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Alternation of Sleeping Groves by Yellow Baboons (*Papio cynocephalus*) as a Strategy for Parasite Avoidance

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ABSTRACT. The primary locus of contact between free-living yellow baboons (*Papio cynocephalus*) in the Amboseli National Park of Kenya and the infective stages of their intestinal parasites is believed to be soil beneath sleeping trees contaminated by the baboons' own fecal emissions. In this report, we present evidence both that infective ova and larvae of intestinal parasites are found at very high densities in the soil beneath sleeping groves and that Amboseli baboons substantially reduce their contact with this reservoir of parasites by alternating periods of a few consecutive nights' use of any particular grove with much longer periods of avoidance of that grove. Although many factors other than the presence of parasite larvae also influence choice of sleeping groves, we propose as a working hypothesis that the temporal pattern of sleeping grove alternation shown by Amboseli baboons reflects a subtle behavioral strategy for parasite avoidance.

INTRODUCTION

During March through October 1977, we investigated behavioral and ecological aspects of parasite transmission among free-living yellow baboons (*Papio cynocephalus*) in the Amboseli National Park of Kenya. For Amboseli baboons, as for many other primate populations, nightly resting sites may be one of the major loci of contact with parasites and pathogens (FREELAND, 1976). Despite the fact that sleeping groves, and to a lesser extent waterholes and abandoned Masai settlements (SCHAEFFER & NJAI, 1978), constitute permanent parasite reservoirs frequently contacted by Amboseli baboons, clinical symptoms of parasite infection are only rarely seen in this population and such infections do not appear to be a major factor contributing to either adult or juvenile mortality (ALTMANN et al., 1977). Certainly, it has been well demonstrated that baboons and other primate species possess immunological mechanisms to reduce their chances of infection under conditions of chronic exposure to both bacterial and helminth parasites (COHEN & SADUN, 1976). However, it also seems likely that many primates further reduce their probability of parasite infection through behavioral strategies of avoidance of habitats containing high densities of the infective stages of such organisms (FREELAND, 1976). Specifically, in the present paper, we demonstrate that soil beneath sleeping groves contaminated by the baboons' own fecal material constitutes one of the few microhabitats in Amboseli in which ova and larvae of the intestinal nematodes of baboons are found in large numbers. Furthermore, we present evidence that Amboseli baboons alternate use of the multiple sleeping groves available to them in such a way as to minimize their probability of contact with the infective stages of both these intestinal helminths and many other kinds of parasites.

BACKGROUND INFORMATION

STUDY SITE AND SUBJECTS

This study was carried out in the Amboseli National Park of Kenya. Amboseli is an area of short-grass savannah situated just north of Mt. Kilimanjaro. A series of swamps and permanent waterholes are fed by rainwater percolating through the volcanic soils of Kilimanjaro and provide a year-round source of water for a population of about 200 yellow baboons and a much larger, seasonally fluctuating, complement of plains game and their predators. The dynamics of the Amboseli ecosystem have been described by WESTERN (1972) and WESTERN and VAN PRAET (1973) and the basic ecology of the baboon population in particular has been described by ALTMANN and ALTMANN (1970).

Since 1971 Amboseli has been the site of a systematic longitudinal study of baboon social behavior and ecology (HAUSFATER, 1975; HAUSFATER, ALTMANN & ALTMANN, 1979). As part of the longitudinal study, the entire baboon population has been censused at least annually and all groups in the area habituated to the presence of observers on foot or in vehicles. Additionally, nearly daily demographic and behavioral records have been maintained on our main study group, Alto's Group, including records of sleeping grove utilization. Generally, the group was located each morning prior to, or just shortly after, descent from their nightly resting site. A series of studies (ALTMANN & ALTMANN, 1970; HAUSFATER & BEARCE, 1976; POST, HAUSFATER & MCCUSKEY, 1980) have documented the critical importance of one species of tree in particular, the yellow-barked acacia (*Acacia xanthophloea*), as both a daytime source of food and a nighttime source of refuge for Amboseli baboons.

SLEEPING TREES

Each night, Amboseli baboons spend 10 or more hours resting in groves of yellow-barked acacia trees. These sleeping groves are spatially distinct clusters of 2–12 trees with branching patterns such that baboons can move from one tree to another without returning to the ground (ALTMANN & ALTMANN, 1970). Only one other tree species, *A. tortilis*, occurs in the Park in any numbers, but this low-crowned "umbrella tree" affords baboons little protection from predators and, to the best of our knowledge, has never been used by Amboseli baboons as a nightly resting site.

