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Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution

Abstract The effect of food resources on behavior has been difficult to measure. Here we use animals themselves to describe "effective" food abundance and distribution by comparing, relative to where individuals stopped to eat, movements of (1) adult females living in a small group of vervet monkeys (*Cercopithecus aethiops*) with those living in a large group and (2) vervets and patas monkeys (*Erythrocebus patas*). Although females in the large vervet group travelled farther and stopped to eat more often than females in the small vervet group, these differences resulted from foraging in *Acacia drepanolobium* habitat. In *A. xanthophloea* habitat, females in the large group travelled less far, travelled shorter distances between foods, and stopped as often as females in the small group. Greater foraging costs of females in larger vervet groups may be offset by access to home ranges of better quality. Compared to patas, vervets travelled shorter distances, moved shorter distances between food sites, stopped less often, and had longer feeding bouts, suggesting that foods of vervets are denser and larger, overall, than foods of patas. When vervets foraged in *A. drepanolobium* habitat, also the habitat of patas, their foraging behavior became more like that of patas. Vervets travelled farther, stopped more often, and spent less time at food sites in *A. drepanolobium* habitat than in *A. xanthophloea* habitat, suggesting that foods are smaller and less usurpable in *A. drepanolobium* habitat. Distance between foods, a component of food distribution, did not increase, however. The critical variable underlying usurpability of foods may be food site depletion time, a temporal measure.

Key words Food resources · Sympatry · Dominance · Intragroup aggression · Group size

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Introduction

Food distribution and abundance have wide-ranging effects on animals, including the foraging behavior of individuals and the quality of competitive relationships within and between groups. Unfortunately, food distribution and abundance have been difficult to estimate, although this has not hindered attempts to do so. Food distribution, for example, has generally been considered in the context of a dichotomy between food that is clumped into patches in which food density is greater than the surrounding area and food that is evenly distributed (Wiens 1976; Southwood 1978). Thus, in studies of the feeding ecology of arboreal primates, for example, individual trees are often considered as patches (e.g., Leighton and Leighton 1982; Symington 1988; White and Wrangham 1988; Whitten 1988; Strier 1989; Chapman et al. 1995). Food distribution has also been estimated separately for each plant species (e.g., Whitten 1983; Saito 1996) or determined by the number of individuals that are able to feed together, with high-density foods that cannot accommodate all group members defined as clumped and foods that allow all group members to feed simultaneously defined as uniform or more widely dispersed (e.g., Shopland 1987; Barton et al. 1996). Foods that are small and widely scattered have also been called dispersed (e.g., Barton 1993).

For multiple reasons, however, it can be difficult to interpret the relevance of such measures to the animals being studied. First, animals usually eat from more than one plant species in a given day, and the actual distribution of their foods will be a composite of all the

species from which they have fed during that time. Second, animals feed on different food items across even short time intervals, and food distribution can change depending on what is being eaten at any particular time. Third, group members may feed simultaneously on multiple species while still remaining a cohesive unit, thus enlarging actual patch size beyond individual plant species. Fourth, several types of food items with different distributions can occur within a given plant species (see Isbell, in press). Fifth, numerical estimates of the patchiness of food distribution are both difficult to measure and strongly dependent upon measurement scale and animal species. Thus, patches may be defined as individual food items at the smallest scale and as entire groves of trees at a very large scale. What is clumped on one scale, however, may be dispersed on another scale for the same animal species. Similarly, what is clumped for one animal species may be more widely distributed for another (e.g., smaller) animal species. Scale is also determined by particular research questions. For instance, if one is interested in the ability of individuals to monopolize or usurp foods, the appropriate scale is likely to be far smaller than the scale at which entire groups deplete patches or monopolize or usurp foods from other groups. These first five problems are mainly difficulties in estimating absolute measures of food distribution and abundance. Finally, although it is assumed that our judgement about which items are food coincides with food distribution relative to the animals themselves, animals may make foraging choices within a food type that are not discerned by the researcher sampling at a given time, e.g., decisions involving fruit ripeness or leaf chemistry (Glander 1978), neighbor relations (resource depletion) (Packer and Pusey 1985), individual preferences, or plant induced defense (for a particularly unexpected example, see Isbell, in press). Patchiness, therefore, is "organism-defined, and must be considered in terms of the perceptions of the organisms rather than those of the investigator" (Wiens 1976).

Food distribution and abundance should not therefore be assessed independently of the animals themselves. One way to use animals themselves to make inferences about their foods is to sample their movements relative to where they eat. By measuring the distances individuals move between their food sites and how long they stay at their food sites, one can infer qualities of foods that are presumably relevant to the animals themselves, and that are independent of external decisions of time and scale. Thus, shorter distances between foods should reflect denser foods, and longer distances, more widely dispersed foods (Table 1). Similarly, longer times at food sites should reflect larger foods or longer handling times, and shorter times at food sites should reflect smaller foods or shorter handling times. Foods that are large or require longer handling times are more likely to be usurpable by higher-ranking individuals. Essentially, what we propose are estimators of "effective" resource distribution and abundance, as opposed to absolute measures, which are fraught with technical difficulties, and which may be biologically inappropriate.

Vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) are ideal species with which to address questions about the influence of food distribution and abundance on behavior. The two primate species are probably more closely related to one another than they are to any other guenon (Disotell 1996), they are broadly sympatric in some parts of their biogeographical ranges, and adult females overlap in body size (vervets: 2.5–5.3 kg, patas: 4.0–7.5 kg; Haltendorth and Diller 1977; Turner et al. 1997). Despite their recent common phylogenetic history, female social relationships differ in these two species. Although both species live in cohesive, female-resident social groups, female vervets have stable, linear dominance hierarchies (Seyfarth 1980; Whitten 1983), whereas female patas monkeys have less clearly defined dominance hierarchies (Cords 1987; L.A. Isbell and J.D. Prueta, unpublished data). In addition, the home ranges of patas monkey groups can be up to 100 times larger than those of vervet groups of similar size (Chism and Rowell 1988; Isbell et al. 1990; L.A. Isbell, in press). These differences are presumed to be driven by differences in food distribution and abundance. Although both vervets and patas feed heavily on gums, vervets also feed on fruits, seeds, and inflorescences, which can often be eaten in large quantities without moving, whereas patas feed more heavily on arthropods, which are often found while moving (Struhsaker 1967; Whitten 1983; Chism and Rowell 1988; Chism and Wood 1994; Isbell, in press).

These differences in female social relationships and home range size suggested that the foods of vervets and

	Characteristic	Meaning
Table 1 Suggested biological meanings of measured foraging characteristics	Distance moved per unit time:	Overall habitat richness
	Short distances:	High food abundance
	Long distances:	Low food abundance
	Time per patch (inverse of # of moves):	Richness ("size") of individual food sites
	Short time:	Small food size; short handling times
	Long time:	Large food size; long handling times
	Distance between food sites:	Dispersion or density of foods
	Short distances:	Foods more clumped; high food density
	Long distances:	Foods more widely dispersed; low food density

patas would differ in predictable ways that would also be reflected in the movements of individuals as they foraged. Specifically, we predicted that vervets would move shorter distances between foods and would stay longer at food sites than patas. These movements would presumably reflect foods that are denser and more usurpable on the one hand (the foods of vervets) and foods that are more widely dispersed and less usurpable on the other (the foods of patas). We also predicted that vervets and patas would forage more similarly (though not identically) when they use the same habitat than when they use different habitats, the rationale being that habitats influence and constrain the foraging options that are available. Finally, we predicted that, as is generally true for primates that feed heavily on plant reproductive parts, the larger group of vervets would travel farther per unit time than the smaller group [it has already been established that larger groups of patas do not travel significantly farther than smaller groups (Chism and Rowell 1988)]. Here we test these predictions by examining the movements of adult females relative to where they stopped to eat their foods.

Methods

Study site and species

The study was conducted as part of an ongoing comparative project at Segera Ranch (36°50′E, 0°15′N; elevation 1800 m) on the Laikipia Plateau in north-central Kenya. Segera Ranch is a privately owned cattle ranch and conservation area that supports a wide diversity of wild animals, including over 30 species of large mammals. The ecosystem is semi-arid, with mean annual rainfall of approximately 600 mm, although this varies considerably from year to year. Two major habitat types occur in the study area: riverine areas support woodlands dominated by *Acacia xanthophloea* but that include a smaller woody shrub layer (*Carissa edulis*, *Euclea divinorum*), and, 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 4m or less (Young et al. 1997; Isbell, in press).

Two groups of vervets and one group of patas were studied intensively, and all individuals were habituated to the presence of observers. All vervets were individually identified by natural markings and characteristics. All adult female patas were identified initially with hair dye sprayed on their pelage with a SuperSoaker 300 water gun (Larami Corp.) and then later identified by natural markings and characteristics. It was possible to determine consis-

tent, stable dominance ranks prior to the collection of data presented here for vervets, but not for patas; agonistic interactions were recorded throughout the study to monitor potential changes in status.

The vervet groups live along the Mutara River in adjacent home ranges which are defended against incursions by each other and additional neighboring groups. Both groups of vervets sleep and forage in *A. xanthophloea* habitat but also forage in adjacent *A. drepanolobium* habitat. The patas group is restricted to *A. drepanolobium* habitat.

Data collection

Data on movements were collected from July 1993 until December 1994, excluding July 1994. The analyses presented here are based on data collected over a shorter 11-month period (January–December 1994, excluding July; the first 6 months of data were excluded to increase reliability). Data were collected by J.D.P. on all 11 adult females in the two groups of vervets (including one adult female who matured during the study; Table 2) and all 15 adult females in one group of patas (8–13 adult females in any one month; monthly sample sizes varied mainly because of difficulty in locating particular individuals). Each group was systematically observed on 4 days each month. During each of the 4 days, each adult female was sampled for, ideally, 30 min beginning at the top of the hour. With vervets, the order of sampling was predetermined to allow each female to be sampled once in the morning or once in the afternoon. This order was different each sampling day within each month so that each female was sampled evenly between morning (0800–1200 hours) and afternoon blocks (1200–1600 hours) during each month. With patas, a similar predetermined order of sampling was abandoned because individuals were difficult to locate in time to sample on the hour. Adult females were therefore sampled opportunistically on the hour and were sampled for 30 min without replacement in the morning or in the afternoon.

