A female baboon rakes intently through another female's fur, looking for ticks. The groomee characteristically looks away, wary of direct eye contact that might stop the groomer. Bouts last several minutes and both partners are groomed.

Carol D. Saunders

Little Things That Tick Off Baboons

Yellow baboons at Amboseli National Park can fool some of their parasites some of the time

by Glenn Hausfater and Reed Sutherland

On the plains north of Mount Kilimanjaro, old female Scar walked over and sat next to her daughter Cete in the shade of an acacia tree. After a few seconds, Scar turned her shoulder prominently toward Cete, who immediately responded by picking through her mother's fur. Cete shortly pulled from Scar's shoulder a large, black tick emblazoned with an *art nouveau* design. Both mother and daughter smacked their lips exaggeratedly at this sight. Cete placed the delicacy in her mouth and, while still chewing, resumed grooming her mother's coat.

Scar and Cete are two of the approximately 200 yellow baboons for which the Amboseli National Park of Kenya serves as home. Similarly, this particular tick species, *Rhipicephalus pulchellus*, is one of many different kinds of parasites for which Amboseli baboons themselves provide a home, although in the parlance of parasitology they are more properly called hosts.

Since 1971, Amboseli baboons have been the focus of ecological and behavioral studies by a team of scientists under the direction of Stuart and Jeanne Altmann of the University of Chicago and Glenn Hausfater of the University of Missouri (see *Natural History*, September 1982). The Amboseli studies, like many that have been done of primates in their natural environment, have had a strong emphasis on what baboons eat (foraging ecology) and conversely, on what eats baboons (predator–prey relations). Only recently have researchers begun to explore the complex host–parasite dynamics involving Amboseli baboons and to understand how parasites both affect and are affected by the behavior and ecology of baboons. We would hardly be so brash as to claim that a *Rhipicephalus* tick scrambling through the grass toward a resting baboon is as spectacular a sight as the bounding charge of a snarling leopard. But the Amboseli studies suggest that these almost imperceptible creatures may be just as important as the large cats in influencing the ranging, feeding, and social behavior of baboons and several other primate species.

A parasite is a plant or animal that lives in prolonged, intimate contact with another organism and can grow and reproduce only by feeding on that organism's tissues and resources. The parasites of wild mammals are generally divided into those that live inside the host's body (endoparasites) and those that live attached to the host's skin or fur (ectoparasites). In baboons and other nonhuman primates, common endoparasites include roundworms (or nematodes), tapeworms, and flukes, all three of which are referred to collectively as helminths. Various pathogenic species of protozoans and bacteria found in baboons are also generally considered intestinal parasites, even though other species of these same microorganisms in primate digestive systems are beneficial symbionts. Common ectoparasites of Amboseli baboons and other primates include fleas, ticks, lice, and mites, although a few of the latter (called lung mites) have actually managed to colonize the respiratory pathway and are thus technically endoparasites. Contrary to popular opinion, many endoparasites and ectoparasites cause little pain or damage to their host. This is particularly true of the more highly coevolved and evolutionarily older host–parasite relationships.

The Amboseli project has maintained a strict policy of noninterference with the subject animals, meaning that the baboons are not fed, trapped, or otherwise manipulated. Nevertheless, this did not prevent team members from collecting a small sample of feces from individual baboons shortly after they had defecated and gone on their way. Then, just as a veterinarian might look for parasites in a fecal smear from one's pet, B. Jean Meade and D. F. Watson of Virginia Polytechnic Institute similarly examined samples from each Amboseli study animal. Using other techniques, they were able to extract and identify intestinal parasite ova from small samples of preserved feces and thereby monitor changes over time in ova emissions by individual baboons. This information was then used to determine if the age, reproductive condition, or social status of a baboon influences the number and kinds of parasites that it harbors.

