

Rank Differences in Ecological Behavior: A Comparative Study of Patas Monkeys (*Erythrocebus patas*) and Vervets (*Cercopithecus aethiops*)

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*One of the central dichotomies in primate behavior is between species in which there are relationships among females that include stable dominance relationships, and those in which the relationships include weak or unstable dominance relationships. This dichotomy has been attributed to differences in food resources, with stable dominance hierarchies occurring in species that feed on usurpable foods. We compared rank-related differences in nonagonistic behaviors considered to be tightly linked to ecology in broadly sympatric vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*), two closely related cercopithecines that are exemplars of this dichotomy, with the expectation that vervets would exhibit stronger rank differences than patas monkeys in these behaviors. Overall, rank explained more than twice as much variation among vervets as among patas monkeys in ranging behavior, activity budgets, and diet. Vervets did not, however, exhibit stronger rank differences when they used *Acacia xanthophloea* habitat, in which foods are more usurpable, compared to *Acacia drepanolobium* habitat, in which foods are less usurpable. In *Acacia drepanolobium* habitat, to which patas are restricted, higher-ranking vervets converged in behavior with patas monkeys to a greater extent than lower-ranking vervets, suggesting that social constraints interfere with the foraging efficiency of lower-ranking vervets even in habitats in which there are fewer opportunities to usurp foods.*

KEY WORDS: behavioral ecology; primates; dominance; Laikipia; Kenya; *Acacia drepanolobium*.

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INTRODUCTION

In some Old World primates such as macaques (*Macaca* spp.), savannah baboons (*Papio* spp.), and vervets (*Cercopithecus aethiops*), relationships among females include observable differences among females in preferences for interacting with other females and in preferential access to food resources. For example, grooming is often nonrandom in these species, with certain females being more sought after as grooming partners than other females (Seyfarth, 1980). Similarly, certain females are often more successful than others in gaining access to preferred food resources (Wrangham, 1981; Whitten, 1983; Janson, 1985; Barton and Whiten, 1993). A key characteristic of such species is the presence of stable, linear dominance hierarchies among females, with the highest-ranking females being most sought after as grooming partners and having preferential access to certain food resources.

In contrast, relationships among females in other Old World primates such as gorillas (*Gorilla gorilla*), red colobus (*Colobus badius*), Hanuman langurs (*Presbytis entellus*), blue monkeys (*Cercopithecus mitis*), and patas monkeys (*Erythrocebus patas*), are less focused on rank. Grooming between females is independent of relative dominance position (Rowell *et al.*, 1991; Borries *et al.*, 1994), and linear dominance hierarchies are more difficult for observers to establish with confidence (Struhsaker, 1975; Rowell *et al.*, 1991; Borries *et al.*, 1991; Watts, 1994; Cords, in press; Isbell and Pruettz, 1998).

Ecological differences, particularly in food resources, appear to underlie these behavioral differences (Sterck and Steenbeek, 1997; Koenig *et al.*, 1998; Isbell *et al.*, 1998a; Isbell and Pruettz, 1998), though there is no consensus on the characteristics of foods that ultimately determine the nature of female relationships. Wrangham (1980) hypothesized that foods which are monopolizable lead to dominance hierarchies and differentiated relationships. He attributed monopolizability to foods that have a clumped spatial distribution (see also van Schaik, 1989; Isbell, 1991) and that vary in quality. Isbell *et al.* (1998a) recently suggested, however, that the more critical variable is temporal distribution of foods, which depends on food-site depletion time (FSDT). Foods that are larger or that have longer handling times have longer FSDTs and are more likely to be usurpable by higher-ranking individuals than foods that are smaller and more quickly consumed.

Regardless of the exact ecological cause, if differences in ecology can determine the nature of dominance relationships among female primates, they should also influence non-agonistic behaviors that are more obviously linked to ecology, such as ranging behavior, activity budgets, and diet. Females in species with stable dominance hierarchies might be expected to show stronger rank differences in these behaviors than females in species with unstable dominance hierarchies.

