WARRIORS

of the Kalahari

BY MILES ROBERTS

"We could be in for an interesting morning," Rob said over the radio. "The Balrog group is starting to forage and they're headed straight toward you."

"We're on the move but our guys haven't seen your guys yet," I replied. "Will keep you posted."

I was with the Gattaca group, composed of more than 30 meerkats. Gattaca wasn't the largest in the area but certainly larger than the Balrog gang of about 20 animals that Rob was monitoring. The previous night the two groups retired only about a couple of hundred yards apart, apparently without noticing each other. Rank sourgrass may have obscured them as they settled down in the fading light. Usually, groups don't tolerate being so close, and when they are a showdown erupts, ending with one group giving way, sometimes after losing a member or two—even pups—in battle.

So far, Gattaca showed no evidence of having seen Balrog. Pups were playing around the den and the dominant male and female were slowly mobilizing after warming up. No one was foraging yet, and no sentinels had taken position on a shrub or snag to scan for predators, as they would shortly. After spending two and a half weeks with eight meerkat groups, I was beginning to get a sense of their daily routine. Today seemed pretty typical, but Balrog's proximity promised to change the schedule.

I was working as a volunteer on Tim Clutton-Brock's meerkat project in the southern Kalahari; Rob is a student on Clutton-Brock's team. A professor of ecology at the University of Cambridge in England, Clutton-Brock and his team, along with collaborators that include Steven Monfort, associate director for conservation and science at the Smithsonian's National Zoo, have been studying meerkats since 1993, trying to sort out their complex social lives.

Social Desert Dwellers

Meerkats (*Suricata suricatta*) are small, social mongooses that breed cooperatively and live in groups of six to 40 or more individuals. They spend the night huddled together underground in sleeping burrows dug by springhares, aardvarks, and other burrowing denizens of this harsh desert environment.

In the Kalahari, where summer daytime temperatures can reach 115°F, burrows offer meerkats security as well as respite from the searing dry heat. But when I was there, it was almost winter, when nighttime temperatures routinely dip to near freezing. Huddling in a mass belowground is the best way for meerkats to stay warm. Still, despite the thermal benefit of huddling, meerkats lose heat and emerge after a night's sleep up to ten percent lighter than they were the night before, because it takes a considerable amount of energy for these small mammals to keep warm.

In early winter, meerkats go underground at sunset, about 5:30 p.m., and stay there until sunrise, about 7:15 a.m. In the morning, meerkats slowly emerge one by one and it may take 20 minutes or more for everyone to surface. Then, the long process of completely waking up begins. The animals, some alone and some in small groups, stand on their hind legs and face the sun to soak up solar energy until their droopy heads finally snap to attention. (Like some other small, insectivorous mammals I have studied, such as big hairy armadillos (*Chaetophractus villosus*), southern tamanduas (*Tamandua tetradactyla*), and dwarf mongooses (*Helogale parvula*), meerkats may reduce their core body temperatures and metabolic rates at night to save as much energy as possible. If so, this would explain their drowsy emergence and prolonged wake-up time.) After a 30-or-so minute warm-up, the meerkats start to interact, groom, and engage in burrow maintenance. Gradually, the orbit of activities shifts from the area immediately outside burrow entrances to the surrounding vegetation. Soon a few individuals start to forage nearby, but it isn't until the dominant male and female head out, often signaling the rest with a "follow-me" call, that the group begins its daily foraging sojourn in earnest. It may travel as far as a couple of miles away to a new sleeping den by day's end.

