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Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats

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Abstract Food distribution is hypothesized to be important in determining the nature of female relationships within social groups of primates. When food limits female reproductive success, spatially clumped foods are expected to produce strong, linear dominance hierarchies within groups, whereas more spatially dispersed foods are expected to produce weaker or non-existent dominance hierarchies. The association between food distribution and competitive relationships presumably occurs because clumped foods are usurpable but dispersed foods are not. We examined the spatial distribution of food patches (trees) and patch size relative to feeding behavior and agonistic interactions in vervets and patas monkeys, two closely related and sympatric species that nonetheless differ in the strength of the female dominance hierarchy. Food patches of both patas monkeys and vervets were small in size and randomly distributed in *Acacia drepanolobium* habitat. In contrast, in *A. xanthophloea* woodland, the habitat type that was exclusively used by vervets, food patches were larger and more spatially clumped. These similarities and differences between and within species were correlated with similarities and differences in the strength and linearity of their dominance hierarchies. Patas monkeys and vervets in *A. drepanolobium* habitat had dominance hierarchies that were weakly defined because there were relatively few agonistic interactions between females. By

contrast, in *A. xanthophloea* habitat, vervets had a stronger, linear dominance hierarchy characterized by a higher rate of agonistic interactions over food. The covariation of agonistic interactions with patch size is discussed in relation to depletion time, another characteristic that may covary with food distribution, and resource renewal rate, an important determinant of agonistic interactions in insectivorous birds, fishes, insects, and mammals.

Keywords Dominance hierarchy · Contest competition · Vervets · Patas monkeys · Hierarchy · Food distribution · Patch size · Renewal rate

Introduction

A potential cost of living in groups is competition with group members over food resources (Alexander 1974; Wrangham 1980; Pulliam and Caraco 1984). Interference, or contest competition, in which dominant individuals usurp resources from others (i.e., subordinates, by definition) through overt behavioral acts such as supplantation or aggression (Schjelderup-Ebbe 1922; Drews 1993), has long been a major focus in behavioral research but has only relatively recently received attention from behavioral ecologists. For group-living animals, agonistic interactions that are sufficiently frequent and consistent between competitors allow observers to derive linear dominance hierarchies based on the outcome of those agonistic interactions (Martin and Bateson 1993). When agonistic interactions are infrequent or inconsistent between competitors, however, it becomes difficult to rank individuals relative to each other. In such cases, hierarchies are considered to be weaker and less linear or even non-existent.

Although the processes of competitive interactions between individuals have been extensively studied in taxa ranging from plants to primates, the underlying ecological factors that elicit competition have become a focus of research in behavioral ecology largely since

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Trivers' (1972) seminal paper clarified the importance of ecological factors in determining reproductive success. For females, access to food is often critical to reproductive success. In many taxa, females avoid direct, or interference, competition for food by living solitarily. Nonetheless, stable groups of females do occur in many taxa, including mammalian taxa such as viverrids, carnivores, cetaceans, and primates. Living in such groups can interfere with gaining access to food. Females in groups are thus expected to compete with each other over foods when it is worth doing so. The question is: what ecological conditions favor competition over foods?

Generally, although different foods may have different specific properties, the value of competing over foods is hypothesized to increase as foods become more spatially clumped (Wrangham 1980; Whitten 1983; Harcourt 1987; van Schaik 1989; Isbell 1991), larger in patch size (van Schaik 1989), less divisible (Elgar 1986), more slowly renewed (Waser and Waser 1985; Blanckenhorn 1991; Grant and Kramer 1992; Bryant and Grant 1995), or more slowly depleted (Janson 1990; Isbell et al. 1998; J. Mathy and L.A. Isbell, unpublished data).

Empirical support is growing for the hypothesis that clumped foods are more easily usurped than dispersed foods (but for evidence that this may be mostly an artifact of increased depletion time see Isbell et al. 1998; J. Mathy and L.A. Isbell, unpublished data). Both natural and experimental studies, particularly of primates, have found that aggression increases when foods become more clumped in space (rabbits, *Lepus europaeus*: Monaghan and Metcalfe 1985; capuchins, *Cebus capucinus*: Phillips 1995; bonnet macaques, *Macaca radiata*: Boccia et al. 1988; rhesus macaques, *M. mulatta*: Southwick 1967; Brennan and Anderson 1988; long-tailed macaques, *M. fascicularis*: Sterck and Steenbeek 1997; Japanese macaques, *M. fuscata*: Saito 1996; vervets, *Chlorocebus aethiops*: Wrangham 1981; baboons, *Papio anubis*: Barton 1993; Johnson 1989). Variation in the spatial distribution of foods is hypothesized ultimately to cause variation in the nature of dominance relationships within groups (Wrangham 1980, 1987; van Schaik 1989; Isbell 1991; van Hooff and van Schaik 1992; Sterck et al. 1997).