Associated with yellow-barked acacias is typically a dense understory of the shrubs *Azima tetracantha* and *Salvadora persica* as well as thick cover of *Cynodon* spp. and *Sporobolus* spp. grasses. The sheer mass of vegetation associated with the groves as well as the relatively high canopy of the trees themselves produces a distinct microhabitat beneath groves in the otherwise arid Amboseli environment. Specifically, recent studies have shown that the area beneath sleeping trees is characterized by generally higher relative humidity, lower solar input, more moderate temperatures, and reduced wind speeds compared to areas of open savannah in proximity to the groves (STELZNER & HAUSFATER, 1980). Such open areas, which characterize the vast majority of the habitat used by baboons in Amboseli, generally have sparse low grass cover punctuated by isolated umbrella trees, clumps of bushes and shrubs, or areas of nearly barren soil.

Alto's Group contained approximately 45 individuals and had nearly exclusive use of at least 15 different sleeping groves during the study period. However, on any given night the entire group slept in only one grove, or occasionally, two adjacent groves. In either case, just

one or two nights of grove occupancy was sufficient to result in substantial fecal accumulation beneath a grove. Each morning, after descent from their sleeping grove, the baboons spent from a few minutes to several hours resting, feeding or socializing on the ground beneath these same trees.

The Parasites

Baboons in Amboseli, as elsewhere in Kenya (Kuntz & Moore, 1973), are known to harbor a wide range of epizootics. However, three genera of intestinal nematodes—namely, *Oesophagostomum*, *Strongyloides* and *Trichostrongylus* (Hausfater & Watson, 1976)—account for the vast majority of parasite ova recovered in fecal samples from Amboseli baboons. Although these nematode parasites differ slightly in life-cycle, all three genera share in common the trait that they are transmitted from host to host through contact with, or ingestion of, infective soil-living larvae (Flynn, 1973; Olsen, 1974). Moreover, ova and rhabditiform (i.e., preinfective) larvae of these genera are commonly recovered in fecal samples from Amboseli baboons and can give rise to infective larvae from one to six days after fecal passage (Sheldon, 1937; Soulsby, 1968).

As emphasized by Ollerenshaw and Smith (1969) a complete understanding of parasite transmission in natural environments involves more than a simple laboratory determination of the optimal incubation temperature for specific parasite species. Likewise, maintenance of larvae in cultures at constant temperature and humidity generally provides little information on larval development times in natural habitats where climatic conditions fluctuate both diurnally and seasonally. Below, we describe a series of experimental studies aimed at documenting the environmental distribution and life-cycle characteristics of the major nematode parasites of Amboseli baboons in so far as this information is relevant to understanding the process of parasite transmission. In general, our procedure in this work was to examine fecal samples and larval cultures for signs of parasite activity or viability following a timed exposure of such materials either to actual ambient environmental conditions or to our best efforts to simulate those conditions in the laboratory. As such, the design of these studies reflected an intentional choice on our parts to accept wherever necessary a reduction in the rigor of experimental controls or in the precision of resultant numerical estimates so as to enhance the overall external validity of our conclusions. Thus, while we are not able to present, for example, an extensive plot of larval development time against temperature, we are able to describe with scientifically acceptable reliability and precision the distribution, survival and hatching schedule of the nematode parasites of Amboseli baboons under the climatic conditions to which these parasites are typically exposed and to which their life-cycles are presumably adapted.

EXPERIMENTAL STUDIES

Ecological Attenuation of Parasite Transmission

Sleeping Groves as a Reservoir of Baboon Parasites

Our first analyses were aimed at determining if the microhabitat beneath sleeping groves did in fact constitute an area of high parasite larvae density. Specifically, soil and grass samples were collected beneath known sleeping sites, beneath groves not used by baboons as sleeping sites and from open areas in proximity to these groves. It is important to note, how-

ever, that regardless of usage patterns by baboons, all three habitats were still subject to use as feeding and resting sites by many other bird and mammal species, including vervet monkeys (*Cercopithecus aethiops*). Soil and grass samples from each area were separated and subjected to extraction of adult and larval nematodes using a Baermann apparatus (GEORGI, 1974; CABEL, 1960). Examination of 1,146.5 g (wet weight) of soil from beneath known sleeping groves yielded 4,620 larvae and adult nematodes, or an average of 402.9 nematodes per 100 g of soil. Grass samples from beneath these same groves yielded an additional 473.1 nematodes per 100 g ($N = 146.9$ g, wet weight). For both grass and soil samples, nematode yield was lowest in samples collected at the greatest distance from the geometric center of the groves.