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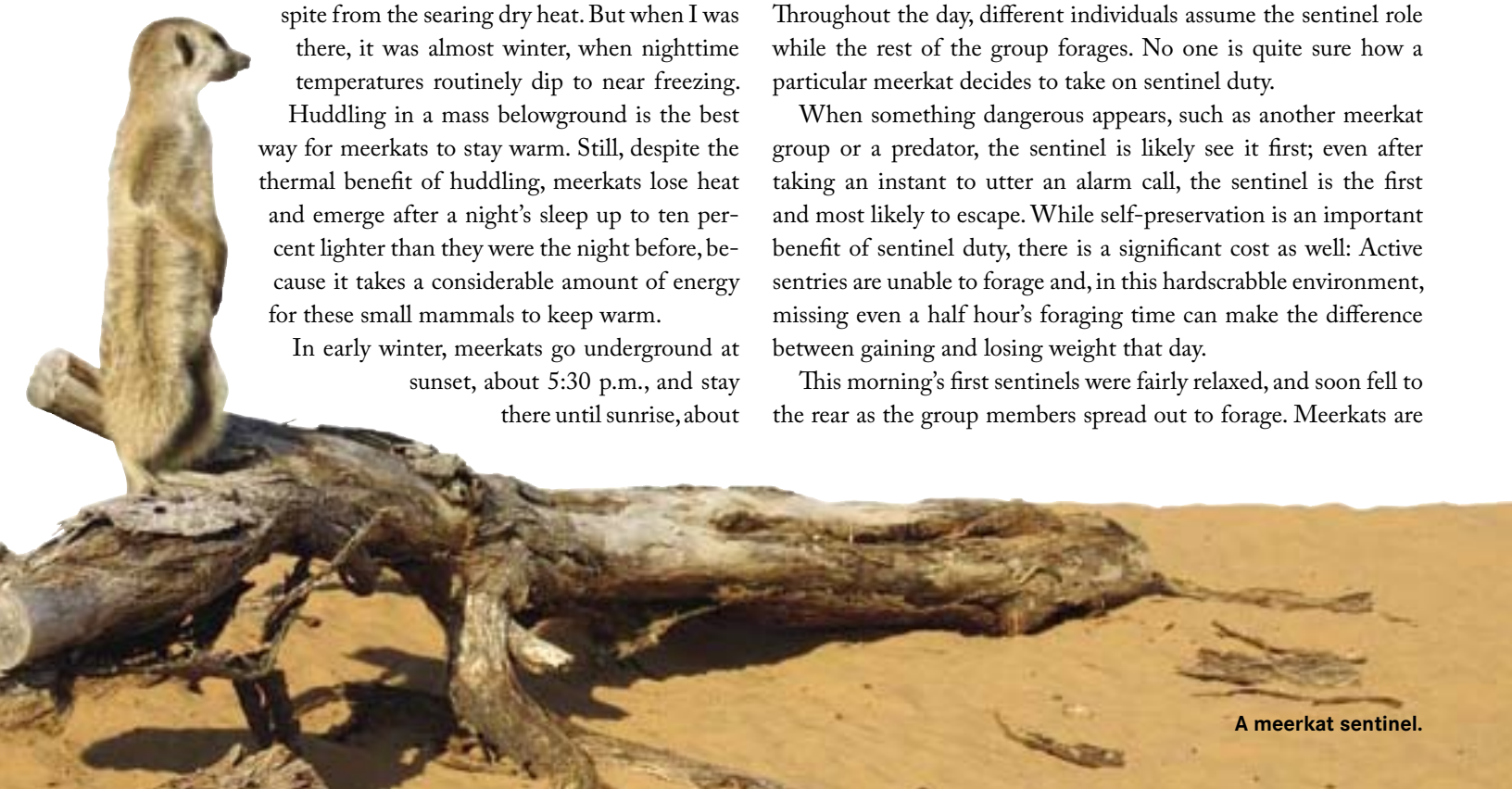
This morning, after a clear, freezing-cold night, Gattaca is particularly slow getting up, and if these meerkats were aware Balrog was nearby they weren't letting on. As the group moved out, a few meerkats climbed up on fallen logs and shrubs to scan the environment to act as sentinels. This behavior is characteristic of meerkats. Throughout the day, different individuals assume the sentinel role while the rest of the group forages. No one is quite sure how a particular meerkat decides to take on sentinel duty.

When something dangerous appears, such as another meerkat group or a predator, the sentinel is likely see it first; even after taking an instant to utter an alarm call, the sentinel is the first and most likely to escape. While self-preservation is an important benefit of sentinel duty, there is a significant cost as well: Active sentries are unable to forage and, in this hardscrabble environment, missing even a half hour's foraging time can make the difference between gaining and losing weight that day.

This morning's first sentinels were fairly relaxed, and soon fell to the rear as the group members spread out to forage. Meerkats are



A meerkat sentinel.

All photos by Miles Roberts

After the day's foraging is done, meerkats gather near their burrows to capture the last rays of the sun and reestablish social ties.

primarily insectivorous and scratch incessantly at the ground to search for subterranean insects, spiders, scorpions, millipedes, larvae, pupae, and even the occasional lizard. Foraging is hard work and the meerkats frantically excavate the crusty soil surface where they are likely to find prey, usually near the base of a grass tussock or shrub. Every third or fourth scrabble becomes a major excavation—a meerkat can dig out a quantity of red Kalahari sand equivalent to its own body weight in 30 seconds or less. These scrabbles appear random and speculative, but are successful surprisingly often. Meerkats have excellent senses of hearing and smell, so excavations may be prompted by the sound or scent of a prospective meal.