Variation in female competitive relationships also appears to have a strong phylogenetic component in primates. Within the family Cercopithecidae, for example, most species of baboons and macaques have stable, linear dominance hierarchies (Hausfater 1975; Seyfarth 1976; Deag 1977; Samuels et al. 1987; Chapais 1988; Barton and Whiten 1993), whereas within the Colobidae most species of colobus monkeys and langurs do not (Struhsaker 1975; Hrdy and Hrdy 1976; Borries 1993; Sterck 1997). It has been difficult to determine whether the variation in female relationships results from phylogenetic inertia or ecological conditions, or a combination of the two through "niche conservatism" (Harvey and Pagel 1991).

Vervets and patas monkeys (*Erythrocebus patas*) are phylogenetically closely related primate species (Disotell

1996) that differ in the nature of female competitive relationships (Isbell and Pruettz 1998; Pruettz 1999). Despite their close evolutionary history, female vervets have clearly defined, linear dominance hierarchies that are stable over long periods of time (Seyfarth 1980; Whitten 1983; Isbell and Pruettz 1998) whereas unprovisioned patas monkeys have weaker, non-linear dominance hierarchies that are unstable over long periods of time (Isbell and Pruettz 1998). This difference cannot be explained easily by phylogenetic inertia. Although vervets and patas monkeys are apparently more closely related to each other than to any other species (Disotell 1996; Groves 2000), vervets differ from patas monkeys in their expression of female relationships while the more distantly related guenons apparently do not (Rowell 1988; Cords 2000).

In most primate species with weak or non-existent dominance hierarchies, females also emigrate from their natal groups. The relative lack of familiarity with non-kin has also been suggested to result in weak or non-existent dominance hierarchies (Harcourt 1978; Watts 1985, 1994; Harcourt and Stewart 1987; van Schaik 1989). This does not apply to patas monkeys, however. In both patas monkeys and vervets, females typically remain in their natal groups throughout life. The explanation for differences between female vervets and patas monkeys is likely to be found in their ecology.

In central Kenya, vervets and patas monkeys both feed in *Acacia drepanolobium* habitat, but vervets also feed and sleep in *A. xanthophloea* riverine habitat. This combination of shared and exclusive use of two habitats offers the opportunity to compare foods of the two species in the same habitat and foods of vervets in two different habitats. Moreover, unlike most primate habitats, which have a high diversity of food species and are therefore exceedingly difficult habitats in which to measure the distribution of foods, the *Acacia* habitats of vervets and patas monkeys are low in food species diversity. If the spatial distribution of foods has an effect on agonistic interactions, it is likely to be most obvious in such simple systems.

Here we examine feeding behavior, food distribution, patch size, and agonistic interactions in female vervets and patas monkeys living in simple habitats. Knowing that patas monkeys and vervets differ in the strength of their dominance hierarchies, we predicted that the major foods of patas monkeys would be more dispersed than the major foods of vervets, but only relative to the habitat that is exclusively used by vervets. In the habitat that the two species share, we predicted that the major foods of both species would be distributed similarly. We also predicted that if food distribution influences female agonistic interactions, the dominance hierarchy of vervets would be less like that of patas monkeys in the habitat with a more clumped distribution of major foods and more like that of patas monkeys in the habitat with more dispersed major foods.

Methods

Study site and subjects

The study was conducted from July 1993 to August 1995 on Segera Ranch, a commercial cattle ranch and conservation area in the central plains of the Laikipia Plateau, north-central Kenya (36°50' E, 0°15' N, altitude 1,800m). A wide diversity of ungulates and a full complement of potential predators on primates occur on Segera, including lions (*Panthera leo*), leopards (*Panthera pardus*), cheetahs (*Acinonyx jubatus*), black-backed jackals (*Canis mesomelas*), and martial eagles (*Polemaetus bellicosus*). Rainfall is seasonal, with peaks in April and May, July and August and October–December (Young et al. 1997). Mean monthly rainfall during the study was 48.7 mm; total rainfall for 1993 and 1994 was 565 and 629 mm, respectively.

Most of the study site (>90%) consists of “black cotton” soils, which are vertisols characteristic of impeded drainage that support *A. drepanolobium* wooded grassland habitat (Young et al. 1997). *A. drepanolobium* is the dominant tree species on black cotton soils, and accounts for 98% of all woody species in *A. drepanolobium* habitat in our study area (Young et al. 1997). Individual *A. drepanolobium* trees rarely exceed heights of 7 m (Coe and Beentje 1991; Isbell et al. 1998). The other vegetation type is *A. xanthophloea* riverine woodland, consisting of an overstorey monoculture of *A. xanthophloea* trees with associated understorey woody shrubs such as *Carissa edulis* and *Scutia myrtina*. *A. xanthophloea* trees can grow to 25 m (Coe and Beentje 1991). While *A. xanthophloea* habitat is used only by vervets for food and sleeping sites, both vervets and patas monkeys feed in *A. drepanolobium* habitat. Detailed descriptions of the study site can be found in Isbell (1998), Isbell et al. (1998), and Young et al. (1997, 1998).

