

Eat or be Eaten

Predator Sensitive Foraging Among Primates

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10 • Predator (in)sensitive foraging in
sympatric female vervets (*Cercopithecus*
aethiops) and patas monkeys
(*Erythrocebus patas*): A test of ecological
models of group dispersion

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Introduction

Competitive relationships result from competitive interactions over resources that can affect survival and reproduction. For male mammals, prospective mates are one such resource. For female mammals, food is more important than mates as a contestable resource (Trivers 1972). Its importance has been recognized by three ecological models that invoke either food distribution (van Schaik 1989, Wrangham 1980) or both food distribution and abundance (Isbell 1991) to explain variation in competitive relationships within and between groups of female primates (see also Isbell and Van Vuren 1996, Sterck *et al.* 1997, van Hooff and van Schaik 1992, Wrangham 1987). For both sexes, survival is also affected by other factors, such as disease and predation, and it is possible that individuals also compete for resources that in some way minimize exposure to disease or predators. In fact, one of the three models (here called the 'predation hypothesis') considers predation to be more important than food in its effects on the grouping behavior of females (van Schaik 1989).

The predation hypothesis assumes that predation ultimately forces females to live together and that variation in predation pressure causes variation in spatial cohesion within groups and among species (Sterck *et al.* 1997, van Hooff and van Schaik 1992, van Schaik 1989). Where predation pressure is high, females are predicted to decrease interindividual distances and thus live in groups that are spatially cohesive. The advantages of living closer to other group members to reduce predation may be gained if one places others between oneself and the predator (Hamilton 1971), or if the predator's ability to target particular individuals during an attack is reduced (Pulliam and Caraco 1984), or if more neighbors reduce

detection time (van Schaik *et al.* 1983). Close proximity to others may increase food competition, however, and group members are expected to increase interindividual distances if given the opportunity. One such opportunity might arise when the risk of predation is low. Under low predation pressure, females are predicted to increase interindividual distances, either uniformly or between subgroups (fission-fusion grouping), thereby living less cohesively. In some species, dispersion is greatest while animals are foraging (Boinski *et al.* 2000). This has been interpreted as enhancing foraging efficiency at the cost of increasing vulnerability to predation (Boinski *et al.* 2000). The predation hypothesis thus implies that trade-offs exist between foraging efficiency and vulnerability to predation and that primates decrease foraging efficiency in exchange for greater safety from predators.

Contrasted with this model are two models that, although differing in the hypothesized effects of food on competition between groups, are similar in hypothesizing that food distribution is sufficient to explain variation in group dispersion (Isbell 1991, Wrangham 1980). The 'food distribution' hypothesis predicts that, where foods are spatially clumped, females decrease interindividual distances, and where foods are more spatially dispersed, females increase interindividual distances. The food distribution hypothesis also implies that if there are trade-offs between foraging and risk of predation, animals will maintain foraging efficiency at the risk of being more vulnerable to predators.

The predation hypothesis and the food distribution hypothesis present mutually exclusive predictions that can be tested under field conditions provided one factor varies while the other does not. For example, one might compare two populations of one species whose foods are distributed similarly but that live in habitats that differ in predation pressure. Alternatively, one might compare two closely related species whose food differs in distribution but which live in habitats with similar predation pressure. Comparison of closely related species reduces the chances that any differences could be explained by phylogenetic inertia.

Vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) are two species that allow the latter comparison. Vervets and patas monkeys are more closely related to one another than they are to other primates (Disotell 1996), thus enabling us to exclude phylogenetic inertia as an explanation for observed behavioral differences between the two species. Vervets and patas monkeys are also sympatric in parts of their biogeographic ranges and overlap

in body size (female vervets weigh 2.5–5.3 kg and female patas, 4.0–7.5 kg; Haltenorth and Diller 1977, Turner *et al.* 1997), making them vulnerable to the same predators in areas of sympatry. Although vervet groups typically have multiple males whereas patas groups have single males (most of the time), males in both species are similar to females in their responses to predators and in both species, males and females avoid predators more often than confront them (Cheney and Seyfarth 1981, Cheney and Wrangham 1987, Chism *et al.* 1983, LAI, unpublished data).