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I often spent entire mornings following individual meerkats to see what they caught. But most of the prey the meerkats consumed with an audible crunching chew (usually the only way to tell that something had been caught) was too small for us to see, let alone identify. "Small something" was the most frequently recorded item in our notes. A meerkat's day's work consists mostly of foraging for dozens and dozens of these small somethings with, if it's lucky, an occasional medium or large something.

Centipede prey.

Although it is important for meerkats to find enough food for themselves, they sometimes donate food to others, almost always to young pups that are just learning to forage. Litters, which on average contain three to five pups, typically emerge from their burrows for the first time when they are about three weeks old, and accompany the foraging group for the first time when they are about five weeks old. While they can keep up with the group, pups are still developing their digging and foraging motor skills and are unable to feed themselves effectively. To get something to eat, they stand near an adult and constantly emit a begging call that seems to become harsher and more annoying as the day wears on. Occasionally, an adult captures a prey item, usually a relatively large one such as a beetle larva or scorpion, then drops it in front of a begging pup that greedily and noisily accepts it. Why an adult donates a particular food item at a particular time is unclear, but all of us working on the project agreed that if we were meerkats we would donate whatever food it took to make the horrible begging sound stop!

Some pups are more successful at garnering feedings than others, and we noted that adult "helpers" in some groups are more generous pup feeders than in others. Over the course of the study, Clutton-Brock and his collaborators have learned that female helpers tend to feed pups more than males do, and they preferentially feed female pups. Regardless of sex, adults are more likely to feed pups larger items than smaller ones, and to feed the nearest pup even if it means running ten yards or more to find one. This helping behavior affects the pup directly but also benefits the group as a whole. Clutton-Brock has found that groups with higher ratios of helpers to pups have faster-growing pups that are more likely to survive and become future helpers themselves.

Pups are highly vulnerable to predators, and when they first embark on foraging forays, there is palpable tension in the group. Frequent stops are made at bolt-holes—entrances to burrows the animals can dive into for safety—where the pups play while edgy adults stand at high alert looking nervously all around. While they are traveling between bolt-holes, the least suspicion results in an alarm call and a mass scurrying for the nearest bolt-hole, with most of the meerkats heading for the same one or two holes even when the group is spread out. In experimental field studies, Marta Manser, a collaborator of Clutton-Brock's, found that even though a meerkat group may have more than 1,000 bolt-holes in its territory, individuals seem to have very detailed knowledge of the location of and distance between bolt-holes, even if they haven't recently visited them. It is likely that pups learn the locations of the bolt-holes on their early foraging expeditions.

Meerkats have many predators, both aerial and terrestrial. Among the terrestrial are jackals (*Canis mesomelas*), bat-eared foxes (*Otocyon megalotis*), wildcats (*Felis silvestris*), and caracals (*Caracal caracal*); all but the jackals are nocturnal, so they are not serious threats when meerkats are huddled in their burrows at night. Among the aerial predators, a variety of raptors are a threat, especially the massive martial eagle (*Polemaetus bellicosus*)—the meerkats' worst nightmare.

All predators elicit alarm calls from sentinels, but the alarm call alerting the group to a terrestrial predator is different from the one for an aerial predator. The magnitude of the predator threat is also encoded in the intensity and structure of the alarm call. Thus, the alarm-call system appears to convey the type and urgency of a threat, so as soon as the alarm is heard, the listeners know its immediacy and whether the threat is by ground or by air. A glance at the caller reveals the direction from which the threat is coming because it has its eyes glued to the source of its concern.

A potentially dangerous but not immediately threatening animal, such as a sluggish puff adder (*Bitis arietans*), elicits another response called "mobbing." In mobbing, most or all group members cluster around the threat with tails held high and heads bobbing to harass it into retreating. I can testify to its effectiveness. One evening, I was lying next to the burrow of a group called Moomins, eyeball to eyeball with the animals, when my broad-brimmed straw hat fell from my head to the ground. Apparently, as long as the hat was on my head it was acceptable to the meerkats. But as soon as it became a separate entity, it was like a puff adder. Within seconds, all 30 Moomins were mobbing my hat and my face next to it. From my ground-level perspective, I was suddenly among what seemed like a huge, multitailed, pulsating, feinting, swerving, threatening alien organism. Unnerved, I retreated like any puff adder would.

Leaders of the Pack

Back with Gattaca, I saw the sentinels stiffen at their posts and it was clear they had seen something in Balrog's direction. "Looks like you've been spotted, Rob," I said into the radio. "Get ready!"