This study includes data collected from adult females in one group of vervets (mean group size 27.6, range 26–30; 8–9 adult females) and one group of patas monkeys (mean group size 37.5 individuals, range 32–45; 13–14 adult females), whose home ranges were separated by circa 4 km. All vervets and all adult patas monkeys were individually identified by wounds, scars, differences in the color of the pelage, differences in the shape and length of nipples, and body size. Individuals were habituated to human observers at 5–20 m distances.

Data collection and analyses

Feeding behavior

Data on feeding behavior of individual adult females in each group were collected by J.D.P. during 30-min focal samples between 0800–1500 hours over 4 days per month per group from July 1993 to December 1994 (excluding July 1994). The data analyzed here include those from January to December 1994 (vervet, $n=215$ focal samples; patas, $n=241$). Vervets were sampled in a predetermined random order without replacement to allow each female to be sampled at a different hour each day during each month and only once per day. This sampling procedure had to be modified for patas monkeys because individual patas monkeys proved more difficult to locate than individual vervets. Within this constraint, an effort was made to randomize samples and to observe female patas monkeys at different times of the day and only once per day. Detailed methods are presented in Isbell et al. (1998).

Whenever a focal adult female was observed feeding during a focal sample, J.D.P. recorded the habitat type, food species, number of feeding sites for each individual of a given species, the location of a feeding site (defined as any location at which a monkey fed while stationary), and food type eaten at each feeding site. Analyses of feeding behavior were conducted on the number of food items eaten by each primate species within each habitat type, weighted by month to control for uneven monthly sample sizes. Time spent feeding was calculated as an overall mean based on means per female during focal samples collected from September to December 1994.

Patch distribution and size

Individual *A. xanthophloea* and *A. drepanolobium* trees most often constituted separate patches, where a patch was defined as an area in which a monkey could move and feed continuously (after White and Wrangham 1988). L.A.I. used the *T*-square distance sampling method (Ludwig and Reynolds 1988, p. 55), with 92 randomly chosen sample points, to measure the distribution of *A. drepanolobium* trees, or patches, in the home range of the patas monkey group. Spatial distribution was calculated by the *T*-square index of spatial pattern (Ludwig and Reynolds 1988, p. 56). While this method was appropriate for the habitat of the patas monkeys, it was not appropriate for the *A. xanthophloea* habitat of the vervets, which is linear with sharp boundaries. L.A.I. determined the distribution of *A. xanthophloea* trees in the home range of the vervet group by counting all trees within 52 20×20 m plots and then calculating whether the distribution was more clumped than expected based on a Poisson distribution. The distribution of *A. drepanolobium* trees in the home range of the vervet group was not measured.

J.D.P. used a variation on the point-center-quarter (PCQ) method (Cottam and Curtis 1956) to measure *A. drepanolobium* trees along transects in the home ranges of each species and *A. xanthophloea* trees along transects in the home range of vervets. This method has an advantage over the other methods because it could be used in both habitats. For patas monkeys, transects were chosen using stratified random sampling in which a set of map coordinates were randomly chosen from the area used by the monkeys during the previous month. The distribution of trees in the home range of patas monkeys was sampled every 20 m along these transects (total transect length 360 m). For vervets, transects were sampled in a stratified manner, with transects oriented perpendicular to the river along which vervets travelled each month. The distribution of trees in the home range of vervets was sampled every 75 m along these transects (total transect length 680 m). Along the transects, J.D.P. measured the nearest tree from a center point in each of five different height categories in each of four equal quadrants, where each quadrant extended infinitely outwards from the center point in one of four compass directions ($n=20$ /PCQ point). In other words, the space around the center point was divided into four equal (and infinite) sections in which the distances to the nearest trees in each of the height categories were measured. Samples within the different height categories (i.e., four samples per height category) were averaged, and analyses were conducted on these averages. Patch size was calculated from average crown width and crown height for each of the two tree species.