One area of sympatry is in Laikipia, Kenya, where a long-term comparative study of vervets and patas monkeys was initiated in 1992. At this study site, the food trees of vervets are more spatially clumped than the food trees of patas monkeys (Pruetz and Isbell 2000). In addition, the distance between food sites is greater for patas than for vervets (a food site is defined as any location where an animal stops to feed and that is separated from other food sites by hindlimb movement of the animal; Isbell *et al.* 1998). The home range of the study group of vervets can be further separated into two habitat types that also differ in food distribution at the scale of individual trees. Food trees in the part of their home range that includes *Acacia xanthophloea* riverine habitat are more clumped than food trees in the part of their home range that includes *A. drepanolobium* habitat (Pruetz and Isbell 2000) (the distance between food sites does not differ; Isbell *et al.* 1998). Comparison of the same group in these two habitats decisively eliminates any potential confounding influences of phylogenetic history, body size, group size, individual differences, and predation pressure, while allowing food tree distribution to vary.

Here we test opposing predictions generated by the predation and food competition models by examining group dispersion in sympatric vervets and patas monkeys sharing the same guild of predator species. Group dispersion is measured here by group spreads and interindividual distances. If the predation model is correct, there should be no significant difference between vervets and patas in group dispersion because both species are vulnerable to the same predators. Similarly, among vervets, there should be no significant difference in group dispersion between habitats within the group's home range because their predators are not constrained to one or the other habitat type. In addition, for individuals reducing foraging efficiency in return for greater safety from predators, interindividual distances are expected to be closer than interfood distances.

If, on the other hand, the food competition models are correct, vervets should be less dispersed than patas because their food trees are more clumped than are the food trees of patas. Vervets should also be less dispersed in that part of their home range where food trees are clumped and more dispersed in that part of their home range where food trees are less clumped. In addition, for individuals either not making trade-offs between foraging efficiency and vulnerability to predators or maintaining foraging efficiency at a risk of increasing their vulnerability to predators, interindividual distances are expected to be similar to interfood distances. We focus on females because the models were developed largely to explain variation in female grouping behavior.

Methods

Study site and subjects

The study was conducted as part of an ongoing comparative project begun in 1992 at Segera Ranch (36° 50' E, 0° 15' N; elevation 1800 m) on the Laikipia Plateau in central Kenya. The ecosystem is semi-arid, with mean annual rainfall of approximately 700 mm, although this varies considerably from year to year. Segera Ranch is a privately owned cattle ranch and conservation area that supports a wide diversity of wild animals, including most of the potential predators of vervets and patas monkeys, including leopards (*Panthera pardus*), lions (*P. leo*), black-backed jackals (*Canis mesomelas*), and martial eagles (*Polemaetus bellicosus*) (Table 10.1). Two major habitat types occur in the study area. Riverine areas support woodlands dominated by *Acacia xanthophloea* but that includes a smaller woody shrub layer (*Carissa edulis*, *Euclea divinorum*). Away from streams and rivers, vertisolic soils of impeded drainage ('black cotton soil') (Ahn and Geiger 1987) support woodlands dominated by *A. drepanolobium* and several species of grasses (predominantly *Pennisetum mezianum*, *P. stramineum*, and *Themeda triandra*) (Young *et al.* 1997). The two *Acacia* species differ considerably in height and canopy volume. While *A. xanthophloea* can grow to 25 m or more (Coe and Beentje 1991), *A. drepanolobium* only rarely grows to 7 m; 98% of individuals are 4 m or less (Isbell 1998, Young *et al.* 1997).

