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Nutritional Benefits of *Crematogaster mimosae* Ants and *Acacia drepanolobium* Gum for Patas Monkeys and Vervets in Laikipia, Kenya

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ABSTRACT Patas monkeys (*Erythrocebus patas*) are midsized primates that feed extensively on the gum of *Acacia drepanolobium* and the ants are housed in swollen thorns of this Acacia. Their diet resembles that expected more of smaller bodied primates. Patas monkeys are also more like smaller bodied primates in reproducing at high rates. We sought to better understand the convergence of patas monkeys with smaller bodied primates by comparing their feeding behavior on ants and gum with that of closely related, sympatric vervets (*Chlorocebus pygerythrus*), and analyzing the nutrient content of the gum of *A. drepanolobium* and of *Crematogaster mimosae*, the most common ant species eaten by patas monkeys in Laikipia, Kenya. All occurrences of feeding and moving during focal animal sampling revealed that 1) patas monkeys seek *A. drepanolobium* gum but vervets avoid it; 2) both species open swollen thorns most often in the morning when ants are less active; 3) patas monkeys continually feed on swollen thorns and gum while moving quickly throughout the day, whereas vervets reduce their consumption of these items and their travel rate at mid-day, and; 4) vervets eat young swollen thorns at a higher rate than patas monkeys. Patas monkeys are able to spend little time acquiring substantial amounts of energy, protein, and minerals from *A. drepanolobium* gum and *C. mimosae* ants each day. These findings, when coupled with evidence of causes of infant and adult female mortality, suggest that reproductive success of female patas monkeys is more immediately affected by illness, disease, interactions between adults and infants, and access to water than by food. Am J Phys Anthropol 150:286–300, 2013. © 2012 Wiley Periodicals, Inc.

A gummivorous/insectivorous diet is generally considered manageable only for smaller bodied primates (500 g or less) because insects are sparse and often difficult to capture, and gums are usually not widely available (Kay, 1975; Gaulin, 1979). The patas monkey (*Erythrocebus patas*) is an exception because it is not small-bodied (females, mean: 6.5 kg, range: 5.4–8.0 kg; males, mean: 12.4 kg, range: 5.4–18.0 kg; Isbell, in press) but is nonetheless highly gummivorous and insectivorous (Isbell, 1998; Nakagawa, 2000). In Cameroon, patas monkeys feed primarily on gums and arthropods, especially grasshoppers (Nakagawa, 2000). In Kenya, at least 76% of the diet of patas monkeys included gums and arthropods, mainly ants, based on a combination of all occurrences and scan sampling (Isbell, 1998). Gums and ants are common, easily accessible, and eaten throughout the year, and they are staple foods for patas monkeys in Kenya (Isbell, 1998; Isbell and Young, 2007). Most of the gums and ants are obtained from one tree species, *Acacia drepanolobium*, which provides domatia for ants within swollen thorns in exchange for their defense against herbivores. Nearly all *A. drepanolobium* trees have ants and about one-third of all *A. drepanolobium* trees have visible gum sites (Isbell, 1998). With *A. drepanolobium* occurring at densities of over 1,300 trees/ha (Young et al., 1997), ants and gum are easily located.

Patas monkeys and smaller bodied primates also converge in their reproductive rates. Controlling for body size, patas monkeys are able to reproduce earlier in life and more often than any other primate for which data exist, except for ruffed lemurs (*Varecia variegata*) (Isbell et al., 2009, 2011). The age at first birth is 3 years, and most adult females reproduce yearly after that (Chism et al., 1984; Nakagawa et al., 2003; Isbell et al., 2009, 2011). The convergence of patas monkeys with other gummivorous/insectivorous primates in reproductive output suggests that gums and arthropods somehow contribute to high reproductive rates.

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This may seem paradoxical in part because gums are considered difficult to digest for animals without digestive specializations (Lambert, 1998, 2002; Caton et al., 2000; Power, 2010). Gums consist primarily of polysaccharides that are difficult to digest unless animals can slow the passage of food through the digestive system enough to allow microbial fermentation (Lambert, 1998). For example, when gum is added to the diet of captive callitrichids, food passage rates slow down in highly gummivorous common marmosets (*Callithrix jacchus*) and pygmy marmosets (*Cebuella pygmaea*) but not in less gummivorous saddle-back tamarins (*Saguinus fuscicollis*), cotton-top tamarins (*S. oedipus*), and golden lion tamarins (*Leontopithecus rosalia*) (Power and Oftedal, 1996). Fermented gums are a good source of energy and minerals, particularly calcium, compared to other primate foods such as leaves and fibrous fruits (Nash, 1986; Lambert, 1998).

Several species within the Cercopithecini have long food retention times, and it has been suggested that long retention times are typical of cercopithecines, enabling them to be generalist feeders that can take advantage of gum and/or arthropods as well as leaves and fruit (Lambert, 1998, 2002). The proportions of the gastrointestinal tract of patas monkeys are similar to other cercopithecine monkeys, including macaques and vervets (*Chlorocebus pygerythrus*, syn. *Ch. aethiops, Cercopithecus aethiops*) (Chivers and Hladik, 1980; Chivers, 1989). Vervets (females, mean: 4.1 kg, range: 3.4–5.3 kg; males, mean: 5.5 kg, range: 3.9–8.0 kg; Isbell and Jaffe, in press) have a large colon that hosts cellulolytic bacteria (Brourton et al., 1991; Stevens and Hume, 1995), suggesting that they are well equipped to digest fiber, especially soluble fiber. The diets of vervets and other guenons include substantial amounts of plants (Jaffe and Isbell, 2011) that comprise high concentrations of insoluble fiber (Blaine and Lambert, 2012; Lambert and Fellner, 2012). In a meta-analysis of the digestive tracts of vertebrates, Stevens and Hume (1995) noted that, at 110–229 mmol/L, vervets have among the highest concentrations of short-chained fatty acids of hindgut fermenting herbivores. These qualities suggest that cercopithecins, including vervets and patas monkeys, easily digest gums.

Although arthropods typically contain high concentrations of energy and protein, they can also be difficult to digest if their exoskeletons include a high proportion of the polysaccharide chitin. They become easier to digest if their chitin is not yet developed (as with larvae), removed, or degraded (Janson and Boinski, 1992; McGrew, 2001; BANR, 2003). In a study of the chitin of four insect species fed to captive animals, Finke (in press) found that amino acids represented 14–69% of the chitin, suggesting that if it is degraded, the amino acids would be available for digestion. Numerous adaptations exist to deal with chitin, including mechanical removal from the rest of the arthropod, thorough mastication, and enzymatic or microbial degradation of chitin (Lambert, 1998). Capuchins (*Cebus* spp.) and squirrel monkeys (*Saimiri* spp.) avoid eating the exoskeleton of arthropods by mechanically removing it with their fingers (Janson and Boinski, 1992). Galagos (*Galago senegalensis*) digest chitin more effectively by masticating it with the high shearing crests on their molars (Kay and Scheine, 1979). Pottos (*Perodicticus potto*) have chitinase in their digestive tracts, an enzyme that breaks down chitin in the digestive system (Cornelius et al., 1976). Although pottos are predominantly frugivorous (Jones, 1969; Nekaris and Bearder, 2011), chitinase is still useful to them because they also consume arthropods, especially ants (Charles-Dominique, 1977).

The discovery that chitinase can exist in the digestive system of a primate species that is not a committed insectivore suggests that it could be more widespread than previously thought. Indeed, chitinase has recently been identified in the digestive systems of humans (Paoletti et al., 2007), rhesus macaques (*Macaca mulatta*), and long-tailed macaques (*M. fascicularis*) (Krykbaev et al., 2010), none of which is highly insectivorous. In this light, it is possible that patas monkeys have chitinase or other chitinolytic enzymes in their digestive systems. Conversely, there is enough chitinous material in the fecal samples of patas monkeys that ant species can often be identified (L.A. Isbell, unpublished data), so that even if patas monkeys do have chitinolytic enzymes, the enzymes are not likely to be completely effective. In addition to being high in protein, arthropods provide minerals that may be rare in other foods, particularly iron and zinc (Christensen et al., 2006).