Agonistic interactions between adult females

All observed occurrences of agonistic interactions that could result in the interruption of feeding activity were recorded during 618 contact hours with vervet monkeys and 577 contact hours with patas monkeys. Such agonistic interactions included (1) physical contact in which one animal bit, grappled with, or slapped another, (2) unidirectional chasing, (3) supplantation, in which an individual replaced another in its exact location and engaged in the same activity as the one replaced, (4) approach-leaves, in which the leaver moved ≥ 2 m away, (5) approach-avoidances in which the avoider moved < 2 m away, and (6) approach-charge interactions in which the avoider cringed, flinched, or crouched without leaving. All agonistic interactions were, by definition, unidirectional, and thus each agonistic interaction had a clear winner and loser.

Each agonistic interaction was recorded along with the identities of individuals involved, the resource over which the interaction occurred if clearly identified (e.g., food, grooming partners, mating partners, or space), and the habitat in which the interaction occurred, i.e., *A. drepanolobium* or *A. xanthophloea* habitat. The interaction was considered food related when at least the loser was engaged in feeding or foraging behavior (actively searching and/or processing food) at the onset of the interaction. Small sample sizes precluded analyzing individual rates of agonistic interactions; rates were calculated on pooled data.

Dominance hierarchies of adult female vervets and patas monkeys were organized to minimize the number of reversals (interactions below the diagonal). Statistical significance of the linearity of dominance hierarchies and the degrees of linearity, K , were determined from Appleby (1983) and de Vries (1995). For the larger patas monkey dominance matrix, the approximation to the χ^2 distribution was used (Appleby 1983). Statistical linearity of the dominance hierarchy, which considers both the extent of reversals against the hierarchy and the number of unknown relationships, is described here along with the “strength” of the dominance hierarchy. The strength of the dominance hierarchy describes only the relative extent of unknown relationships, as expressed by empty cells in the matrix. Thus, weak dominance hierarchies are those in which the number of unknown relationships is high, reflecting the absence of agonistic interactions between individuals in numerous dyads. By inference, individuals in groups with weak dominance hierarchies have few opportunities or little incentive to compete with each other. In contrast, strong dominance hierarchies are those in which the number of unknown relationships is low, reflecting the occurrence of agonistic interactions between individuals in most, if not all, dyads. By inference, individuals in groups with strong dominance hierarchies frequently take opportunities to compete with each other. Two females (GEO and MND, one from each species) were excluded from analyses because they died before being observed in more than two agonistic interactions. Analyses of feeding behavior and female agonistic behavior were conducted with the Systat statistical program. All tests are two-tailed.

Results

Feeding behavior

Among patas monkeys, foods on *A. drepanolobium* accounted for 53.6% of the diet ($n=3,558$; Table 1). Foods on *A. drepanolobium* were eaten five times more often than the second most frequently eaten species. Patas

monkeys fed in 10.0 ± 0.6 *A. drepanolobium* trees/h ($n=220$ 30-min focal samples; Fig. 1) and fed in 2.8 ± 0.1 feeding sites/tree ($n=220$; Fig. 2).

Among vervets, *A. drepanolobium* accounted for 35.4% and *Acacia xanthophloea* for 21.8% (total 57.2%) of the total diet ($n=3,154$). In *A. drepanolobium* habitat, food items from *A. drepanolobium* accounted for 47.6% of the vervets’ diet ($n=2,549$; Table 1). In that habitat, foods on *A. drepanolobium* were eaten four times more often than the next most frequently eaten food species. As with patas in *A. drepanolobium* habitat, vervets fed in several *A. drepanolobium* trees per unit time ($9.4 \pm$

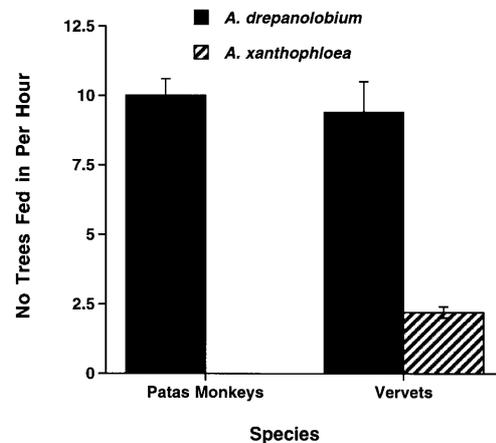


Fig. 1 Number of *Acacia drepanolobium* and *A. xanthophloea* trees in which patas monkeys and vervets fed per hour (error bars ± 1 SE)

Table 1 Major food species and food items (percentages) in the diets of vervets and patas monkeys