The behavioral data come from one group of vervets averaging 18.3 individuals (seven adult females and two adult males) and one group of patas monkeys averaging 24.2 individuals (nine to ten adult females and one adult male), all of whom were habituated to the presence of observers. All animals were individually identified

Table 10.1. Signs of potential predators from November 1997–August 1999 in the home ranges of the study groups of vervets and patas monkeys. For each potential predator, the number of sightings by observers is given first, followed by the number of sightings of tracks and dung and reliable sightings of predators by cattle herders. The presence of nocturnal predators, such as hyenas, lions, and leopards, is more often determined by signs than by actual sightings whereas the presence of strictly diurnal predators, such as cheetahs, and martial eagles, is more often determined by sightings

Species	Vervets	Patas
Lion (<i>Panthera leo</i>)	1/3	3/17
Leopard (<i>P. pardus</i>)	2/4	0/0
Cheetah (<i>Acinonyx jubatus</i>)	4/1	2/0
Spotted hyena (<i>Crocuta crocuta</i>)	0/4	0/3
Black-backed jackal (<i>Canis mesomelas</i>)	3/0	9/1
African wild cat (<i>Felis libyca</i>)	1/0	10/0
Serval (<i>F. serval</i>)	3/0	0/0
Caracal (<i>F. caracal</i>)	0/0	2/0
Martial eagle (<i>Polemaetus bellicosus</i>)	2/0	3/0

by natural markings and physical characteristics or by hair dye sprayed on their pelage with a syringe.

The vervet group lives along the Mutara River and defends its home range against incursions by neighboring groups. The vervets sleep and forage in *A. xanthophloea* habitat but also forage in adjacent *A. drepanolobium* habitat. Food trees in *A. xanthophloea* habitat are more spatially clumped than those in *A. drepanolobium* habitat (Pruetz and Isbell 2000). In addition, on average, in *A. xanthophloea* habitat, *A. xanthophloea* trees are 13.3 m from other *A. xanthophloea* trees and food sites are 5.8 m from other food sites, whereas in *A. drepanolobium* habitat, *A. drepanolobium* trees are 2.4 m from other *A. drepanolobium* trees and food sites are 6.2 m from other food sites for the vervet group (Isbell *et al.* 1998, Pruetz 1999). The divergence between inter-tree distance and inter-food site distance in these two habitats likely reflects the fact that individual *A. xanthophloea* are large, have multiple food sites within them, and are seldom passed without being fed in whereas individual *A. drepanolobium* trees are small, have few food sites, and are often passed without being fed in as vervets forage. With both habitat types combined, distances

between trees and between food sites are 7.8 m and 6.1 m, respectively, in the home range of the vervet group (Isbell *et al.* 1998, Pruetz 1999). The patas group is restricted to *A. drepanolobium* habitat. On average, trees are 4.3 m from other trees and food sites are 16.5 m from other food sites in the home range of the patas monkey group (Isbell *et al.* 1998, Pruetz 1999), again reflecting the fact that not all trees are fed in as monkeys forage.

Data collection

Demographic data (births, deaths, disappearances, emigrations, and immigrations), dominance interactions, alarm calls, and predator sightings in conjunction with alarm calls have been recorded regularly since 1992 (number of observation days per month: patas monkeys, mean = 7.4, mode = 5, range = 0–24; vervets: mean = 7.4, mode = 10, range = 0–18). All predator sightings and signs within the home ranges of the monkeys, including those not associated with alarm calls, have been recorded since November 1997. From January to August, 1999, data on interindividual distances were collected from all adults using focal animal sampling. Focal animals were sampled beginning on the hour for 30 minutes using a predetermined random sampling procedure without replacement. Point samples were taken every 5 minutes during the 30-minute sample, with the identities of the three nearest neighbors of any age and of either sex and their distances from the focal female recorded. When the focal animal was 50 m or more away from any other animals, it was considered separated from the group, and alone or peripheral.