During each focal sample, the observer recorded the distance the focal individual moved between each of two successive food sites. A move was defined as any locomotion involving the hindlimbs. A food site was defined as any location at which an adult female stopped to eat food. Food sites could be as small as a single arthropod or as large as several branches with flowers as long as all were within either arm's reach. Food sites therefore differed from "patches" (as defined above) in that the movements of the animals, rather than the relative density or distribution of food, determined the scale of measurement.

Distances between foods were estimated by eye while in close proximity (most often < 10 m) to the focal animal. These distances could also include non-food-related movements, such as moving to groom another individual. Because there was no way of knowing whether the animal's movements for apparently non-food related reasons included assessment of foods nearby, this potential bias could not be avoided. The accuracy of the observer's ability to estimate variable distances was checked each month at the research camp by estimating distances between flags set up by another person (monthly $n = 40$–80). Estimates of distances were within 5% of true distances in each of the 11 months involved in this analysis (data collected during the first 6 months were excluded from analyses because estimates were more than 5% off true distances in two of these months).

Table 2 Age/sex compositions of the study groups at the beginning (January 1994) and end (December 1994) of the study period

	GG (small vervet group)		PG (large vervet group)		LP (large patas group)	
	Beginning	End	Beginning	End	Beginning	End
Adult males	2	2	10	8	1	1
Adult females	2	2	9	8	12	12
Immatures	6	4	11	10	20	28
Total	10	8	30	26	33	41

When the focal animal stopped to eat, the food species and item eaten were recorded whenever they were clearly observed. Unidentified foods were described as fully as possible. The habitat type in which the focal animal moved was classified as *A. drepanolobium*, *A. xanthophloea*, or, when the focal animal moved within both habitats during a given sample, both *A. drepanolobium* and *A. xanthophloea*. When individuals moved out of sight, their time out of sight was recorded, and their minimum travel distance was estimated based on where they disappeared and where they reappeared.

As part of a separate study, durations of feeding bouts for individuals in the large vervet group and the patas group were recorded. Feeding bouts began when the animal began feeding, chewing, swallowing, or making hand-to-mouth or mouth-to-substrate movements. Bouts ended when the animal stopped feeding for more than 10 s, moved two body lengths between foods, or changed food types. During each feeding bout, the number of bites was also recorded. A bite was operationally defined as one hand-to-mouth or one mouth-to-substrate movement. Note that each feeding bout is not necessarily identical to feeding at each food site. These data are presented because, unlike the measure of minutes per food site (see below), they exclude non-feeding times and therefore may be more representative of actual time spent feeding at food sites (although they may err in the opposite direction by underestimating times at feeding sites). They also provide estimates of numbers of items eaten within each feeding bout.

Statistical analyses

All data were entered into Microsoft Excel and imported into JMP (SAS Institute) for statistical analyses. Before running statistical tests, we obtained mean scores for each adult female from all respective focal samples. Parametric tests were conducted on these individual means (type I ANOVA) and were two-tailed unless specified.

The following means (per female) were used in the statistical analyses below: total distance travelled in 30 min (total travel distances do not include estimates of minimum distances moved while out of sight; 90% of all focal samples had less than 20% of meters estimated while out of sight, the average focal sample included less than 7% of travel distance out of sight, and 72% of all focal samples had no meters moved while out of sight), number of moves between food sites in 30 min, distance moved between food sites, and minutes spent at each food site. Distance between food sites was calculated by dividing the total distance travelled during a 30-min focal sample by the number of moves made to cover that distance. The inverse of the number of moves between food sites (multiplied by 30 min) represents the more intuitive "minutes per food site". This value (and all the others) was calculated for each individual before averaging over all individuals, so the statistics are not the same as for the number of moves made between food sites because the mean of inverses is different from the inverse of the mean (Templeton and Lawlor 1981).

When in habitats characterized as mixed (i.e., observations of focal animals in both habitats), vervets foraged quite similarly to when they were in *A. drepanolobium* habitat (values were within 15% of each other for all traits; all *P* values > 0.20), but very differently than when they foraged in purely *A. xanthophloea* habitat (5- to 7-fold differences in three out of four traits; *P* values for these < 0.001). Therefore, the category of mixed use (by vervets) of both *A. drepanolobium* and *A. xanthophloea* habitats was reclassified for analysis as *A. drepanolobium* habitat.

Of the 566 focal samples conducted between January and December 1994, we excluded all focal samples that were not exactly 30 min ($n = 81$), focal samples with ambiguously identified females or habitat types ($n = 2$), focal samples with obvious errors in estimated moves, e.g., estimated distance out of sight was greater than the estimated total distance ($n = 4$), and all samples for individuals with fewer than three samples in either habitat type ($n = 3$; see below). After these exclusions, 476 focal samples remained for analysis (Table 3).

Table 3 Number of 30-min focal samples per adult female, January–December 1994

GG (small vervet group)	PG (large vervet group)	LP (large patas group)
HGL 35	CRV 26	BOZ 3
NIT 27	CHL 34	CEZ 14
	FRJ 28	DAL 22
	SAL 33	GEO 5
	TOR 28	GYA 12
	MOO 8	MIC 11
	QSO 25	MNT 11
	BUR 23	PEN 20
	MND 3	PIC 28
		REM 3
		REN 5
		SCO 7
		TAZ 15
		VNC 25
		WAR 25

T-tests were conducted on mean feeding bout durations calculated for eight adult female vervets and for two classes of adult female patas, those with infants and those without infants. The adult female patas were compressed into these two classes because the data on feeding bouts were collected on unidentified females and this approach avoided the risk of pseudo-replication.

