

RESEARCH ARTICLE

Interspecific and Temporal Variation of Ant Species Within *Acacia drepanolobium* Ant Domatia, a Staple Food of Patas Monkeys (*Erythrocebus patas*) in Laikipia, Kenya

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The ants that live in the swollen thorns (domatia) of *Acacia drepanolobium* are staple foods for patas monkeys (*Erythrocebus patas*). To obtain a better understanding of these insects as resources for patas monkeys, we sampled the contents of 1,051 swollen thorns (ant domatia) over a 22-month period from December 1999 to September 2001, in Laikipia, Kenya. First, we confirmed that of the four species of ants that live on *A. drepanolobium*, *Crematogaster sjostedti*, the competitively dominant ant in this system, does not rear significant brood in the swollen thorns and is therefore not a major food item of patas monkeys. Second, across the other three species that do use swollen thorns for rearing their brood, *C. nigriceps*, *C. mimosae*, and *Tetraponera penzigi*, the number of worker ants per swollen thorn increased with increasing competitive dominance. Third, although there was considerable month-to-month variation in the number of workers, immatures, and especially alates (winged reproductives) within species, there was less variation across species because ant production was asynchronous. Variation in domatia contents was poorly related to rainfall for each of the three species. Finally, distal thorns held more alates and fewer workers than interior thorns, and branches higher off the ground held more alates and more workers than lower branches. For the numerically dominant *C. mimosae*, higher branches held significantly more immature ants than did lower branches. Ants are reliable food resources for patas monkeys, and are probably more reliable than many plant resources in this highly seasonal environment. We estimate that patas monkeys may get as much as a third of their daily caloric needs from these ants year-round. As ants and other insects are widely consumed by primates, we suggest that greater consideration be given to species differences in animal food choices and that further studies be conducted to examine the degree to which ants influence

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INTRODUCTION

The majority of insectivorous mammal species are small-bodied because insects and other arthropods usually represent small, highly dispersed resources [Kay, 1984]. However, larger body size does not preclude the consumption of insects. Indeed, individuals of many larger-bodied primate species not normally considered insectivorous, e.g., chimpanzees (*Pan troglodytes*), gray-cheeked mangabeys (*Lophocebus albigena*), and patas monkeys (*Erythrocebus patas*), spend considerable time eating ants, for example [Isbell, 1998; McGrew, 2001; Redford, 1987; R.L. Chancellor, unpublished data].

Ants are estimated to constitute as much as 30–40% of the diet of patas monkeys in East Africa, and they are consumed year-round [Isbell, 1998]. Hocking [1970] estimated that in the *Acacia drepanolobium* ecosystem characteristic of the “black cotton” soils in East Africa, there are more than 4,000 kg of ant biomass per km². This makes *acacia* ants one of the dominant animals in this ecosystem. They are thus likely to have profound effects on the ecosystem they inhabit, as predators of their invertebrate prey, as tenders of scale insects, as consumers of plant nectar, as protectors of their host trees, and as food items for their own predators.

Patas monkeys are, in fact, the major mammalian predators of the ants that inhabit the swollen thorns (ant domatia) of *A. drepanolobium* [Isbell, 1998]. As insectivorous larger primates [females: 4–7.5 kg; males: 7.5–13 kg; Haltenorth & Diller, 1977], patas monkeys surpass the proposed threshold of about 1,000 g for the upper size limit for insectivorous primates [Richard, 1985:185], partly because the ants that inhabit *A. drepanolobium* represent an abundant resource and occur in fairly large “parcels” readily accessible for any mammal that can reach and break into the swollen thorns that house them [Isbell, 1998; Isbell et al., 1998a; Pruetz & Isbell, 2000]. Although adult *acacia* ants are chitinous and produce a variety of chemicals, e.g., alkaloids, that may serve as deterrents [Garraffo et al., 2001; Laurent et al., 2003], it is likely that their broods (eggs, larvae, pupae, and alates, the winged reproductives) are less protected, and are potentially rich dietary sources of proteins, fats, and carbohydrates [Auger et al., 2004; McGrew, 2001].

Patas monkeys live in highly seasonal, semi-arid environments in which plant productivity increases with rainy periods and decreases with dry periods [Chism et al., 1984; Enstam & Isbell, 2007]. Primates living in seasonal environments often have seasonal reproduction, and patas monkeys are no exception [Butynski, 1988; Cords, 1987; Enstam & Isbell, 2007]. However, patas monkeys are also prolific breeders both relative to other guenons and for their body size, with individuals consistently reproducing every year [Enstam & Isbell, 2007; L.A. Isbell, unpublished data]. Seasonal yet reliably annual (or shorter) reproduction is more typical of the more classically insectivorous primates, e.g., Demidoff’s bushbabies (*Galago demodovii*) and gray mouse lemurs (*Microcebus murinus*) [Bearder, 1987; Richard, 1987]. Their convergence with insectivorous

smaller primates in having short interbirth intervals suggests that ant eating may help patas monkeys sustain their high reproductive rates. They may compensate for the shortfall that a highly seasonal plant diet creates by consuming a food that is presumably available year-round.