Food species/item	Patas	Vervets ^a	
		<i>Acacia drepanolobium</i> habitat	<i>A. xanthophloea</i> habitat
<i>A. drepanolobium</i> (total)	53.6	47.6	
Swollen thorns	19.6	11.7	
Exudate	18.0	2.3	
Flowers	1.8	1.1	
Seeds	0.7	6.4	
New leaves	0.7	7.8	
Unidentified	12.8	18.3	
<i>A. xanthophloea</i> (total)	0.2		61.6
Exudate	0.2		40.4
Seeds			10.2
Flowers			5.7
Unidentified			5.3
<i>Commelina</i> spp.	10.5	1.1	
Arthropods (various species)	5.9	2.7	0.2
<i>Acacia seyal</i>	5.6	12.5	1.0
<i>Lycium europaeum</i>	1.9	3.8	0
Grass species	0.7	5.0	3.3
Mushrooms	0.4	1.9	0.8
<i>Acacia gerrardii</i>	0.1	3.2	3.8
<i>Euclea divinorum</i>		0.9	2.8
Minor foods (>14 plants/animal species)	21.1	21.3	26.5
Total	100.0	100.0	100.0

^a Excludes foods eaten by vervets during focal samples that obviously included both habitats

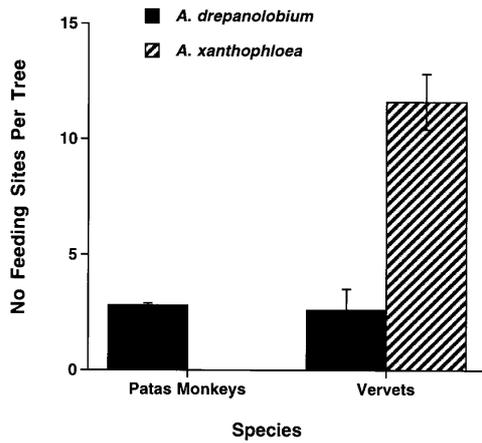


Fig. 2 Number of sites per tree in which patas monkeys and vervets fed per hour (error bars ± 1 SE)

1.1 trees/h, $n=214$; Fig. 1) while feeding at only a few sites within them (2.6 ± 0.9 feeding sites/tree, $n=116$; Fig. 2). In *A. xanthophloea* habitat, food items from *A. xanthophloea* accounted for 61.6% of the diet of vervets ($n=605$). Foods on *A. xanthophloea* were eaten 16 times more often than the second most frequently eaten food species in that habitat (Table 1). Vervets fed in 2.2 ± 0.2 *A. xanthophloea* trees/h (Fig. 1), and at 11.6 ± 1.2 feeding sites per tree ($n=130$; Fig. 2).

Distribution and size of major tree species

By itself, *A. drepanolobium* accounted for over half the food items in the diet of patas monkeys, and nearly as much for vervets when they were in that habitat. *A. xanthophloea* accounted for more than half of the foods of vervets in *A. xanthophloea* habitat (Table 1). We therefore focused on measuring the distributions of these tree species. The spatial distribution of *A. drepanolobium* trees was not significantly clumped in the home range of patas monkeys (PCQ: $\chi^2=11.55$, $df=13$, $P>0.50$, based on the divergence of the standard deviation from the mean

number of trees; T -square: $C=0.54$, $z=1.31$, $n=92$, $P>0.20$), nor was the distribution of *A. drepanolobium* trees significantly clumped in the home range of vervets (PCQ: $\chi^2=22.11$, $df=29$, $P>0.80$). In contrast, the spatial distribution of *A. xanthophloea* trees in the home range of vervets was more clumped than expected [PCQ: coefficient of dispersion=2.16 (Sokal and Rohlf 1997); Poisson distribution: $\chi^2=20.3$, $df=6$, $P<0.01$].

The mean height of *A. xanthophloea* patches was 5.4 m; the mean width was 5.1 m. *A. drepanolobium* patches follow a J-shaped height distribution (Young et al. 1997) dominated by smaller individuals. Mean height was 1.2 m and mean width was 1.5 m.

Agonistic interactions between adult female patas monkeys

Adult female patas monkeys had 208 decided agonistic interactions during 577 h at a rate of 0.36/h. Per dyad ($n=90$ possible dyads), the rate was 0.004 interactions/h. Food-related interactions accounted for 75 (48.4%) of the total number of interactions for which context could be determined, while interactions in which food was not involved accounted for 80 (51.6%) of the total number of such interactions ($n=155$; Table 2). Weighted by the time spent feeding (38.7%), agonistic interactions during feeding occurred at a rate of 0.34/h (0.004 interactions/dyad per hour), almost 50% more often than when animals were not feeding (0.23/h, 0.003 interactions/dyad per hour; $\chi^2=6.1$, $df=1$, $P<0.02$).

The dominance hierarchy of adult female patas monkeys was not significantly linear ($d=90$, $df=20.02$, $\chi^2=15.2$, $P>0.70$, $K=0.196$; higher values of K indicate stronger degrees of linearity: Appleby 1983). Four reversals accounted for 4% of all agonistic interactions, with more than half ($n=48$) of all dyadic relationships remaining unknown.