Vervets and patas monkeys are two closely related Old World primates (Disotell, 1996) that differ from one another in the expression of dominance

relationships among females. Female vervets form linear dominance hierarchies that are stable over time, even when maturing females enter the adult dominance hierarchy (Cheney *et al.*, 1981; Cheney, 1983; Lee, 1983; Whitten, 1983; Isbell and Pruettz, 1998). Reversals against the hierarchy, in which lower-ranking females occasionally win over higher-ranking females in agonistic interactions, account for $\leq 2\%$ of the total interactions (Cheney *et al.*, 1981; Isbell and Pruettz, 1998). Although provisioned patas monkeys can have stable, linear dominance hierarchies (Kaplan and Zucker, 1980; Jacobus and Loy, 1981; Loy and Harnois, 1988; Nakagawa, 1992; Goldman and Loy, 1997), unprovisioned female patas monkeys have statistically non-linear dominance hierarchies that are less stable than those of vervets, with a higher percentage of reversals (18%), especially when maturing females enter the dominance hierarchy (Isbell and Pruettz, 1998). Consistent with these differences in dominance relationships are differences in the foods of vervets and patas. Although both vervets and patas eat a high proportion of gums, vervets also feed frequently on fruits, seeds, and flowers, whereas patas feed more on arthropods (Wrangham and Waterman, 1981; Whitten, 1983; Chism and Wood, 1994; Isbell, 1998; Isbell *et al.*, 1998a). Food sites with fruits, seeds, and flowers, in particular, are often contested among vervets (Whitten, 1983; Wrangham and Waterman, 1981), and they are likely to be more usurpable than arthropods because they are larger or require longer handling times.

Here we examine whether the differences between vervets and patas monkeys in dominance relationships are also apparent in nonagonistic behaviors that are more obviously linked to ecology. We also compare these same measures in the same vervets using two habitat types that differ in the temporal distribution of their foods to examine whether rank differences are reduced when vervets use the habitat with apparently less usurpable foods.

METHODS

Study Site and Animals

We have studied vervets and patas on Segera Ranch (36°50'E, 0°15'N; elevation 1800 m) on the Laikipia Plateau in Kenya continuously since 1992. Annual rainfall from mid-1992 to mid-1997 has ranged from 568 to 833 mm (mean: 700 mm) and is generally seasonal, with drier periods occurring on average in September and January-March, but rainfall patterns are inconsistent and can vary considerably from year to year.

The study site has two main habitat types: woodland dominated by *Acacia xanthophloea* along rivers, and wooded grassland dominated by *A. drepanolobium* in areas away from water. *Acacia xanthophloea* grows to 30 m (Coe and Beentje, 1991), whereas *A. drepanolobium* seldom grows to >7 m in the study area (Young

et al., 1997; Isbell, 1998). Patas are restricted to *Acacia drepanolobium* habitat, whereas vervets sleep in *A. xanthophloea* and feed in both *A. xanthophloea* and *A. drepanolobium* habitats. Young *et al.* (1998) described the ecosystem in detail.

We collected the data presented here on ranging behavior, activity budgets, and diets of adult females from July 1993–December 1994 on one group of vervets ($n = 26–30$, with 8–9 adult females) and one group of patas monkeys ($n = 33–41$, with 12–15 adult females). All monkeys were habituated to the presence of observers, and all adults were individually recognizable. For vervets, the sampling protocol was as follows: each female was sampled once each of four days per month using a predetermined random sampling order without replacement. The samples for each female alternated morning (0800–1200 h) with afternoon (1200–1600 h) sampling blocks of time. Within these blocks, we sampled each female only once during a given hour, always at the top of the hour. For patas monkeys, this protocol had to be abandoned because females were difficult to find in time to sample on the hour: group spreads of >300 m were common. We sampled female patas monkeys opportunistically at the top of the hour, and no female was sampled more than once per day. During the first 30 min of focal sampling, we recorded the number of moves that the female made and the distance she travelled between successive food sites.

Food sites are any location where the focal female stopped to eat. A move is a movement involving hindleg locomotion that terminated when the female stopped to eat. Total travel distance is a summation of all distances between food sites per 30 min. We calculated the average distance between food sites for each focal sample by dividing the total distance travelled per 30 min by the number of moves made during that same time. Minutes per food site is the inverse of the number of moves between food sites multiplied by 30 min (see Isbell *et al.*, 1998a). We noted each food species and food item whenever the female stopped to eat. We also noted food species and items that were not identifiable. Categories of ranging behavior and diet used in analyses are in Table I.