Whether ants are indeed continuously available is unknown, however. Although the feeding behavior of the monkeys suggests that ants are available in the swollen thorns throughout the year [Isbell, 1998], and casual observations indicate that adult ants are ubiquitous on trees, it is unclear how much temporal variation exists in the availability of ants, particularly the more nutritionally valuable immature ants. The uncertainty arises partly because it is impossible for observers to identify exactly what or how much the monkeys consume as they eat the contents of swollen thorns and partly because tropical environments with distinct rainfall patterns, as are found in Kenya, may affect insect reproduction and availability [Kaspari et al., 2001b; Rhine et al., 1986]. Indeed, previous work has shown that ant colonies in the ecosystem inhabited by Kenyan patas monkeys contract during dry periods, even abandoning smaller trees. These trees are then reoccupied (either by new colonization by alates or by existing colony expansion) during wet periods [Palmer et al., 2000]. Thus, there could be periods during the year when nutritious, immature ants are not available.

At an average density of 1,335 trees/ha, *A. drepanolobium* accounts for >90% of the woody cover in the study area in Laikipia, Kenya [Young et al., 1997, 1998]. In Laikipia, individual *A. drepanolobium* trees are occupied by one of four species of ants (in order of their successional series, increasing colony size, and increasing competitive dominance): *Tetraponera penzigi*, *Crematogaster nigriceps*, *C. mimosae*, and *C. sjostedti* [Palmer, 2004; Young et al., 1997]. Virtually all trees larger than seedlings are occupied by one of these species, and all four species co-occur at fine spatial scales at the study site. Colonies of the first three species inhabit swollen thorns produced by the tree. In contrast, colonies of *C. sjostedti* rarely use the swollen thorns, instead raising brood in dead woody crevices and the excavations of long-horn beetle (Cerambycidae) larvae [Palmer et al., in prep]. Since patas monkeys get most of their ants from the swollen thorns of *A. drepanolobium*, *C. sjostedti* appears to be less attractive than the other ant species as foods for patas monkeys. Other differences in ant behavior may also contribute to their differential consumption. For instance, *C. mimosae* is far more likely to tend scale insects than the other two species that inhabit these domatia [Young et al., 1997]. Though rarely emphasized as food items for primates, scale insects are eaten nonetheless. Chacma baboons (*P. hamadryas ursinus*) and Hanuman langurs (*Semnopithecus entellus*) even pass up their normal foods to eat scale insects during scale insect outbreaks [Hamilton et al., 1978; Srivastava, 1991].

After several decades of investigating the plant foods of primates, we have learned a great deal about their food choices when those choices involve plants [Lambert, 2007]. Unfortunately, our understanding of food choice is not as sophisticated when animal foods are involved. We do know, however, that variability exists among primates in the extent of ant-eating, the ant species that are consumed, the temporal consumption of ants, and the means by which they are procured [e.g., Deblauwe et al., 2003; Ganas & Robbins, 2004; McGrew, 2001; Schöning et al., 2007; Tutin & Fernandez, 1992]. Black and white colobus monkeys (*Colobus guereza*), for example, do not eat any ants whereas sympatric gray-cheeked mangabeys do [Struhsaker, 1978; Waser, 1977]. Mangabeys frequently eat the arboreal, vine-dwelling ant, *Tetramorium aculeatum*, but rarely eat army ants (*Dorylus* spp.) [R.L. Chancellor, unpublished data]. On the

other hand, chimpanzees invest much time, effort, and ingenuity to obtain army ants [Hamle & Matsuzawa, 2002; McGrew, 2001] whereas gorillas (*Gorilla gorilla*) use little ingenuity and simply scoop them up with their hands [Watts, 1989].

To more fully understand the choices of primates for different animal foods, it is important to examine the behavior of the animals they eat, because food animals undoubtedly differ in ways that affect their desirability. Here we help to fill the gap in knowledge about the behavior of food animals of primates by relating temporal and small-scale spatial variation in the abundance of four ant species associated with *A. drepanolobium* in Laikipia, Kenya, to the feeding behavior and reproductive characteristics of patas monkeys. Our broader goal is to encourage others to examine ant species eaten or avoided by primates at their own study sites for greater understanding of the choices primates make about their animal foods and the repercussions of those choices.