To better understand how gums and arthropods contribute to the ability of patas monkeys to reproduce so rapidly, we compared the feeding behavior of patas monkeys on gum and ants with that of sympatric vervets, which are less insectivorous and have a slower reproductive rate (Isbell et al., 1998a, 2009). We also determined the nutritional composition of *Crematogaster mimosae*, the most common ant found on *A. drepanolobium* (Isbell, 1998; Palmer et al., 2008), and the gum of *A. drepanolobium*, both of which are regularly eaten by patas monkeys.

METHODS

Study site and subjects

This study was conducted on Segera and Mpala Ranches on the Laikipia Plateau in central Kenya. Patas monkeys and vervets were observed from 1992 to 2002 as part of a long-term comparative socioecological study conducted with approval from the government of Kenya and in compliance with Rutgers University and the University of California Institutional Animal Care and Use policies.

Patas monkeys are largely restricted to *A. drepanolobium* woodlands, whereas vervets use both *A. drepanolobium* woodlands and *A. xanthophloea* woodlands. *Acacia drepanolobium* woodlands are typically associated with vertisolic "black cotton" soils that are seasonally waterlogged and difficult to navigate by vehicle when wet. *Acacia xanthophloea* woodlands are typically found along rivers, streams, and swamps. The home range of the vervet study group included the Mutara River. Further details of the study site and groups can be found in Isbell et al. (1998a, 2009).

Behavioral data collection

The data presented here on feeding behavior and diet are from an 11-month period between January and December 1994, excluding July, of focal sampling of all 15 adult females in one group of patas monkeys and all nine adult females in one group of vervets. Each group was systematically observed 4 days each month. On each of the 4 days, each adult female was sampled ideally for 30 min beginning on the hour. For vervets, the sampling order was predetermined to allow each female to be sampled once in the morning or once in the afternoon. This order was different each sampling day within each month so that each female was sampled evenly between morning (08:00–12:00 h) and afternoon blocks (12:00–16:00 h). A similar predetermined sampling order could not be sustained for patas monkeys because individuals proved difficult to locate in time to sample on the hour. Adult females were therefore sampled opportunistically without replacement for 30 min on the hour in the morning or in the afternoon.

During focal sampling, all occurrences of gum and swollen-thorn destruction or consumption by tree species were recorded when clearly seen. Young and mature or old swollen thorns were also noted by their color; young swollen thorns are reddish, whereas mature or old swollen thorns are black or gray. In some cases, it was possible to identify the species of ant on the tree on which the monkeys fed. Locomotor gaits of the focal animal (walking, loping, running, climbing, and leaping; see Isbell et al. (1998b) for definitions) were also recorded, along with the distances moved while using those gaits when the animal moved between food sites. Food sites were defined as any location where the animal stopped moving its hindquarters to eat food. Distances between food sites were estimated by eye. The observer's accuracy in estimating variable distances was checked each month by comparing estimated against true distances between flags set up at the research camp by another researcher (n = 40–80 per month). Estimates of distances between flags were within 5% of true distances in each of the 11 months. Gait and distance data provided the opportunity during data analyses to distinguish between feeding on gum or swollen thorns at the same tree (which would have involved only climbing or leaping between food sites) versus multiple trees (which would have included walking, loping, or running but no climbing or leaping between food sites). We included only those focal samples in which adult females were never out of sight, resulting in 142 focal samples (4,260 min) for patas monkeys and 105 focal samples (3,150 min) for vervets.

Specimen collection and nutritional analyses

Fresh weights of *C. mimosae* ants within swollen thorns were obtained by harvesting 12 swollen thorns from 12 trees in July 2012, freezing the ants to inactivate them, and then weighing all extracted ants. The mean fresh weight of ants (workers, pupae, and larvae combined) per swollen thorn was 0.4461 g ± 0.084 SE. Fresh weights were used only to estimate how many grams of ants the monkeys ate per day.

For nutritional analyses, *C. mimosae* ants were collected in July 2011 by harvesting individual swollen thorns from multiple trees and in August 2011 by fumigating entire trees with a pyrethroid insecticide (Mortein Doom). Ants extracted from swollen thorns on multiple trees were combined, whereas adults, pupae, and larvae from the fumigated trees were separated into workers only, brood (both pupae and larvae), pupae, and larvae. All were dried in a solar oven.

For nutrient intake estimates, dry weights were used and were corrected for additional moisture using the average dry matter coefficient of ant samples (Rothman et al., 2012). Workers and brood were weighed on a dry matter basis from samples collected in 2010 and 2011. Average dry weight of a single worker was 0.00078 g ± 0.05 SE and a single immature was 0.0016 g ± 0.40 SE. We calculated the average ant dry matter per swollen thorn based on a range of 188–261 ants per swollen thorn, with workers constituting 61.3% of the contents, and brood 30.8% (alates were not weighed but there were fewer than 10 alates per thorn; Isbell and Young, 2007). We estimate from this that the average swollen thorn holds 0.183–0.253 g of *C. mimosae* ants (dry weight).

Globules of gum were scraped off 13 trees in July 2011, placed in three plastic containers and stored at ambient temperature until shipping. Sampled gums were variable in color (opaque yellow, amber, reddish brown, and dark brown) and shape (bulbous or oblong), but similar in having a hard consistency.

Gum and ant samples were analyzed for their nutritional composition in the Department of Anthropology at Hunter College, New York, USA using standard methods (Rothman et al., 2012). Upon arrival, the samples were ground through a 1 mm sieve in a Wiley Mill and stored in plastic containers with desiccant until they were processed for analysis. All samples were analyzed for crude protein ($N \times 6.25$) via combustion using a Leco TruSpec Nitrogen Analyzer (St. Joseph, Michigan), gross energy using an IKA C200 bomb calorimeter (Wilmington, North Carolina), and ether extract using an ANKOM XT15 Fat Analyzer (Macedon, NY). Gums were analyzed for neutral detergent fiber (NDF) using an ANKOM A200 Fiber Analyzer (Macedon, NY) without sodium sulfite and with α-amylase (Van Soest et al., 1991). Soluble fiber was estimated via AOAC method 991.43 (Lee et al., 1992). Chitin was estimated in ant samples via acid detergent fiber (ADF) analysis using an ANKOM A200 Fiber Analyzer (Van Soest et al., 1991; BANR, 2003). To determine the amount of nitrogen that was bound to fiber in gums and chitin in ants, the nitrogen remaining on the residues of NDF (NDIN) and ADF (ADIN) was measured (Licitra et al., 1996; Finke, 2007; Rothman et al., 2008). The ADIN or NDIN multiplied by 6.25 provides an estimate of the protein that is unlikely to be digested. Thus, we considered the available (digestible) protein to be crude protein (CP)—(ADIN [for ants] or NDIN [for gums] × 6.25). Various reports discuss the appropriateness of correction factors used to estimate protein digestibility by primates (Milton and Dintzis, 1981; Conklin-Brittain et al., 1999; Rothman et al., 2008, 2012). Based on the amino acid profiles of numerous invertebrates, 6.25 is apparently a good correction factor to estimate the usable protein contained within invertebrates (Finke, in press). Gums were assessed for the presence of condensed tannins using the acid-butanol assay after the milled samples were sonicated three times in 70% (v/v) aqueous acetone to a concentration of 10 mg/mL (Porter et al., 1986; Rothman et al., 2009). Mineral analysis was conducted at Dairy One Forage Laboratory (Ithaca, NY) via a Thermo Jarrell Ash IRIS Advantage Inductively Coupled Plasma Radial Spectrometer after samples were ashed in a muffle furnace at 550°C. The concentration of total nonstructural carbohydrates (TNC) in gums was estimated by subtracting the soluble fiber, available protein, ash, ether extract, and NDF from 100. This estimate of TNC is not completely accurate because all of the (albeit small) errors from other analyses will affect this measure (Rothman et al., 2012), and we are not sure whether this fraction represents oligosaccharides, simple sugar, or other unmeasured compounds as it is an estimation by difference. All results are presented as a percentage of dry matter (Shreve et al., 2006).