Immediately following each 30-min sample of diet and ranging behavior of females, we recorded start and end times of the activities of the same focal female for 15 min (or, in some samples at the beginning of the study, 30 min) using a Pision Organiser hand-held data logger and the Observer software package (Noldus Information Technology). Operational definitions of activities used in analyses are in Table I.

We determined relative ranks of adult females over the same time period on the basis of observed responses to approaches by other adult females. Females are low-ranking if they avoid other females or are supplanted or chased by other females. We constructed dominance matrices to assign relative ranks while minimizing reversals (scores below the diagonal) (Isbell and Pruettz, 1998). We assigned females that were indistinguishable from others in their positions in the hierarchy, i.e., they could be switched with other females without increasing the number of reversals, equal ranks in analyses.

Table I. Categories of ranging behavior, diet, and activity budgets used in analyses

Ranging behavior

1. Total distance traveled in 30 min
2. Number of moves made in 30 min
3. Distance between food sites
4. Minutes per food site

Diet

1. Flowers (mostly *Acacia xanthophloea* and *A. drepanolobium*)
2. Fruits (mostly *Scutia myrtina*, *Carissa edulis*, and *Commelina* spp.)
3. Seeds (mostly of *Acacia xanthophloea* and *A. drepanolobium*, removed from their pods)
4. Swollen thorns (of *Acacia drepanolobium*, often eaten in their own right when young and mainly for the invertebrates in them when old; see Isbell, 1998)
5. Gum (mostly *Acacia xanthophloea* and *A. drepanolobium*)
6. Leaves (mostly *Lycium europaeum*, grass spp.)
7. Fungi, and other plant parts (mushrooms on termite mounds, tubers, roots, stalks, stems)
8. Animals (arthropods, geckos, young birds, and birds' eggs)
9. Unknown foods
10. Water

Activities

1. Walk: Identified as slowest gait; when feet visible, only one foot off the ground at any given time
2. Forage while walking: Scan vegetation while walking
3. Feed while walking: Chew or ingest food while walking
4. Lope: Identified as faster than walking with a rocking motion; when feet visible, front and hind feet alternating suspension off ground
5. Run: Identified as fastest gait; when feet visible, all feet suspended simultaneously off ground at some point in the stride
6. Climb: Quadrupedal movement within trees or bushes
7. Leap: Substantial vertical movement with all four feet off the substrate at height of vertical movement
8. No movement: Resting, sleeping, or being still; excludes other categories
9. Forage without moving: Search, scan, or manipulate food item at close range while stationary
10. Feed without moving: Chew or ingest food item while stationary
11. Autogroom: Scratching, combing through one's own fur
12. Social groom: Combing through another's fur

Data Analysis

We entered all data on ranging behavior of individual adult females into Excel (Microsoft) and then imported them into JMP (SAS Institute). We excluded samples if they were not exactly 30 min, were conducted on ambiguously identified females or habitat types, or included time out of sight. Resultant sample sizes range from 4 to 22 30-min samples for individual vervets (median = 16; n for group = 134) and 4 to 24 30-min samples for individual patas (median = 13; n for group = 165). We calculated mean values for each female and conducted regression analyses (on rank) using JMP on the individual means (sample sizes: vervets, 7 adult females in *Acacia xanthophloea* habitat, 8 in *A. drepanolobium* habitat, and 9 in both habitats combined; patas, 12 adult females). We conducted t-tests using JMP on individual means of the three highest-ranking and the three lowest-ranking females in each species.

We transferred all data on the activities of individual adult females from Observer files to Excel. To minimize bias resulting from diurnal variation in activities, we calculated the percent of time spent in each activity for each focal sample and then averaged across samples for each female, excluding the time that the focal animal was out of sight (Isbell and Young, 1993). Sample sizes range from 6 to 31 focal samples for individual vervets (median = 23; n for group = 180) and 3–14 focal samples for individual patas (median = 8; n for group = 93). We conducted regression analyses (on rank) using JMP on individual means (sample sizes: vervets, 9 adult females in each habitat; patas, 12 adult females). We conducted t-tests using JMP on individual means of the three highest-ranking and the three lowest-ranking females in each species.