STUDY SITE AND METHODS

The research was carried out over 22 months as part of a long-term research project on patas monkeys and vervets (*Cercopithecus aethiops*) (the long-term project was approved by the UC Davis IACUC and the Kenya government) on Segera ranch (36°50'E, 0°15'N; elevation 1,800 m) on the Laikipia Plateau in north-central Kenya. Segera Ranch is a cattle ranch that encourages a wide diversity of wild animals typically found in semi-arid or dry habitats. In addition to vervets and patas monkeys, olive baboons (*P. h. anubis*), and lesser bushbabies (*Galago senegalensis*) occur there. Other mammal species characteristic of East African savannah-woodlands also occur there, e.g., lions (*Panthera leo*), leopards (*P. pardus*), zebras (*Equus burchelli* and *E. grevyi*), Grant's gazelles (*Gazella granti*), giraffes (*Giraffa camelopardalis*), and elephants (*Loxodonta africana*) [see also Young et al., 1998]. The ecosystem is semi-arid, with variable annual rainfall, but with a mean annual rainfall of 600–700 mm. Two tree species predominate at the study site: *Acacia xanthophloea* (fever tree), which occurs along streams and rivers, and *A. drepanolobium* (whistling thorn acacia), which occurs away from streams and rivers on vertisolic soils of impeded drainage ("black cotton" soil) [Ahn & Geiger, 1987].

At regular intervals from December 1999 to September 2001, individual swollen thorns were collected from *A. drepanolobium* trees in and around the 4,000 ha home range of a group of patas monkeys that was systematically studied from 1992 to 2002 [Carlson & Isbell, 2001; Enstam & Isbell, 2004; Isbell, 1998; Isbell et al., 1998b]. Each sampled tree was carefully approached, and the exit holes of the targeted swollen thorns were sealed by inserting thorn tips to keep ants from leaving the domatia. The swollen thorns were then removed with clippers, placed in a plastic bag, and then deposited at the end of the day in a freezer, which killed the occupant ants. At the time of collection, we recorded the ant species identity, height of each tree (with a meter stick), height of the branch from which each swollen thorn was taken, and the location of the swollen thorn along that branch (distance from branch tip, and distance from the canopy center). One to three swollen thorns were sampled on each tree. No attempt was made to select trees systematically; with a density of about 1,335 trees/ha, it was not difficult to sample individual trees only once. Swollen thorns were chosen randomly without regard to ant activity that indicates the presence of ants in the swollen thorns.

At a later date (within several weeks for each collection), we opened the swollen thorns and counted the ants inside. Initially we attempted to distinguish

between eggs, pupae, early and late instar larvae, and workers, but counting eggs and early instar larvae (the smaller larvae) proved impractical. Therefore, after the first 120 swollen thorns (out of 1,051), we counted workers, small alates (males), large alates (females), and “immatures”, which were pupae and later instar larvae. Over the 22-month sampling period, data are available from all months except May–July 2001. We also recorded from each swollen thorn the presence of other material: carton (plant material modified by ants to create multiple floors, or levels, within a single dwelling), frass (insect excreta), leaves, unidentified (usually large lepidopteran or coleopteran) larvae, and spiders’ webs.

Statistical Analysis

Data were analyzed with JMP statistical software. Mean ant contents per swollen thorn were calculated for each tree. Differences among ant species were analyzed with one-way analysis of variances, and individual means were compared with Tukey’s HSD tests, with sample size being the number of trees sampled. Relationships among quantitative traits were analyzed with Pearson product-moment correlations, both for all species combined, and for each species separately. Thorn contents of other materials were scored on a presence/absence basis, and compared across ant species with χ^2 analysis. Statistical significance was set at an α level of 0.05.

RESULTS

Frequency of Ant Life Stages in Swollen Thorns

We counted 60,152 workers, 30,085 immatures, and 8,148 alates from 1,051 swollen thorns harvested from 817 individual trees. Less than 1% ($n = 2$) of the trees had more than one ant occupant (trees in successional transition). These are not included in the following analyses.

The average numbers of workers, immatures, and large (female) and small (male) alates differed among ant species (Table I). As anticipated, swollen thorns on trees occupied by *C. sjostedti* contained very few ants at any life stage. The remaining results reported here are restricted to the other three species. These species were similar to each other in their use of swollen thorns for brooding, averaging 30.0–37.3 immatures ($F = 1.91$, $P = 0.15$), and 7.6–9.6 alates per domatium ($F = 1.02$, $P = 0.36$). In contrast, the mean number of worker ants per swollen thorn increased with increasing competitive dominance (*T. penzigi*, 39.9; *C. nigriceps*, 60.4; *C. mimosae*, 74.2, $F = 28.2$, $P < 0.001$).