Results

Comparison between the large and the small vervet group

The large vervet group was more than three times the size of the small vervet group (Table 2). At the beginning of the sampling period, the large vervet group included eight adult females, whereas the small vervet group included only two adult females. This difference remained throughout the study due to the death of one adult female and the maturation of a female in the large vervet group (who then took the dead female's place in the sampling protocol).

As predicted based on theoretical expectations and empirical studies on the general diet of vervets, individual adult females in the large vervet group travelled significantly farther per 30-min sample than did adult females in the small vervet group (large group: $\bar{x} = 82.6$ m ± 6.7 SE; small group: $\bar{x} = 43.8$ m ± 11.1; $F = 6.41$, $P = 0.032$; Fig. 1). This difference was driven by differences in distances travelled in *A. drepanolobium* habitat (large group: $\bar{x} = 138.2$ m ± 12.2; small group: $\bar{x} = 73.4$ m ± 18.0; $F = 6.02$, $P = 0.040$). Unexpectedly, however, individuals in the large group travelled significantly shorter distances than individuals in the small group when they were in *A. xanthophloea* habitat (large group: $\bar{x} = 20.7$ m ± 3.0; small group: $\bar{x} = 40.9$ m ± 13.9; $F = 5.83$, $P = 0.042$).

Individual adult females in the large group made over three times as many moves between food sites per 30-min sample as adult females in the small group (large
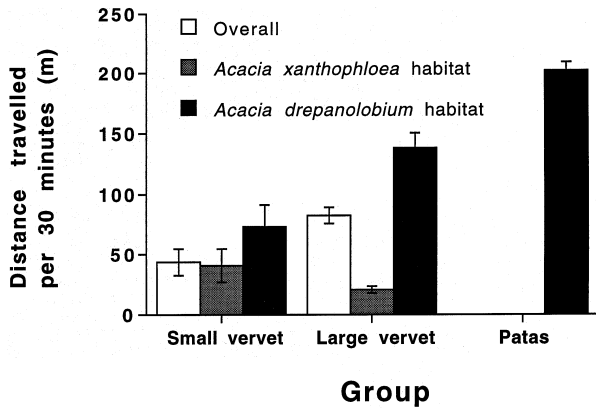
Fig. 1 Intra- and inter-specific differences in mean distances moved by adult female vervet and patas monkeys during 30-min focal samples. Sample sizes are the number of adult females in each group: small vervet group, $n = 2$; large vervet group, $n = 8$; patas group, $n = 13$. *Error bars* are 1 SE
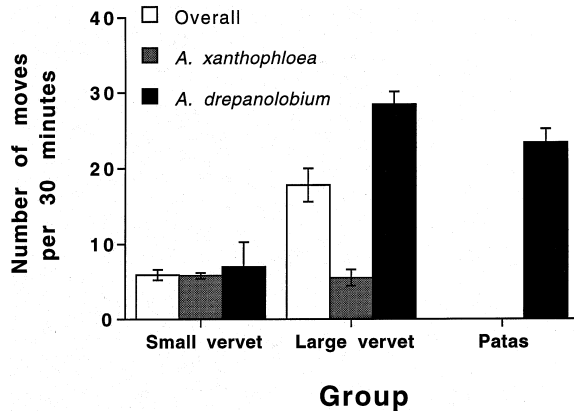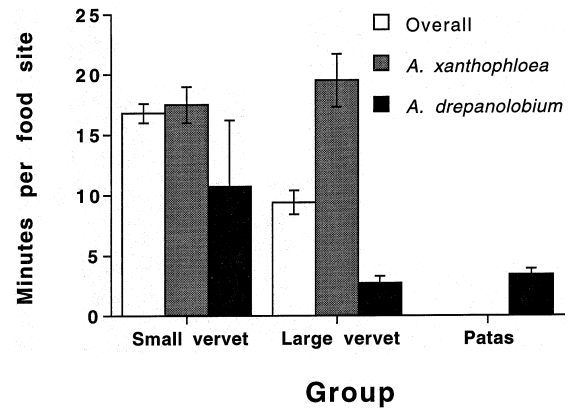

Fig. 3 Intra- and inter-specific differences in time spent at food sites by adult female vervet and patas monkeys

Fig. 2 Intra- and inter-specific differences in mean number of moves per unit time by adult female vervet and patas monkeys

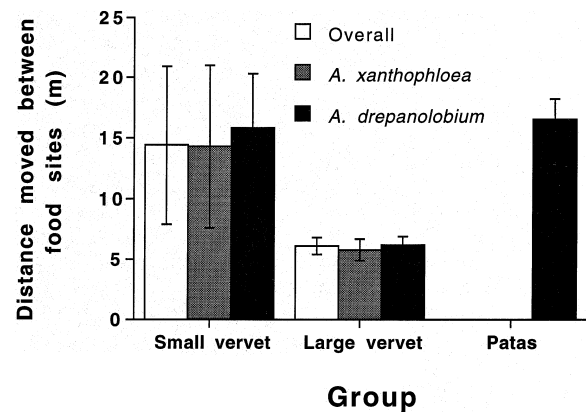**Fig. 4** Intra- and inter-specific differences in distances between food sites by adult female vervet and patas monkeys

group: $\bar{x} = 17.8 \pm 2.2$; small group: $\bar{x} = 5.9 \pm 0.7$; $F = 5.89$, $P = 0.038$; Fig. 2). This was due to differences in number of moves in *A. drepanolobium* habitat (large group: $\bar{x} = 28.7 \pm 1.7$; small group: $\bar{x} = 7.0 \pm 3.3$; $F = 31.85$, $P = 0.0005$). In *A. xanthophloea* habitat this difference did not exist; adult females in the two groups made similar numbers of moves (large group: $\bar{x} = 5.5 \pm 1.1$; small group: $\bar{x} = 5.8 \pm 0.4$; $F = 0.02$, $P = 0.89$).