Although gross energy provides a reasonable estimate of energy obtained by patas monkeys and vervets because the majority of ants and gums are digestible, the chitin in ants is largely indigestible and soluble fiber requires microbial digestion. To more accurately estimate the energy of gums and ants available for digestion to patas monkeys and vervets, we also present estimates of their metabolizable energy (ME) using summative equations (BANR, 2003; Conklin-Brittain et al., 2006). The ME was calculated by estimating that available protein provides 4 kcal/g, fat provides 9 kcal/g, TNC provides 4 kcal/g, and soluble fiber provides 3 kcal/g. To estimate caloric contributions of soluble fiber, we subtracted 1 kcal/g to account for the energy used by microbes during fermentation (Conklin-Brittain et al., 2006). In our estimations of ME, we also estimated the TNC of ants by subtraction and assigned this fraction a caloric value of 4 kcal/g. It is not clear whether ants would have considerable amounts of carbohydrates other than chitin, although in some insects it can be substantial (Raubenheimer and Rothman, in press). In addition, this estimate by subtraction probably contains other noncarbohydrate compounds present in ants, such as formic acid and other chemicals secreted by ants (Attygalle and Morgan, 1984); consequently, we report the ME with and without the inclusion of TNC. For some ant samples, we did not analyze ash because our sample was too small, so we subtracted the average ash concentration of all other ants in our TNC calculation. We assumed that the NDF in gums, and chitin in ants, was not being digested.

RESULTS

Consumption of ants by patas monkeys and vervets

Patas monkeys were clearly observed to open up or eat 376 swollen thorns of *A. drepanolobium* during 142 30-min focal samples. On average, adult female patas monkeys opened or ate 2.6 swollen thorns from *A. drepanolobium* per focal sample or 63 swollen thorns per adult female per 12-h day. At least 21% of the swollen thorns were young and unlignified (80/376), and were more likely to be consumed entirely than mature thorns, which were often simply cracked open to gain access to ants (Isbell, 1998). When the species of ant was identified, most were *C. mimosae*, the most common ant species on *A. drepanolobium* (Isbell, 1998; Isbell and Young, 2007; Palmer et al., 2008). Based on ant contents of sampled swollen thorns weighing 0.4461 g (fresh weight), we estimate that adult female patas monkeys ate 28.1 g of ants per day.

In five of 142 focal samples, patas monkeys opened up or ate a total of six *A. seyal* var. *fistula* swollen thorns (range: 1–2 per sample), three of which were young thorns. Several species of ants (*C. sjostedti, C. castanea, Lepisota canescens,* and *Camponotus rufoglaucus*) are found on *A. seyal*, but only *C. castanea* and *L. canescens* are known to rear their brood in swollen thorns (Young et al., 1997).

Adult female vervets were clearly observed to open up or eat 124 *A. drepanolobium* swollen thorns during 105 30-min focal samples, less than half as many per focal sample (mean: 1.2 swollen thorns) as patas monkeys. We estimate that each adult female vervet ate, on average, 28 *A. drepanolobium* swollen thorns per day. At least 73% of the swollen thorns were young, unlignified thorns (91/124), significantly more than eaten by patas monkeys ($\chi^2=110.22$, $P < 0.0001$, df=1), suggesting that, unlike patas monkeys, vervets eat *A. drepanolobium* swollen thorns more for their inherent nutritional value than for the ants housed in the thorns. If they ate the swollen thorns for the ants inside, we estimate that each adult female vervet ate 12.5 g (fresh weight) of ants per day.

In four of 105 focal samples, vervets ate 26 swollen thorns of *A. seyal* (range: 1–12 per sample). All the swollen thorns were young, suggesting that vervets also eat *A. seyal* swollen thorns more for their nutritional value than for the ants themselves. *Crematogaster sjostedti*, *C. castanea*, and *Camponotus rufoglaucus* were recorded on *A. seyal* trees that were fed on by vervets. None of these ant species is highly aggressive in defending the tree from herbivory.

Consumption of gums by patas monkeys and vervets

Patas monkeys were clearly observed to eat *A. drepanolobium* gum on 365 occasions, for an average of 2.5 bouts per focal sample. We estimate that each adult female ate *A. drepanolobium* gum 61 times per 12-h day, on average. Less frequently they ate *A. seyal* gum ($n=11$) and *A. xanthophloea* gum ($n=2$).

Vervets were clearly observed to eat *A. xanthophloea* gum most often ($n=164$ bouts), followed by *A. seyal* ($n=51$), *A. drepanolobium* ($n=14$), and *A. gerrardii* ($n=5$). Although their time spent in *A. drepanolobium* habitat was more than double that in *A. xanthophloea* habitat (Pruetz and Isbell, 2000), vervets ate *A. drepanolobium* gum (mean: 0.13 bouts per 30-min focal sample; 3.2 bouts per day) 12 times less often than they ate *A. xanthophloea* gum (mean: 1.6 bouts per 30-min focal sample; 37.5 bouts per day). Although *A. seyal* is less common than *A. drepanolobium* (Young et al., 1997) vervets fed on *A. seyal* gum nearly four times more often (mean: 0.45 bouts per focal sample; 11.6 bouts per day) than they fed on *A. drepanolobium* gum.

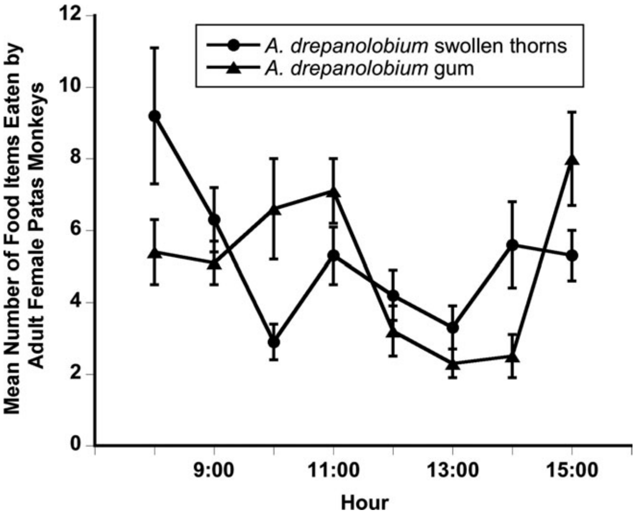

Fig. 1. Mean numbers of *Acacia drepanolobium* swollen thorns opened or eaten and *Acacia drepanolobium* gum sites fed upon by adult female patas monkeys across hours of the day. Bars represent ± 1 SE.

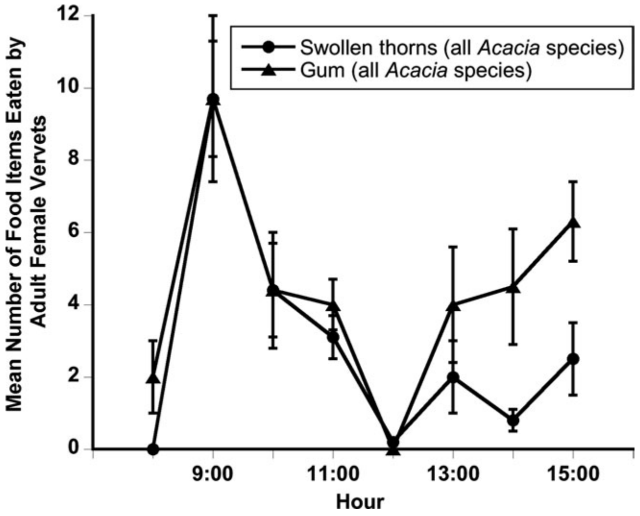

Fig. 2. Mean numbers of *Acacia drepanolobium* and *A. seyal* swollen thorns opened or eaten and *A. drepanolobium*, *A. seyal*, and *A. xanthophloea* gum sites fed upon by adult female vervets across hours of the day. Bars represent ± 1 SE.