Inter-individual distances were calculated for all adult males and females in both groups (vervets: $n = 297$ point samples, range, 12–49 per individual; patas: $n = 481$ point samples, range 24–79 per individual), with the exception of one patas monkey (MIC), who was excluded because she died after being sampled only five times. The last two months of data on interindividual distances of vervets were excluded because the study group fused with another group in July, 1999 and the sudden and unusual addition of strange females to the group could have created a new group that was atypical in dispersion.

Data on group spreads were recorded from January to August, 1999 (data from July and August were excluded from analyses for vervets; see above), once every observation hour on the three-quarter-hour. While one observer stood at one edge of the group, another walked to the farthest visible edge and estimated the

distance between himself and the other observer. Distances were always estimated by the same observer, and were consistent with estimates from previous studies (e.g., Isbell *et al.* 1998, 1999). Habitat type was recorded for a subset of these group spreads for vervets as part of another study (Enstam, unpublished data). No obvious bias could be detected with this subset.

Data analysis

Because female vervets and patas monkeys typically remain in their natal groups throughout life, permanent disappearances of adult females were considered deaths. The criteria for determining cause of death follow Cheney *et al.* (1988) as modified by Isbell (1990). Females that disappeared were considered to have died of suspected predation when they were in apparently good health within 72 h preceding their noted disappearance. Predation was confirmed if the predator was observed feeding on the monkey or if remains were found that could be assigned to a missing individual.

The data on group spreads and interindividual distances were entered into Excel (Microsoft) and then imported to JMP (SAS Institute, Cary, SC) for analysis. Analyses were conducted on mean interindividual distances per focal animal for each of the first, second, and third nearest neighbors.

With all data points on nearest neighbors of adult females included, the mean distance for the third nearest neighbor was actually smaller (9.3 m) than the mean for the second nearest neighbor (10.1 m) for vervets. This occurred because in several cases (QSO: 5; SAL: 6), the second nearest neighbor was less than 50 m from the focal animal while the third closest neighbor was greater than 50 m away from the focal animal and therefore not counted as a neighbor. By definition, however, the second nearest neighbor is always closer than the third. We therefore excluded those data points and recalculated the means so that the third nearest neighbor was indeed farther away, on average, than the second nearest neighbor.

Results

Predator presence

From November 1997 to August 1999, nine potential predator species of vervets and patas monkeys were observed either directly or via signs at least once, and six of these occurred in the home ranges of both study groups (Table 10.1). Although leopards

(*Panthera pardus*) were not seen during this time in the home range of the patas monkeys, they had been seen there in the past. Servals (*Felis serval*) were seen only in the vervets' home range, whereas caracals (*F. caracal*) were seen only in the patas monkeys' home range. These congeners are similar in body size and general diets, with caracals replacing servals in drier habitats (Dorst and Dandelot 1969, Estes 1991). Given that the home ranges of the two study groups are separated by only about 4 km, the overlap in predator species is not surprising. Although an analysis of densities of individual predator species cannot be done here, the number of sightings suggest that black-backed jackals, lions, and African wild cats (*F. libyca*) were more common in the habitat of patas monkeys, whereas leopards were more common in the habitat of vervets during this study. Only martial eagles and leopards are confirmed predators of vervets and only jackals are confirmed predators of patas at this site. It is unlikely that hyenas (*Crocuta crocuta*) are actual predators of primates because these nocturnal carnivores do not climb trees. With the exception of martial eagles and cheetahs, all of the potential predators hunt mainly at night.