Since Amboseli baboons showed few

clinical signs of parasite infection, research team members were surprised to discover that nearly all individuals, including young infants, have a large complement of intestinal helminths. In fact, the average adult animal harbors four to five species of helminths, as well as several species of protozoan parasites; a single fecal sample might contain as many as 100 nematode ova per gram. Several previous laboratory and field studies have shown that a well-fed host can often support large numbers of parasites without showing any external signs of blood loss, tissue damage, or inflammation. However, if a drought reduces the availability of food or an injury prevents the host from feeding, clinical symptoms appear rapidly and may kill the animal. More frequently, the weakened and malnourished host falls victim to one of its predators or to disease.

Far and away the most common intestinal parasites recovered from Amboseli baboons are helminths of the genera *Trichuris, Trichostrongylus*, and *Abbreviata*. The first two have very similar life cycles. Baboons become infected with *Trichuris* and *Trichostrongylus* by swallowing their eggs or larvae, which are found as contaminants in the soil adhering to the baboons' food plants. The larvae mature in the gut of the host baboon, then mate and produce eggs, which are dispersed via the host's feces. The third common helminth, *Abbreviata*, undergoes the first part of its development in an insect such as a grasshopper or dung beetle. Baboons get infected with this parasite when they eat the insect intermediate host, and the worm then spends the rest of its life in the baboon's intestinal tract. Other helminths found in Amboseli baboons infect their host by penetrating the skin, the way hookworms do, rather then by an oral route.

Clearly, baboons get infected with all these intestinal nematodes by direct contact with larvae or ova. Thus, a major research effort has focused on trying to determine the most likely site of this contact. Since parasite ova and larvae are dispersed in the baboons' feces, members of the research team faced the very nasty job of finding out where and how frequently baboons defecate and if the choice of defecation site influenced parasite transmission. Sparing the reader details of methodology, we will say merely that fresh feces desiccate rapidly on the open savanna and that this is generally lethal to parasite ova and larvae. In contrast, both ova and larvae remain viable and infective for a substantially longer time directly beneath the trees where baboons sleep.

Although baboons spend most of their waking hours feeding on the open savanna, their day always begins and ends at one of several groves of acacia trees within their home range. Baboons sleep in the trees at night as a refuge from large cats, and in just a few nights they deposit a considerable amount of fecal matter on the ground below.

Early in the morning, baboons spend some time resting, feeding, grooming, and sunning themselves beneath their trees. During this period, which may last a few minutes or a few hours, they are exposed to infective ova and larvae in their own feces. Multiple soil samples obtained beneath baboon sleeping trees averaged more than 100 adult and larval nematodes per ounce. The yield from these samples was proportional to the soil's distance from the center of the grove. Samples obtained just outside the shadow of the grove or in the open savanna contained virtually no larvae at all. These data point to the obvious conclusion that the baboons' own sleeping sites were the primary source of contact with their intestinal parasites.

Even in the relatively moist soil beneath the baboons' sleeping trees, parasite ova and larvae cannot live forever. The eggs are rapidly attacked by soil fungi, and both eggs and larvae may be eaten by the myriad dung beetles active in Amboseli. Hausfater and Meade wondered if baboons might outsmart their parasites by avoiding a grove with a high density of infective parasites until the natural causes of egg and larval mortality had reduced parasite numbers to a minimum.

Through a series of controlled experiments, these researchers were able to determine that the ova and larvae in baboon feces have a fairly regular hatching and mortality schedule, based partly on environmental conditions and partly on their species-specific life cycles. Larval hatching hits a peak two to four days after fecal deposition, and the larvae become infective shortly thereafter. However, four to five days later, larvae will have died off to nearly the same level as when baboons first used the grove. Thus, approximately nine days from the first time baboons use a grove, it becomes "safe" for reuse.