Unfortunately, given our relatively simple laboratory facilities and equipment as well as the large number of larvae recovered from these samples, there was no practical way to differentiate among nematodes parasitic for baboons, parasitic for other animals, plant parasites, or even free-living forms. However, comparison of the above recovery figures to those for soil from groves not used by baboons and from open areas does provide a means of assessing the quality of the microhabitat beneath baboon sleeping trees for parasite survival as well as the effects on parasite density of periodic grove use by baboons. Thus, soil from beneath groves not used by baboons yielded only 74.8 nematodes per 100 g ($N = 426.2$ g, wet weight) while soil from open areas adjacent to groves, and typical of the habitat in which baboons spend most of their day, yielded no larvae or adult nematodes at all ($N = 900.0$ g, wet weight). Thus, we concluded that the area beneath sleeping groves not only constituted one of the few microhabitats in Amboseli suitable for survival of parasites, but was also probably the primary locus of contact between baboons and the infective stages of their intestinal nematodes.

Dry Season Attenuation of Parasite Transmission

Long-term rainfall records for Amboseli show distinct peaks in the months of November–December, the "short rains," and in the months of March through May, the "long rains." In fact, year-to-year variability in the amount and timing of rainfall is substantial, and in the best of years a total of only 500 mm of rain is accumulated. As a result, feces deposited in open habitats generally desiccated very rapidly, particularly during the six or more months each year in which there is little or no rainfall. Specifically, our studies showed that nearly all fecal samples passed by baboons during the dry season months of May through October desiccated *in situ* with no more than 5% (dry weight, estimated) of the samples removed by the action of the only diurnally-active dung beetles during that time of year, *Onthophagus* sp.

The effects on parasite ova and larvae of direct exposure to daytime open plains' climatic conditions were assessed in the following experiments. A total of 60 fecal samples were collected in the field shortly after passage. Approximately one-half of each sample was placed in a closed, moistened jar and maintained indoors at ambient laboratory temperature. (Mean minimum and maximum indoor temperatures were 17.3 and 28.0°C, respectively.) The second portion of each sample was placed in a Stender dish, covered loosely with gauze to prevent contamination, and then placed outside of the laboratory on an area of open soil. (Mean minimum and maximum shade temperatures outdoors were 10.9 and 32.6°C, respectively; soil surface temperatures typically exceeded 50°C, however.)

The contents of both the Stender dishes and the sealed jars were subjected to Baermann

extraction of larvae after intervals from 6 hr to five days. A total of 488 nematode larvae were recovered from 2,325.8 g (wet weight) of feces incubated in the moistened jars, an average of 20.9 larvae per 100 g of feces. In contrast, the samples exposed to open plains' environmental conditions yielded four larvae, an average of only 0.18 larvae per 100 g ($N = 2{,}207.4$ g, wet weight), and in fact all four of these larvae were recovered from samples exposed to open plains' conditions for 24 hr or less.

Although the samples exposed on open soils did not yield large numbers of larvae, it seemed plausible that the ova contained in these samples might remain viable, presumably awaiting an increase in moisture or other environmental cue before hatching. We tested this hypothesis by exposing one-third (692.4 g, wet weight) of 18 freshly collected fecal samples to ambient open plains' conditions following the same protocol as above. However, at the end of the five day exposure to outside conditions, the samples were rehydrated with warm distilled water and incubated at ambient indoor temperature for three days prior to Baermann extraction. These samples yielded five larvae, or an average of 0.72 larvae per 100 g of feces. This yield was approximately four times greater than that obtained from another third of each sample that was also placed outdoors for five days, but not subjected to rehydration before larvae extraction. However, the yield of 0.72 larvae per 100 g from the rehydrated samples was still less than one-eighth of the average yield of 6.1 larvae per 100 g obtained from the one-third of each sample incubated in moist jars indoors for three days and then subjected to larval extraction ($N = 643.5$ g, wet weight). Thus, while some parasite ova were indeed resistant to desiccation, in general direct exposure of parasite-containing materials to the dry season climatic regime attenuated parasite transmission, at least in unprotected open plains habitat, through increased mortality of parasites at both the ova and larval stages.