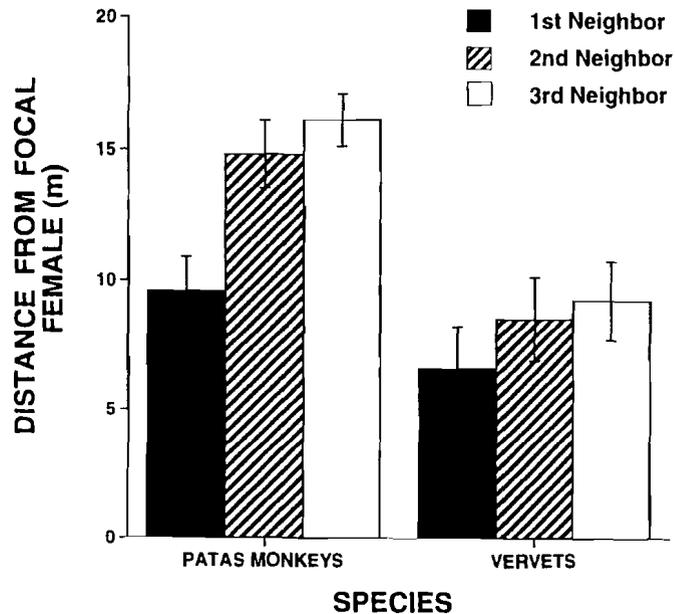
Predation on adult females

Since the long-term study began, a minimum of ten of 18 (56%) adult female vervets and five of 34 (15%) adult female patas monkeys have died of suspected or confirmed predation. Remains of five of the ten adult female vervets were found, and signs of leopards near the group's locations around the dates of death suggest that most of these females were killed by leopards (see also Isbell 1990). In one episode of predation in which three vervets died overnight, claw marks were seen on the trunks of the vervets' sleeping trees, and remains of the vervets in and below the trees were found (V. Cummins and S. Robbins, personal communication). No remains of adult female patas monkeys that were suspected of being killed by predators have ever been found.

Interindividual distances

Since vervets were observed more often in early morning, and patas monkeys in mid-morning to late afternoon, we examined the possibility that the data could be biased by time of day before conducting further analyses. Interindividual distance was not correlated with time of day in either species, however (patas, first nearest neighbor: $r^2=0.44$, $p=0.15$, $df=48$; second nearest neighbor: $r^2=0.02$, $p=0.35$; third nearest neighbor: $r^2=0.04$, $p=0.19$; vervets, first

Fig. 10.1. Distances in meters (± 1 SE) between the focal female and her three nearest neighbors. Nearest neighbors are significantly closer ($p = 0.001$) in vervets than in patas monkeys.



nearest neighbor: $r^2 = 0.0002$, $p = 0.93$; $df = 43$; second nearest neighbor: $r^2 = 0.02$, $p = 0.31$; third nearest neighbor: $r^2 = 0.02$, $p = 0.32$), suggesting that such a bias was not present.

The nearest neighbor of focal female patas monkeys was, on average, 45% farther away than was the nearest neighbor of focal female vervets (patas: $9.6 \text{ m} \pm 1.3$ standard error; vervets: $6.6 \text{ m} \pm 1.6$; t -test: $t = 1.43$, $p = 0.17$, $df = 14$; Fig. 10.1). The second nearest neighbor of focal female patas was 74% farther away than that of vervets (patas: $14.8 \text{ m} \pm 1.3$; vervets: $8.5 \text{ m} \pm 1.6$; $t = 3.04$, $p = 0.009$; Fig. 10.1). The third nearest neighbor of focal patas was 75% farther away than that of vervets (patas: $16.1 \text{ m} \pm 1.0$; vervets: $9.2 \text{ m} \pm 1.5$; $t = 4.03$, $p = 0.001$; Fig. 10.1). Together, the three nearest neighbors of adult female patas monkeys were significantly farther away from focal females than were those of adult female vervets (Fisher's combined test: $\chi^2 = 26.41$, $p < 0.001$, $df = 6$). Interindividual distances could not be analyzed for vervets in the two different habitats because sample sizes per female were too small.