Table 2 Frequency of agonistic interactions under different contexts among adult female vervets and patas monkeys

Context	Patas monkeys		Vervets in <i>A. drepanolobium</i> habitat		Vervets in <i>A. xanthophloea</i> habitat	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
While feeding	75	48.4	37	86.0	18	62.1
While grooming	24	15.5	1	2.3	4	13.8
Over spatial location	24	15.4	0		0	
While resting	7	4.5	1	2.3	1	3.0
Access to male	7	4.5	0		0	
Redirected agonism	5	3.2	0		0	
Proximity to other	4	2.6	0		0	
During coalition	4	2.6	0		0	
Access to infant	2	1.3	2	4.6	4	13.8
Other	3	1.2	2	4.6	2	6.8
Total	155	99.9	43	99.8	29	99.9

Agonistic interactions between adult female vervets

Overall, adult female vervet monkeys had 138 decided agonistic interactions with other adult females during 618 h, at a rate of 0.22 interactions/h. Per dyad ($n=28$), agonistic interactions occurred at a rate of 0.007 interactions/h. Of these interactions, 55 (39.9%) clearly involved food while 83 (60.1%) did not (Table 2). Weighted by the percentage of time spent feeding (53.6%), agonistic interactions during feeding occurred at a rate of 0.17/h (per dyad, 0.006 interactions/h); agonistic interactions while the animals were not feeding occurred at a rate of 0.29/h (per dyad, 0.010 interactions/h).

Overall, with both habitats combined, the dominance hierarchy of adult female vervet monkeys was relatively strong and statistically linear ($d=4.75$, $df=21$, $P=0.01$, $K=0.76$), with one reversal (0.6%) and two unknown relationships ($n=151$ dyadic interactions).

When agonistic interactions were separated by habitat and the context of the interaction was known, adult female vervets had 29 decided agonistic interactions in *A. xanthophloea* habitat and 43 decided agonistic interactions in *A. drepanolobium* habitat. However, vervets spent less time in *A. xanthophloea* habitat (31%) than *A. drepanolobium* habitat (69%, $n=618$ h). Weighted by the percentage of time spent in each of these habitats, the rate of agonistic interactions among adult female vervets was 50% greater in *A. xanthophloea* habitat (0.15 interactions/h) than in *A. drepanolobium* habitat (0.10 interactions/h), but the difference was not significant ($\chi^2=2.9$, $df=1$, $P=0.11$). Of the total number of context-determined agonistic interactions in each of the two habitats, 18 (62.1%) occurred over food in *A. xanthophloea* habitat, whereas 37 (86%) occurred over food in *A. drepanolobium* habitat. Weighted by the percentage of time spent feeding in each of the habitats (*A. xanthophloea*: 31%, *A. drepanolobium*: 76%), the rate of food-related agonistic interactions was nearly three times greater in *A. xanthophloea* than in *A. drepanolobium* habitat (0.30 vs 0.11 interactions/h; per dyad, 0.010 vs 0.004 interactions/h; $\chi^2=11.3$, $df=1$, $P<0.0008$; Fig. 3). Non-food-related agonistic interactions among vervets in *A. xanthophloea* and *A. drepanolobium* habitats were not significantly different, however (0.08 vs 0.06 interactions/h; per dyad, 0.003 vs 0.002 interactions/h; $\chi^2=0.47$, $df=1$, $p=0.66$; Fig. 3).

The dominance hierarchy of female vervets in *A. xanthophloea* habitat was strong and statistically linear ($d=4.75$, $df=21$, $P=0.01$, $K=0.76$). There were two unknown relationships (7% of all dyads) and one reversal. In contrast, their dominance hierarchy in *A. drepanolobium* habitat was weaker and not statistically linear ($d=8.75$, $df=21$, $P>0.09$, $K=0.56$). There were nine unknown relationships (32% of all dyads) and no reversals. Unknown relationships of vervets in *A. drepanolobium* habitat were more than four times more frequent than in *A. xanthophloea* habitat. The dominance hierarchy of vervets was more similar to that

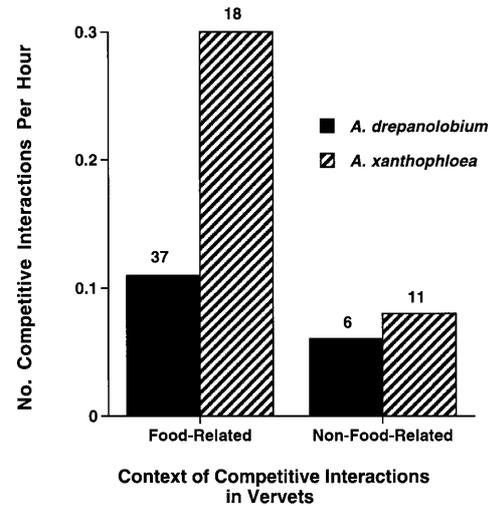


Fig. 3 Rate per hour of competitive interactions of adult female vervets in *A. xanthophloea* and *A. drepanolobium* habitats within their home range. The rate for food-related interactions was weighted by the percentage of time spent feeding in each habitat; the rate for non-food-related interactions was weighted by the remaining percentage of time. Total numbers of interactions are given above the bars

of patas monkeys when they were in *A. drepanolobium* habitat than when they were in *A. xanthophloea* habitat.

