

Diet for a Small Primate: Insectivory and Gummivory in the (Large) Patas Monkey (*Erythrocebus patas pyrrhonotus*)

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A 17 month field study of unprovisioned patas monkeys (*Erythrocebus patas pyrrhonotus*) in Laikipia, Kenya, using both ad libitum and scan sampling techniques, revealed that the diet of patas monkeys consists primarily of gum of *Acacia drepanolobium*, arthropods (both free-living and concentrated in the swollen thorns of *A. drepanolobium*), and other animals. This type of diet is normally found only in smaller-bodied primates. Results from vegetational transects suggest that the larger-bodied patas monkey can subsist on such a diet because gum and arthropods are relatively easily found in their habitat, thereby minimizing search time. Patas monkeys also spend more time moving and less time feeding (while not moving) than other Old World primates. The characteristic long limbs of patas may have evolved in response to feeding on small, nonusurpable, and widely distributed foods, in which access to foods is maximized while time and energy spent in terrestrial travel between food sites are minimized. *Am. J. Primatol.* 45:381–398, 1998.

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INTRODUCTION

Patas monkeys (*Erythrocebus patas*) are superlative primates. Among cercopithecids, they have the longest legs relative to their body size [Strasser, 1992; see also Gebo & Sargis, 1994]. They are considered the fastest of all primates, having been estimated to run as fast as 55 km/h [Hall, 1965]. Among cercopithecines, patas have the earliest age at first reproduction (3 years) [Chism et al., 1984; Harvey et al., 1987] and, along with *Cercopithecus neglectus*, *C. campbelli*, *Miopithecus talapoin*, and some *C. aethiops*, the shortest interbirth intervals (1 year) [Cheney et al., 1986; Butynski, 1988]. Despite their high reproductive potential, they occur at the lowest densities of any cercopithecoid [Cords, 1987;

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Stammback, 1987; Melnick & Pearl, 1987; Struhsaker & Leland, 1987] and have the largest home ranges for their group biomass of any primate [Clutton-Brock & Harvey, 1977]. This contribution adds yet two more superlatives: East African patas monkeys (*E. p. pyrrhonotus*) are the most insectivorous and gummivorous of cercopithecoids and the largest gummivore/insectivore of all the primates.

A general principle of physiological ecology is that although smaller animals eat absolutely less food than larger animals, they require more food per unit body weight because their metabolic rates are higher per unit body weight [Bell, 1971; Jarman, 1974]. Thus, although smaller animals can subsist on relatively small and rare foods, their foods must be of high quality (e.g., gum and insects). In contrast, larger animals must subsist on more abundant foods, but their foods can be of lower quality (e.g., grasses and mature leaves). Low-quality foods are generally more abundant than high-quality foods [Jarman, 1974; Gaulin, 1979; Terborgh, 1983].

Among primates, those that feed primarily on leaves tend to be large-bodied. The largest primate, *Gorilla gorilla*, is a folivore in parts of its biogeographic range. In contrast, primates that feed primarily on gum or arthropods are small-bodied. The largest reported primate specialist on gum and/or arthropods, *Galago crassicaudatus* [Gaulin, 1979; Richard, 1985; Nash, 1986], weighs no more than 1.8 kg [Bearder & Doyle, 1976]. In this paper, I present data showing that patas monkeys in Kenya also feed primarily on arthropods and gum. With adult female patas monkeys weighing 4–7.5 kg and adult males 7.5–13 kg [Haltenorth & Diller, 1977], patas monkeys are two to seven times heavier than *Galago crassicaudatus*. The highly gummivorous and insectivorous diet of East African patas monkeys appears at first to contradict the Jarman/Bell principle. I suggest here that, on the contrary, the patas monkey is not an exception but for a confirmation of the principle. I also provide supporting evidence that the long limbs of patas are, at least in part, an adaptation for efficiency in travel [Chism & Rowell, 1988] between numerous small and widely dispersed food sites.

METHODS

Study Site

The behavioral data included here were collected on Segera Ranch on the Laikipia plateau, Kenya (36° 50' E, 0° 15' N; elevation 1,800 m). Segera Ranch is a cattle ranch and conservation area that supports at least 17 species of ungulates, four likely mammalian predators of patas (lion [*Panthera leo*], leopard [*P. pardus*], black-backed jackal [*Canis mesomelas*], and cheetah [*Acinonyx jubatus*]), and three other primate species (vervets, baboons (*Papio anubis*), and galagos [*G. senegalensis*]). Researchers, water troughs, fences, cattle, and cattle herders are the only introduced intrusions into the lives of the monkeys (the latter two have coexisted with patas for several centuries). Climatological data were collected approximately 10 km away at my research camp. Laikipia is a semiarid ecosystem in the rainshadow of Mt. Kenya. Rainfall, on average, peaks in April and May, although there is considerable year-to-year variation in both total and monthly amounts of rain (Fig. 1). Total yearly rainfall in 1993 was estimated at 568 mm. During the 17 month study period, an average of 43.4 mm of rain fell per month (range: 0–144 mm). Mean minimum and maximum temperatures during this period were 12.0°C and 28.3°C, respectively.