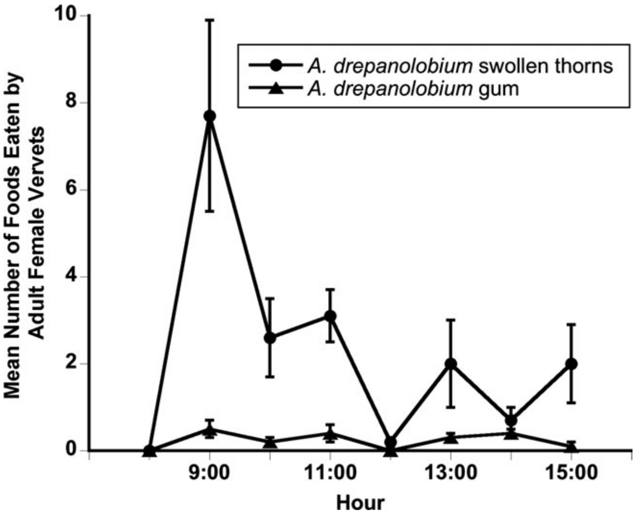

Fig. 4. Mean numbers of *A. drepanolobium* swollen thorns and gum sites fed upon by adult female vervets across hours of the day. Bars represent ± 1 SE.

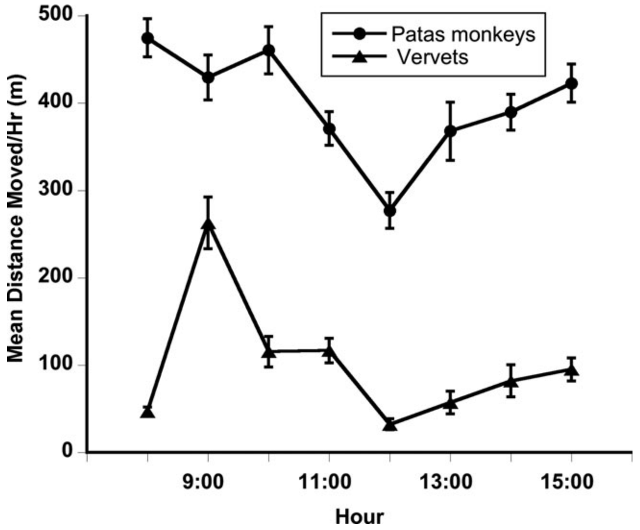

Fig. 3. Mean distance (*m*) adult female patas monkeys and vervets moved per hour of the day. Bars represent ± 1 SE.

Feeding on ants versus gum

Over the course of the day, patas monkeys fed relatively continuously on both *A. drepanolobium* swollen thorns and gum (Fig. 1). Peak swollen-thorn destruction occurred in the first hour of sampling, likely because colder temperatures slowed ants' defensive behavior (Hocking, 1970). Although they ate swollen thorns and gum nearly equally across all focal samples, numbers of swollen thorns were not correlated with numbers of gum sites per focal sample ($r_s=0.14$, $P=0.09$, $n=142$, df=140, two-tailed), perhaps because gum sites are much less common than swollen thorns and thus are not encountered as often as swollen thorns (Isbell, 1998). Nonetheless, patas monkeys ate more of each food item the farther they traveled per focal sample (swollen thorns: $r_s=0.23$, $P=0.006$, $n=142$, df=140, two-tailed; gum: $r_s=0.38$, $P < 0.0001$, $n=142$, df=140, two-tailed).

A previous study suggested that patas monkeys made a stronger effort to find and feed on gum than swollen thorns because the percentage of gum records in the diet was similar to that of swollen thorns, despite the fact that gum is less common on trees than swollen thorns (Isbell, 1998). If patas monkeys eat swollen thorns in passing while actively searching for gum, then they might be expected, once they find trees with rich gum sites (i.e., taller trees; Isbell, 1998), to stay to harvest the gum from those trees. We examined this by comparing feeding records on gum that involved moving to successive gum sites within a tree (involving climbing or leaping) versus between trees (involving walking, running, or loping). Excluding 12 records that were unclear in distinguishing between the two conditions (because the order of different gaits was not recorded), we found that feeding at single gum sites within trees occurred 76% (80 of 106 bouts) of the time that patas monkeys stopped to feed on gum whereas feeding at multiple gum sites within trees occurred 24% of the time (26/106 bouts). Although these differences indicate that patas monkeys did not often harvest multiple gum sites on trees, it was not because they passed up opportunities. Given that only 3% of sampled trees (5 of 167) had more than one globule of gum (Isbell, 1998), it is evident that patas monkeys specifically sought out trees with multiple gum sites ($\chi^2=27.77$, $P < 0.0001$, df=1).

Vervets also showed a peak of swollen-thorn eating in the morning. Consumption of swollen thorns and gum was not continuous over the day, however, but showed a decline at mid-day (Fig. 2). The lull coincided with slower travel at this time, suggesting that the vervets were resting rather than switching to different foods, in contrast to patas monkeys, who continued to move and feed throughout the day (Fig. 3). Particularly striking is the obvious avoidance by vervets of *A. drepanolobium* gum even when they had the opportunity to eat it, as indicated by their consumption of *A. drepanolobium* swollen thorns (Fig. 4).

Nutritional composition of *C. mimosae* ants and *A. drepanolobium* gum

Samples within both ants and gum varied in their composition (Table 1). Both gross energy and crude protein in *C. mimosae* were roughly similar in samples with multiple life stages and in larvae and pupae analyzed separately (Table 1). Because it is as yet unknown whether patas monkeys can digest chitin, it is not clear how much energy or protein is actually available from ants. We estimated the amount of protein available for digestion if they cannot digest the nitrogen bound to chitin by running a nitrogen assay on the residue of the chitin and found that a large percentage of nitrogen would still be digestible (Rothman et al., 2008).

Based on our calculation that *C. mimosae* ants (workers and brood combined) provide 3.5–4.0 kcal/g ME (with and without TNC; Table 1), we estimate that ants from *A. drepanolobium* provide patas monkeys with 38–60 kcal of energy per day (the range is derived from consumption of 11.5 g dry weight/day×3.5 kcal/g×0.94 [average dry matter coefficient] to 15.9 g dry weight/day×4.0 kcal/g×0.94), whereas they provide vervets with 17–27 kcal of energy per day (5.1 g dry weight intake/day×3.5 kcal/g×0.94 to 7.08 g dry weight intake/day×4.0 kcal/g×0.94).

Acacia drepanolobium gum is composed primarily of soluble fiber (71–76% of dry weight) and secondarily, TNC (15–19%), both of which are rapidly digested (but see the Methods for caveats about measuring nonstructural carbohydrates in this way). As expected, it is low in protein (~2%) and insoluble (hard to digest) fiber (2.5–5%). Gross energy is close to expected for carbohydrates (4 kcal/g). Because we did not collect gum samples systematically, we cannot estimate daily energy intake from gums but we can estimate how much gum would need to be ingested per bout and per day to make their diet feasible. The energy requirements for patas monkeys are unknown, but a rough estimate of their energy requirements may be derived from data that exist for captive, provisioned rhesus macaques. The basal metabolic rate of adult female rhesus macaques, which are similar to patas monkeys in body weight, has been estimated at 277 kcal/day (BANR, 2003). Primates in general are estimated to require approximately double the energy of their basal metabolic rates for their daily needs (BANR, 2003) and so adult female rhesus macaques might require 554 kcal/day. If ants supply 38–60 kcal of energy per day, then gum would need to supply 494–515 kcal per day. Dividing those values by 2.61 (3 kcal/g×0.87 as a standard correction factor) yields 189–197 g of gum required per day, or 3.1–3.2 g per bout. Unsystematically collected gum samples from *A. drepanolobium* (dry weight minimum, 23 g; mean, 33.4 g, $n=6$) suggest that ingesting such amounts per bout is achievable.