TABLE I. Mean Contents (± 1 SE) of Swollen Thorns for Trees Occupied by Each of the Four Ants Inhabiting *Acacia drepanolobium*

Ant	Workers	Immatures	Female alates	Male alates	Total alates
<i>C. sjostedti</i>	23.0 \pm 4.9 (28)	1.0 \pm 0.6 (28)	0.5 \pm 0.5 (28)	0.1 \pm 0.1 (28)	0.6 \pm 0.5 (28)
<i>C. mimosae</i>	74.2 \pm 3.7 (331)	37.3 \pm 2.9 (331)	1.6 \pm 0.3 (271)	8.1 \pm 1.0 (271)	9.7 \pm 1.1 (271)
<i>C. nigriceps</i>	60.4 \pm 2.8 (265)	30.0 \pm 2.4 (265)	2.7 \pm 0.4 (230)	4.9 \pm 1.0 (230)	7.6 \pm 1.1 (230)
<i>T. penzigi</i>	39.9 \pm 2.5 (191)	35.2 \pm 3.5 (191)	1.3 \pm 0.3 (181)	6.4 \pm 1.2 (181)	7.7 \pm 1.3 (181)

Sample sizes (number of trees, in parentheses) differ slightly within species because, for a few initial samples, we did not count alates.

Temporal Variation in Ant Life Stages Within Swollen Thorns

There was considerable month-to-month variation in the presence of workers, and in the production of immatures and alates (Fig. 1). Significantly more monthly variation existed in the number of alates than in the number of workers or immatures ($F = 24.6$, $P = 0.006$), and there was a non-significant tendency for *T. penzigi* to have more temporal variation in the number of alates, workers, and immatures than the two *Crematogaster* spp. ($F = 4.1$, $P = 0.11$). However, because variation in domatia contents was asynchronous across ant species, coefficients of variation across the entire community were lower than for any particular species (Fig. 2). Although eight out of nine correlations between rainfall and the three life stages of the three ant species in thorns were negative, all relationships were weak and none was statistically significant (all P values ≥ 0.25).

Small-Scale Spatial Variation in Ant Life Stages Within Trees

Across all three ant species, distal thorns (more toward the branch tips) held more alates than interior thorns ($F = 3.59$, $P = 0.05$) and branches higher off the ground held significantly more immatures and workers than lower branches (immatures: $F = 11.6$, $P = 0.0007$; workers: $F = 73.0$, $P < 0.0001$). For the numerically dominant *C. mimosae*, branches higher off the ground also held significantly more alates ($F = 4.36$, $P = 0.04$).

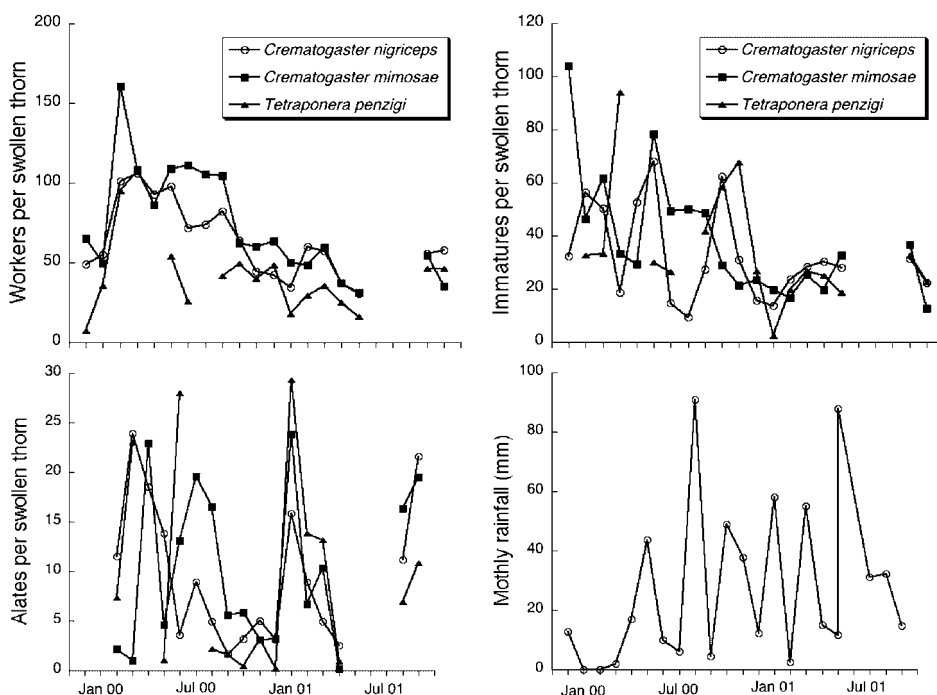


Fig. 1. Temporal variation in rainfall and the contents of swollen thorns, by ant species. In addition to the 2 months where there were no data for any of the species, there were 2 months when our collections did not include any trees occupied by *T. penzigi*.

