1981; Enstam and Isbell, 2002], and resident males were often observed to bark-grunt from tall trees, descend and run in the direction they were scanning [Enstam, pers. observation].

Third, they may scan to detect predators. Two lines of evidence suggest that patas monkeys may scan from tall trees to detect predators: (1) focal animals gave alarm calls from trees that were taller than the average height of trees in the tall *A. drepanolobium* microhabitat, and (2) focal animals were as high up in trees as they could go while giving alarm calls (fig. 6). Scanning the environment from 'emergent' trees (i.e. the tallest trees available) may enable patas monkeys to detect predators and to detect them at greater distances because their view is not hampered by shorter trees [Rasa, 1986; Yasukawa et al., 1992]. Enhanced visibility is important because increased ability to detect predators affords prey better chances of escape [Pulliam, 1973; Bertram, 1978; van Schaik et al., 1983].

Previous research on patas monkeys suggests that they are responsive to the risk of predation. At Kala Maloue, Cameroon, patas monkeys use open grassland more often than at the Laikipia study site, apparently because of relaxed predation pressure from mammalian predators [Nakagawa, 1999]. In areas with higher predation rates, many of the behaviors of patas monkeys, including diurnal births [Chism et al., 1983], sleeping site selection [Hall, 1965; Chism and Rowell, 1988] and night-resting behaviors [Hall, 1965; Chism and Rowell, 1988] appear to be adaptations to deal with nocturnal predators in habitats with few refuges. Observations of patas monkey behavior at the edge of riverine woodland (e.g. cautious behavior, extensive scanning) and before crossing open areas (e.g. extensive scanning, rapid advance) [Chism and Rowell, 1988] indicate that they are also wary in these areas during the day and tend to use these areas less than woodlands. While patas monkeys do not appear to modify interindividual distances based on the risk of predation [Isbell and Enstam, 2002], the results reported here do suggest that patas monkeys attempt to reduce predation by diurnal predators by scanning their surroundings from taller trees [Chism and Rowell, 1988].

Our results add to the growing literature on primate habitat use and preference and indicate that patas monkeys are sensitive to differences in microhabitat struc-

ture. Although previous research has shown that patas monkeys prefer certain habitat types over others [Chism and Rowell, 1988], this is the first study to show the fine-grained nature of microhabitat preference in patas monkeys. Indeed, our results show that patas monkeys distinguish between, and preferentially use for different purposes, not only particular microhabitats, but trees of different heights within preferred microhabitats. These findings underscore the importance of differences in habitat on variation in primate behavior.

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