FEATURES

By Elizabeth Pennisi, in Amboseli National Park, Kenya

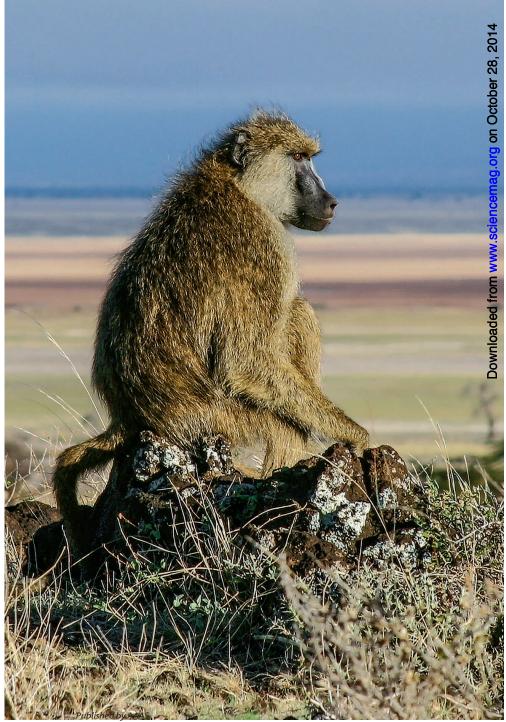
everal yellow baboons are sitting on their haunches pulling up grass, tearing off the stems, and shoving the corms into their mouths. The scene looks sleepy but a frisson of sexual tension is in the air. Glenn, the troop's dominant male, clearly has eyes for Hokey, whose swollen rear end means she's ready to mate. He's hanging out nearby, hoping to get lucky.

Suddenly a commotion erupts; squealing baboons are mixing it up in a cloud of dust. Within a few heartbeats it's over. Hokey ambles away, grunting. Was she hurt? I ask. No, says Kinyua Warutere, a tall, unassuming Kenyan who has spent much of the past 20 years observing baboons here on the savanna northwest of Mount Kilimanjaro. He recounts in detail what to me had been a blur. Wily old Lobo had coaxed three other males to charge Glenn, then grabbed Hokey and mated with her. Hokey's grunt was her copulation call. To my astonishment, Glenn had lost his fertile female to a middle-aged has-been.

Similar play-by-play details, captured painstakingly over 43 years and combined with a wealth of genetic and physiological data, have brought renown to the Amboseli Baboon Research Project. Begun by Stuart and Jeanne Altmann, a husband-and-wife team, the project is the world's longest running baboon study, and it set a standard for behavioral fieldwork 40 years ago when Jeanne devised a method of making systematic observations now implemented worldwide. "They have transformed the field," says Larissa Swedell, a primatologist at Queens College of the City University of New York who has studied baboons elsewhere in Africa.

Many other primate researchers have gravitated to baboons, which spend most of their time on the ground and thus are easy to observe. Robert Sapolsky, a neuroscientist at Stanford University in Palo Alto, California, for example, has explored social interactions and stress in the animals, a theme of his captivating 2002 book, *A Primate's Memoir: A Neuroscientist's Unconventional Life Among the Baboons.* Other teams have also studied baboons over the years. But none can match the decades of cradle-tograve observations at Amboseli, which have yielded what Sapolsky calls "stunningly

Babaga



An epic baboon study shows how social interactions shape health and reproduction in all primates—including humans



large and detailed data sets stretching over decades," from which a varying cast of researchers "mine incredibly subtle, interesting behavioral findings."

Some of those findings lay bare the workings of baboon troops, showing how conflict, habitat loss, predation, and drought shape the lives of these Old World primates. The work is also ever more relevant to our own species. Amboseli researchers are probing how baboons age to understand why women outlive men but are apparently sicker over the course of their lives. They're dissecting how social relationships among baboons influence longevity, and they are using new molecular tools to document the interplay between behavior and two hot research areas: epigenetics and the microbiome. And in an extraordinary new twist, Amboseli is helping peel away the mystery of a decadesold human catastrophe.

IN THE FINAL MONTHS of World War II, the German-occupied Netherlands cut food rations to less than one-quarter of normal caloric levels. Some 4.5 million people starved, and 18,000 died. To assess the famine's long-term toll, researchers in 2001 tracked down 2400 babies born in an Amsterdam hospital between 1943 and 1947. They discovered that the famine babies—those born in the winter of 1944 to 1945—suffered higher rates of diabetes, heart disease, obesity, and other ills in later life than babies born earlier or later.

Scientists have floated two possible explanations. One holds that the harsh conditions crippled embryonic development, cheating children out of a healthy life. The other idea holds that malnutrition during development tweaked the metabolism, brain function, and circulatory system of famine babies as a coping mechanism for starvation. Later, when food was abundant, those adaptations went awry and led to illnesses. That idea, says Laura Clamon Schulz, a reproductive physiologist at the University of Missouri, Columbia, "is one of the most provocative and difficult to test in the field."