Soils in the study area are poorly drained, seasonally waterlogged (“black cotton”) vertisolic soils [Ahn & Geiger, 1987] supporting wooded grasslands dominated by *Acacia drepanolobium* in the overstory and *Pennisetum* spp. and

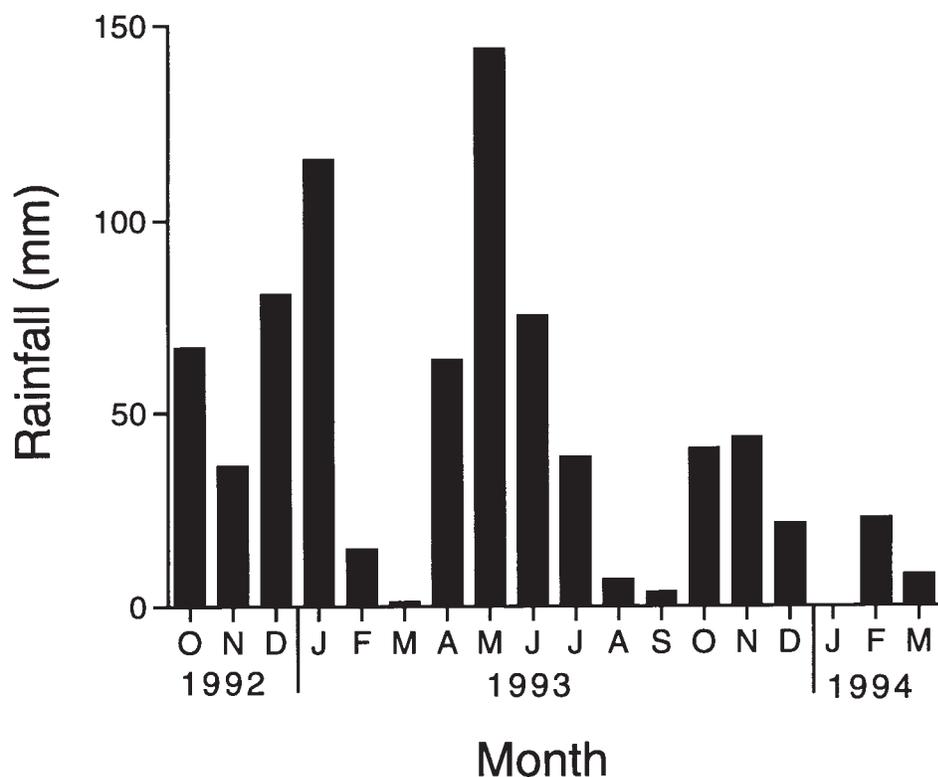


Fig. 1. Monthly rainfall (mm) from October, 1992, through March, 1994, 10 km from the study area.

Themeda triandra in the understory [Taiti, 1992; Young et al., 1997]. *A. drepanolobium* is a small leguminous tree ranging in height from less than 1 m to 7 m. The distribution of heights is consistent with that expected of a population with a stable age structure [Young et al., 1997]. *Acacia drepanolobium* has hollow stipular swellings (swollen thorns or "galls") that are part of a complex mutualism existing between *A. drepanolobium* and several species of protective ants [Hocking, 1970; Madden & Young, 1992; Young et al., 1997]. Colonies of these ants live in the swollen thorns and harvest extrafloral nectaries on the leaves. Virtually every individual of *A. drepanolobium* taller than 0.5 m houses a colony of ants [Young et al., 1997]. In addition, numerous other invertebrates and small vertebrates occur on *A. drepanolobium*, many inside swollen thorns. The ants, especially those of the genus *Crematogaster*, swarm and bite when the thorns are disturbed [Hocking, 1970; Madden & Young, 1992]. The study site is characteristic of habitats to which patas are now largely restricted in Kenya and Tanzania.

Subjects

Patas monkeys live in single male, multifemale groups for most of the year. Females remain in their natal groups throughout life, whereas males disperse from their natal groups when they become juveniles or subadults [Hall, 1965; Chism et al., 1984]. Extragroup males are solitary or form small associations with other males and converge upon groups of adult females, their offspring, and

the one resident male during the breeding season [Chism et al., 1984]. The resident male is often replaced at this time [Chism et al., 1984; Chism & Rowell, 1986; L.A.I., unpublished data]. Females can reproduce yearly, beginning at 3 years of age [Chism et al., 1984].

As part of a comparative study of vervets and patas monkeys that began in August, 1992, and is continuing, I have studied one group of patas ranging in size from 28–47 individuals. Adult females were identified as individuals by variation in the color, size, and shape of their nipples, tail kinks, tail carriage, color of ischial callosities, and temporary dye marks (black Nyanzol D powder mixed with an aqueous solution of alcohol, water, and hydrogen peroxide [Belmar Inc., North Andover, MA] sprayed on their fur with SuperSoaker 30 and SuperSoaker 300MDS (Larami Corp., Mt. Laurel, NJ) water guns. Adult males that came into proximity with the study group were identified as individuals by variation in coat color and the length of the tail. Only a few juveniles could be recognized individually or by sex. The group ranged over at least 2,850 ha and overlapped minimally with two smaller groups of eight and 15 animals. Intergroup encounters were infrequent but invariably aggressive, with adult females and juveniles, and occasionally the resident adult male, actively involved [Chism et al., 1984].

Data Collection and Analysis

Data on feeding behavior presented here were collected for 17 months, from October, 1992, until March, 1994 (excluding April, 1993). For the first 8 months, the food species and food item were recorded whenever animals were observed feeding to determine the range of food items found in the patas diet. Foods that were not identified were noted as such with a description whenever possible of the motor patterns used to get the foods. I assumed quick movements were used solely for obtaining animals. Beginning in July, 1993, feeding, moving, and other activities were recorded for all animals seen during instantaneous scan samples conducted for 1 min every 15 min during systematic observations. Feeding was scored and the food species and item noted when an animal was observed chewing, gnawing, or placing an item into its mouth. Moving was scored when an animal was observed walking, loping, running, climbing, or leaping. An animal observed chewing while moving was scored as moving. The group was scanned each time from left to right to avoid potential biases toward obvious behaviors such as grooming and fighting.

Analyses of activities are based on 6,265 records over 9 months. Monthly scores for each activity were calculated both within and among age/sex classes as percentages to give equal weighting to months with unequal sample sizes. Monthly percentages were then averaged to obtain overall percentages of time devoted to moving and feeding for each age/sex class and for the group over the entire study.