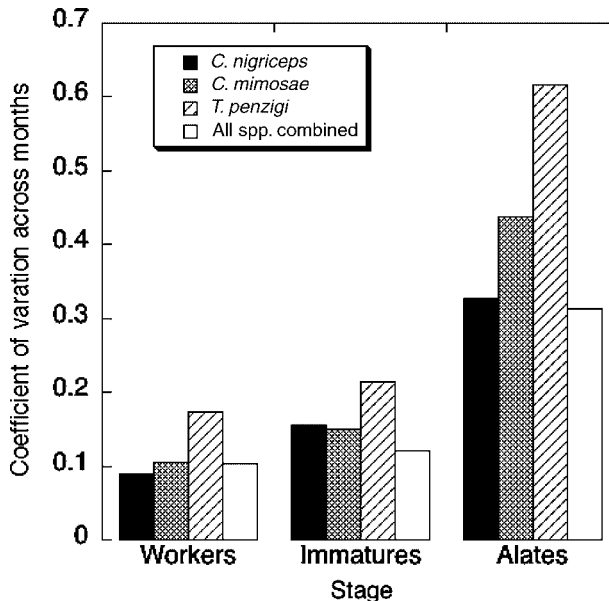


Fig. 2. Coefficients of variation (across 18 months) for the contents of swollen thorns. For the “All spp. combined” category, all three species were weighted equally.

Variation in Non-Ant Contents of Swollen Thorns by Ant Species

The swollen thorns on trees occupied by different ant species also differed in other contents (Table II). Swollen thorns occupied by *C. mimosae* were far more likely to contain carton and unidentified larvae of other species than were other ant species (Table II). Swollen thorns occupied by *C. nigriceps* were virtually the only ones in which we found the leaflets of *A. drepanolobium*. Swollen thorns occupied by *T. penzigi* uniquely contained frass. Spiders’ webs were found in all three species that brood their young in swollen thorns.

DISCUSSION

The four ant species that inhabit *A. drepanolobium* are major components of the wooded grassland habitats that dominate the impeded drainage (“black cotton”) soils of East Africa. Patas monkeys mainly consume ants of three of the four species—those that rear their brood in the swollen thorns of *A. drepanolobium*. Our data indicate that although there is large temporal variation in the number of workers, immatures, and alates within each of these three ant species, together they provide patas monkeys with a consistent supply of all life stages throughout the year, even during dry periods. The adult ants and their brood contained in these swollen thorns thus represent an abundant and reliable resource for patas monkeys.

As the reproductive members of ant colonies, alates are a particularly good source of dietary fat [Redford & Dorea, 1984], and may even provide the highest quality insect foods [McGrew, 2001], since there is more energy in fat than in other macronutrients per unit weight. For this reason, it is notable that although the monthly presence of alates varied more than workers or immatures, there was no consistent relationship between rainfall and alate presence for any ant species, and no consistent pattern across ant species. This contrasts with some neotropical

TABLE II. The Number (and Percent) of Swollen Thorns that Contained Different Material, by Ant Species

Ant	<i>N</i>	Carton (%)	Frass (%)	Leaves (%)	<i>N</i>	Unid. larvae (%)	Spiders' webs (%)
<i>C. sjostedti</i>	35	8 (23)	0 (0)	0 (0)	26	1 (4)	0 (0)
<i>C. mimosae</i>	341	<i>190 (56)</i>	5 (1)	7 (2)	192	<i>17 (9)</i>	5 (3)
<i>C. nigriceps</i>	301	23 (8)	3 (1)	<i>106 (35)</i>	152	3 (2)	8 (5)
<i>T. penzigi</i>	243	11 (5)	<i>168 (69)</i>	1 (0.5)	99	2 (2)	3 (3)
χ^2		273.3	553.8	172.1		11.05	2.92
<i>P</i>		<0.0001	<0.0001	<0.0001		0.012	0.40

Italicized numbers highlight sources of significant interspecific variation. Sample sizes were smaller for the last two traits.

plant ants, which match alate production to seasonal temperatures [Frederickson, 2006] or rainfall [Kaspary et al., 2001b] and show synchrony among some species [Kaspary et al., 2001a,b]. In addition, more alates were found on higher branches and in more distal swollen thorns. Although patas monkeys feed mainly from the ground [Pruetz, 1999] and thus eat more swollen thorns from lower branches, they are also more likely to eat distally located swollen thorns and so increase their chances of consuming alates.