We entered data on food items eaten by individual adult females into Excel. To minimize biases resulting from uneven monthly sample sizes, we first calculated the percentage of each food item in the diet for each month and then averaged the percentages across months by habitat for each female. Months in which there were <5 records for any female were excluded from analysis (Isbell and Young, 1993). Resultant sample sizes range from 7 to 17 months for individual vervets (median = 16; n , group-months = 117) and 3 to 14 for individual patas (median = 9; n , group-months = 115). For vervets, we calculated overall diet per individual (both habitats combined) by multiplying the proportions of food items in each habitat by the average proportion of days spent feeding in each habitat, averaged across all months (median % days feeding in *Acacia xanthophloea* = 28.2%, range = 18–67.7%; median % days feeding in *A. drepanolobium* habitat = 71.8%, range = 33.3–82.1%). We conducted regression analyses (on rank) using JMP on individual means using arcsine-transformed data (sample sizes: vervets, 8 females; patas, 13 females). We conducted t-tests using JMP on individual means of the three highest-ranking and the three lowest-ranking females in each species.

We examined data both with correlation tests on activity budgets, diets, and ranging behavior of all adult females within each species and with t-tests on activity budgets, diets, and ranging behavior of the three highest-ranking adult females and the three lowest-ranking adult females within each species. We analyzed the resultant correlation coefficients (r^2 values) to reduce bias from unequal sample sizes (vervets had fewer females than patas monkeys, which could differentially decrease their effect sizes) using two-way ANOVAs with monkey species and correlate type (diet vs. activity vs. ranging) as the independent variables. Similar ANOVAs were carried out with the data for vervets only, testing the effects of habitat on rank differences. All statistical tests are two-tailed. Effect sizes described below are from fitted regression lines on untransformed data; the statistical analyses reported are from either untransformed data, or for activity budgets, transformed data. When a result is statistically significant, we specify the particular test, i.e., correlation test using all females or t-test using rank classes.

Table II. Two-way analysis of variance for the effects of species (patas monkeys, vervets) and behavioral categories (ranging behavior, activity budgets, and diet) on the correlation coefficients between behavioral categories and rank (all females examined)

Source	Degrees of freedom	F ratio	p
Species (patas vs. vervets)	1	6.52	0.01
Correlate type (diet vs. activity vs. ranging)	2	1.29	0.28
Species × Correlate type	2	2.84	0.07
Error	44	—	—

RESULTS

Comparison Between Patas and Vervets

When correlation coefficients were analyzed across all categories of ranging behavior, activity budgets, and diets, a strong effect of species was evident (Table II). With all females examined, rank explained more than twice as much of the variance in ranging behavior, diets, and activities in vervets as in patas (21% vs. 9%; $F = 6.52$, $p < 0.01$; Fig. 1). The species correlate type interaction term indicates that the strength of overall species differences varied among these categories. Rank differences explained four times as much variance in diet (20% vs. 5%), and three times as much variance in ranging (33% vs. 11%), in vervets as in patas. In contrast, rank explained a similar amount of variance in activities (11–12%) in vervets and patas.

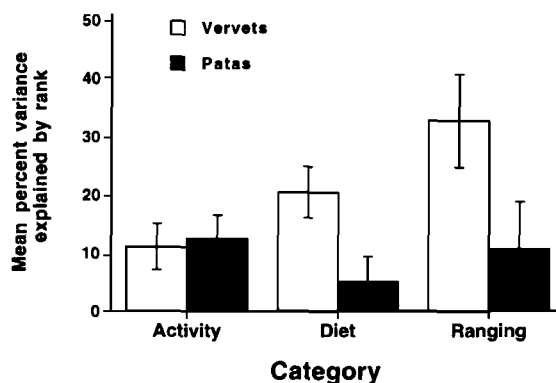


Fig. 1. Mean (\pm one S.E.) percent variance explained by rank (r^2 values $\times 100$) for ranging behavior, activity budgets, and diet for patas and vervet monkeys ($F = 6.52$, $p = 0.01$).