Comparing the two food types, although gross and ME are high in *Acacia drepanolobium* gum, they are lower than those of *C. mimosae* ants, even when workers are separated from immatures. Protein is substantially higher in ants than gum. The mineral content in *C. mimosae* ants is also higher than in *Acacia drepanolobium* gum except for calcium.

TABLE 1. Intersample variation in nutrient composition of Acacia drepanolobium gum and Crematogaster mimosae ants[a]

	Gum sample 1	Gum sample 2	Gum sample 3	Ants, all ages	Ants, mixed brood 1	Ants, workers only	Ants, mixed brood 2	Ants, mixed brood 3	Ants, pupae only	Ants, larvae only	BANR (2003) estimated adequate requirements, non-human primates
GE (kcal/g)	3.61	4.05	3.88	5.88	5.61	6.0	6.02	5.97	5.92	5.52	
NDF (%)	4.99	2.61	3.6								10–30
ADF (%)				24.78	11.08	27.09	9.12	9.14	9.45	1.86	5–15
CP (%)	2.39	2.08	1.83	54.24	48.47	60.01	50.94	49.86	50.89	47.23	15–22
Fat (%)				21.17	23.22	23.57	24.88	25.83	26.45	24.81	
Unavailable CP (%)	1.26	1.92	0.78	13.39	3.77	15.98	3.79	3.29	3.52	2.22	
Available CP (%)	1.13	0.16	10.5	40.85	44.7	44.63	47.15	46.57	47.37	45.01	
Soluble Fiber (%)	71.5	76.4	75.8								
TNC (%)	19.93	18.81	15.77	13.2	17.33	0.56	15.37	14.47	12.94	24.53	
ME including TNC/100 g	298.76	305.09	294.66	406.72	457.06	392.86	473.99	476.63	479.25	501.39	
ME without TNC/100 g				353.92	387.75	390.62	412.51	418.77	427.47	403.29	
Ash (%)	2.45	2.02	3.78		3.67	4.15	3.48	3.99	3.8	3.8	
Ca (%)	0.78	0.61	0.77		0.25	0.19					0.8
P (%)	0	0	0		0.61	0.64					0.6
Mg (%)	0.09	0.08	0.06		0.16	0.11					0.08
K (%)	0.11	0.17	0.13		0.95	0.83					0.4
Na (%)	0.14	0.032	0.014		0.11	0.115					0.2
Fe (ppm)	94	29	792		141	446					100
Zn (ppm)	2	1	4		107	192					100
Cu (ppm)	2	1	<1		24	38					20
Mn (ppm)	16	4	39		32	107					20
Mo (ppm)	<0.1	<0.1	<0.1		0.7	1.3					
Tannin	negative	negative	negative								

[a] Based on dry weights.

GE, gross energy; NDF, neutral detergent fiber; ADF, acid detergent fiber; CP, crude protein; TNC, total nonstructural carbohydrates; ME, metabolizable energy.

DISCUSSION

Why do patas monkeys and vervets differ in their ant consumption?

Although vervets eat a wide variety of invertebrates (Isbell and Jaffe, in press), and ants are available in their home ranges, only patas monkeys take full advantage of them as a food source. Harvey et al. (1987) pointed out that larger primates usually cannot obtain enough insects but this cannot explain the species differences because vervets are smaller than patas monkeys and ants are ubiquitous in the study area. Why do vervets not eat them more often?

Among the many possibilities are that 1) vervets have mechanical difficulty opening up mature, lignified swollen thorns; 2) ants are unpalatable to them; 3) ant defenses are effective against them, and; 4) their digestive systems cannot tolerate ants in substantial quantities. All these need further investigation, but there is indirect evidence of a mechanical difficulty. In a study of fruit and seed eating among cercopithecine primates, vervets were deterred by the hardest fruit pericarps, whereas patas monkeys were not (Happel, 1988). There is also anecdotal evidence that ants are unpalatable to vervets in concentrated amounts. Captive vervets offered mashed bananas with *Crematogaster* spp. mixed in often spit the bananas out (L.A. Isbell, unpublished data).

What determines preferences for particular *Acacia* gums?

Galagos and cercopithecine primates living in semiarid environments in Africa feed on gums of multiple *Acacia* species but appear to be selective. Vervets and yellow baboons (*Papio cynocephalus*) in Amboseli National Park, Kenya, eat the gum of *A. xanthophloea* while rarely eating the gum of *A. tortilis* (Struhsaker, 1967; Hausfater and Bearce, 1976; Wrangham and Waterman, 1981). Wrangham and Waterman (1981) showed that *A. xanthophloea* gum is lower than *A. tortilis* gum in secondary compounds, especially condensed tannins, and suggested that vervets avoid *A. tortilis* because of the tannins. Like patas monkeys in this study, lesser galagos (*Galago senegalensis braccatus*) in Laikipia eat *A. drepanolobium* gum more than *A. xanthophloea* gum (Nash and Whitten, 1989). Nash and Whitten (1989) argued that condensed tannins could not explain the preference of galagos for *A. drepanolobium* gum because condensed tannins are low in both species. The two *Acacia* species did differ in other secondary compounds, however, and they suggested that galagos might be choosing *A. drepanolobium* gum for its higher levels of flavonoids. Flavonoids appear to have growth- and estrogen-related functions (Nash and Whitten, 1989).

Oddly, vervets in Laikipia express the opposite preference, favoring the gum of *A. xanthophloea* (and *A. seyal* var. *fistula*) over that of *A. drepanolobium* (this study). Their low consumption of *A. drepanolobium* gum cannot be ascribed to a lack of opportunity as might be argued for the low consumption of *A. xanthophloea* gum by patas monkeys; they clearly had opportunities to eat *A. drepanolobium* gum while they ate swollen thorns from that tree species.

Appendix A (available online) provides a compilation of *Acacia* gum nutrient compositions from 10 species or subspecies. Although diverse *Acacia* species tend to be similar in several nutrients, there is also occasionally wide variation among studies, perhaps because of natural variation or different analytical methods. The nutritional profile of *A. drepanolobium* gum does not stand out from other *Acacia* species in any nutrient except that it is higher in manganese and iron (perhaps due to one sample that had bark and lichen within it) and lower in zinc. Analyses of additional species are needed to identify why some species are eaten and others are not.

How do patas monkeys reproduce so well on a diet mainly of gum and arthropods?

Females ultimately turn food into offspring, and thus information about the nutritional components of food is helpful for understanding differences in reproductive rates within and between species. Vervets tend to reproduce at a rate expected for their body size (Isbell et al., 2009). Like patas monkeys, they eat gum and arthropods but they eat arthropods to a lesser extent (Struhsaker, 1967; Wrangham and Waterman, 1981; Cheney et al., 1988), and they eat more plant reproductive parts than patas monkeys (Isbell et al., 1998a). Patas monkeys, in contrast, reproduce at a rate well above that expected for their body size (Isbell et al., 2009). How are they able to acquire enough energy and nutrients on ants and gum to mature quickly and reproduce every year?

Gum and ants are always available. One notable difference between patas monkeys and other cercopithecines is that patas monkeys eat gum and arthropods throughout the day, all year long (see also Isbell, 1998; Isbell and Young, 2007). It has long been assumed that gums and arthropods are rare or difficult to find, but patas monkeys reveal that this need not be the case. Gums, in particular, may be more reliably available than flowers, fruits, seeds, and young leaves as persistently stationary and renewing resources (Génin et al., 2010), and they are all the more reliable because few other species eat them. The only other nonprimate animal reported to eat *A. drepanolobium* gum is the Kori bustard (*Ardeotis kori*) (Nash, 1986).