Wet Season Attenuation of Parasite Transmission

Following periods of heavy rainfall, an extensive invertebrate fauna utilized baboon feces, including both dung beetles and numerous dipteran species. Two dung beetle species in particular, *Kheper purpurascens* and *Gymnopleurus vireus*, dispersed and buried a very large proportion (estimated at greater than 85%, wet weight) of all dung deposited by baboons during periods of heavy rainfall. Adult dung beetles use buried feces as a food source for themselves and, following oviposition in the buried dung ball, for their own larvae (HALFFTER & MATTHEWS, 1966). Ova of only a few nematode species are able to withstand mastication by dung beetles, and thus the action of dung beetles is generally to reduce eventual parasite numbers (MILLER & CHI-RODRIGUEZ, 1961). However, we also know that baboons dig up and eat larval dung beetles (POST, HAUSFATER & MCCUSKEY, 1980). Thus, these invertebrates are almost certain to serve as intermediate hosts for some baboon parasites (e.g., Spiruroid nematodes) and are also probable mechanical transmitters for several other groups of intestinal helminths and protozoa. Yet another factor relevant to understanding wet season attenuation of parasite transmission is that a substantial proportion of parasite ova exposed to moist soil are rapidly invaded and destroyed by fungi, especially *Fusarium* sp. and *Cephalosporium* sp., and other soil microorganisms (LYSEK, 1966). In sum, although much more work is still needed on the precise role of both dung beetles and soil microorganisms in parasite transmission among baboons, it seems likely at present that with respect to most nematode species, wet season ecological conditions result in at least as great an attenuation of larval hatching and survival as do the desiccating climatic conditions of the Amboseli dry season.

Table 1. Baboon sleeping grove utilization patterns in relation to larvae hatch and mortality schedules.

Night	Baboons	Parasites	Expected larval numbers (per 100 g, wet weight of feces)[1]	Days since last use of grove	Grove reuse probability[2]
1	First night of grove usage	Negligible ova and larvae	—	—	— —
2	Second night of grove usage	Ova numbers increasing; infective larvae negligible	—	1	+ (.40)
3	Avoidance or use of grove (depending on seasonal conditions)	Ova hatch begins (night 1 ova only); infective larvae numbers low	24	1	+ (.40)
4	Avoidance of grove	Ova hatch rate high (nights 1 and 2 ova); infective larvae numbers increasing	53	2	− (.26)
5	Most extreme avoidance of grove	Ova hatch continues; infective larvae numbers high	73	3	− (.19)
6	Avoidance of grove	Ova hatch continues; infective larvae numbers high	80	4	− (.23)
7	Avoidance of grove	Ova hatch diminishing; infective larvae numbers decreasing	63	5	− (.23)
8	Avoidance of grove	Infective larvae numbers decreasing	49	6	− (.26)
9	Return to grove	Infective larvae numbers decreasing	40	7	+ (.29)
10	Return to grove	Infective larvae numbers low	33	8	+ (.28)
11	Highest likelihood of return to grove	Infective larvae numbers low	27	9	+ (.33)
12	Return to grove unless used on night 9, 10 or 11 above	Dependent on usage patterns on nights 10 and 11 above	22	10	− (.26)

(For footnotes, see opposite page.)

Parasite Larvae Hatching and Mortality Schedules

Larval Hatching Schedules

Our next analyses were aimed at estimating the number and hatching schedule of nematode larvae potentially resulting from fecal emissions by baboons overnight at sleeping groves. For these analyses, fecal samples were again collected in the field shortly after passage. Samples were maintained in moist, sealed jars at ambient laboratory temperature for one to ten days and then subjected to Baermann extraction of larvae. Extraction of samples carried out from 6–24 hr after deposition yielded 5 larvae per 100 g of feces (N = 840.6 g, wet weight). In contrast, samples examined at 48, 72 and 96 hr after deposition averaged 28 larvae per 100 g of feces (N = 2,082.2 g, wet weight). Extraction of samples incubated for 120 hr or longer again yielded only low larval numbers, just over 9 larvae per 100 g (N = 2,295.2 g, wet weight). Thus, a distinct peak in larval hatching occurred during the relatively restricted period from roughly 48 to 96 hr after fecal deposition. Additionally, many of the larvae recovered in these samples had reached the third-stage larval development and hence were potentially infective if contacted by baboons.