Discussion

Both vervets and patas monkeys fed heavily on acacia trees at this site, a finding not unexpected given that there are few other tree species available. In these simple habitats, foods from *A. drepanolobium* (including ants from within swollen thorns; see Isbell 1998) accounted for most of the identified food items of patas monkeys and for those of vervets when they were in *A. drepanolobium* habitat. Unidentified foods were often small and accompanied by movements of monkeys that suggested feeding on insects and other arthropods (Isbell 1998; Isbell et al. 1998).

Both vervets and patas monkeys exhibited relatively weak, non-linear dominance hierarchies in this habitat. Such hierarchies resulted more from the low rate of agonistic interactions between many dyads than from reversals between dyads (at least over a short period of time; see Isbell and Pruettz 1998) or from an inability to compete. Although patas monkeys appear to have more coalitions than vervets (Table 2), in both species, coalitions were very rare. Coalitions were not observed in vervets during this study, but this is an artifact of both the rarity of coalition formation and small sample size; as in other populations (e.g., Cheney 1983), coalitions have been observed in this vervet population, although not as often as in other populations (L.A. Isbell, unpublished data).

The distribution of *A. drepanolobium* was not clumped but was instead randomly distributed in the

home range of the patas monkeys and where those trees occurred in the home range of the vervets. Arthropods are also generally considered to be widely dispersed and relatively evenly or randomly distributed (Terborgh 1983; Zhang 1995). Such over-dispersed foods are hypothesized to create the ecological conditions for weak or non-existent dominance relationships among female primates (Wrangham 1980; van Schaik 1989; Isbell 1991).

Vervets also fed heavily on *A. xanthophloea*, a tree species typically found in a narrow belt along rivers in East Africa. Unlike *A. drepanolobium*, the spatial distribution of *A. xanthophloea* within that narrow belt was clumped. Clumped foods are hypothesized to be the ecological basis for strong, linear dominance hierarchies in primates, presumably because clumped foods are usurpable, thus making it profitable for females to behave competitively toward other females (Wrangham 1980; van Schaik 1989; Isbell 1991).

Although our results may be interpreted as providing support for the hypothesis that spatial distribution is important in determining agonistic interactions, we do not yet know if the scale at which our ecological measurements were taken is the scale that actually determines the outcome of agonistic interactions, i.e., whether food patches are monopolizable at the scale of the individual tree. With their small size and only a few food items eaten per tree, individual *A. drepanolobium* trees may indeed be monopolizable by individual monkeys. It is common to see one patas monkey or vervet feeding alone in an *A. drepanolobium* tree. Individual *A. xanthophloea* trees, however, are unlikely to be monopolizable by individual monkeys given the larger size of such trees, the greater number of food sites within individual trees, and the more frequent agonistic interactions in them. Vervets are rarely seen feeding by themselves in single mature *A. xanthophloea* trees.

These observations suggest that patch size may be more important than the spatial distribution of those patches in determining agonistic interactions. *A. xanthophloea* trees grow substantially larger than *A. drepanolobium* trees (Coe and Beentje 1991), and vervets had more agonistic interactions in the larger patches. Similarly, in two congeneric species of squirrel monkeys (*Saimiri oerstedii* and *Saimiri sciureus*), females had a greater number of agonistic interactions in larger trees (Mitchell et al. 1991). Agonistic interactions decreased in the largest trees, however, and Mitchell et al. (1991) suggested that this was because the largest trees had sufficient feeding sites for all group members. Patch size per se may not be particularly informative and may depend on the interaction between the number of potential feeders (van Schaik 1989) and the number of feeding sites within the patch. For vervets, even the large patches may not have had enough feeding sites for all animals to feed together. Agonistic interactions may have been more frequent in large patches because they held feeding sites (mean number of feeding sites/*A. xanthophloea* tree per focal sample=11.6) perhaps sufficient to attract multiple individuals but not to feed the entire

group (mean group size=27.6), whereas agonistic interactions may have been reduced for both species in the smaller *A. drepanolobium* patches because the feeding sites (mean number of feeding sites/*A. drepanolobium* tree <3/focal sample for both species) were usually insufficient to attract multiple individuals (mean group size of the patas group=37.5). The mean group spread of the vervet group was smaller in *A. xanthophloea* habitat than in *A. drepanolobium* habitat (Isbell and Enstam, in press), which would be expected if this interpretation is correct.