Rank-Related Differences Among Patas Monkeys

When the individual traits within ranging behavior, activity budgets, and diets were examined separately, patas monkeys showed no statistically significant rank-related differences in ranging behavior, regardless of whether all females or just rank classes were compared (all p values >0.09). Higher-ranking female patas ate a significantly smaller proportion of seeds than lower-ranking female patas did (all females, $r^2 = 0.30$, $p = 0.05$, fitted line ranging from 0.0% to 3.0%, i.e., the highest-ranking individuals had seeds as 0% of their diet, and the lowest-ranking individuals had seeds as 3.0% of their diet). Higher-ranking females did not differ significantly from lower-ranking females in the proportion of any other food item in the diet (all p values >0.25). Higher-ranking females climbed more often than lower-ranking females did (rank classes, $t = 3.5$, $p = 0.02$, $\bar{x} = 11\%$ vs. 7%). No other rank differences in activities are statistically significant (all p values ≤ 0.06).

Rank-Related Differences Among Vervets

Overall, with both habitats combined, higher-ranking adult female vervets traveled significantly farther than lower-ranking females did (all females, $r^2 = 0.66$, $p = 0.01$, fitted line ranging from 108 to 59 m; rank classes, $t = 4.9$, $p = 0.008$, $\bar{x} = 20$ m vs. 11 m). There are no statistically significant differences between higher- and lower-ranking females in other ranging behaviors (all other p values ≥ 0.06). Higher-ranking vervets ate a greater proportion of fungi and miscellaneous plant parts than lower-ranking vervets did (all females, $r^2 = 0.50$, $p = 0.05$, fitted line ranging from 8% to 0%; rank classes, $t = 5.3$, $p = 0.006$, $\bar{x} = 7\%$ vs. 0%) and a lower proportion of fruits than lower-ranking vervets did (rank classes, $t = 6.3$, $p = 0.003$, $\bar{x} = 3\%$ vs. 10%). There are no other statistically significant rank differences in other dietary categories (all p values ≥ 0.11). Higher-ranking vervets do not differ significantly from lower-ranking vervets in any of the activities (all p values ≥ 0.15).

Comparison of Vervets in Different Habitats

In *Acacia xanthophloea* habitat, where foods are apparently more abundant and have longer depletion times (Isbell *et al.*, 1998a), higher-ranking female vervets spent nearly twice as much time as lower-ranking females did at food sites (all females, $r^2 = 0.58$, $p = 0.04$; Fig. 2). Not surprisingly, higher-ranking females also made fewer moves per unit time than lower-ranking females (number of moves per unit time is the inverse of minutes per food site) (all females, $r^2 = 0.59$, $p = 0.04$, fitted line ranging from 4.5–9 moves). They do not differ significantly from lower-ranking females in the other ranging behaviors (all p values ≥ 0.30).

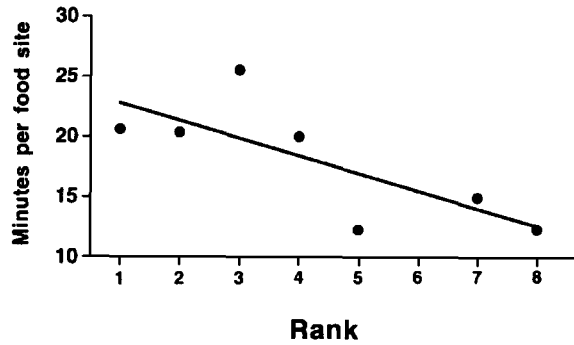


Fig. 2. Relationship between rank and mean time spent at food sites per 30 min for individual adult female vervet monkeys in *Acacia xanthophloea* habitat ($r^2 = 0.58$, $p = 0.04$).

There are no significant rank-related differences in diet (all p values ≥ 0.12), nor is there a statistically significant rank-related difference in any of the activities (all p values ≥ 0.12).