Larval Mortality Schedule

The low larval numbers obtained from samples incubated for greater than 120 hr indicated not only that negligible numbers of larvae hatched during this interval, but also that larvae hatched earlier must have suffered heavy mortality. The mortality schedule of these larval nematodes was estimated as follows: Larvae extracted by Baermann apparatus from samples incubated 48–96 hr were transferred to covered culture dishes and maintained at ambient laboratory temperature in a shallow layer of physiological saline and fecal extract. This culture method is a modified version of a standard parasitological technique (Garcia & Ash, 1975), but with the advantage that larvae can be readily examined for any signs of movement under a low power microscope. The number of active, and presumably viable, larvae in each culture was determined daily until all larval movement ceased and mortality presumed to be total. It seems likely that survival of larvae in these cultures was at least as good as that experienced by larvae exposed to the actual ambient conditions within the Park, even conditions beneath sleeping groves. A survivorship plot of the larvae recount data was closely fit by the exponential mortality function:

$$Y = \exp(-.22t),$$

where Y equals the proportion of larvae still active after t days (r = −.98, N = 541). In

1) Values for expected larval numbers given in this table were obtained by considering only larvae hatched in the interval from 48–96 hr after any previous night of grove occupancy. The model assumed that all larvae recovered from samples at 48 hr post-deposition were hatched in the preceding 24-hr interval. Larvae recovered at 72 hr post-deposition were assumed to represent the survivors (calculated from the equation on p. 293) of larvae hatched at 48 hr post-deposition plus additional larvae newly hatched in the interval from 48–72 hr post-deposition. Larvae recovered at 96 hr were similarly treated as representing survivors from the hatches at 48 and 72 hr post-deposition as well as larvae newly hatched in the 72–96 hr interval. Larvae numbers on all subsequent days were considered to represent only survivors from the 48, 72 and 96 hr hatchings.

In the table, night 4 constitutes both the interval 72 hr after the first night of grove occupancy and the interval 48 hr after the second successive night of grove occupancy. In this case, the expected number of larvae was taken as the sum of larval numbers expected from both the 72 and 48 hr hatchings as calculated in the above model. 2) Plus (+) and minus (−) symbols indicate grove reuse probabilities above and below the mean value (.27), respectively. See text for grove reuse probability calculation procedures.

Table 2. Consecutive nights of sleeping grove occupancy and mean return times. (See text for further explanation.)

Dates	Season	Rainfall (mm)	Grove-nights of occupancy
Sept. 8, 1976–Oct. 31, 1976	Dry	0.8	54
Nov. 1, 1976–Dec. 20, 1976	Wet	53.8	50
Mar. 19, 1977–May 11, 1977	Wet	102.1	57[1)]
Sept. 4, 1977–Oct. 12, 1977	Dry	1.7	43[1)]
Total			204
Total (less "unknown" intervals)			193

1) Group split between two different groves on three nights.

(continued)

essence, the above function indicated that mortality of these nematode parasites occurred at the rate of 0.22 deaths per larvae per day, yielding an average larval life expectancy of 4.5 days.

FIELD STUDIES

Successive Nights of Grove Use

Based upon larval hatch rates alone, it would be advantageous for baboons to use a particular grove for no more than two nights in succession, thereby avoiding the grove during the period from 48 through 96 hr after the first previous night of occupancy (Table 1). Table 2 presents a summary of grove utilization patterns for four periods during 1976–1977 for which we have continuous records of grove occupancy patterns exceeding 30 nights. These data show that for nearly three-fourths of all nights for which the utilization run length could be determined exactly, run length was only one night or two nights in succession ($N = 193$ nights, Table 2).

Mean Return Time

Amboseli baboons could further reduce their probability of contact with infective parasite larvae if they delayed grove reuse not just for the period of peak larval hatching, but also for the additional 4.5 days required for natural mortality to reduce larval numbers to near baseline levels, a total of 8.5 days in all (Table 1). The observed mean return time following any interval of continuous grove usage was 9.1 days (Table 2), very close to the predicted interval of grove avoidance. In fact, the observed mean return time of 9.1 days is most likely an underestimate of the true mean, since this calculation did not include the incomplete return times resulting from truncated (i.e., open-ended) intervals in the data set.