Analyses of diet are based on 974 ad libitum feeding records and 462 scanned feeding records (1,436 total records) collected during 452 observation hours. Feeding records for different food items were first calculated as proportions of the monthly diet to reduce biases resulting from unequal sample sizes. Monthly proportions were then averaged over all 17 months to obtain an overall estimate of the relative contributions of different foods to the diet of patas monkeys. I used the Shannon Index ($H = -\sum p_i \log p_i$, where p_i is the proportion of the diet attributed to food item i) as a measure of monthly dietary diversity.

I obtained larger sample sizes in the first 8 months when I used ad lib sampling than later when I used scan sampling. The diets of patas monkeys during these two periods were not significantly different due to sampling methods. Di-

etary diversity was about 20% greater during the first 8 months of ad lib sampling than during the next 9 months of scan sampling (ad lib: H (mean \pm 1 S.D.) = 0.65 ± 0.16 ; scans: $H = 0.52 \pm 0.19$; Mann-Whitney U test: $U = 23.5$; $P > 0.20$). However, dietary diversity tends to be positively correlated with rainfall ($r = 0.35$, $P < 0.10$), and the months of focal sampling were wetter than the months of scan sampling (Fig. 1). When this rainfall difference is taken into account, the residual difference in dietary diversity between the two sampling methods drops to only half as much ($\sim 10\%$, $U = 35.5$, $P > 0.20$). In addition, there were no consistent differences between the two sampling methods in estimates of the percentages of the staple food items discussed in this article (gum and swollen thorns) (Fig. 3). Therefore, I combined the data obtained by the two methods in the analyses that follow.

I also destructively sampled 573 swollen thorns from 183 trees in November, 1992, to determine their contents. All trees along one 500 m \times 5 m and two 250 m \times 5 m randomly chosen line transects and two randomly chosen 50 m \times 5 m transects within the study group's home range were sampled. Two mature (black or gray) and, when they were present, two young (red or brown) swollen thorns from each tree were opened with scissors or knives while wearing latex gloves to minimize bites from ants. The locations of the swollen thorns on the tree relative to the trunk (distal, medial, or proximal) and the lowest branch (high, middle, or low) and their contents were recorded on checksheets. When present, young swollen thorns were invariably located at the distal ends of branches, whereas mature thorns were more numerous and occurred on all but the oldest stems.

From December, 1992, to June, 1993, the number of swollen thorns eaten per tree was recorded opportunistically for individual patas monkeys as they fed. The species of ant in each of these food trees was also noted.

In March, 1995, I sampled all 167 trees along five additional randomly chosen 50 m \times 5 m transects to estimate the abundance and distribution of gum. I recorded the height of each tree, and, when gum was present, the number of gum sites and their heights in the tree. I also estimated visually the surface area of each gum site, and, for globular gum, the volume.

All statistical tests are two-tailed. Nonparametric statistical tests are from Siegel [1956] and Zar [1984].

RESULTS

General Patterns

The diet of patas monkeys was simple. Only 13 plant species contributed to their diet (Table I). The most heavily used plant species was *Acacia drepanolobium*, which contributed about 83% of the diet (monthly range: 47–100%; but see Animal Foods below). This reflects the ubiquity of *A. drepanolobium* in the habitat of patas monkeys. *A. drepanolobium* occurs as a virtual monoculture in the study area, accounting for over 98% of all woody species and occurring at a mean density of 1,335 individuals/ha [Young et al., 1997]. Other, less important food plant species included *Commelina* spp. (4% overall; monthly range: 0–7%) and *Lycium europeum* (2% overall; monthly range: 0–9%).

The gum of *A. drepanolobium* was the single most numerous food item in the diet, contributing 37% of the records (monthly range: 5.4–87.5%) [see also Chism & Wood, 1994]. Tree surveys revealed that gum was present on 30% of all sampled trees at an average density of 344 trees/ha. Globular forms of gum, which are most often eaten by patas, were found on 24% of the sampled trees; only 3% of

TABLE I. Food Species and Food Items in the Diet of East African Patas Monkeys Over a 17-Month Period (n = 1,436)*

Food species	Food item	Weighted average (%)
<i>Acacia drepanolobium</i>	Gum	36.9
	Young swollen thorns	16.9
	Mature swollen thorns	10.1
	Swollen thorns of unspecified age	9.6
	Flowers	6.1
	Pods/seeds	3.7
	Soft thorns	0.1
	Unidentified	<0.1
<i>A. xanthophloea</i>	Gum	<0.1
<i>A. seyal</i>	Flowers	0.7
	Gum	0.5
	Young swollen thorns	0.3
	Swollen thorns of unspecified age	0.2
<i>Commelina</i> spp. (<i>C. latifolia</i> , <i>C. reptans</i> , <i>C. africana</i>)	Fruits/seeds	3.3
	Stems	0.5
	Flowers	0.2
<i>Lycium europeum</i>	Leaves	1.6
	Flowers	0.2
	Fruits	0.1
Mushrooms		0.5
<i>Sarcostema viminalis</i>	Roots	0.1
<i>Opuntia vulgaris</i>	Leaves	0.1
<i>Hibiscus</i> sp.	Flowers	<0.1
<i>Cucumis aculeata</i>	Stems	<0.1
	Leaves	<0.1
<i>Lippia javanica</i>	Fruits	<0.1
<i>Plectranthus</i> sp.	Leaves	<0.1
Unidentified plants	Grass culm	0.2
	Stems	0.1
	Leaves	0.1
Orthoptera (grasshoppers)		3.1
“Caterpillars” (Coleoptera/ Lepidoptera)		0.9
Coleoptera		0.5
Lepidoptera (moth)		0.2
Hymenoptera (ants)	Larvae	0.1
	Adults	0.1
Hymenoptera (wasp)		<0.1
Gecko (<i>Lygodactylus pictoralis</i>)		0.7
Unidentified items		2.4
Total		100.1

*All months are weighted equally to control for unequal sample sizes.

all trees had more than one glob. The percentage of trees with gum increased with increasing tree height ($r_s = 0.94$; $n = 6$; $P = 0.02$) (Fig. 2).