Regularity and reliability of food, both daily and seasonally, may be key to enabling rapid reproduction in patas monkeys and other gummivorous/insectivorous primates. Reliable and regular access to food may be especially important for smaller bodied primates because they need to eat more regularly and more often than larger bodied primates (Gaulin, 1979). Among gummivorous/insectivorous primates, lesser galagos that live sympatrically with patas monkeys eat the same readily available gums and arthropods (Nash and Whitten, 1989). Gray mouse lemurs (*M. murinus*), needle-clawed galagos (*Euoticus elegantulus*), saddle-back and moustached tamarins (*S. mystax*), and Goeldi's monkeys (*Callimico goeldii*) behave as if they know where gum sites are located and return repeatedly to them, often on the same day/night or over multiple days/nights (Charles-Dominique, 1977; Joly and Zimmermann, 2007; Joly-Radko and Zimmermann, 2010; Garber and Porter, 2010). Like patas monkeys, reddish-gray mouse lemurs (*M. griseorufus*) feed on gums throughout the hours of their active period (Génin et al., 2010). Fork-marked lemurs (*Phaner furcifer*) feed on gums throughout the night and year (Schülke, 2003; Schülke and Kappeler, 2003).

Similarly, in some tropical environments arthropods may be less temporally variable than plant foods. In the Taï Forest, Côte d'Ivoire, for example, there is little seasonal variation in insect abundance, whereas fruits are seasonal (Buzzard, 1996). In Ranomafana National Park, Madagascar, coleopterans, the arthropods most frequently eaten by brown mouse lemurs (*M. rufus*), are eaten throughout the year (Atsalis, 1999). Relative to most other primates, these primate species can reproduce at high rates, for example, litters in galagos and mouse lemurs and twinning twice per year in many callitrichines (Digby et al. 2011) (for callitrichine reproduction in relation to gum feeding, see Ah-King and Tullberg, 2000).

With the exception of patas monkeys, the primates exemplified above are both small and gummivorous/insectivorous. High adult mortality relative to infant mortality has been proposed to have ultimately favored the evolution of rapid reproduction (Young, 1981; Stearns, 1992; Charnov, 1993; Reznick et al., 2001; Reznick and Bryant, 2007; Isbell et al., 2009), but as studies of provisioned primates demonstrate, full reproductive capability is expressed only upon abundant consumption of food (Drickamer, 1974; Mori, 1979; Kirkwood, 1983; Kurita et al., 2008).

Gum and ants can be eaten quickly. Patas monkeys spend, on average, 7.8 s at individual *A. drepanolobium* gum sites and 12.7 s feeding on individual swollen thorns (Pruetz, 1999). If they feed at 61 gum sites and eat the contents of 63 swollen thorns per day, they may be able to obtain their daily energy needs in only 21.3 min, that is, 3% of the 12-h day. This estimate does not include the time involved in walking from tree to tree, but even that can be profitable: the more they walk, the more gum and ants they eat, and the more they find other foods. Orthopterans, for example, accounted for 3% of all feeding records of patas monkeys in Kenya (Isbell, 1998) and 15.8% of their time spent feeding in Cameroon (Nakagawa, 2003). Patas monkeys in Kenya spend quadruple the time vervets spend scanning the vegetation while walking (Isbell et al., 1998b) and orthopterans are often flushed up in the course of walking.

Gums provide abundant energy. If patas monkeys eat 63 swollen thorns per day, they would derive 38–60 kcal/day from ants. This estimate does not include ants captured on the ground, on trunks of trees, or accidentally ingested with other food items and so is a conservative estimate. If patas monkeys are similar to rhesus macaques in their energy needs, they would need much more of their energy to come from gum. This may be entirely possible. Given their frequent visits to gum sites each day, they need only eat approximately 3 g per globule, equivalent to the weight of three almonds.

Ants provide sufficient protein. Ants have comparable amounts of protein to vertebrate animal prey, such as fish, wild game, and beef (DeFoliart, 1975; McGrew, 2001; Dufour, 2009). Concentrations of available protein are high (41–47%) compared to the recommended adequate protein concentrations of 15–22% (BANR, 2003). Based on our estimates of available protein from 11 to 16 g dry weight of ants ingested per day, patas monkeys obtain 5–8 g of protein from ants daily.

Protein requirements for adult female primates are estimated at 0.8–1.0 g/kg (Oftedal, 1991). With adult female patas monkeys weighing about 6.5 kg, we estimate that ants provide 0.8–1.2 g/kg protein, and thus ants may alone meet the monkeys' daily protein requirements. Although few data on the amino acid profiles of ant protein are available (see Yaqin, 1994), profiles of other invertebrates demonstrate that most amino acids are abundant, and the most limiting amino acids in invertebrate prey are the sulfur amino acids (Finke, 2002, in press). However, as invertebrates provide a balanced concentration of all amino acids, if the consumer is eating sufficient quantities, amino acid requirements should be met (Oonincx and Dierenfeld, 2012).

Patas monkeys also obtain protein from other sources such as grasshoppers, geckos, and leaves of *A. drepanolobium*, *Lycium europaeum*, *Cucumis aculeata*, and *Plectranthus* spp. (Isbell, 1998; Isbell et al., 1998a; Pruetz and Isbell, 2000), but these are not staple foods.

Gum and ants provide high amounts of minerals. Mineral acquisition is an apparent advantage of a gummivorous and insectivorous diet. Gum and insects have been suggested to be complementary foods because gums provide a good source of calcium, and insects, phosphorus, within required ratios of 1:1–2:1 (Bearder and Martin, 1980), depending on the amounts eaten of both gums and insects. Our estimate of ant intake from systematic sampling and of gum intake based on energy requirements suggests that calcium is in higher concentrations than phosphorus, although we do not know their bioavailability.

Copper and sodium are suggested to be limited in many primate diets (Rode et al. 2003, 2006) and primates actively seek them (Oates, 1978; Rothman et al., 2006; Fashing et al., 2007). Yellow baboons in Amboseli occasionally develop a copper deficiency so severe that it manifests at a clinical level (Markham et al., 2011). In a study of redtail monkeys in Kibale National Park, Uganda, dietary concentrations of copper and sodium were 9–15 and 96–193 ppm, respectively, so low that it was suggested that these minerals might limit redtail populations in heavily logged areas of the forest (Rode et al., 2006). Copper and sodium provided to patas monkeys through ants were 2–10 times higher than levels reported for redtails. Sodium intake of redtails may have been underestimated, however. Arthropods are a major part of redtail diets and are typically caught and eaten quickly (Struhsaker, 1980). In the nutritional study, however, feeding behavior and the food items being eaten were recorded only after being sustained for at least 15 s (Rode et al., 2006), long enough that if that time frame had been used with patas monkeys, many bouts of swollen-thorn eating would have been missed.

Additionally, ants provide high levels of iron and zinc. Zinc, in particular, can be deficient in plant-based diets (Kies et al., 1983). Zinc deficiency has widespread effects, including negative effects on growth rates, enzyme activity, energy- and sex-related hormone activity, reproduction, and appetite (Kirchgessner et al., 1976). With zinc levels as high as 150 mg/kg, *C. mimosae* ants provide substantially more than the 100 mg/kg considered adequate for primates (BANR, 2003).

Table 2 compares the chemical composition of *C. mimosae* with several other species of African ants that are known to be eaten by primates, along with one species (*Pachycondyla analis*) that has not yet been observed to be eaten by primates. It is interesting to note that *P. analis* is thus far collectively the poorest in nutrients because it has some of the lowest levels of fat and minerals, including iron, calcium, phosphorus, and potassium (excluding "Onyoso mammon," for which the species is unknown).