Each of the two main study groups of Amboseli baboons—Alto's group and Hook's group—uses about fifteen to twenty different acacia groves for sleeping. Often these groves are just a few hundred yards apart, although both groups use sites widely scattered throughout the thirty-square-mile study area. Amboseli baboons are not territorial, but each group has almost exclusive access to a number of groves. Thus, if a group returns to an acacia grove after foraging and sleeping on the other side of its range, the baboons can safely assume that another group has not used the trees in their absence.

Hausfater and Meade analyzed grove use by Amboseli baboons and found that groups typically stayed at any given grove for only two nights and then moved on to another sleeping site. When they analyzed the patterns more closely, they found that the study animals not only avoided groves during times of peak larval hatching but also waited an average of nine days before using a grove again. In other words, grove-use patterns by the baboons seem to minimize the animals' exposure to infective ova and larvae.

The Amboseli team has uncovered no compelling evidence to suggest that baboons actually perceive microscopic ova and larvae in the soil beneath their groves. More likely, the odor from the feces accumulated beneath their sleeping sites is their cue to change groves again. Ernest Hemingway seems to have noted this same phenomenon in his novel *The Green Hills of Africa*:

> Instead of the cool early morning smell of the forest there was a nasty stink like the mess cats make.
>
> "What makes the stink?" I whispered to Pop.
>
> "Baboons," he said.

Ticks sometimes spend months atop grass stems waiting to hop aboard a baboon host. These Rhipicephalus *ticks go through three of their four life cycles on different hosts, dropping off between cycles to molt.*

Bob Campbell

A whole tribe of them had gone on just ahead of us and their droppings were everywhere.

Although Amboseli researchers hypothesize that baboons leave groves because of the buildup of feces and parasite larvae beneath their trees, there may be other reasons. For example, if the animals are attacked by a leopard or lions during the night, they may abandon their current grove immediately and stay away for a long time. Thus, one alternative hypothesis about sleeping site changes is that the moves help baboons and other primates avoid predators.

Another hypothesis about grove use evolves from the baboons' foraging behavior: when baboons wander on their home range during the day, they don't stray too far from their nightly rest sites. Some researchers think the baboons might switch groves as a way of getting at new feeding grounds.

Neither of these hypotheses seems very likely, however. When baboons move to a new sleeping grove, it is frequently only a few hundred yards away, hardly far enough to give them access to entirely different foraging areas or to fool a leopard.

Thus, the grove-change pattern by Amboseli baboons may well be the result of "fecal buildup" since that is the hypothesis that best accounts for the frequent, short-distance relocations of Amboseli baboons and of primates at other study sites.

In addition to their intestinal parasites, Amboseli baboons are also host to a wide range of arthropod ectoparasites. Ticks, fleas, and similar small creatures give irritating bites and are vectors for a variety of diseases transmissible to animals and humans. Ticks are known to carry several forms of typhus, including an attenuated variety, appropriately called tick fever, that has laid low more than a few Amboseli researchers. One indication of the seriousness of ectoparasite-borne diseases is that baboons and other primates have a ritualized behavior for removal of ectoparasites—grooming.

Scar, Cete, and other female baboons spend more time grooming each other than in any social activity except infant care. About 7 percent of their day is given over to grooming. Since baboon groups are basically made up of a series of matriarchies, females direct much of their grooming attention toward their offspring and siblings. This tendency is so strong that if an adult female and young female frequently groom each other, they are almost certainly a mother–daughter pair. Grooming is also one of the most important ways that baboons from different families build social bonds with each other, and the various matriarchs in a group often groom each other.

Adult males, by contrast, hardly spend any time at all grooming each other. Unlike females, males generally leave their parental group and thus have few relatives available as grooming partners. However, males do spend an extraordinary amount of time grooming the rump fur of estrous females.

A grooming sequence generally begins when one baboon approaches another and inclines its chest, neck, or cheek toward the prospective groomer. The "groomee" simultaneously assumes the characteristic stiff-legged solicitation posture, while cocking its head to the side and assiduously avoiding direct eye contact with the groomer. Avoiding eye contact is exceedingly important if the groomee ranks higher in dominance status than the groomer, for even a glance from the higher-ranking baboon may be perceived as a threat and the prospective groomer would then probably break off the interaction and move away.