Swollen thorns of *A. drepanolobium* were the second most numerous food item, accounting for 36% of the records (monthly range: 8.7–77.1%). Swollen thorns are found on all *A. drepanolobium* individuals; on average, about 20% of all thorns on each tree are swollen [Hocking, 1970]. Although all trees have swollen thorns and only a quarter of the trees have gum, swollen thorns and gum were eaten nearly equally. Gum had a higher selection ratio (the number of feeding records

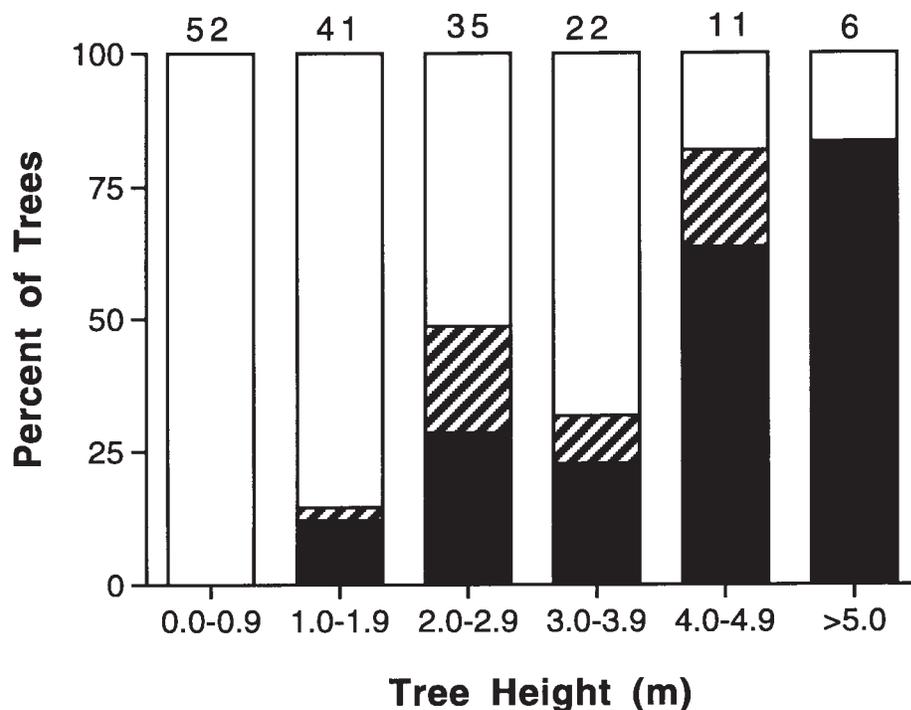


Fig. 2. Percentage of sampled trees without gum (white bars), with gum but without globs (striped bars), and with globs of gum (black bars). The percentage of trees with gum and with globs of gum tends to increase with the height of the tree. Sample sizes are above the bars.

divided by the number of trees/ha [Oates, 1977] than swollen thorns (1.54 vs. 0.39), indicating that patas made a stronger effort to eat gum than swollen thorns. Gum and swollen thorns together accounted for 74% of the diet of patas and were staples whose combined contribution to the diet dropped below 45% of the monthly diet only once (Fig. 3).

Young swollen thorns were eaten proportionately more than mature thorns in months with greater rainfall ($y = 0.36\text{Log}(x) + 0.076$; $r = 0.91$; $P < 0.01$). This is likely due to greater stem growth and thorn production during rainy periods.

Animal Foods

When patas monkeys fed on *A. drepanolobium*, they fed only briefly at each food tree before moving away. Individuals ate only one swollen thorn per tree in 72 of 88 (82%) observations for which the number of thorns eaten per tree was recorded. Two swollen thorns were taken from the same tree during 13 observations (15%), three thorns twice, and four thorns once. Ants were found on all but one of these 88 trees. *Crematogaster mimosae*, the most aggressive ant species, was the most frequently found species on these trees (60%). This probably reflects its greater abundance relative to other ant species (Table II) [see also Hocking, 1970]. *C. nigriceps* was also common, occurring in 25% of the trees. *C. sjostedti*, a less aggressive ant, was found only on the one tree in which four swollen thorns were eaten.