More moves per unit time indicates that individuals spent fewer minutes at each food site (this former is the mathematical inverse of the latter). Adult females in the large group spent significantly less time at each food site than adult females in the small group (large group: $\bar{x} = 9.4$ min ± 1.0; small group: $\bar{x} = 16.8$ min ± 0.8; $F = 11.45$, $P = 0.008$; Fig. 3). Again, this was driven by differences in their foraging behavior while in *A. drepanolobium* habitat. In that habitat, adult females in the large group spent significantly less time at each food site than adult females in the small group (large group: $\bar{x} = 2.8$ min ± 0.6; small group: $\bar{x} = 10.7$ min ± 5.5;

$F = 9.95$, $P = 0.014$). In *A. xanthophloea* habitat, individuals in the two groups spent similar time at food sites (large group: $\bar{x} = 19.5$ min ± 2.2; small group: $\bar{x} = 17.5$ min ± 1.5; $F = 0.19$, $P = 0.68$).

Finally, adult females in the large group travelled less than half the distance between food sites as adult females in the small group (large group: $\bar{x} = 6.1$ m ± 0.7; small group: $\bar{x} = 14.4$ m ± 6.5; $F = 8.60$, $P = 0.017$; Fig. 4). This difference was consistent regardless of habitat type (*A. drepanolobium*: large group: $\bar{x} = 6.2$ m ± 0.7; small group: $\bar{x} = 15.8$m ± 4.4; $F = 18.06$, $P = 0.003$; *A. xanthophloea*: large group: $\bar{x} = 5.8$ m $+ 0.9$; small group: $\bar{x} = 14.3$ m ± 6.7; $F = 6.71$, $P = 0.032$).

These results suggest that foods in the home ranges of the vervet groups differ in density and size. In *A. xanthophloea* habitat, the preferred habitat of vervets, foods in the two home ranges are effectively similar in size, but denser in the home range of the large vervet group. In *A. drepanolobium* habitat, foods in the home range of the larger vervet group are effectively smaller but still denser than foods in the home range of the small vervet group.

Examination of the diets of the small and large vervet groups shows that the small vervet group fed more heavily than the large group on gum, regardless of habitat (although this might be biased by relatively small sample sizes for the small vervet group; Table 4). The percentage of gum in the small group's diet may have been higher; many of the observations of unidentified plant parts were of *A. xanthophloea* in months when gum was a large percentage of their identified diet. Gum is a preferred food item of vervets, particularly the gum of *A. xanthophloea* (Wrangham and Waterman 1981). The small group fed on fruits, flowers, and seeds less often than the large group, also regardless of habitat. The small group was not observed to eat swollen thorns, or grasses in either habitat.

Comparison between vervets and patas

Because of the potential for differences between species to be confounded by group size effects (such as those above), analyses that follow compare only the larger of the two vervet groups with the patas group. The patas group was close in size to the large vervet group at the beginning of the study (Table 2). By the end of the study, the patas group was 36% larger than the large vervet group, mainly due to recruitment of infants. Although female membership changed over the study period (three adult female patas were lost and three adult females were recruited through maturation; see above for vervets), the number of adult females remained the nearly same in both groups.

As predicted based on theoretical expectations and observed species differences in home range size, adult female vervets moved less than half the distance between food sites (vervets: $\bar{x} = 6.1$ m ± 0.7; patas: $\bar{x} = 16.5$ m ± 1.7; $F = 21.94$, $P = 0.0001$; Fig. 4) and less than half the total distance per unit time than did adult female patas (vervets: $\bar{x} = 82.6$ m ± 6.7; patas: $\bar{x} = 201.9$ m ± 7.1; $F = 128.2$, $P < 0.0001$; Fig. 1). Vervets made fewer moves per unit time than did patas, although this difference was not statistically significant at the 0.05 level (vervets: $\bar{x} = 17.8 \pm 2.2$; patas: $\bar{x} = 23.3 \pm 1.8$; $F = 3.79$, $P = 0.064$; Fig. 2), and vervets spent significantly longer at each food site (vervets: $\bar{x} = 9.4$ min ± 1.0; patas: $\bar{x} = 3.4 \pm 0.5$; $F = 37.76$, $P < 0.0001$; Fig. 3).

These latter two results were substantiated by the separate data set that excluded non-foraging behavior. Vervets had longer feeding bouts (vervets: $\bar{x} = 28.9$ s ± 2.9; patas: $\bar{x} = 12.0$ s ± 2.0; $t = 2.71$; $df = 8$; $P < 0.03$) and more bites/bout than patas (vervets: $\bar{x} = 8.64 \pm 0.96$; patas: $\bar{x} = 3.92 \pm 0.59$; $t = 2.32$; $df = 8$; $P < 0.05$). Feeding bouts were shorter than time spent at feeding sites partly because several individual bouts could occur at a given feeding site if they were separated by more than 10 s of non-feeding behavior.