Meerkats in Exile


Miles Roberts

Dominant female meerkats may kill any young her subordinates dare to produce, but subordinate females are no less ruthless. They too may kill the dominant female's pups–but they aren't often given the chance. Instead, the usually friendly relationships between a dominant female and some subordinates begin to sour as a dominant enters the last weeks of her 70-day pregnancy. The dominant, which is usually the heaviest female in the group, becomes a virago. She hits, bites, charges, and chases some subordinate females until they leave the group to escape the constant harassment.

The exiles stay in the group's territory but forage and sleep alone or with other exiles. Whenever the dominant female runs into an exile, she chases and attacks her some more. Then, about three days after the dominant gives birth, many of the exiled females return to their group; once her young are a few days old, the subordinates will not kill them. Peace reigns again among the females, until the dominant is well into her next pregnancy.

The dominant is selective about which subordinates she forces into exile. Females younger than about nine months, which rarely conceive, are left alone. In contrast, older females, especially those that are pregnant, as well as females more distantly related to the dominant, are exiled on more than 40 percent of the possible occasions, according to a recent study published in the ***Proceedings of the National Academy of Sciences***. The findings are the result of a long-term collaboration between the Smithsonian National Zoo's Steven Monfort,

But nothing was likely to happen until the still-oblivious dominant male and female led the way.

The dominant couple controls much that happens in meerkat society; the dominant female, in particular, wields great power. Dominant females produce more than 80 percent of the pups that survive their first month. Subordinate females may breed from time to time, but the dominant female usually kills their pups to maintain reproductive supremacy. Older subordinate females may also be temporarily exiled from the group during the latter part of the dominant female's pregnancy (see sidebar). It is during these exiles that subordinate females are most likely to mate with males from other groups that are prospecting for breeding opportunities (although conception rates are low), because they, too, are reproductively suppressed by the dominant male in their own groups. Sometimes alone and sometimes in small coalitions, males search for females to mate, insinuate themselves into another group (where, unlike females, they may be accepted), or even form a group of their own with footloose females in exile.

Females rarely disperse from their natal groups; instead they stay and wait for the chance to become dominant if and when something happens to the reigning matriarch. An older subordinate female in exile sometimes forms a new group with a prospecting male, but a female is never accepted into an established group. New group formation is hazardous because small groups are much less likely to survive than large ones during a prolonged drought or other difficult conditions.

Thus, individual meerkats are confronted with a rather harsh life decision: stay with the group as a nonreproductive helper and accept the low probability of becoming a reproductive dominant, or leave the group, breed almost immediately, and try to form a new group, but with much lower odds for success. Before taking one or the other of these courses, subordinate meerkats undergo

Miles Roberts

Like most pups, this youngster is probably the offspring of the dominant female.

a kind of apprenticeship during which they learn how to forage, locate bolt-holes, take turns being sentinel, provision pups, and babysit at the den. Of all these assignments, babysitting seems to be the most demanding.

When her pups are born, the dominant female almost immediately leaves them in the care of babysitters that spend the entire day at the burrow keeping guard and nursing them. Some of the wet-nurses are females whose own pups have been killed by the matriach, but there are also cases of spontaneous lactation in nonreproductive subordinates. Other than nursing, the dominant female gives little care to her pups, and spends most of her time foraging. This gives the dominant female the energy to breed more frequently and produce larger litters. For their work, the babysitters

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the University of Cambridge's Tim Clutton-Brock, and their colleagues.

It is clearly advantageous for a dominant female to exile infanticidal subordinates. But this study revealed an additional twist. The stress of being exiled wreaks havoc with the subordinates' own chances of reproducing, explaining, at least in part, how the dominant maintains her breeding monopoly.

The chronic stress of an exile, measured by elevated levels of stress hormones produced by her adrenal glands, makes an exiled female more likely to abort if she is already pregnant, and much less likely to conceive if she mates during exile. In fact, only one female in the study conceived during her exile.

A dominant female benefits from suppressing reproduction in subordinates by reducing or eliminating competition for the child care provided by subordinate helpers. The more helpers per pup, the faster the pup grows and the greater its odds of surviving. Up to a point, dominants are more likely to exile subordinates as group size increases and competition intensifies. In very large groups, however, the chances of a subordinate being exiled decreases, suggesting that it's just too expensive energetically for the pregnant dominant to force out many subordinates at the same time. Similarly, dominant females with low body weights are less likely to use energy to exile subordinates than heavier females are.