A catastrophe offered the Amboseli team a chance to evaluate what happens when food runs short for pregnant baboons and their infants. After a dry year in 2008, severe drought hammered East Africa in 2009, taking a heavy toll on wildlife. Most baboons survived, but females stopped ovulating and some infants starved to death. The next year brought record rains.

Now, those infants are fully grown. If starvation prepared them for lean times in adulthood, then those born in 2009 should do better in later drought years than those born in 2010. But if conditions when they were in the womb left them physiologically damaged, they would do worse in later hard times—and that's what was observed. Susan Alberts, Jenny Tung, and graduate student Amanda Lea, of Duke University in Durham, North Carolina, first compared the reproductive success of female baboons born during the 2009 drought with those born in years in which food and water were not scarce. During later dry years, they found, baboons born in 2009 were less likely to conceive and much slower to resume menstruation. (Female baboons become sexually mature at age 4.5.)

Now, the Amboseli team is factoring in other stresses, such as social status or loss of a parent. Infants experiencing three or more stressors in their first year of life tend to die a year or two earlier than those who led a charmed infancy, Tung says. Alberts, Tung, and Lea also found that drought-year infants born to high-ranking mothers do better during subsequent droughts than those born to low-ranking females, perhaps because they get more food and are less harassed.

The findings suggest that infants who were malnourished in the 2009 drought suffered



Babies born during the Dutch "Hunger Winter" of 1944 to 1945 had health problems as adults. Findings from Amboseli may help explain why.

irreversible physiological changes. They also support a converse idea, the silver spoon hypothesis, which holds that "kids born in really good years to high-ranking moms do much better," Tung says. The same effects could explain the patterns seen after the Dutch famine. "I can certainly see the parallel between the baboon study and ours," says Tessa Roseboom, an epidemiologist at the Academic Medical Center in Amsterdam who studied the fate of the famine babies. "This is a fascinating story."

Like Roseboom's group, the Amboseli researchers are now trying to unravel the molecular causes of these long-lasting effects. Suspecting the subtle hand of epigenetics which modifies gene activity without altering a DNA sequence—they are sizing up differences in patterns of methylation, in which the attachment of methyl groups to DNA can silence nearby genes. They compared baboons subsisting on wild foods with those that live near a tourist lodge and feast on calorie-rich garbage. Lodge baboons are known to forage less and have 20% body fat compared with the usual 2%, high cholesterol, and bad teeth.

The pilot study of 66 males in the two troops revealed significant differences in methylation, Lea reported in May at the Biology of Genomes meeting in Cold Spring Harbor, New York. Most intriguing are differences affecting a gene called *PFKP* that responds to insulin and is involved in breaking down sugar, and a gene called *KCNIP4* that seems to play a role in human obesity. The researchers suspect that dietary shifts trigger epigenetic changes that affect the activity of these genes, although they don't know how these changes play out in baboon health.

SUCH CUTTING-EDGE STUDIES wouldn't be possible without detailed data on the life histories and behavior of the more than 1500 baboons monitored over the decades at Amboseli. And those data are the fruits of a methodology pioneered by Jeanne Altmann. When she arrived with Stuart in Kenya in 1963, she could not have imagined immersing herself in the world of baboons. The behavior she planned to watch was that of her toddler, Michael. Stuart, however, had planned to spend a year studying baboon communication, so the Altmanns struck out in search of a field site. Baboons at Nairobi



Jenny Tung, part of the third generation of women running the Amboseli project, collects a fecal sample.

National Park had adapted to tourists, so the couple settled on Amboseli, where open savanna and passable terrain allow for easier fieldwork, and the baboons were not perturbed by their presence.

After the Altmanns returned to the United States in 1964, Jeanne resumed her undergraduate studies (in math) and worked part time as a computer programmer. But her Kenya experience had kindled an interest in baboons, and eventually, egged on by Stuart, she began pondering how to reduce biases in observational studies.

Researchers of the time tended to jot down whatever caught their eye. With that approach, "the biggest, flashiest individuals doing the most dramatic things are going to be disproportionately recorded," says Jeanne, now a professor emeritus of behavioral ecology at Princeton University. In 1974, she published a method of observing individuals in a predetermined random order for preset lengths of time, greatly reducing bias.

The paper may be the most cited in animal behavior, says Karen Strier, a behavioral ecologist at the University of Wisconsin, Madison, who has studied New World monkeys for decades. "It was a bible for me."

Jeanne Altmann also drove a shift of focus away from male baboons. In 1975, she began observing females and discovered the intricate links between social relationships and raising offspring. That work earned her a Ph.D. in behavioral sciences just in time for her son Michael's high school graduation. More recently, Amboseli researchers have found that higher ranked females have more offspring, on average, than lesser peers and that their young mature faster, creating larger lineages. But rank isn't everything: No matter what a female baboon's status, having friends correlates to a longer lifespan-and it's even better if some friends are males, Amboseli researchers reported last month in the Proceedings of the Royal Society B.