In *Acacia drepanolobium* habitat, where foods are apparently less abundant and have shorter depletion times, higher-ranking female vervets made significantly more moves per unit time than lower-ranking female vervets did (all females, $r^2 = 0.59$, $p = 0.03$, Fig. 3). They also moved farther than lower-ranking females did (rank classes, $t = 2.8$, $p = 0.05$, $\bar{x} = 154$ m vs. 110 m). They do not differ significantly from lower-ranking females in other ranging behaviors (all p values ≥ 0.08). Higher-ranking females ate a significantly greater proportion of fungi and miscellaneous plant parts than lower-ranking females (all females, $r^2 = 0.51$,

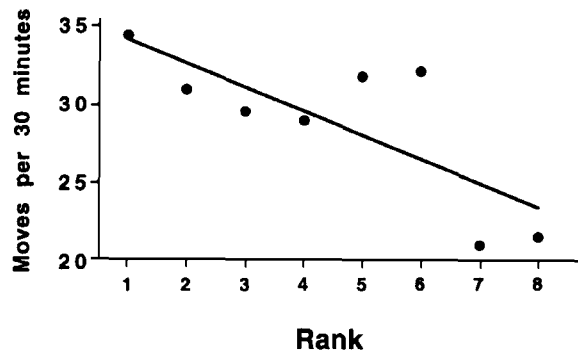


Fig. 3. Relationship between rank and number of moves between food sites per 30 min for individual adult female vervet monkeys in *Acacia drepanolobium* habitat ($r^2 = 0.59$, $p = 0.03$).

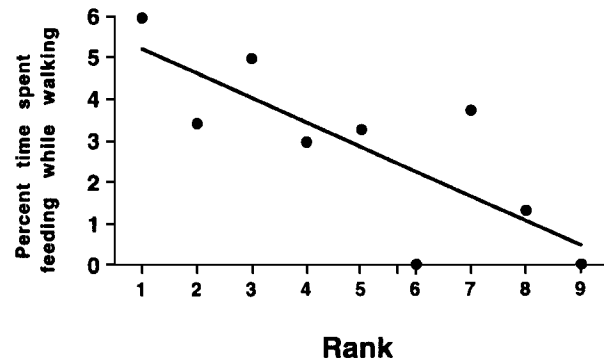


Fig. 4. Relationship between rank and time spent feeding while walking for individual adult female vervet monkeys in *Acacia drepanolobium* habitat ($r^2 = 0.61$, $p = 0.01$).

$p = 0.04$, fitted line ranging from 8% to 2%; rank classes, $t = 3.6$, $p = 0.02$, $\bar{x} = 6\%$ vs. 2%) but they do not differ from lower-ranking females in dietary proportions of other foods (all p values ≥ 0.15). Higher-ranking females spent significantly more time feeding while walking than lower-ranking females did (all females, $r^2 = 0.61$, $p = 0.01$, Fig. 4) and more time foraging while stationary (all females, $r^2 = 0.43$, $p = 0.05$; Fig. 5), but they did not differ from lower-ranking females in any other activities (all other p values ≥ 0.08).

Based on correlation coefficients analyzed by habitat across categories of ranging behavior, activity budgets, and diet, the effect of rank is either not significantly weaker in *Acacia drepanolobium* habitat than in *A. xanthophloea* habitat

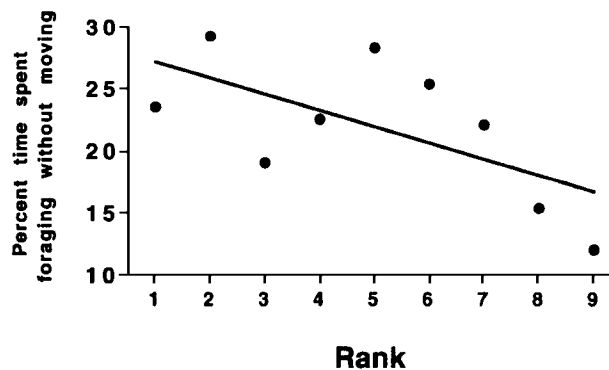


Fig. 5. Relationship between rank and time spent foraging while stationary for individual adult female vervet monkeys in *Acacia drepanolobium* habitat ($r^2 = 0.43$, $p = 0.05$).