Although young swollen thorns are likely to have nutritional value by them-

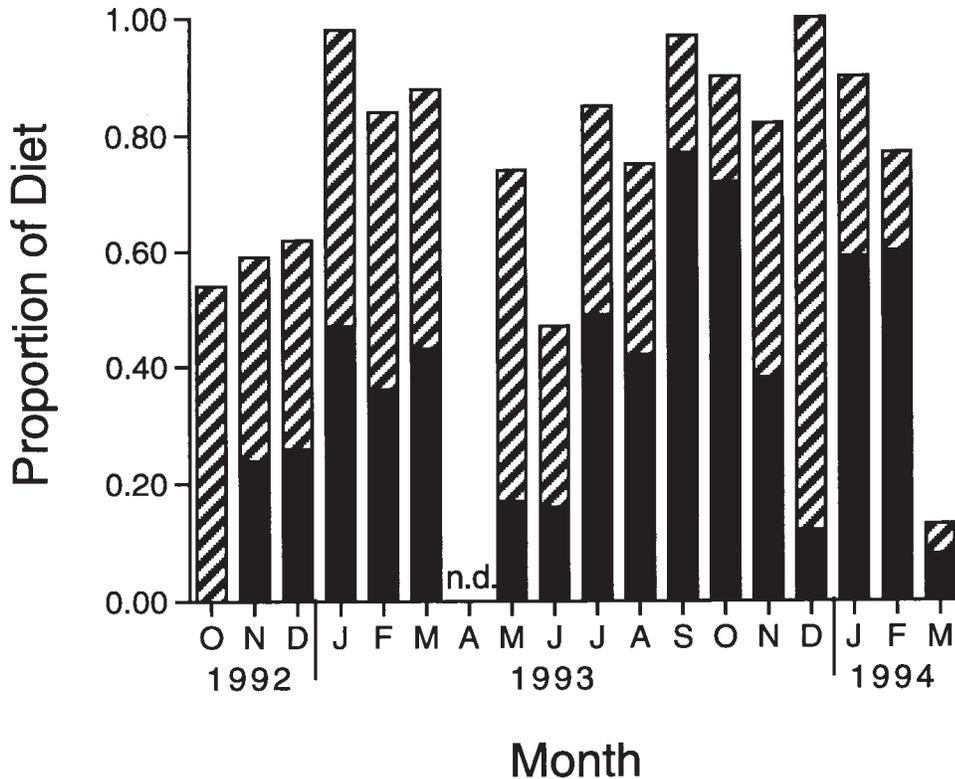


Fig. 3. Proportion of gum (striped bars) and swollen thorns (black bars) in the monthly diet of patas monkeys on Segera Ranch, Laikipia, Kenya. No data are available for April, 1993.

selves (they taste sweet, and local children eat them), mature swollen thorns are dry and lignified and apparently have no nutritional value (although Redford [1987] suggested the possibility that indigestible matter detoxifies chemicals produced by ants). Patas do not, in fact, generally eat mature swollen thorns but open them up mainly for the animals that live inside the thorns. Animals were found in the swollen thorns of 84% of all trees from which swollen thorns were destructively sampled and in 73% of all sampled swollen thorns (Table II). Ants were by far the most numerous animal; they were present in 78% of all young thorns and 47% of all mature thorns opened by observers. In young and mature thorns combined, immature (eggs, larvae, and pupae) and adult ants were found together more often than adults alone (32% vs. 26%). The most common ants found inside thorns in order of frequency were *C. mimosae*, *C. nigriceps*, *C. sjostedti*, *Tetraponera penzigi*, and *Camponotus* spp. Each swollen thorn occupied by *C. mimosae* ants has been estimated elsewhere in East Africa to hold, on average, 70 eggs, 74 larvae, and 55 pupae as well as numerous adults [Hocking, 1970]. The combined biomass of *C. mimosae* and *C. nigriceps* has been estimated at 4,375 kg/km² [Hocking, 1970], which is comparable to the total biomass of large (>5 kg) herbivorous mammals in other African ecosystems with similar annual rainfall [Owen-Smith, 1988]. Although these estimates seem higher than what I observed at Segera, the numbers of ants can nonetheless be considerable. Adult *Crematogaster* are particularly aggressive in defense of their colonies,

TABLE II. Contents of Swollen Thorns of *Acacia drepanolobium* Opened by Destructive Samples (See Text for Sampling Methods)

	Mature thorns (n = 364)		Young thorns (n = 209)		All thorns (n = 573)	
		%		%		%
Adult ants present only						
<i>Crematogaster mimosae</i>	48	13.2	45	21.5	93	16.2
<i>C. nigriceps</i>	6	1.6	6	2.9	12	2.1
<i>C. sjostedti</i>	4	1.1	1	0.5	5	0.9
<i>Tetraponera penzigi</i> , <i>Camponotus</i> sp., and unidentified ants	21	5.8	18	8.6	39	6.8
Subtotal	79	21.7	70	33.5	149	26.0
Adults and immatures present						
<i>Crematogaster mimosae</i>	54	14.8	46	22.0	100	17.4
<i>C. nigriceps</i>	14	3.8	19	9.1	33	5.8
<i>C. sjostedti</i>	2	0.6	0	0.0	2	0.4
<i>Tetraponera penzigi</i> , <i>Camponotus</i> sp., and unidentified ants	22	6.0	27	12.9	49	8.6
Subtotal	92	25.3	92	44.0	184	32.2
Total thorns with ants	171	46.9	162	77.5	333	58.2
Other animals present						
“Caterpillars”	10	2.7	4	1.9	14	2.4
Larvae of non-ant arthropods	13	3.6	0	0.0	13	2.3
Spiders	9	2.5	1	0.5	10	1.7
Orthopterans	2	0.6	0	0.0	2	0.3
Dipterans	2	0.6	0	0.0	2	0.3
Mites	2	0.6	0	0.0	2	0.3
Frog (<i>Hyperolius</i> sp.)	1	0.3	0	0.0	1	0.2
Gecko eggs (<i>Lygodactylus pictorialis</i>)	1	0.3	0	0.0	1	0.2
Other	23	6.3	15	7.2	38	6.6
Subtotal	63	17.5	20	9.6	83	14.5
Total animal matter	234	64.3	182	87.1	416	72.6
Empty thorns	130	35.7	27	12.9	157	27.4

swarming rapidly and biting when they detect disturbances, particularly at the distal ends of the tree [personal observation; Hocking, 1970; Madden & Young, 1992]. Other animals found within the thorns included spiders, beetles, and frogs (Table II). Of these other animals, only scale insects (young thorns: n = 4; mature thorns: n = 3) were found with ants in the same thorn.

In addition to feeding on animals within the swollen thorns, patas were observed to eat geckos (*Lygodactylus pictorialis*), chameleons (*Chameleo senegalensis*), and a variety of invertebrates outside the thorns, including grasshoppers and “caterpillars” (free-living animals = 5% of all food items) (Table I).