Greater interindividual distances in patas monkeys relative to vervets were mirrored by greater distances between food sites in the home range of patas. The mean distance between food sites was 16.5 m for patas and 6.1 m for vervets (Isbell *et al.* 1998). The average

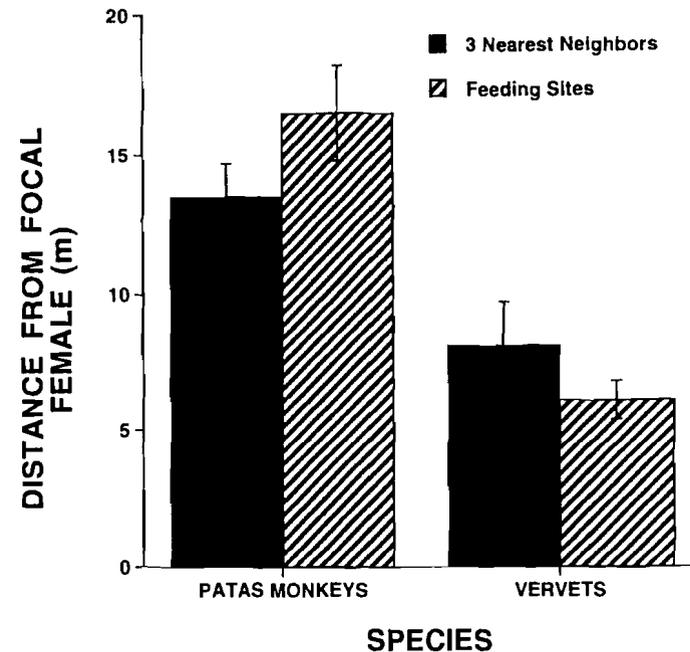


Fig. 10.2. Mean inter-individual distances of the three nearest neighbors of focal animals relative to mean inter-food site distances for vervets and patas monkeys. Inter-food site distances are from Isbell *et al.* 1998.

distance of the three nearest neighbors combined corresponded remarkably well with average interfood sites for both species (Fig. 10.2).

Group spreads

Group spread was not correlated with time of day (vervets, $r^2 = 0.03$, $p = 0.25$, $n = 48$; patas, $r^2 = 0.001$, $p = 0.73$, $n = 88$). The mean group spread for patas monkeys was $151.8 \text{ m} \pm 6.8$ whereas the mean group spread for vervets was $128.0 \text{ m} \pm 10.2$. Group spread was probably underestimated for patas monkeys. When group spread is estimated by multiplying the mean nearest-neighbor distance (9.6 m) by the mean number of animals in the group minus one (23.2), the group spread is 223 m, 47% greater than the estimate derived from observations in the field. Group spread probably was not underestimated for vervets. The mean nearest-neighbor distance of 6.6 m multiplied by the vervets' mean group size minus one (17.3) yields an estimated group spread of 114 m, only 11% off the estimate derived from observations in the field. The greater difficulty in locating individual patas monkeys for focal sampling (see Isbell *et al.* 1998) suggests that the difference in estimates of group spread

in patas monkeys occurred because patas monkeys are more difficult than vervets to see in the field. Even without adjusting for the underestimation, vervets had significantly smaller group spreads than patas ($t = 2.0$, $p = 0.05$, $n = 134$, two-tailed).

The greater group spread of patas was not caused by the resident male. Although the resident male patas monkey may be socially peripheral (Carlson 2000), he is apparently not spatially peripheral. The nearest neighbor of the focal adult male patas monkey was, on average, 58% farther away than the nearest neighbor of focal adult male vervets (patas: 11.2 m; vervets: 7.1 m \pm 0.8), but the difference was not statistically significant ($t = 2.63$, $p = 0.23$). Assuming that the resident male patas was always on the edge of the group, he would have contributed, at most, about half the difference of 23.8 m between species in group spread because he was, on average, 11.2 m from his nearest neighbor.