In *A. drepanolobium* habitat alone, vervets and patas converged in the number of moves between food sites (vervets: $\bar{x} = 28.7 \pm 1.7$; patas: $\bar{x} = 23.3 \pm 1.8$; $F = 3.93$, $P = 0.061$; Fig. 2) and in time spent at each food site (vervets: $\bar{x} = 2.7$ min ± 0.6; patas: $\bar{x} = 3.4$ min ± 0.5; $F = 0.78$, $P = 0.39$; Fig. 3). Nonetheless, vervets still travelled almost one-third as far per unit time as patas (vervets: $\bar{x} = 138.2$ m ± 12.2; patas: $\bar{x} = 201.9$ m ± 7.1; $F = 23.71$, $P < 0.0001$; Fig. 1). More surprising, vervets still travelled less than half as far between foods as did patas (vervets: $\bar{x} = 6.2$ m ± 0.7; patas: $\bar{x} = 16.5$ m ± 1.7; $F = 19.31$, $P = 0.0003$; Fig. 4).

How do these results correspond with what the animals actually ate? Gum and free-living arthropods and other animals constituted at least 20% of the diet of patas (Table 4). Swollen thorns of *A. drepanolobium*, a

Table 4 Proportion of food items in the diets of vervets (large group) in *Acacia xanthophloea* and *A. drepanolobium* woodlands and patas in *A. drepanolobium* woodland in Laikipia, Kenya. Proportions are means weighted equally by month

	Vervet groups				Patas group
	Large	Small	Large	Small	
Habitat	*A. xanthophloea*		*A. drepanolobium*		*A. drepanolobium*
Food:					
Gum	38.9%	56.8%	17.0%	62.0%	13.8%
Swollen thorns	0.7	0	11.0	0	14.5
Animals (mostly arthropods)	0.8	0.6	1.8	8.3	6.7
Grasses	9.4	0	6.7	0	0.4
Fruits	11.8	2.2	3.4	0	6.5
Flowers	9.2	5.9	4.0	0.6	1.5
Seeds	8.3	12.1	6.6	6.6	0.6
(Fruits, flowers, seeds combined)	(29.3)	(19.3)	(14.0)	(7.2)	(8.6)
Leaves	1.6	0	6.3	0	3.0
Unknown plant parts	2.4	20.2	7.4	10.5	10.2
Other	7.2	0.6	5.8	0	1.8
Unidentified	*9.8*	*1.6*	*29.9*	*12.0*	*41.0*
Total	100.1%	100.0%	99.9%	100.0%	100.0%
Sample size	3429	318	679	58	5079

major component of the patas diet, also include animals, however (Hocking 1970; Isbell, in press), and may be eaten for this reason. The estimated percentage of gum and animal matter in the patas diet when the arthropod contents of swollen thorns are included was minimally 35% (59% of all identified foods). A previous study using different methods estimated gum and animal matter to be as high as 70% (Isbell, in press). The diet of vervets in *A. drepanolobium* (compared to *A. xanthoph-loea*) was more similar to the diet of patas in *A. drepanolobium*. Vervets ate fruits and flowers more often in *A. xanthophloea* habitat but ate swollen thorns more often in *A. drepanolobium* habitat. In *A. drepanolobium* habitat, vervets ate grasses and seeds more often, and animals less often, than patas.

Perhaps the most striking similarity between the two species was the high percentage of unidentified food items in their diets while in *A. drepanolobium* habitat. In this habitat, unidentified food items constituted the single largest category for both patas (41%) and vervets (30%). In contrast, unidentified food items comprised only 10% of the vervet diet in *A. xanthophloea* habitat. It is unlikely that this difference was a result of poorer visibility (for the observer) in *A. drepanolobium* habitat. If the proportion of focal samples in which individuals moved out of sight can be used as an indication of visibility, it appears that there was no consistent effect of habitat on visibility. Vervets moved out of sight (for short periods of time) during 26.0% of focal samples in *A. xanthophloea* habitat ($n = 154$), and during 49.1% of samples in *A. drepanolobium* habitat ($n = 114$). However, patas (in *A. drepanolobium* habitat) moved out of sight even less frequently than vervets in either habitat (17.5%; $n = 206$). The high proportion of unidentified foods for both primate species in *A. drepanolobium* habitat more likely reflects diets high in foods that are difficult to identify because they are small and quickly consumed.

Discussion

The utility of animal movements as bioassays of qualities of food resources

Using the movements of animals relative to their food sites avoids the problems inherent with current approaches of estimating the qualities of foods as outlined above. Since observers routinely watch focal animals move during sampling (indeed, focal sampling requires continuous observation; Altmann 1974), it should be relatively easy to estimate how far animals travel between foods during these movements as long as focal sampling is at all possible. Moreover, this approach readily allows comparisons across individuals, groups, and species.

Distances between foods as an estimate of food density

For species that consistently move ahead while foraging, food density can be estimated by measuring the distances individuals travel from one food site to the next. Travel distance between sites should vary depending on differences in food density, with poorer habitats requiring greater travel between foods, and on differences in animals' use of the habitat, with slower rates of resource depletion occurring in habitats with greater densities of foods (Table 1). Travel distances between food sites should be independent of group size in swath feeders, but may easily increase with group size when food sites in one's path are depleted before arrival at the (former) food sites, thereby increasing the distance required to reach the next still-existing food site (see below).