According to the etiquette of grooming, the groomer and groomee must exchange roles every few minutes. Baboons that fail

Each morning baboons descend from trees to feed and sun. Baboons ingest most of their intestinal parasites at their sleeping groves. Parasite larvae and ova, dispersed through baboon feces on to the soil and grass beneath the trees, cling to plants the monkeys eat.

Glenn Hausfater

to reciprocate in this manner or that consistently do a lackluster job of grooming have great difficulty finding partners.

Once a grooming bout begins in earnest, the groomer combs through the groomee's fur with great concentration, using specific finger and hand movements to capture and remove ectoparasites. A groomer will often use his or her fingertips and nails to rake the groomee's skin in short strokes—movements called comb and scrape by Amboseli researchers—thereby loosening ectoparasites and other debris. Another pair of movements—termed lift and bite—are used to remove the loosened ectoparasite from the groomee's fur or skin and then transport it to the groomer's mouth, where it is eaten. Carol D. Saunders, who recently completed a study of the grooming behavior of Amboseli baboons and the ecology of their ectoparasites, has thus far identified more than a dozen such motor patterns.

The most common ectoparasites that Amboseli baboons remove from each other during grooming are hard ticks of the family *Ixodidae*. Hard ticks generally have four life stages, of which three are spent on a succession of vertebrate hosts. Mating takes place while the adult ticks are riding about on a baboon or some other mammal. About a week later the gravid female drops to the ground and deposits thousands of eggs on the soil. The eggs hatch into tiny six-legged larvae, called pepper ticks in East Africa, and the larvae in turn climb to the top of grass plants and wait for any appropriate vertebrate host to walk by. The larvae feed on their hosts for about a week and then drop off prior to molting into larger eight-legged nymphs. The nymphs feed for about a week on yet another vertebrate host before they drop off one last time and undergo their final molt to adulthood.

As adults, these ticks are quite mobile. They are attracted to carbon dioxide because it may be a cue to the presence of a living, breathing mammal in their vicinity. Saunders was able to capitalize on this attraction by slowly releasing CO_2 from metal cylinders and luring ticks from vegetation. Similarly she found that "questing" ticks, those perched high atop grass stems, would readily jump onto a sheet of wool flannel dragged through the grass. Both of these methods of collecting ticks were used to estimate seasonal changes in tick density in Amboseli and to determine where the greatest number of ticks lived.

Saunders found that tick densities in Amboseli have two major peaks. The first is in January-February, following a rainy period late in the preceding year, and the second occurs between April and June, following a second rainy period that begins between March and May. As with helminth larvae, the baboons' own sleeping groves proved to be the major reservoir of ixodid ticks. Another important concentration of ticks was found directly beneath "umbrella" trees, the squat, flat-topped acacias scattered about the African savanna and under which baboons take their midday siestas.

The aim of obtaining such detailed information on the distribution of ticks in the study area is to determine how tick densities in the baboons' home range influence their movements and grooming patterns. Although formal analyses are still in progress, casual examination of the data suggests that baboons often go into a "burst" of grooming after moving through

A group of baboons lounge under an acacia tree on the savanna at Amboseli National Park in Kenya. These shady areas are infested with parasites, mainly hard ticks.

Glenn Hausfater

a habitat infested with ticks. But at this point we cannot draw any conclusions beyond the obvious one: ticks seem to play an extremely important role in the social life and ecology of Amboseli baboons.

Analyses like the ones described so far only tell one side of the host–parasite coevolution story. Although none of the Amboseli researchers likes parasites very much, a spirit of fairness requires us to admit that parasites are entitled to make a living as much as baboons. From the parasites' point of view, the evolution by baboons of behavior to avoid them is unfortunate. On the other hand, parasites might have evolved a few tricks of their own. For example, parasites might time their reproduction and dispersion to maximize their chances of landing a baboon host, especially a relatively parasite-free infant.