Appendix B (available online) reveals that the ants analyzed thus far represent only a small proportion of the ant species that primates have been documented to eat. At least 18 genera of ants are consumed by primates, with *Crematogaster* (nine identified species eaten by at

TABLE 2. *Known chemical compositions of ant species, based on fresh weights unless noted*

Ant species[a]	GE (kcal/g)	ADF (%)	CP (%)	Fat (%)	Unavailable CP (%)	Ash (%)	Ca (%)	P (%)	Mg (%)	K (%)	Na (%)	Fe (ppm)	Zn (ppm)	Cu (ppm)	Mn (ppm)	Mo (ppm)
Crematogaster mimosae[b] (dry)	5.83	14.96	53.33	23.21	7.59	4.0	0.22	0.63	0.14	0.89	0.11	303.5	149.5	31.0	69.5	1.0
Crematogaster depressa?[c]	1.4	19.0	57.0	3.0		5.0	0.23	0.46	0.12	0.24	0.02	630	197	38	164	
Camponotus brutus[c]	1.2	13.0	68.0	4.0		4.0	0.31	0.84	0.17	0.48	0.04	458	155	18	317	
Dorylus sjostedti[c]	2.3	45.0	76.0	7.0		2.0	0.13	0.41	0.10	0.49	0.32	304	821	7	39	
Oecophylla longinoda[c]	1.1	10.0	56.0	15.0		4.0	0.11	0.60	0.07	0.29	0.05	233	276	27	288	
Pheidole crassinoda?[c]	2.0	16.0	72.0	5.0		3.0	0.24	0.57	0.17	0.46	0.08	1402	287	33	222	
Tetramorium aculeatum[c]	1.8	9.0	63.0	13.0		3.0	0.25	0.71	0.22	0.44	0.11	890	501	60	217	
Onyoso mammon (Luo name)[d] (dry)						1.7	0.03					177	111			
Pachycondyla analis (not known to be eaten by primates)[c]	2.3	39.0	72.0	3.0		2.0	0.08	0.26	0.07	0.17	0.05	476	192	19	47	

[a] Species' names and spellings confirmed or corrected using Bolton (1995).

[b] Source: this study.

[c] Source: Deblauwe and Janssens (2008).

[d] Source: Christensen et al. (2006).

least six primate species), *Dorylus* (12 identified species eaten by four primate species), and *Pachycondyla* (six identified species eaten by three primate species) being especially common. Although it is intriguing that chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla* spp.), two large-bodied primate species, eat many species of ants, their strong representation is likely to be at least partially a result of better viewing conditions (i.e., with animals feeding on or near the ground). Guenons are undoubtedly underrepresented because their arboreality makes it difficult to determine specifically what arthropod prey is being consumed (Struhsaker, 1978; Cords, 1986; Gautier-Hion, 1988). However, documentation is also likely a matter of observer interest. Arboreal gray-cheeked mangabeys (*Lophocebus albigena*) are identified as consumers of multiple ant species because effort was made to document their ant-eating behavior (Appendix B). We hope that others will build on this list in the future.

Do gums provide other benefits that affect reproduction? Finally, it has also been suggested that phytoestrogens kaempferol and apigenin, two flavonoids found in *A. drepanolobium* gum, have a positive effect on growth and reproduction (Nash and Whitten, 1989). This possibility should be explored further as phytoestrogens can have beneficial and detrimental effects (Kurzer and Xu, 1997).

In summary, gums and ants provide patas monkeys in Laikipia, Kenya, with readily obtained, predictably found, and continually available foods that easily meet their energy, protein, and mineral requirements. These findings suggest that ants and gum contribute substantially to the high reproductive rate of female patas monkeys. Indeed, we have no evidence that the food nutrients we examined limit female reproductive success in this population. These findings lend further support that illness, predation, interactions between adults and infants, and reduced access to water limit female reproductive success more immediately than food in this population (Isbell and Chism, 2007; Isbell et al., 2009).

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APPENDIX A

Nutrient composition of *Acacia* gums.

TABLE A1. Literature survey of nutritional components of gums from Acacia trees in Africa. Values are from dry weights unless noted.

Tree species (Country of Collection)	GE (kcal/g)	NDF (%)	CP (%)	Fat (%)	Soluble fiber (%)	Soluble carbs (%)	Ash (%)	Ca (%)	P (%)	Mg (%)	K (%)	Na (%)	Fe (ppm)	Zn (ppm)	Cu (ppm)	Mn (ppm)	Condensed tannins (%)	Total phenolics (%)	Source
A. drepanolobium (Kenya)	3.85	3.7	2.1		74.57	16.85	2.75	0.7	0	0.08	0.14	0.03	305	2.33	1.5	19.67	negative		This study
A. drepanolobium (Kenya)																	0.04	0.2	Nash and Whitten (1989)
A. drepanolobium (Tanzania)								0.6 wet wt		0.07 wet wt	0.16 wet wt	0.08 wet wt	58.9	28.9	4.36	10.7	0.49 ("Tannins") wet wt		Mhinzi et al. (2008)
A. drepanolobium (Tanzania)			3.6–7.75				0–2.56												Anderson and Dea (1967)
A. xanthophloea (S. Africa)			2.4				5.5												Anderson et al. (1984)
A. xanthophloea (Kenya)			0.87				2–6										0	0.02	Nash and Whitten (1989)
A. xanthophloea (Kenya)																	0.23–0.31	0.09–0.23	Wrangham and Waterman (1981)
A. xanthophloea (Kenya)							1.6 wet wt												Hausfater and Bearce (1976)
A. xanthophloea (Kenya)			0.6–1.7 wet wt	0.5–1.6 wet wt			3.1–15.1 wet wt												Altmann et al. (1987)
A. tortilis (Kenya)			1.8 wet wt	0.2 wet wt			2.0 wet wt												Altmann et al. (1987)
A. tortilis (Kenya)																	27.99–70.96	37.82–56.0	Wrangham and Waterman (1981)
A. tortilis (Kenya)							10.7 wet wt												Hausfater and Bearce (1976)
A. tortilis (Sudan, Zimbabwe, Botswana)			2.9–9.4				1.3–2.0												Anderson and Bell (1974)
A. nilotica (Location?)			0.5				2.5												Anderson et al. (1972)
A. elatior (Kenya)																	0.13	0.38	Nash and Whitten (1989)
A. seyal (Location?)			0.9				2.8												Anderson et al. (1984)
A. seyal var senegalensis (Tanzania)							3.91 wet wt			0.16 wet wt			62.38	18.81	2.26	3.88	0.45 ("Tannins") wet wt		Mhinzi (2003)
A. seyal var. *fistula* (Tanzania)							2.7 wet wt			0.07 wet wt			22.12	19.32	1.1	4	0.85 ("Tannins") wet wt		Mhinzi (2003)
A. kirkii var. *kirkii* (Tanzania)								0.98 wet wt		0.06 wet wt	0.46 wet wt	0.11 wet wt	29.8	111.0	13	3.55	0.51 ("Tannins") wet wt		Mhinzi et al. (2008)
A. karroo (S. Africa, Namibia)			0.9	0.1			3.2	0.96–1.04	0.01	0.11	0.99–1.03								Anderson and Pinto (1980); Bearder and Martin (1980)
A. sieberiana (Ghana)			1.2				1.5												Anderson et al. (1984)
A. hockii (Ghana)			1.4				1.3												Anderson et al. (1984)

APPENDIX B

Ant species eaten by African primates.