The consumption of ants by patas monkeys could very well compensate for seasonal fluctuations in plant foods, enabling them to maintain their high reproductive rates while living in highly seasonal environments. In particular, the high protein and energy content of immatures and alates [McGrew, 2001] remains obtainable throughout the year, even during dry periods, in part because the different ant species are not synchronous in their brood production. Similarly, the other primary food of patas monkeys in the habitat, acacia gum, appears to be fairly reliable [Isbell, 1998]. Although no comparable systematic data are available on the seasonal availability of other foods of patas monkeys, the monkeys readily eat these other foods (e.g., seeds, fruits, flowers, and mushrooms) as they become available, and such reproductive plant foods are far less constant over time than the brood of acacia ants in this highly seasonal ecosystem. The reliability of ants (and gum) throughout the year may even protect patas monkeys during frequent droughts when many other wildlife and domestic animal species become less robust [personal observation] and suffer population declines [Georgiadis, in press]. Indeed, patas monkeys show no physical signs of nutritional distress during droughts nor are their reproductive rates negatively affected [Isbell & Chism, in press; L.A. Isbell, unpublished data].

Just how much energy do ants provide patas monkeys? Using previously published data [Pruetz & Isbell, 2000], we calculated that each adult female patas monkey in the study group eats on average the contents of 44 swollen thorns per day (% swollen thorns eaten from *A. drepanolobium* × no. trees fed on per hour × 12 h daylight). From data on body weights of ants in Hocking [1970] (means of 0.00135 and 0.00155 g per worker for *C. nigriceps* and *C. mimosae*, respectively) and the numbers of ants per swollen thorn found in this study, we estimated that individual female patas monkeys minimally eat 6 g of ants per day (assuming immatures weigh at least as much as workers), with the additional assumption that they choose swollen thorns as randomly as we chose them. The behavior of patas monkeys suggests, however, that they do not choose swollen thorns randomly. In a sample of 88 trees that were examined directly after patas monkeys fed on them, ants occupied 87 trees (98.9%) [Isbell, 1998]. In contrast,

when we sampled 183 trees and 573 swollen thorns without regard to the behavior of the monkeys, ants and other insects were found on 153 (84%) of the trees and in only 333 (58%) of the thorns [Isbell, 1998].

The average *C. nigriceps* thorn had 95 ants, and the average *C. mimosae* thorn had 121 (Table I). If patas monkeys are discerning enough to only open thorns in the upper halves of these distributions, they would average 152 *C. nigriceps* ants and 188 *C. mimosae* ants, or about 60% more ants per thorn than the average found through random sampling, i.e., about 11 g of ants daily. If the monkeys were even more discerning, this number would increase further. The upper 25% of thorns had 109% more *C. nigriceps* ants (199), and 126% more *C. mimosae* ants (261) than their means, resulting in the consumption of about 15.3 g of ants daily. Note that these are underestimates because *T. penzigi* is not included.

With ants averaging 5,361 kcal/kg [Ramos-Elorduy & Pino, 1990, cited in DeFoliart, 1992], 11–15 g of ants would generate about 57–82 kcal/day/adult female patas monkey. Although data on energy requirements for patas monkeys are not available, comparable data for female rhesus macaques (*Macaca mulatta*) weighing 6 kg (this is within the weight range of adult female patas monkeys), estimates metabolizable energy requirements of about 277 kcal/day [CAN, 2003:46]. Assuming the energy needs of patas monkeys are roughly similar, 11–15 g of ants could provide adult female patas monkeys with about 20–30% of their daily energy requirement. The energetic contribution from ants is substantial, and could contribute to their consistently annual reproduction.

Interspecific variation in domatia contents other than ants and their brood (Table II) may also influence the food choices of patas monkeys. It is doubtful that patas monkeys benefit much, if at all, from eating leaflets inside the domatia of *C. nigriceps* (which are also readily available and fresher outside the domatia), frass (insect excreta) inside the domatia of *T. penzigi*, or carton inside the domatia of *C. mimosae*. On the other hand, non-ant larvae and scale insects are more often found in the domatia of *C. mimosae* than in those of other ants [see also Seufert & Fiedler, 1996; Weeks, 2003; Young et al., 1997] and they are undoubtedly eaten by patas monkeys in the course of eating *C. mimosae*. These non-ant foods may help to explain why, of all the ant species in the study area, patas monkeys disturb the domatia of this, the most aggressive ant species, most often [Isbell, 1998].