Dominant individuals that suppress the reproduction of subordinates and use them as helpers exist in a variety of vertebrates that breed cooperatively, including African wild dogs (***Lycaon pictus***), Florida scrub jays (***Aphelocoma coerulescens***), and ring-tailed lemurs (***Lemur catta***). But in these and several other cooperatively breeding species, scientists have ruled out chronic stress as the cause of suppression. The results of this study show, however, that stress may play a role in other species not yet tested—or that meerkats are unique.

—Susan Lumpkin

Miles Roberts

Resting at the end of the day.

get little directly in return. A day of babysitting is a day without foraging, and babysitters may lose substantial amounts of weight. As is the case for sentinels, we don't know how a meerkat decides to babysit or not: There is no obvious rotation or schedule. All subordinate adults and yearlings guard the den and take turns babysitting, but older males spend less time doing so, in part because they go off prospecting and aren't around. There also appear to be "generous" and "lazy" helpers in meerkat groups, but lazy helpers don't seem to suffer any negative consequences and generous ones don't seem to be rewarded.

Gattaca Versus Balrog

Helpers also contribute in times of crisis, like the one I saw brewing in the Gattaca group. Some of Gattaca's frontline foragers were on high alert, clearly having detected the Balrogs nearby. Gattaca had been relatively spread out, but now all of its members were headed toward Balrog. The front line was in full pursuit while the rest, including the pups, ran to catch up, heads bobbing up and down as first one, and then another meerkat stopped for a second, assumed an elevated vigilant position to get a better view of the prospective field of battle, and scurried back to the group. I had been warned that these intergroup interactions, or "iggies" in the vernacular of the seasoned meerkat watcher, could erupt suddenly and be very chaotic. Iggies are all about territory, and they usually result in the establishment of new territorial boundaries, with the smaller group typically losing ground to the larger one.

Meerkats vigorously defend their territories because they contain the precious resources needed for survival; food and shelter are of utmost importance. In the Kalahari's very harsh, semi-arid climate, food resources fluctuate considerably between wet and dry seasons and between years. At the study site, mortality due to food competition within the large groups may be higher than mortality due to predation. Clutton-Brock's studies have also shown that during one year of extremely low rainfall, all meerkat groups consisting of nine or fewer individuals went extinct, probably due to lack of food. So acquiring and maintaining a quality territory, through iggies if necessary, is an important part of meerkats' survival strategy.

For the most part, iggies are bloodless power plays, but occasionally groups engage fiercely and meerkats are injured or killed. If one group invades another's burrow when only pups and babysitters are at home, the gruesome fact of meerkat life is that the pups are almost always killed.

Gattaca was united and moving purposefully toward the smaller Balrog group. It was my last day in the Kalahari and, while iggies are exciting departures from the norm, I had gotten to know some of the animals well enough to not want to see any of them get hurt. This is unscientific, but anyone who has spent time with meerkats knows what I'm talking about: Their individual personalities had emerged. Meerkat sentinels had climbed on me to find the highest available perch. Tiny pups had leaned against my leg while warming up in the morning sun. I had spent part of an afternoon foraging like a meerkat, searching for insects, grubs, pupae—anything—and failed so miserably that I was humbled by the meerkats' abilities and work ethic. I had witnessed their clan skirmishes and family squabbles; been scent marked and mobbed; and had chilled out with my groups at the end of long workdays, watching the sun go down. The prospect of spending my last day discovering the meerkats' dark side did not appeal to me.

Fearing the worst, I followed the group with trepidation. Then Rob called by radio. "Looks like Balrog is opting out, heading off away from Gattaca," he reported. Fortunately for me, discretion was the better part of valor for Balrog as, outnumbered, the group scooted away. Gattaca assembled around a large pile of brush that served as an excellent vantage point for several sentinels, a safe haven for the rest, and a playground for the pups. The group seemed content to declare victory and take a midday break a few hours early.

I returned to camp and hadn't planned to go out again. But meerkats can cast a spell on you. A few hours later, I heard their siren call and decided to try to find Gattaca one last time. I started my search where I left the group in the morning but the meerkats were nowhere to be found. A little disappointed, I headed toward camp along a game trail. About halfway back, I heard a rustle and looked up to see three Gattaca pups running through the grass and down the trail toward me, an adult following close behind. I felt elated—as if my family were greeting me as I returned home at the end of the day. Of course they weren't, and the meerkats ran past me, giving me one of those "oh, you with the hat again" looks. Everything was back to normal. It was a good time to leave. Z

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