Number of moves between foods and food site depletion time

The richness of food sites can be estimated by the total number of moves that individuals make between food sites. The more quickly a food site is depleted, the earlier an animal moves on, and the more moves the animal makes per unit time. Food site depletion times should be quicker for individuals when food sites (1) are inherently smaller in size, (2) involve shorter handling times, or (3) have already been visited by other individuals. Food site depletion time (FSDT) may be the single most important characteristic of food resources that affects female social relationships within groups.

Total distance per unit time and travel costs to individuals

Finally, travel costs to individuals can be estimated by calculating the total distance that individuals travel per unit time (Janson and van Schaik 1988; Wrangham et al. 1993; Chapman et al. 1995; Janson and Goldsmith 1995). Distances should be greater in one area than another when food sites are poorer in quality, i.e., smaller or less abundant. Total distances may also be greater for individuals in larger than in smaller groups simply because larger groups have more mouths to feed. Estimating travel costs to individuals is preferable to the more frequently calculated distances an entire group moves per unit time (e.g., Struhsaker 1975; Isbell 1983; Janson 1988), because it has greater potential to elucidate fitness consequences for individuals (L.A. Isbell, J.D. Pruetz, M. Lewis and T.P. Young, unpublished work).

Differences within species

Compared to the small vervet group, adult females in the large vervet group travelled nearly twice as far per unit

time, spent about half as long at each feeding site, and made more than three times as many stops for food, but they travelled less than half as far between feeding sites. This was almost entirely driven by differences in the use of *A. drepanolobium* habitat; in *A. xanthophloea* habitat, the two groups moved nearly the same number of times and stayed as long at each food site. In *A. xanthophloea* habitat, the large group actually travelled half as far per unit time as the small group and half as far between food sites. Interestingly, distances between foods were consistently shorter for the larger group regardless of habitat type.

These results suggest that although FSDT is similar in the parts of their home ranges that include *A. xanthophloea*, foods in the home range of the small group are less dense (i.e., the habitat is of lower quality), even in the small group's core area, than the foods in the home range of the larger group. Alternatively, this variation may not have been due to absolute differences in food resources, but due to differing ways these two groups used those resources, with the smaller group being more selective about which foods they actually ate (although we think this less likely; see Cramer and Gallistel 1997).

It is unlikely that travel distances in the *A. drepanolobium* habitat were greater for the large vervet group because food sites in *A. drepanolobium* habitat are of inherently lower quality for the large group. It is also unlikely that their greater travel distances in *A. drepanolobium* habitat resulted from resources being depleted in the foraging paths of neighbors because (1) distances between food sites were actually shorter for the large group than for the small group in that habitat, and (2) distances between food sites were similar for the large vervet group regardless of habitat. It is more likely that the large group was required to travel farther in *A. drepanolobium* habitat because absolutely more food had to be obtained and the smaller foods in *A. drepanolobium* habitat exacerbated travel costs by providing less food per food site.

These results provide qualified support for the hypothesis that scramble competition for food increases in larger groups of primates that feed primarily on plant reproductive parts (flowers, fruits, and seeds) (Waser 1977; Isbell 1991; Wrangham et al. 1993; Oluput et al. 1994; Chapman et al. 1995; Janson and Goldsmith 1995). However, they also suggest that although larger groups can incur greater foraging costs than smaller groups, they may be able to reduce these costs to some degree by having better quality home ranges than smaller groups (see Wrangham 1980; Cheney and Seyfarth 1987; Robinson 1988; Isbell et al. 1990). Given the demonstrated ability of larger groups to usurp resources from smaller groups in many species (reviewed in Cheney 1987), one possibility for the persistence of small groups is that the presence of small and large groups together represent an evolutionarily stable strategy in which the costs and benefits of living in small groups (inhabiting poorer quality home ranges but minimizing travel costs) are balanced by those of living in large groups (incurring increased travel costs but inhabiting higher quality home ranges).

Differences between species

In almost all measures, vervets and patas differed significantly in their movements. Patas travelled more than twice as far as vervets between food sites, spent one-third the amount of time at food sites, and travelled more than twice as far per unit time. These results suggest that the foods of patas are less abundant, more widely dispersed, and smaller (i.e., less usurpable) than the foods of vervets. These results are consistent with the negative relationship between food abundance and home range size across mammalian species, in general (McNab 1963; Clutton-Brock and Harvey 1977), and the difference between these two species in the stability of the female dominance hierarchy (L.A. Isbell and J.D. Pruetz, unpublished data).

Vervets moved and fed more like patas when they were in *A. drepanolobium* habitat, the habitat to which patas are restricted in the study area, and less like patas when they were in *A. xanthophloea* habitat, the habitat with which vervets are typically associated in East Africa. This is apparent by comparing the large vervet group in each habitat and by comparing vervets and patas in *A. drepanolobium* habitat alone. Adult females in the large vervet group travelled farther, made more moves between food sites, spent less time at each food site, and ate smaller foods more often in *A. drepanolobium* habitat than in *A. xanthophloea* habitat. Differences between vervets and patas in the number of moves made per unit time and the time spent at each food site were greatly reduced when they used the same habitat. Use of the same habitat resulted in a convergence in the foraging and ranging behavior of these two closely related species. These qualities of foods are presented schematically in Fig. 5.