TABLE B1. Literature survey of ant species consumed by primates living in Africa

Ant species	Country	Known primate consumers	Source
Anochetus spp.	Cameroon	Gorillas	Deblauwe and Janssens (2008)
Anoplolepis tenella	Cameroon	Gorillas	Deblauwe and Janssens (2008)
Atopomyrmex cryptoceroides	Cameroon	Gorillas	Deblauwe and Janssens (2008)
Camponotus brutus	Tanzania, Gabon, Cameroon	Chimpanzees	Nishida and Hiraiwa (1982); Tutin and Fernandez (1992); Deblauwe and Janssens (2008)
Camponotus maculatus	Tanzania	Chimpanzees	Nishida and Hiraiwa (1982)
Camponotus vividus	Tanzania, Gabon	Chimpanzees, gorillas	Nishida and Hiraiwa (1982); Tutin and Fernandez (1992)
Camponotus spp.	Uganda[b], Gabon, Senegal, Cameroon, Tanzania	Chimpanzees, gorillas, gray-cheeked mangabeys	Nishida and Hiraiwa (1982); McGrew (1992); Deblauwe and Janssens (2008); R. Kaserengenyu, personal communication
Crematogaster castanea	Cameroon	Gorillas	Deblauwe and Janssens (2008)
Crematogaster clariventris	Gabon, Cameroon	Mandrills, gorillas	Lahm (1986); Deblauwe and Janssens (2008)
Crematogaster concava	Cameroon	Gorillas, chimpanzees	Deblauwe and Janssens (2008)
Crematogaster depressa?	Gabon	Gorillas	Tutin and Fernandez (1992); Deblauwe and Janssens (2008)
Crematogaster mimosae	Kenya	Patas monkeys, vervets	Isbell (1998); this study
Crematogaster nigriceps	Kenya	Patas monkeys, vervets	Isbell (1998); LA Isbell, unpublished data
Crematogaster sjostedti	Kenya	Patas monkeys	Isbell (1998); LA Isbell, unpublished data
Crematogaster stadelmanni	Gabon	Gorillas	Tutin and Fernandez (1992)
Crematogaster striatula	Gabon, Cameroon	Mandrills, gorillas, chimpanzees	Lahm (1986); Deblauwe and Janssens (2008)
Crematogaster spp.	Tanzania, Gabon, Cameroon, Uganda[b]	Pottos, gorillas, chimpanzees, mandrills, gray-cheeked mangabeys	Charles-Dominique (1976); Nishida and Hiraiwa (1982); Lahm (1986); Deblauwe and Jannsens (2008); R. Kaserengenyu, personal communication
Dorylus burmeisteri	Senegal, Guinea, Cote d'Ivoire	Chimpanzees	Schöning et al. (2008)
Dorylus emeryi	Guinea, Cote d'Ivoire, Cameroon	Chimpanzees	Schöning et al. (2008)
Dorylus gerstaeckeri	Guinea, Cote d'Ivoire	Chimpanzees	Schöning et al. (2008)
Dorylus kohli	Cameroon, D.R. Congo, Tanzania	Chimpanzees	Deblauwe and Janssens (2008); Schöning et al. (2008)
Dorylus mayri	Cameroon, Guinea, Cote d'Ivoire	Chimpanzees	Deblauwe and Janssens (2008); Schöning et al. (2008)
Dorylus molestus	Tanzania	Chimpanzees	Schöning et al. (2008)
Dorylus nigricans	Gabon, Guinea, Cote d'Ivoire	Mandrills, chimpanzees	Lahm (1986); Schöning et al. (2008)
Dorylus opacus	Cameroon	Chimpanzees	Deblauwe and Janssens (2008)
Dorylus rubellus	Nigeria	Chimpanzees	Schöning et al. (2008)
Dorylus sjostedti	Cameroon	Gorillas, chimpanzees	Deblauwe and Janssens (2008)
Dorylus terrificus	Uganda	Chimpanzees	Schöning et al. (2008)
Dorylus wilverthi	Cameroon, D.R. Congo, Uganda	Gorillas, chimpanzees	Deblauwe and Janssens (2008); Schöning et al. (2008)
Dorylus sp.	Rwanda, Tanzania, Senegal, Guinea, Cote d'Ivoire	Gorillas, chimpanzees, kipunji	Watts (1989); McGrew (1992); McGrew et al. (2005); Davenport et al. (2010)
Megaponera sp.	Senegal	Chimpanzees	McGrew (1992)
Monamorium afrum	Tanzania	Chimpanzees	Nishida and Hiraiwa (1982)
Myrmicaria natalensis	Uganda[b]	Gray-cheeked mangabeys	R. Kaserengenyu, personal communication
Myrmicaria sp.	Gabon	Mandrills	Lahm (1986)
Odontomachus assiniensis	Uganda[b], D.R. Congo, Cameroon	Gorillas, gray-cheeked mangabeys	Yamagiwa et al. (1991); Deblauwe and Janssens (2008); R. Kaserengenyu, personal communication
Odontomachus troglodytes	D.R. Congo	Gorillas	Yamagiwa et al. (1991)
Odontomachus spp.	Gabon	Mandrills	Lahm (1986)
Oecophylla longinoda	Tanzania, Gabon, Cameroon	Chimpanzees, gorillas	Nishida and Hiraiwa (1982); Tutin and Fernandez (1992); Deblauwe and Janssens (2008)
Oecophylla sp.	Tanzania, Senegal, Cote d'Ivoire	Chimpanzees	McGrew (1992)
Pachycondyla brunoi	Cameroon	Chimpanzees	Deblauwe and Janssens (2008)
Pachycondyla crassa	Uganda[b]	Gray-cheeked mangabeys	R. Kaserengenyu, personal communication
Pachycondyla lamottei	Cameroon	Chimpanzees	Deblauwe and Janssens (2008)
Pachycondyla (Euponera) subiridescens	D.R. Congo	Gorillas	Yamagiwa et al. (1991)
Pachycondyla talpa	D.R. Congo	Gorillas	Yamagiwa et al. (1991)
Pachycondyla (Paltothyreus) tarsata	Gabon, D.R. Congo; Cameroon	Gorillas, Chimpanzees	Yamagiwa et al. (1991); Tutin and Fernandez (1992); Deblauwe and Janssens (2008)
Pachycondyla spp.	D.R. Congo	Gorillas	Yamagiwa et al. (1991)
Pheidole crassinoda?	Cameroon	Gorillas, chimpanzees	Deblauwe and Janssens (2008)
Pheidole pulchella	Cameroon	Chimpanzees	Deblauwe and Janssens (2008)
Pheidole speculifera	Cameroon	Gorillas, chimpanzees	Deblauwe and Janssens (2008)
Platythyrea sp.	Cameroon	Gorillas	Deblauwe and Janssens (2008)
Polyrachis concava	Cameroon	Gorillas	Deblauwe and Janssens (2008)
Polyrachis laboriosa	Cameroon	Gorillas	Deblauwe and Janssens (2008)
Polyrachis militaris	Cameroon	Gorillas	Deblauwe and Janssens (2008)
Polyrachis spp.	Gabon, Cameroon	Mandrills, gorillas, chimpanzees	Lahm, 1986; Deblauwe and Janssens (2008)
Solenopsis sp.	Gabon	Mandrills	Lahm (1986)
Technomyrmex spp.	Cameroon	Gorillas	Deblauwe and Janssens (2008)
Tetramorium aculeatum	Tanzania, Cameroon, Uganda	Chimpanzees, gorillas, gray-cheeked mangabeys	Nishida and Hiraiwa (1982); Isbell and Young (2007); Deblauwe and Janssens (2008)
Tetramorium guineense	Cameroon	Gorillas	Deblauwe and Janssens (2008)
Tetraponera penzigi	Kenya	Patas monkeys, vervets	LA Isbell, unpublished data
Onyoso mammon (Luo name)	Kenya	Humans	Christensen et al. (2006)
Unspecified	Ghana	Roloway monkeys	Curtin (2002)

TABLE B1. (Continued)

Ant species[a]	Country	Known primate consumers	Source
Unspecified	Cameroon	gray-cheeked mangabeys; patas monkeys, tantalus monkeys	Poulsen et al. (2001); Nakagawa (2003)
Unspecified	Gabon	Mandrills, talapoins, moustached monkeys, crowned monkeys, putty-Nosed monkeys	Norris (1988); Gautier-Hion (1988)
Unspecified	Cote d'Ivoire	Olive baboons	Kunz and Linsenmair (2008)
Unspecified	Tanzania	Kipunji	Davenport et al. (2010)
Unspecified	S. Africa	Samango monkeys	Lawes (1991)
Unspecified	Kenya	Galagos (*Otolemur* (*Galago*) *garnetti* and *Galagoides* (*Galago*) *zanzibaricus*)	Harcourt and Nash (1986)

[a] Species' names and spellings confirmed or corrected using Bolton (1995).
[b] Ants identified by P. Ward.

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