This temporal pattern of grove avoidance following two successive nights of utilization may be a direct response by baboons to the odor associated with fecal accumulation beneath sleeping groves. Obviously, a behavioral response mediated by such a proximate mechanism would be influenced by a wide variety of environmental factors, for example, rainfall, relative humidity and the burial of feces by dung beetles. In this regard, the high proportion of three night runs of grove utilization during the 1976 dry season may be significant (Table 2). The 1976 dry season actually comprised the end of a nearly two year long drought; soil beneath sleeping trees was very dry and fecal debris desiccated rapidly with a concomitant reduction in odor. Hence, the increased frequency of three night grove occupancy sequences during this

Table 2. (continued)

Consecutive nights of grove occupancy					Return time		
1 night	2 nights	3 nights	>3 nights	Unknown	$\bar{X}$	*S.D.*	*N*
14 (25.9)	6 (11.1)	27 (50.0)	4 (7.4)	3 (5.6)	8.1	6.9	23
23 (46.0)	16 (32.0)	9 (18.0)	0 (0)	2 (4.0)	9.0	7.7	24
25 (43.9)	22 (38.6)	6 (10.5)	0 (0)	4 (7.0)	11.2	7.1	28
32 (74.4)	6 (14.0)	3 (7.0)	0 (0)	2 (4.6)	7.6	5.3	26
94 (46.1)	50 (24.5)	45 (22.1)	4 (1.9)	11 (5.4)	9.1	6.9	101
94 (48.7)	50 (25.9)	45 (23.3)	4 (2.1)				

season may have reflected the longer time required to reach any given level of odor (or other stimulus) build-up beneath sleeping trees. Likewise, the relatively high proportion of one night runs of grove utilization in the 1977 dry season, which followed a period of heavy rains, and the longer mean return times in both wet seasons compared to the adjacent dry seasons were consistent with this fecal build-up hypothesis of sleeping grove avoidance (Table 2).

Grove Reuse Probabilities

The temporal pattern of sleeping grove usage by Amboseli baboons may also have been constrained by a preference for returning as soon as practicable to certain groves having such desirable qualities as superior protection from predators or proximity to important food resources. Data on sleeping tree utilization were examined for such an effect by calculating the conditional probability, over the entire 1976–1977 field study ($N = 428$ grove nights of occupancy), that Alto's Group would return to a grove on night 1, 2, 3, ..., t following any previous night of occupancy of that grove. The conditional probability values for individual nights were then compared to the mean probability of grove reuse averaged over the entire study period ($\bar{x} = .27$).

Table 1 shows that grove reuse probabilities were lower than average on nights 4–8 following the start of a typical sequence of grove occupancy, the nights of peak larval hatching and highest larval numbers beneath the groves. The single lowest probability of grove reuse, 0.19, occurred on night 5 of a typical grove occupancy sequence. Conversely, grove reuse probabilities were higher than average on nights 9–11 after the start of any previous period of grove use, nights by which larval numbers were expected to have returned to baseline levels. The highest probabilities of grove reuse, 0.40 and 0.33, occurred on nights 2–3 and night 11, respectively, of a typical grove occupancy sequence. Thus, available data on the temporal pattern of grove utilization by Amboseli baboons were consistent both with the hypothesis that baboons avoided sleeping groves during periods of high larval numbers beneath groves and the hypothesis that the baboons in general returned to specific groves as soon as larval numbers were reduced to baseline levels by natural mortality.

DISCUSSION AND SPECULATION

Obviously, many factors besides parasite larvae density must influence choice of sleeping groves by Amboseli baboons, for example, availability of nearby food resources or the presence of predators in the immediate area. However, many of the groves considered in this study

were located just a few hundred meters apart, such that were baboons to occupy two groves simultaneously, as happened periodically, all individuals would still be in visual and vocal contact with each other. Thus, a shift from one set of trees to another set located just a short distance away would not be expected to have a significant effect on either the distribution of foods accessible to baboons or the distribution of predators to which the baboons were themselves accessible. The parasite avoidance hypothesis provides one plausible alternative explanation for the observed pattern of frequent, typically short-distance, shifts in sleeping groves on a night-to-night basis.

On the other hand, contact with the infective stages of intestinal nematodes and other parasites can be avoided by means other than change of sleeping groves or modification of the temporal pattern of grove reuse. For example, sleeping groves might be approached by routes that circumvented zones of heavy fecal accumulation, or fallen tree limbs might be used as parasite-free access ramps to sleeping sites. Nevertheless, we propose as a working hypothesis that the temporal pattern of sleeping grove utilization by Amboseli baboons reflects a subtle behavioral strategy for parasite avoidance. Hopefully, the present analyses will stimulate further field and laboratory research both on basic mechanisms of parasite transmission in natural primate populations and on the parasite avoidance hypothesis in particular. More generally, the present report calls the attention of primate biologists to the fact that the distribution of microscopic creatures, such as nematode worms, bacteria, protozoa and fungi, may actually have exerted as strong a selective pressure on the evolution of primate behavior as has the distribution of food, water, or those frequently-invoked macroscopic creatures, the terrestrial carnivores.

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