(all females, $F = 1.43$, $p = 0.24$) or it is significantly stronger (rank classes, $F = 9.71$, $p = 0.003$). In either case, the results did not support the prediction that vervets have stronger rank differences on behavior in the habitat having the more usurpable foods.

DISCUSSION

Differential Rank Differences in Patas and Vervets

This is the first evidence that closely related, sympatric species differing in the stability of female dominance hierarchies also differ in the extent of rank effects on nonagonistic behaviors that are tightly linked to ecology. The existence of rank differences in both ecological behavior and agonistic behavior in vervets and the relatively weak rank differences in both these behaviors in patas monkeys suggest these characteristics share a common underlying ecological cause, the most likely one being differential usurpability of foods. Provisioned groups of patas monkeys have stable, linear dominance hierarchies (Kaplan and Zucker, 1980; Jacobus and Loy, 1981; Loy and Harnois, 1988; Nakagawa, 1992; Goldman and Loy, 1997). Provisioning often increases the frequency of agonistic interactions such that relative ranks become more obvious (Rowell, 1967; Southwick, 1967; Boccia *et al.*, 1988; Brennan and Anderson, 1988; Isbell and Pruettz, 1998). The Laikipia patas monkey group is the only non-provisioned patas group for which dominance interactions have been described, and their dominance hierarchy was not statistically linear over a four-year period (Isbell and Pruettz, 1998). Relative ranks of non-provisioned adult female patas monkeys are difficult to determine partly because reversals within dyads of females constitute a high percentage of their agonistic interactions and partly because maturing females appear to create instability as they enter the dominance hierarchy. Conversely dominance relationships among female vervets are stable over time—at Laikipia ≥ 4 years—with virtually no reversals within dyads (Isbell and Pruettz, 1998). The differences in stability or strength of the dominance hierarchy between provisioned and nonprovisioned patas monkeys and between patas monkeys and vervets have been attributed ultimately to differences in their food resources by Isbell (1991), Isbell *et al.* (1998a), and Isbell and Pruettz (1998). Provisioned patas monkeys undoubtedly feed on foods that are temporally and spatially more clumped and thus more easily usurped than food eaten by nonprovisioned patas. Similarly, vervets typically feed on foods that have longer depletion times, which may make their foods more usurpable than those of patas monkeys (Isbell *et al.*, 1998a).

On the basis of the difference between nonprovisioned patas monkeys and vervets in the strength and stability of the dominance hierarchy, we expected that higher- and lower-ranking female vervets would differ more than higher- and lower-ranking patas monkeys in behaviors that are closely linked with ecology.

The ANOVA on correlation coefficients (Table II) was not biased by sample size, and it had the power to combine effects that were individually not statistically significant. This test showed that vervets have stronger rank differences than patas monkeys. Indeed, rank explained more than twice as much of the variance in ranging behavior, activity, and diet in female vervets as in female patas monkeys.

Higher- and lower-ranking female patas monkeys differ significantly from one another in only the proportion of time spent climbing (based on the t-test) and in the proportion of seeds in the diet (correlation test). No other rank-related difference is apparent. Given the number of individual tests that we conducted, some tests could result in statistical significance by chance alone. On the other hand, the existence of real rank differences is more convincing when both kinds of statistical tests are consistent with each other. Among patas monkeys, in no case was there a statistically significant rank difference using both the t-test and the correlation test. Female patas monkeys, as expected, do not appear to be strongly influenced by rank in behaviors that are closely associated with their habitat or the qualities of their food resources.

In both habitats combined, vervets differed significantly in two food types: higher-ranking females ate a greater proportion of fungi and miscellaneous plant parts than lower-ranking females did, based on both tests; and higher-ranking females ate a smaller proportion of fruits than lower-ranking females did, based on the t-test. Fungi, in particular, are usurpable, perhaps because they have a long FSDT. A low-ranking female may not be able to consume many mushrooms while sitting in one spot because mushrooms are usurpable, being abundant in restricted areas, e.g., on top of termite mounds. They also differed in one ranging behavior: higher-ranking females travelled farther than lower-ranking females, based on both tests. Greater travel distance among higher-ranking female vervets was an unexpected result, but it is explicable when each habitat is considered separately.