One of the features of baboons that makes them convenient to study is a flashy, hot-pink swelling, called the sexual skin, on the backsides of females. This peculiar anatomical structure (restricted to baboons and certain other Old World monkeys and apes) is an area of perineal skin that cyclically swells, deflates, and changes color in relation to female hormonal changes. By keeping daily records of the size, shape, and color of each female's sexual skin, one can obtain a fairly good idea of her hormonal and reproductive conditions on any given day.

When data on parasite ova emissions were compared with records on sexual skin swelling, Amboseli researchers discovered that reproduction by the intestinal helminths of the study females was strongly influenced by the females' reproductive cycles. In particular, just after female baboons gave birth there was a very sharp rise in egg production by their intestinal helminths, apparently tied to a series of rapid changes in the female's progesterone level.

Such reproduction clearly facilitates an early assault on newborn infants, but some baboons may develop parasites before they are even born. Amboseli researchers believe that one endoparasite species, *Strongyloides fulleborni*, is acquired by infants while still in the womb or possibly very shortly after birth, through the colostrum. This form of mother–infant parasite transmission has previously been recorded in domestic animals, but never in a wild primate.

One other aspect of our work at Amboseli has been to examine whether baboons might be infecting other primate species with their parasites. Although most of the intestinal parasites of Amboseli baboons can infect many other host species, only half of the helminths found in the baboons are also found in the two other primates with which they share their home range—vervet monkeys (*Cercopithecus aethiops*) and the indigenous Masai pastoral people. The similarities and differences in the parasites of these three sympatric hosts can probably be accounted for by similarities and differences in diet.

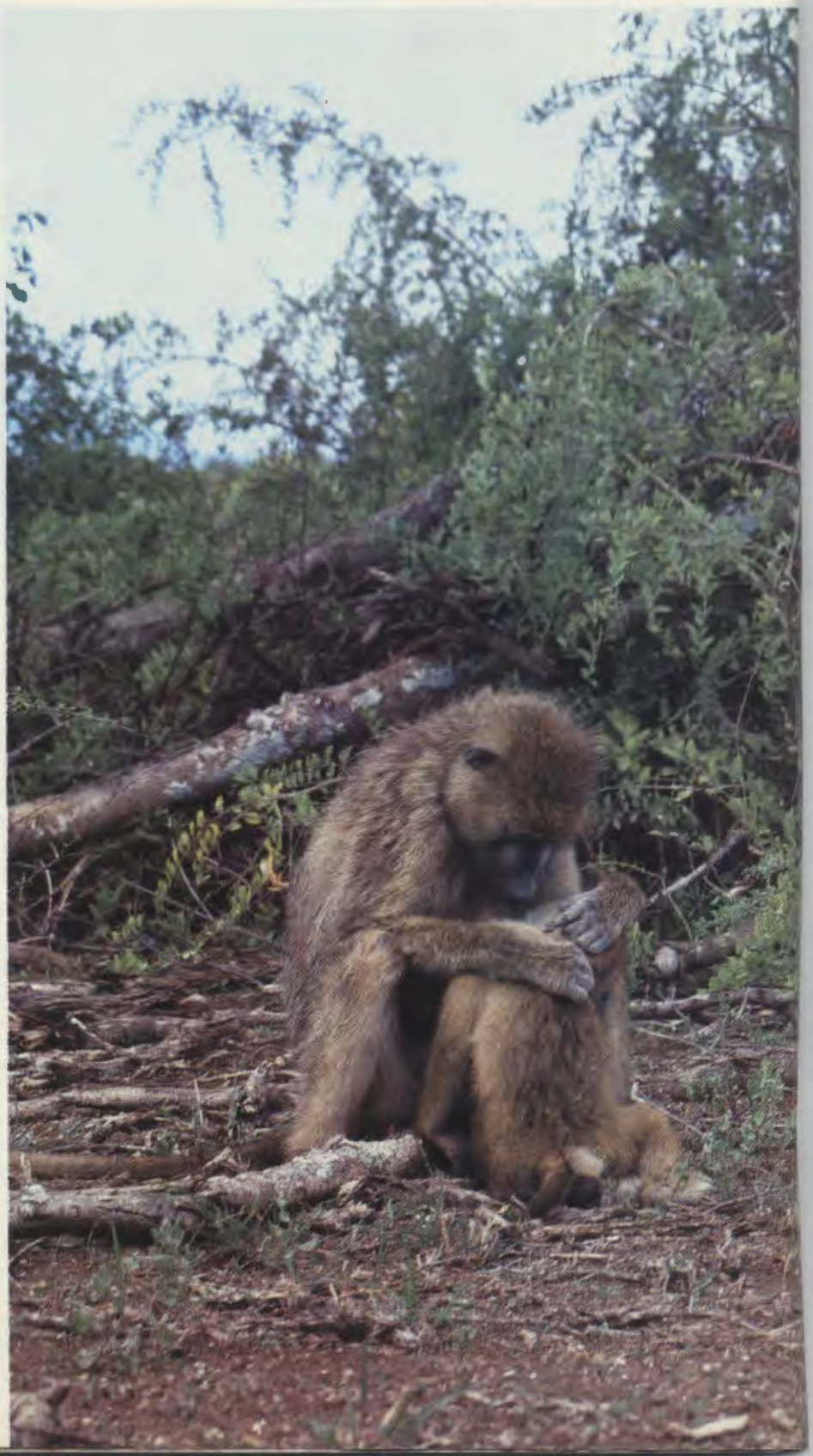
For example, the Masai harbor tapeworms that they probably pick up from eating meat. Baboons and vervet monkeys eat very little meat and thus rarely have tapeworms. On the other hand, baboons and vervets eat grasshoppers, an item not usually found on the Masai menu.