When vervets used *A. xanthophloea* habitat, their mean group spread was 93.0 m \pm 4.6. When they used *A. drepanolobium* habitat, their mean group spread was 165.8 m \pm 18.2, 78% wider than in *A. xanthophloea* habitat ($t = 3.54$, $p = 0.006$, $n = 11$). The wider group spread of vervets in *A. drepanolobium* habitat is consistent with other findings that vervets converge to some extent with patas monkeys in foraging and ranging behavior when they use the same habitat (Isbell *et al.* 1998).

Discussion

Vervets have been described as living in 'compact' groups (van Hooff and van Schaik 1992: 362), whereas patas monkeys have been described as living in less cohesive groups in which group members are widely dispersed and 'separated by tens of meters most of the time' (van Hooff and van Schaik 1992: 364). While this study does not confirm the magnitude of separation within patas groups, the data, none the less, support the point that vervets are generally less dispersed than patas monkeys.

The estimates of group spreads and interindividual distances do not support the hypothesis that the differences in dispersion between vervets and patas monkeys are caused by differences in predation. According to the predation hypothesis, the smaller group spreads and interindividual distances of vervets occur because vervets are at high risk of predation and patas are at low risk. At this study site, however, neither species can be argued to be at low risk of predation. Females in both species died of predation, and the

same predators occurred in the home ranges of both vervets and patas. The more numerous items of hard evidence of predation in vervets, that is, remains of monkeys, could perhaps be taken to suggest that vervets suffer greater predation than patas. However, the larger size of the home range of the patas group (100 times the size of the home range of the vervet group) makes it much more difficult both to find the remains of patas monkeys that have disappeared and to find the group within the 72-h time limit for categorizing an apparently healthy female's disappearance as suspected predation. In support of the latter statement, the patas group was found most frequently on 5 days per month, not sufficiently often to determine probable cause of death for most females. In contrast, the vervet group was found most frequently on 10 days per month, enough to be within the 72-h time limit for classifying disappearances of apparently healthy females as suspected predation. With twice the annual mortality rate of female vervets (Isbell and Young, unpublished data), it is even possible that female patas suffer greater predation than female vervets.

The predation hypothesis is further undermined by the differences in dispersion in the same group of vervets using two different habitat types within their home range. It is difficult to argue that predation pressure differs significantly within the 40-ha home range of the vervet group during the day when the vervets are foraging. Predators typically have larger home ranges than their prey and, although two of the potential predators of vervets (servals and caracals) are apparently more constrained than the other predators to one or the other habitat type (Table 10.1), they do not leave a void but instead replace each other. There is no indication that the riverine habitat presents a barrier to other predators.

The comparison between species in group spreads and interindividual distances is, however, consistent with the food distribution hypothesis. Food trees of vervets in *A. xanthophloea* habitat are more clumped than foods of both vervets and patas in *A. drepanolobium* habitat (Pruetz and Isbell 2000). Moreover, distances between food sites are shorter in the home range of the vervets than in the home range of the patas monkeys. As predicted by the food distribution models, vervets were more spatially cohesive than patas, and more spatially cohesive in *A. xanthophloea* habitat than in *A. drepanolobium* habitat. Furthermore, distances between neighbors mirrored quite well the distances between food sites for both species.

Animals often have greater interindividual distances while foraging than while engaged in other activities (e.g., spider monkeys

(*Ateles belzebuth*): Klein and Klein 1975, squirrel monkeys (*Saimiri oerstedii*): Boinski 1987). The assumption is that they spread out to reduce competition with each other, even to the extent of increasing their vulnerability to predators (Boinski *et al.* 2000). We know of no studies that have actually examined food intake of individuals at different interindividual distances, however. In the absence of such data, the alternative explanation, that foraging requires the mapping of interindividual distances onto inter-food distances whereas other activities do not, cannot be ignored (see also Phillips 1995).

To conclude, we suggest that vervets and patas do not need to be particularly sensitive to predators as they forage because they feed during the day when most of their predators, including leopards, their most deadly predator, are least active.

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