Although vervets foraged more like patas when they were in *A. drepanolobium* habitat, the differences between the two species in total distance moved and distance between food sites were not completely eliminated. One explanation for this is that, like intraspecific differences in vervets, interspecific differences could be driven by a difference in group size. This is unlikely, however, because patas, regardless of their group sizes, have among the longest daily travel distances of any cercopithecine for their body size (Clutton-Brock and Harvey 1977; Chism and Rowell 1988). A more likely explanation is that patas rely more heavily than vervets on small, widely dispersed foods, which require longer travel distances to obtain sufficient food per individual (Chism and Rowell 1988; Isbell, in press; see also above for the same trend in vervets). Patas have limb adaptations that increase stride length (Hurov 1987; Hildebrand 1988; Strasser 1992; Gebo and Sargis 1994), enabling them to move more quickly per unit time than vervets. Most of the locomotor differences between these
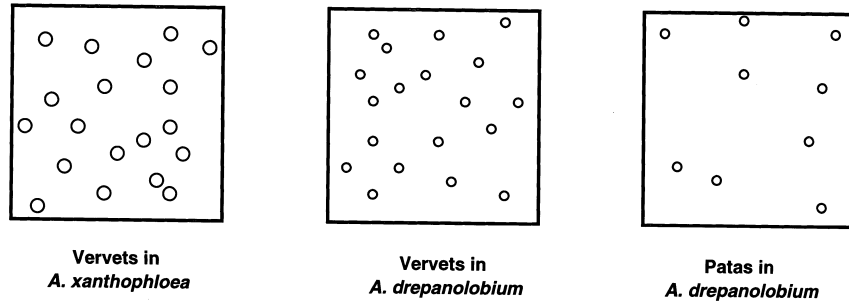
Fig. 5 A schematic view of the variation in the size and distribution of food sites of a large group of vervets in *Acacia xanthophloea* and *A. drepanolobium* habitats and a group of patas in *A. drepanolobium* habitat. Each *circle* represents a food site at which an animal can feed without having to travel. *Larger circles* represent food sites that have longer depletion times (FSDT); *greater distances between circles* represent effectively more widely separated (less dense) food sites. Vervets in *A. xanthophloea* and *A. drepanolobium* habitat feed on foods that are similar in distribution but that differ in FSDT, with foods in *A. xanthophloea* having longer FSDT. Vervets and patas in *A. drepanolobium* habitat feed on foods that are similar in FSDT but that differ in distribution, with patas having effectively more widely separated foods

two species occur while foraging: patas spend about four times longer than vervets in foraging while walking (Isbell et al., in press). The ability to move long distances rapidly might also be advantageous for patas because they live in habitats with few trees or bushes that serve as appropriate refuges from predators. Patas and vervets do not differ, however, in the time they spend in running (Isbell et al., in press).

Food distribution and its relation to food site depletion time (FSDT)

Noticeably absent from this discussion is consideration of food "patchiness". This may be surprising given that at least two socioecological phenomena have been linked to food patchiness. Species that have more clearly defined dominance hierarchies also show greater increases in day range length with increasing group size, whereas species that have only weakly defined dominance hierarchies show no group size effect on day range length (Isbell 1991). The former association has been hypothesized to result from feeding on foods with a clumped distribution; the latter, from feeding on foods with a dispersed distribution (Isbell 1991).

The hypothesized reason that species feeding on clumped resources have greater daily travel distances when in larger groups has been that patches of foods are more quickly depleted by larger groups, forcing them to visit more patches per day (Waser 1977; Isbell 1991). All else being equal (such as overall food abundance, which may instead differ between groups of different sizes; see above), this would force larger groups to travel farther each day. Conversely, species feeding on dispersed resources would feed in a swath with little overlap of in-

dividual foraging paths, and larger groups would simply forage in broader swaths, and not have longer daily travel distances. This is largely consistent with the foraging and ranging patterns of vervets and patas (Chism and Rowell 1988; this paper).

Dominance heirarchies are likely to be influenced by patchiness on a very different and smaller scale (Schaub 1995; but see Whitten 1983). Foods are more likely to be worth fighting over if they cannot be quickly depleted at a given individual feeding site (Post et al. 1980; Shopland 1987). It is often presumed that clumped resources are more readily monopolizable or usurpable than dispersed resources (e.g., Southwick 1967; Chalmers 1968; Robinson 1981; Whitten 1983; Monaghan and Metcalfe 1985; Harcourt 1987; Altmann and Muruthi 1988; Boccia et al. 1988; Brennan and Anderson 1988; Saito 1996). However, the variable of interest here is probably not clumpiness of foods per se, which is a spatial measure, but rather the depletion times of individual feeding sites, such as those reported here (see also Shopland 1987), which is a temporal measure.

Clumpiness is only one of the variables that can affect FSDT. Because of this, and also because food distributions are difficult to measure and perhaps less than useful, we suggest moving away from attempts to describe food distributions independently of animals, and toward describing characteristics that can affect FSDT, such as food size, handling time, number of animals feeding at the same spot, or latency to move away from food sites. These measures are easily obtainable with experimental (see Janson 1996) and descriptive studies.

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Communicated by P.M. Kappeler