In this study, agonistic interactions covaried with both spatial distribution of patches and patch size. These results are similar to those of other studies which have found that competition increases with clumped resources of sizes that can support some but not all group members and decreases with more dispersed resources that are very small (Mitchell et al. 1991; Barton and Whiten 1993; Barton et al. 1996; Koenig et al. 1998). Although numerous studies support the hypothesis that spatial distribution, or a combination of spatial distribution and patch size, influences female agonistic relationships, Isbell et al. (1998) cautioned that the correlation between spatial distribution of foods and competition could be confounded with another, more important, factor – feeding site depletion time. Foods that are more clumped, e.g., fruits or corms, may also be larger and or they may require more processing time consumed slowly, whereas foods that are more evenly dispersed, e.g., many arthropods, may be consumed more quickly (Post et al. 1980; Shopland 1987; Janson 1990; Isbell et al. 1998). An experimental study of captive, group-living rhesus macaques (*M. mulatta*), in which the effects of spatial distribution and food size were separated, revealed that food size predicted aggression better than did spatial distribution (J. Mathy and L.A. Isbell, unpublished data).

Primates are perhaps unusual among mammals in having an extremely high diversity of food items in their diets. For example, folivorous red colobus monkeys (*Procolobus badius*) in Uganda consumed various plant parts including foliar buds, young leaves, mature leaves, leaf petioles, floral buds, flowers, seeds, unripe fruit, ripe fruit, and exudates from over 60 plant species (Struhsaker 1975; Isbell 1983). In addition to consuming arthropods, squirrel monkeys in Peru consumed fruits of more than 150 species (Mitchell et al. 1991). Hanuman langurs (*Semnopithecus entellus*) in Nepal consumed fruits, floral buds, flowers, leaves, pith, and petioles from at least 69 plant species (Koenig et al. 1998). The langurs often competed for leaves, plant parts which are typically considered not worth competing over. As Koenig et al. (1998) pointed out, however, even leaves may be contestable if they vary in quality. The vervets and patas described here have simple diets, making it easier than for many primates to identify and measure characteristics of food resources that favor agonistic interactions.

Even with their simple diets, however, in these two primate species, individuals easily feed simultaneously within a short distance of each other (Isbell and Enstam,

in press). Species that are committed to insectivory also have comparatively low dietary diversity, but their foods are typically eaten quickly, making simultaneous feeding by multiple individuals more difficult. In such species, renewal rate may be more important than patch size or depletion time in determining agonistic interactions. Waser and Waser (1985) suggested that rapid renewal rates favor tolerance of others in white-tailed mongooses (*Ichneumia albicauda*) and other insectivorous viverrids. Renewal rate or arrival time also influences agonistic interactions in insectivorous fish and insects. Aggression decreased with rapidly arriving foods and increased with more slowly arriving foods in zebra-fish (*Branchydanio rerio*: Grant and Kramer 1992), medaka (*Oryzias latipes*: Bryant and Grant 1995), and water striders (*Aquarius remigis*: Blanckenhorn et al. 1998). When foods become available simultaneously, more individuals can feed at the same time, and agonistic interactions decrease. Similarly, house sparrows (*Passer domesticus*) had greater tolerance for others when their foods were simultaneously provided than when their foods were asynchronously provided (Elgar 1986). Although Elgar described the difference between the two treatments as a difference in divisibility, it may also be interpreted as a difference in the timing of availability.

Because different species can have vastly different diets, a universal ecological characteristic of food that determines competition probably does not exist. For insectivorous species, whether they may be mammals, birds, fishes, or insects, individual feeding sites (or food items) are depleted quickly because the foods can be consumed quickly. With faster depletion times, the likelihood decreases that multiple foods will be available for multiple individuals to feed simultaneously. Any ecological characteristic that affects the ability of multiple individuals to feed simultaneously, e.g., renewal rate, arrival time, or divisibility, may be important in determining agonistic interactions. For carnivorous species, individual feeding sites are depleted more slowly because they are larger or have longer processing times. Slower depletion times increase the likelihood that multiple feeding sites will be available simultaneously. For such species, feeding site depletion time, number of feeding sites per "patch," or spatial distribution of "patches" may be more important in determining agonistic interactions. For frugivorous/folivorous species with broad diets, the effect of slow depletion time is compounded by broad diet to enable even greater numbers of individuals to feed simultaneously. Broad diets also increase the probability of variation in food quality, however, and for such species, food quality may be an additional ecological characteristic that determines agonistic interactions.

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