Such cross-species comparisons of parasites is a controversial subject, for medical researchers in some tropical countries argue that wild nonhuman primates pose a serious health risk to humans who have traditional life styles. Some experts even go so far as to say that nonhuman primates such as baboons or vervets should be controlled, that is, trapped or shot, to reduce the frequency of parasite transmission to humans.

However, nearly the only finding of human health concern from Amboseli was that a few baboons carry the protozoan

Baboons get infected with parasites very early in life, in some cases while they are still in the womb. Intestinal parasites often step up reproduction just after female baboons give birth. This baboon at Mikumi National Park in Tanzania will have a full complement of parasites by age three.

Duncan Anderson and Rachel Wilder; Animals Animals



parasites *Balantidum coli* and *Entamoeba histolytica*, species that can cause dysentery in humans but that have little effect on baboons. Humans and baboons could potentially pass these dangerous protozoans to each other through their communal use of certain water holes. However, since Amboseli baboons fastidiously avoid defecating around their water holes, these protozoan parasites are probably transmitted only in one direction—from humans to monkeys. In sum, there seems to be little evidence that controlling wild primates in Amboseli would improve the health of the Masai people or other local inhabitants.

Much to their chagrin, several Amboseli researchers have begun to find the parasites of baboons nearly as interesting as the baboons themselves. Although they cannot be sure where this strange fascination will lead, the goal of their ongoing work is to learn more about the behavioral and ecological factors responsible for the transmission of parasites and disease to primates in their natural environment. Of course, for Scar, Cete, and the other Amboseli baboons, the goal of their efforts is much more basic: to avoid both predators and parasites and thereby live a long and healthy life. □

When baboons pass through a woody habitat, they often go into an intense burst of grooming, below, when several groom simultaneously. A burst may enable baboons to purge the ticks before they can embed themselves.

Carol D. Saunders