The presence of ants and other animals inside the swollen thorns suggests that patas ingested more animal matter than is readily apparent from Table I. Although I was often able to see larvae, pupae, and adults on the mouths and chins of monkeys, I was not able to observe directly the contents of swollen thorns eaten by the monkeys. Therefore, I have produced three estimates of the proportion of total animal matter in the diet eaten from thorns. I multiplied the monthly proportion of young and mature swollen thorns in their diet by 1) 0% and 100%, respectively, 2) 87% and 64% (the proportion of young and mature destructively sampled thorns with animals), and 3) 100% and 100%. The first estimate as-

sumes that the monkeys ate the young thorns only for their own nutritional value but that the monkeys ate the mature thorns only for the animals inside and that they could unerringly judge which thorns had animals. The second estimate assumes that the monkeys ate thorns randomly and only for the animals inside the thorns. The third assumes that they ate all the thorns entirely for the animals inside and that they could unerringly judge which thorns had animals. All estimates assume no major seasonal fluctuations in ant presence in thorns. Months in which the age of swollen thorns in the patas diet was not specified were given values based on the overall mean proportions of young and mature thorns eaten by patas monkeys during the other months (young swollen thorns = 64%; mature swollen thorns = 36%). When the proportion of swollen thorns with animal matter thus estimated is combined with the proportion of free-living animals in the diet (5%), the estimated proportion of animal food increases to 19%, 34%, or 42%, depending on which of the three assumptions is used. The first estimate is undoubtedly an underestimate because animals would invariably be eaten with young thorns even if patas monkeys were eating them also for the plant material. The second estimate may also be an underestimate because, unlike researchers, patas appeared to open swollen thorns nonrandomly (they often scanned trees before taking swollen thorns) and because many of the unidentified food items (2.4%) outside of thorns were probably animals (unidentified foods were obtained 68% of the time with quick, grabbing movements suggesting capture of fast-moving animals). Therefore, I estimate that 30–40% of the diet of patas monkeys consisted of animals and that most of these were social ants.

Feeding Behavior by Age and Sex

There were minor differences in the diet of individuals of different age/sex classes. The adult male and infants ate gum most often, followed by swollen thorns, whereas adult females and juveniles ate swollen thorns most often, followed by gum (Table III). Flowers were the third most numerous food item for all age/sex classes. Seeds were the fourth most numerous food item for the adult male and infants, whereas arthropods were the fourth most numerous food item for adult females and juveniles.

There were also minor age/sex differences in the percentage of time spent

TABLE III. Proportions of Food Items in the Diet of Different Age/Sex Classes of Patas Monkeys Over 16 Months During Which Age/Sex Classes Were Noted

Food item	Adult male diet (%)	Adult Females diet (%)	Juvenile diet (%)	Infant diet (%)
Gum	44.3	34.4	36.5	37.8
Swollen thorns	35.6	41.1	38.8	30.9
Flowers	7.0	6.2	8.1	16.4
Acacia seeds/pods	4.1	4.0	3.9	7.5
Leaves/soft thorns	2.5	3.2	1.7	1.3
Non-Acacia fruits/seeds	0.7	2.9	2.5	0.8
Arthropods	1.6	5.1	5.4	3.8
Vertebrates	2.2	0.5	0.1	2.6
Roots	0.0	0.0	0.7	0.0
Mushrooms	0.0	0.0	0.1	0.0
Unidentified	2.1	2.6	2.3	0.7
Total	100.1	100.0	100.1	101.8

feeding. The adult male spent 8% of his time feeding ($n = 439$), whereas adult females spent an average of 11% of their time feeding ($n = 2,880$). Similarly, juveniles and infants spent 13% and 9% of their time feeding, respectively (juveniles, $n = 1,309$; infants, $n = 1,637$). More variation existed in the time spent moving. Infants were the most active, spending half their time moving, whereas juveniles spent 42% of their time moving. Adult females spent 37% of their time moving. The adult male was least active, spending 29% of his time moving. Overall, the group spent 11% of its time feeding and 39% moving.

DISCUSSION

Body Size and an Insectivorous/Gummivorous Diet

Although patas monkeys weigh about four times more than the next largest primarily gummivorous or insectivorous primate, results from this study suggest that at least two-thirds of their diet in Kenya (estimated by frequency of ingestion) consisted of gum and arthropods [see also Olson, 1985; Chism & Wood, 1994; Isbell et al., 1998]. Gum and arthropods (including larvae) contain high amounts of carbohydrates, protein, and lipids and are therefore high in quality [Gaulin, 1979]. Arthropods are generally smaller and more widely dispersed than fruits, flowers, seeds, and leaves [Terborgh, 1983]. (Relative dispersion is operationally defined here by the distance between two or more individual prey items or units of food. Foods are considered more clumped, or less dispersed, when the distance between two or more prey items or units of food is so small that no hind limb locomotion is required to obtain them. Foods are considered more dispersed when the distance between two units of food requires, minimally, hind limb locomotion to obtain them. As units of food become more widely dispersed, more travel is required [see Isbell et al., in press a]). I have also shown here that *A. drepanolobium* gum is a dispersed resource, occurring on less than one-third of all trees and, when present, limited most often to one site per tree (Fig. 2). Searching for small and widely dispersed foods is usually considered time-consuming, and larger-bodied primates usually cannot subsist to a great extent on gums and arthropods because they cannot obtain sufficient quantities to meet their dietary needs [Terborgh, 1983; Richard, 1985].