LIKE MOST AMBOSELI NEOPHYTES, I

find it impossible to tell the baboons apart. But Raphael Mututua, who keeps the Amboseli project running smoothly, is on a first-name basis with all 300-odd baboons. He and his colleagues have honed "baboon eyes": an ability to recognize individuals and notice subtle changes in behavior. With time, Mututua says, "you see them like you see human beings." He coaches me in coat color, tail shape, facial characteristics, posture, and other features. My 2 days in the field are far too few to get the hang of it.

Susan Alberts also has baboon eyes—and a penchant for molecular studies. As Jeanne Altmann's graduate student, she and Altmann in 1989 decided that the project's voluminous behavioral observations would

The baboon chronicles

Amboseli researchers have monitored their subjects for 40 years.

- 1963–4

Jeanne and Stuart Altmann study baboon ecology in Kenya, mostly at what is now Amboseli National Park

- 1971

The Altmanns return to Amboseli and launch what became a long-term study of a baboon troop called Alto's Group

- 1974

Jeanne Altmann publishes a methodological study that sets the standard for behavioral observations

- 1980

The project expands observations to a second troop, Hook's Group

- 1981

Raphael Mututua becomes the first of three Kenyan field assistants

- 1984

The project's first Kenyan student, Philip Muruthi, joins; he goes on to complete a Ph.D.

Susan Alberts joins project as an assistant; she, too, completes a Ph.D.

- 1989

Blood sample collection begins, leading to papers on the influence of social factors on behavior and physiology

- 1994

Fecal sampling starts, enabling larger sample sizes for hormone and DNA studies

- 2003

Amboseli team discovers that male baboons can identify their own offspring and that friends matter for females

- 2009

Severe drought forces baboons to spend much of their time foraging

- 2010

Jenny Tung and Beth Archie sign on as project associate directors under directors Alberts and Jeanne Altmann

2013

Mercy Akinyi determines that grooming leads to fewer ticks and healthier blood



be more meaningful with genetic data. To explore how a male's success at fathering offspring varies with his rank and whether he has migrated from a different troop, Alberts and Altmann began collecting blood for paternity testing. Even though fertile females have multiple mates, the work showed that dominant males father most of their offspring-somehow sperm from the topranking males comes out ahead. Yet dominant males have limited lineages because most don't stav dominant for very long. Alberts and colleagues also discovered that contrary to expectations, fathers know their own offspring and can boost their progeny's survival odds, if they stay in the same troop.

Getting blood samples by darting and tranquilizing animals is difficult and expensive, so Alberts and Altmann honed techniques to cull DNA and hormones from fecal samples, which are now crammed by the thousands in freezers in the United States. They only collect fecal samples they see deposited, so they know the source. Hormone concentrations in the feces have taught them much about how baboons deal with stress, and DNA extracted from the samples has allowed them to build pedigrees for the more than 1500 individuals they've observed over the years.

Biologist Beth Archie of the University of Notre Dame in Indiana has come up with a new use for these samples. Over the past 5 years, studies have linked the microbiomemicrobes that live in and on our bodies-to our health status. Some work has suggested that social connections lead to more similar microbiomes, but it's been hard to tease apart whether social connections or similar diets are responsible. Archie has pulled bacterial DNA out of the feces to characterize baboon microbiomes. Combining that data with behavioral observations allows her to evaluate how baboon social mores affect the microbiome. At the recent Biology of Genomes meeting, she and Tung reported that gut microbiomes are most similar within a social group, and specific bacteria and enzymes strongly correlate with how friendly baboons are to each other. "We show a striking role for social relationships," Archie says, "which has ramifications for the evolutionary costs and benefits of sociality."

For other projects, the Amboseli researchers have had to resume blood collection. This year's effort will start the day after I leave Amboseli: Mututua and colleagues will fan out among a troop, each concealing a meterlong blowgun loaded with a tranquilizing dart, until a target baboon is alone and they Through grooming, baboons not only reduce parasites—they also cement friendships.

can take it down. "Once we cover [the darted animal] with the tarp, [others in the troop] forget all about it," Tung says.

Back at the truck, a team will weigh the drugged animal, make a cast of the teeth, take a skin punch, and check for parasites. They will also draw blood for their studies, which aim to test immune system function and correlate it with age, social rank, and other factors. Tung and Archie are pushing the limits of what can be done in the field. When their colleagues flew in from North Carolina, they brought reagents for testing immune function that must be kept frozen before they are mixed with blood and incubated at baboon body temperature. Using this test on captive primates in the United States, Tung and postdoc Noah Snyder-Mackler found that low social status often dampens immune function. Now, they have a chance to see what happens in wild baboons, which are under far greater stress and are besieged by parasites. By doing so, the baboon watchers hope to uncover a new plot twist in the epic Amboseli story-and perhaps another clue to what shapes our own health.