In conclusion, the combination of ant species that are eaten by patas monkeys provide a significant and reliable food source for them throughout the year and help to buffer them from fluctuations in plant foods during dry seasons and droughts. Although insectivory has traditionally been emphasized in small primates, larger-bodied primates eat insects as well, and even show preferences for certain species. Our results suggest that it may be time to investigate animal food choices in primates more closely and to consider the degree to which insects, especially the widely consumed ants [Redford, 1987], influence nutrient and energy intake, and therefore reproduction, in these larger primates.

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REFERENCES

- Ahn PM, Geiger LC. 1987. Kenya soil survey—soils of Laikipia District. Kabete, Kenya: Ministry of Agriculture, National Agricultural Laboratories.
- Auger J, Ogborn GL, Pritchett CL, Black HL. 2004. Selection of ants by the American black bear (*Ursus americanus*). *West N Am Nat* 64:166–174.
- Bearder SK. 1987. Lorises, bushbabies, and tarsiers: diverse societies in solitary foragers. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 11–24.
- Butynski TM. 1988. Guenon birth seasons and correlates with rainfall and food. In: Gautier-Hion A, Bourlière F, Gautier J-P, Kingdon J, editors. *A primate radiation: evolutionary biology of the African Guenons*. New York: Cambridge University Press. p 284–322.
- Carlson AA, Isbell LA. 2001. Causes and consequences of single-male and multi-male mating in free-ranging patas monkeys (*Erythrocebus patas*). *Anim Behav* 62:1047–1058.
- Chism J, Rowell T, Olson D. 1984. Life history patterns of female patas monkeys. In: Small M, editor. *Female primates: studies by women primatologists*. New York: Alan R. Liss. p 175–190.
- Committee on Animal Nutrition. 2003. *Nutrient requirements of nonhuman primates*, 2nd revised edition. Washington, DC: National Academies Press.
- Cords M. 1987. Forest guenons and patas monkeys: male-male competition in one-male groups. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. *Primate societies*. Chicago: University of Chicago Press. p 98–111.
- Deblauwe I, Dupain J, Nguenang GM, Werdenich D, Van Elsacker L. 2003. Insectivory by *Gorilla gorilla gorilla* in Southeast Cameroon. *Int J Primatol* 24:493–502.
- DeFoliart G. 1992. Insects as human food. *Crop Prot* 11:395–399.
- Enstam KL, Isbell LA. 2004. Microhabitat preference and vertical use of space by patas monkeys (*Erythrocebus patas*) in relation to predation risk and habitat structure. *Folia Primatol* 75:70–84.
- Enstam KL, Isbell LA. 2007. The guenons (genus *Cercopithecus*) and their allies. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. *Primates in perspective*. New York: Oxford University Press. p 252–274.
- Frederickson ME. 2006. The reproductive phenology of an Amazonian ant species reflects the seasonal availability of its nest sites. *Oecologia* 149:418–427.
- Ganas J, Robbins MM. 2004. Intrapopulation differences in ant eating in the mountain gorillas of Bwindi Impenetrable National Park, Uganda. *Primates* 45:275–278.
- Garraffo HM, Spande TF, Jain P, Kaneko T, Jones TH, Blum MS, Ali TMM, Snelling RR, Isbell LA, Robertson HG, Daley JW. 2001. Ammonia chemical ionization tandem mass spectrometry in structural determination of alkaloids. II. Tetraponerines from pseudomyrmecine ants. *Rapid Commun Mass Spect* 15:1409–1415.
- Georgiadis N. In press. Savanna herbivore dynamics in a livestock-dominated landscape: I. Dependence on land use, rainfall, density, and time. *Biol Conser*.
- Haltenorth T, Diller H. 1977. *A field guide to the mammals of Africa including Madagascar*. London: Collins.
- Hamilton WJ, Buskirk RE, Buskirk WH. 1978. Omnivory and utilization of food resources by chacma baboons (*Papio ursinus*). *Am Nat* 112:911–924.
- Hamle T, Matsuzawa T. 2002. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *Am J Primatol* 58:133–148.
- Hocking B. 1970. Insect associations with the swollen thorns acacias. *Trans Roy Entomol Soc Lond* 122:211–255.
- Isbell LA. 1998. Diet for a small primate: insectivory and gummivory in the (large) patas monkey (*Erythrocebus patas pyrrhotus*). *Am J Primatol* 45:381–398.
- Isbell LA, Chism J. In press. Distribution and abundance of patas monkeys (*Erythrocebus*