How can the patas monkey, a relatively large-bodied primate, sustain itself on a diet primarily of arthropods and gum? Patas monkeys have none of the recognized morphological adaptations of other primates for feeding on arthropods and gum, such as specialized anterior dentition, a long caecum and proximal colon, specialized nails [Nash, 1986], or an elongated digit [Sterling, 1994], that might improve their efficiency in finding or ingesting such foods. A superficial examination of their diet would suggest that patas monkeys are an exception to the Jarman/Bell principle and an exception to observed patterns of primate diet. I suggest, however, that patas monkeys do not violate the Jarman/Bell principle but that their food does. Patas monkeys in Laikipia, Kenya, may be able to sustain themselves on a diet largely of arthropods and gum, despite their large body size, because their diet consists of a rare combination of high-quality foods that are small and dispersed but also easily and quickly found. Social ants, which make up the majority of the arthropod foods of patas, are almost certainly more abundant than all of the more asocial arthropods (e.g., grasshoppers, beetles, and caterpillars) on which patas and many other insectivorous primates feed. They are also more quickly and easily found. Ants and other arthropod foods of patas can be found on almost every tree and in most swollen thorns in the study

area throughout the year. Unlike other insectivores, patas are thus required to spend little time searching for many of their arthropod foods. Similarly, although gum is not as common as swollen thorns, it can be found easily as the monkeys move through their home range.

Although easily found, gum and swollen thorns are nevertheless limited in their abundance at any given tree. Trees on which globular gum is found typically have only one globular gum site. Similarly, although every tree has many swollen thorns, patas typically eat only one (or two) swollen thorns per tree. The ant species that live in these swollen thorns are aggressive. Swarming by *Crematogaster* spp. increases rapidly during the first 45 s after their thorns have been disturbed and continues without letup for at least 4 min [Madden & Young, 1992] and perhaps much longer. Ants are effective in minimizing the browsing time of young giraffes (*Giraffa camelopardalis*) [Madden & Young, 1992], apparently by biting tender skin inside their noses. The aggressive behavior of the ants may have the same effect on the browsing time of patas monkeys by minimizing the number of swollen thorns that individual patas monkeys take per tree and lowering the probability that additional monkeys will select swollen thorns from the same tree. Interestingly, ants do not appear to constrain patas in their use of *A. drepanolobium* as resting and sleeping sites. The bodies of patas monkeys, which are covered with long, shaggy hair [Napier & Napier, 1985], may be better protected from ant bites than their sparsely covered lips and noses. The constraints apparently placed on the feeding behavior of patas by aggressive ants results in the ants being a more widely dispersed food resource for patas than is otherwise suggested by their ecological distribution.

Long Limbs as an Evolutionary Consequence of Feeding on Foods That Are Small, Nonusurpable, and Widely Dispersed

Patas monkeys on Segera Ranch in Laikipia spent 11% of their time feeding and 39% of their time moving [see also Isbell et al., 1998]. This contrasts with the activity budgets of many other Old World monkeys regardless of diet, broad habitat type, or phylogenetic grouping. Among arboreal, forest-dwelling folivores, for example, *Colobus badius* spent 30–41% of their time feeding and 7–9% moving [Marsh, 1978; Struhsaker & Leland, 1979]. *Colobus guereza* spent 20% of their time feeding and 5% moving [Struhsaker & Leland, 1979]. Among arboreal, forest-dwelling frugivores, *Cercocebus albigena* spent 42% of their time feeding and 21% moving [Waser, 1977]. *Macaca mulatta* spent 40% of their time feeding and 26% moving [Seth & Seth, 1986]. Among semiterrestrial, savannah-woodland frugivores, *Papio cynocephalus* spent 60–65% of their time feeding and 18–20% moving [Altmann & Muruthi, 1988]. Even the more closely related guenons, *Cercopithecus mitis* and *C. ascanius*, spent more time feeding (33%) and less time moving (~17%) than patas [Struhsaker & Leland, 1979]. It is possible, although not likely, that variation in definitions and sampling methods (all of the above used scan sampling, varying only in sampling interval and the length of time the animals were observed before their activities were recorded) produced the magnitude of the difference between patas and other Old World monkeys. Using similar definitions and methods (differing only by 5 min in the time interval between scans), Isbell and Young (1993) found that adult vervets in Amboseli National Park, Kenya, were again different from patas in spending more time feeding (32%) than moving (13%).

The difference between patas in this study and other Old World monkeys in time spent feeding and moving is not likely to exist because patas eat absolutely

less than other monkeys of similar weight. The short time that patas feed relative to primates in other habitats is more likely to indicate a diet of small and quickly eaten foods. Similarly, the greater time patas spent moving likely reflects both the opportunity afforded to ingest small food items while moving and reliance on foods that are more widely dispersed. Patas monkeys in Uganda have been described as feeding at a steady walk [Hall, 1965]. Patas at this study site spent four times as much time foraging while walking [Isbell et al., 1998] and spent one-third as much time at food sites as broadly sympatric vervets [Isbell et al., 1998].

Patas differ morphologically from their closest allies (*Cercopithecus* spp.) in having longer hind legs and forelegs [Hurov, 1987; Strasser, 1992], longer tarsal bones [Strasser, 1992], and hind foot digitigrady [Meldrum, 1991], all of which increase stride length [Hurov, 1987; Hildebrand, 1988]. Their unique morphology has been viewed as an adaptation for high-speed terrestrial locomotion primarily for escape from predators [Hall, 1965]. The ability to run fast may indeed help patas avoid predation both by chasing and running away from predators. Patas were observed to chase some mammalian predator species (i.e., black-backed jackals (*Canis mesomelas*) and leopards [personal observation; J. Pruett, personal communication; see also Hall, 1965; Struhsaker & Gartlan, 1970]. They also run from mammalian predators, particularly domestic dogs (*Canis familiaris*). However, climbing may also be effective; over a 4 year period, patas climbed trees in response to predators as often as they ran [Isbell et al., 1998]. More importantly, patas did not differ from sympatric vervets (which have shorter limbs) in their escape responses to predators. These points do not support the hypothesis that patas evolved unique responses (i.e., long limbs and high-speed escape) in response to predators [Isbell et al., 1998].