Rank Differences in Vervets Relative to Habitat

While in *Acacia xanthophloea* habitat, higher- and lower-ranking vervet females differed most in their ranging behavior: higher-ranking females spent longer at food sites and made fewer moves than lower-ranking females, based on correlation tests. This difference in time spent at food sites probably reflects the ability of higher-ranking females to feed undisturbed regardless of FSDT, while lower-ranking females get supplanted more easily from foods with longer FSDTs (Shopland, 1987; Janson, 1990).

In *Acacia drepanolobium* habitat, higher-ranking female vervets travelled farther (t-test), made more moves per unit time (correlation test), spent more time feeding while walking (correlation test), spent more time foraging while stationary (correlation test), and ate a greater proportion of fungi and miscellaneous plant

parts than lower-ranking females (both tests). By covering more area, stopping more often for food, and making more efficient use of their travel time in combining feeding with travel, higher-ranking vervets may have been able to eat more food than lower-ranking vervets could in *A. drepanolobium* habitat.

The variation in behavior of the same individuals in different habitats may reflect differential opportunities to use these habitats. Higher-ranking vervets may be able to employ different, but equally good, strategies in different habitats, perhaps depending on FSDT. In *Acacia xanthophloea* habitat, higher-ranking vervets stayed longer at food sites than lower-ranking vervets. In *Acacia drepanolobium* habitat, where average FSDT is shorter and the ability to monopolize access to foods is presumably less effective, higher-ranking vervets foraged more like patas monkeys than lower-ranking vervets did. Previously, we reported that six measures of ranging and activity behaviors (not analyzed by rank) showed differences between patas and vervets (Isbell *et al.*, 1998a, 1998b). Patas monkeys spent fewer minutes per food site and travelled farther between foods, travelled farther per unit time, made more moves per unit time, spent more time foraging while stationary, and more time foraging while walking. Higher-ranking vervets followed these patterns more closely than lower-ranking vervets in *Acacia drepanolobium* habitat, behaving more like patas than lower-ranking vervets in all but one of these behaviors (distance between foods), including three with statistically significant rank differences (total distance per unit time; number of moves per unit time; foraging while stationary). The greater convergence of the behavior of higher-ranking vervets with that of patas monkeys in *Acacia drepanolobium* habitat and the persistence of general rank differences in that habitat despite fewer opportunities to contest over food (Pruetz, in prep.) suggest that social constraints can reduce the foraging efficiency of lower-ranking vervets even in habitats where food is not particularly usurpable.

We expected rank differences to be greater in vervets when they were in *Acacia xanthophloea* habitat than when they were in *A. drepanolobium* habitat because foods in *A. xanthophloea* habitat have longer FSDTs and are thus likely to be more usurpable (Isbell *et al.*, 1998a). This was clearly not the case, and if anything, the results were opposite that expected. Rank explained about 15% of the variation in vervet activities, ranging behavior, and diet in the *Acacia xanthophloea* habitat, but about 25% in the *A. drepanolobium* habitat. The extent of rank differences among vervet females was also expected to converge with that found among patas monkeys when using the same habitat (*Acacia drepanolobium*). This was also not the case. Rank explained about 25% of the variance in vervet behaviors in *Acacia drepanolobium* habitat, compared to about 10% in patas. It is possible that once hierarchies are established, i.e., when animals feed regularly on usurpable foods, they can be maintained despite relatively nonusurpable foods and fewer agonistic interactions because nonecological constraints exist, such as learning, in which only a few interactions are needed to establish consistent asymmetric agonistic relationships (Pusey and Packer, 1997).

In summary, these results suggest that females that have stable dominance relationships show stronger rank differences in nonagonistic behaviors more obviously linked to ecology than females that have unstable dominance relationships. This covariation between agonistic behavior and ecological behavior provides further indirect support for the hypothesis that dominance relationships are ultimately determined by ecological conditions. They also suggest that for females with stable dominance relationships, ecological characteristics and social constraints interact to influence behavior such that higher-ranking females may be better able than lower-ranking females to adjust their behavior in different habitats to obtain their food efficiently.

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