- patas*) in Laikipia, Kenya, 1979–2004. Am J Primatol.
- Isbell LA, Pruettz JD, Young TP. 1998a. Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. Behav Ecol Sociobiol 42:123–133.
- Isbell LA, Pruettz JD, Lewis M, Young TP. 1998b. Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*): implications for the evolution of long hindlimb length in *Homo*. Am J Phys Anthropol 105:199–207.
- Kaspari M, Pickering J, Windsor D. 2001a. The reproductive flight phenology of a neotropical ant assemblage. Ecol Entomol 26:245–257.
- Kaspari M, Pickering J, Longino JT, Windsor D. 2001b. The phenology of a neotropical ant assemblage: evidence for continuous and overlapping reproduction. Behav Ecol Sociobiol 50:382–390.
- Kay RF. 1984. On the use of anatomical features to infer foraging behavior in extinct primates. In: Rodman PS, Cant JGH, editors. Adaptations for foraging in nonhuman primates. New York: Columbia Press. p 21–53.
- Lambert JE. 2007. Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. Primates in perspective. New York: Oxford University Press. p 482–495.
- Laurent P, Hamdani A, Braekman JC, Daloz D, Isbell LA, de Biseau JC, Pasteels JM. 2003. New 1-alk(en)yl-1,3,5-trihydroxycyclohexanes from the Dufour gland of the African ant *Crematogaster nigriceps*. Tetrahedron Lett 44:1383–1386.
- McGrew WC. 2001. The other faunivory: primate insectivory and early human diet. In: Stanford CB, Bunn HT, editors. Meat-eating and human evolution. New York: Oxford University Press. p 160–178.
- Palmer TM. 2004. Wars of attrition: colony size determines competitive outcomes in a guild of African acacia ants. Anim Behav 68:993–1004.
- Palmer TM, Young TP, Stanton ML, Wenk E. 2000. Short-term dynamics of an acacia ant community. Oecologia 123: 245–235.
- Palmer TM, Stanton ML, Young TP, Goheen, Pringle RM, Karban R. In prep. Break-down of an ant-acacia mutualism following the exclusion of large herbivores from an African savanna.
- Pruettz JD. 1999. Socioecology of adult female vervet (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) in Kenya [dissertation]. Urbana-Champaign: University of Illinois. 298p. Available from: University Microfilms, Ann Arbor, MI: 9944972.
- Pruettz JD, Isbell LA. 2000. Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. Behav Ecol Sociobiol 49:38–47.
- Redford KH. 1987. Ants and termites as food: patterns of mammalian myrmecophagy. In: Genoways HH, editor. Current mammalogy. New York: Plenum Press. p 349–393.
- Redford KH, Dorea JG. 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. J Zool Lond 203:385–395.
- Rhine RJ, Norton GW, Wynn GM, Wynn RD, Rhine HB. 1986. Insect and meat-eating among infant and adult baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. Am J Phys Anthropol 70: 105–118.
- Richard AF. 1985. Primates in nature. New York: Freeman. 558p.
- Richard AF. 1987. Malagasy prosimians: female dominance. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 25–33.
- Schöning C, Ellis D, Fowler A, Sommer V. 2007. Army ant prey availability and consumption by chimpanzees (*Pan troglodytes vellerosus*) at Gashaka (Nigeria). J Zool 271: 125–133.
- Seufert P, Fiedler K. 1996. Life-history diversity and local co-existence of three closely related lycaenid butterflies (Lepidoptera: Lycaenidae) in Malaysian rainforests. Zool Anzeiger 234:229–239.
- Srivastava A. 1991. Insectivory and its significance to langur diets. Primates 32: 237–241.
- Struhsaker TT. 1978. Food habits of five monkey species in the Kibale Forest, Uganda. In: Chivers DJ, Herbert J, editors. Recent advances in primatology, vol 1. New York: Academic Press. p 225–248.
- Tutin CEG, Fernandez M. 1992. Insect-eating by sympatric lowland gorillas (*Gorilla g. gorilla*) and chimpanzees (*Pan t. troglodytes*) in the Lopé Reserve, Gabon. Am J Primatol 28:29–40.
- Waser PM. 1977. Feeding, ranging and group size in the mangabey *Cercocebus albigena*. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys, and apes. New York: Academic Press. p 183–222.
- Watts DP. 1989. Ant eating behavior of mountain gorillas. Primates 30:121–125.

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- Weeks JA. 2003. Parasitism and ant protection alter the survival of the lycaenid *Hemiargus isola*. *Ecol Entomol* 28: 228–232.
- Young TP, Stubblefield CH, Isbell LA. 1997. Ants on swollen-thorn acacias: species co-existence in a simple system. *Oecologia* 109: 98–107.
- Young TP, Okello B, Kinyua D, Palmer TM. 1998. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *Afr J Range Forage Sci* 14:94–102.