Alternatively, the long legs of patas have also been viewed as an adaptation to cover long distances efficiently [Chism & Rowell, 1988]. Patas monkeys travel, on average, about 3,800–4,200 m per day [Chism & Rowell, 1988]. Although they are smaller in body size and often have smaller groups than baboons, daily travel distances of patas are comparable to those of baboons [e.g., Sharman & Dunbar, 1982]. If long limbs evolved to travel long distances efficiently, the question, then, is what it is about their circumstances that requires patas but not baboons to be efficient at travelling so far each day. Patas in this study consumed their food quickly because it occurred in small packets and because the defensive behavior of their ant prey limited continued consumption in the same location. Patas elsewhere in Africa apparently also feed on small and widely dispersed foods (although not necessarily on arthropods within swollen thorns of acacias) [see Nakagawa, 1989]. Beyond the obvious fact that small foods provide less energy than large foods (all else being equal), foods that are small and quickly consumed cannot be usurped by other group members through direct, or contest, competition. Other group members may, however, increase the distance between food sites through indirect, or scramble, competition, in which group members may deplete foods in the paths of their neighbors [van Schaik, 1989; Isbell, 1991]. The amount of food an individual patas monkey obtains is thus likely to be maximized by increasing the number of food sites visited per unit time and being the first to visit them. Baboons, in contrast, often feed on foods that occur in larger packets and in a less dispersed distribution (e.g., fruits in trees), making them usurpable by high-ranking individuals [Post et al., 1980; Post, 1982]. Unlike patas, the speed at which an individual baboon arrives at such a food site may be of little advantage when the food can be usurped by a slower but higher-ranking individual.

These two strategies are used by high-ranking adult female vervets living in two habitats that differ in food size [see Isbell et al., 1998]. In *A. drepanolobium* habitat (also the habitat of patas in this study), where the foods of vervets are, like those of patas, relatively small, higher-ranking female vervets (who are presumably free of social constraints) visited more food sites per unit time than lower-ranking females. By contrast, in *A. xanthophloea* habitat, where the foods of vervets are larger, higher-ranking female vervets stayed longer at food sites than lower-ranking females [Isbell et al., unpublished data].

Why Do Patas Monkeys Have Such Large Home Ranges?

Theoretical and empirical data suggest that the size of home ranges is determined partly by body weight or group biomass [McNab, 1963; Milton & May, 1976; Clutton-Brock & Harvey, 1977; Isbell, 1991]. Patas monkeys have exceptionally large home ranges for their group weight [Clutton-Brock & Harvey, 1977]; the home range of patas monkeys in this study was minimally 2,850 ha. McNab [1963] developed a formula, $R = 12.6W^{.75}$ (where R = the home range and W = body weight), by which the home range of solitary, small mammals could be predicted based on body size. Struhsaker [1978] applied this formula to five group-living primate species in Kibale Forest, Uganda, by multiplying the estimated weights of an adult male, adult female, and an immature by the number of individuals in their respective age/sex classes and summing the products. Only *Cercocebus albigena* had a larger home range (410 ha) than predicted (278–308 ha) by the formula. Application of the formula (as calculated in Struhsaker [1978] to the study group (assuming one adult male patas monkey the weight of 10 kg, 12 adult females at 5 kg each and 34 immatures at 3 kg) each reveals an expected home range of 1,553 ha, about half of that observed.

The size of home ranges is also determined by the abundance and density of foods [McNab, 1963; Clutton-Brock & Harvey, 1977]. Primates that spend much of their time feeding on arthropods tend to have large home ranges for their (group) biomass [Clutton-Brock & Harvey, 1977], and patas appear to be no exception. Clutton-Brock and Harvey [1977] suggested that the foods of insectivorous primates may be less abundant than the foods of other primates [see also Isbell et al., 1998]. This is difficult to reconcile, however, with the finding in this study that social ants and other arthropods found within the swollen thorns of *A. drepanolobium*, a staple of the patas diet, are ubiquitous throughout the study group's home range. Patas live in some of the driest habitats of any primate in Africa, and it is possible that their large home ranges are more closely tied to water availability than to food abundance per se. Although the daily movements of the group often appeared to be circuitous or random, the group almost always seemed to move eventually toward cattle troughs or ephemeral pools of water where they drank water if undisturbed by cattle or people. The home range of the main study group also included a river that provided water more continuously in the past before irrigation diverted much of the water upstream. The home range of the larger of the two other patas groups in the area ended at this river. The third group had a long and narrow home range with a dam and a cattle trough at each end of its known home range. Interestingly, this group appears to have disintegrated some time after water was no longer being pumped into that cattle trough. By moving between widely scattered water sources, rather than radiating from a centrally located permanent water source, patas may minimize local depletion of food resources.

Alternatively, or in addition, their large home ranges may be an adaptation

to minimize encounters with predators [see Chism et al., 1983]. By sleeping in different sites each night, they are less predictably found by nocturnal predators [Chism et al., 1983]. Even more intriguing is the possibility that patas abandon use of a localized area within their home range and move to a different, nonoverlapping part of their home range after an encounter with a predator. Preliminary examination suggests such a pattern of home range use; its relationship to predator presence is currently being investigated.

CONCLUSIONS

1. In East Africa, patas monkeys feed primarily on gum of *Acacia drepanolobium* and arthropods, found at ground level in and around herbaceous vegetation and in the swollen thorns of *A. drepanolobium*.

2. Heavy reliance on gum and arthropods is unusual for such a large-bodied primate and appears to violate the Jarman/Bell principle. In fact, it is their food that "violates" the assumptions of the Jarman/Bell principle by being easily and quickly found despite being relatively small and widely dispersed.

3. Patas monkeys in this study can apparently subsist on such a diet because, unlike other gummivore/insectivores, they spent little time searching for their arthropod foods.

4. Many of the superlatives that describe patas monkeys, including their very long limbs and very long daily travel distances, may be associated with a diet of small, widely dispersed, and nonusurpable foods.

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