

Dance of the Sexes

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The primate order is exceedingly diverse. Taken as a whole, primates—a group that includes the major subdivisions of prosimians (lemurs and lorises), monkeys (from both the Old and New Worlds), and apes (lesser and greater)—are generalized mammals. They can eat practically anything from seeds to sap, or grass to grubs, as well as varying amounts of fruit, leaves, and animal protein. Some live in tropical forests, while others survive in near-desert conditions. Throughout their ancient history, primates moved into, and subsequently become better adapted for, a great array of environments. Thus, over time, and through natural selection, primates' generalized nature—their mammalian ability to function as the jack-of-all-trades in the natural world—supported their evolution into a diverse taxonomic order.

If we wanted to choose a primate that exemplifies that diversity, we'd certainly want to look among the lemurs of Madagascar. The primate featured in this article, the Milne-Edwards's sifaka, is no exception. Indeed, primatologists Pochron and Wright, the authors of this selection, remark that this species resembles something from The Muppet Show. Their uniqueness among primates is attributed to several factors. It's hypothesized that the ancestors of modern lemurs rafted to Madagascar, the third largest island in the world, over 60 million years ago, thereby severing their kin ties with their original population. Once settled onto the island, members of the ancestral lineage moved into various econiches and subsequently evolved their distinctive features through natural selection. This phenomenon, known as an adaptive radiation, worked in concert with another force—isolation—to further shape the genetic makeup of lemurs. Consequently, Madagascar's lemurs demonstrate many unique behavioral and anatomical features.

As you read this article, identify some distinguishing traits seen among various lemurs, while paying particular attention to the author's research questions about the Milne-Edwards's sifaka. The authors start with a seemingly simple question, "Why are females of this species dominant over males?" To answer this question, they must consider many variables, as is often the case in science. Variation in social behaviors, group size and composition, reproductive rate, longevity, and the environment all figure into an intriguing topic that is still under study.

The group of lemurs, known as Milne-Edwards's sifakas, was small—an adult male, an adult female, and two large offspring. With only four animals, distinguishing them should have been easy.

"That's the male," said Georges Rakotonirina, pointing. Rakotonirina was the lead field technician, a native of Madagascar who had been studying the sifakas with one of us (Wright) since 1986.

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"And that's the female." The novice among us (Pochron), new to the study in 2000, stared at the dark forms up in the tree and blinked. They all looked the same.

"Look," said Rakotonirina. "They're eating vahia-banikondro."

"What?" Pochron thought to herself. "How can he tell from down here what they're eating? And can I possibly learn to pronounce and spell . . . whatever it is?" Hearing chattering in the forest canopy, Pochron then asked aloud, "What bird is that?"

Rakotonirina laughed. "That's the sifaka," he said. "It means he wants to stop fighting." Pochron knew then and there she had some catching up to do, notwithstanding her previous experience studying baboons in Tanzania. But like Wright and many others whose first encounter with lemurs was life-changing, she was hooked.

The lemurs of Madagascar are the surviving members of a lineage that has been genetically isolated from the rest of the primate family for at least 65 million years. The island became separated from the African mainland 160 million years ago, and from the Indian landmass 80 million years ago. The ancestors of lemurs probably colonized the island by rafting there on drifting vegetation. Until relatively recently, lemurs lived in a separate world. Meanwhile, primates elsewhere evolved into monkeys, apes, and humans.

That ancient genetic split is surely one reason lemurs often boast such unusual traits, compared with humanity's closer primate relatives. For example, dwarf lemurs store up fat in their tails and then draw on it while hibernating; in contrast, no monkey or ape hibernates. Members of one lemur family, the indriids, maintain an upright, kangaroolike posture as they leap from one tree trunk and cling to another; monkeys, however, are quadrupedal, like squirrels. All lemurs have toothcombs—a set of teeth ideally shaped for grooming; monkey and ape teeth are shaped for biting and chewing.

Especially surprising to evolutionary biologists, in most groups of lemurs, females are dominant over males. In some lemur species female dominance becomes manifest only in conflicts over food; in other species it emerges in all social settings. Yet in mon-

keys and apes—indeed, in mammals generally—female dominance is rare. What has led to such an unusual social characteristic among lemurs, with its far-reaching implications?

Female mammals that do dominate males are usually well equipped physically to do so. Female spotted hyenas are often bigger than males. Female reindeer rule over males during the short season when males have shed their antlers prior to growing new ones and the females have not yet shed theirs. Female golden hamsters call the shots when they are fatter than males.

But female lemurs are not usually larger than males, nor do they have any special weapons for enforcing dominance, such as bigger teeth. Members of the two sexes are virtually monomorphic, or similar, when it comes to physical strength. How do females manage to get their way without the brawn to back up a threat? We and our colleagues do not yet have a definitive answer to that question, but after eighteen years studying one indriid species, we have some inklings.

The center of our universe is the Milne-Edwards's sifaka (*Propithecus edwardsi*). Until recently it was considered a subspecies of the diademed sifaka, but geneticists have now determined that it is a separate species. Weighing in at about thirteen pounds and looking like something out of the Muppet studio, the animal lives throughout Ranomafana National Park, a 170-square-mile emerald forest set in cloud-covered mountains, and in adjacent regions. . . . It has orange eyes and woolly, water-resistant fur (a useful trait in a rainforest), which is colored dark brown to black except for two large, white patches on the animal's back. The females have a lemony, maple-syrupy smell; the males, which have more glands for scent marking, smell muskier.

Active by day, Milne-Edwards's sifakas prefer to hang out some forty feet up in the trees, and they travel, as do other indriids, by leaping from one tree trunk to the next. Adults are mainly leaf eaters, but they also rely heavily on fruits and seeds.

Females and males do not often come into conflict, but when they do, the females win about 95 percent of the time. Apparently males are letting females win such altercations. What are they giving up

by submitting? The answer may be calories. Adult females, for instance, appear to eat more seeds than adult males do. The difference is most pronounced during the mating season. Seeds are generally high in fat, and storing up fat is good preparation for a female on her way to becoming reproductively active. When you see males and females fighting, you will probably find tempting seeds nearby.

If males are allowing females to enjoy more seeds, what are they getting in return? The answers that jump to mind are: sex and offspring. And that would make sense in evolutionary terms. Unfortunately for the theory, the annual estrus cycle of the female lasts only ten hours, and in that short period she may mate with several males. None of those mating males is likely to know whose baby the female is having. If he allows a female to take his food, and she uses it to raise another male's offspring, he has not helped himself at all. So why would he allow her to win extra calories? Nature is hardly known for its generosity. In our years of field observations seeking answers to this question, we have found ourselves bumping into some other unusual and fascinating lemur traits. Our goal, then, is to find a coherent explanation that makes sense of it all: with apologies to the high-energy physicists, our holy grail is a kind of grand unified theory of the lemur.

Milne-Edwards's sifakas usually occur in small groups ranging from two to nine individuals. Typically, the groups include three adults (either two males and one female, or vice versa), infants, and older offspring. A female may come into her brief period of estrus at any time during the mating season, which runs from late November through mid-January. The babies are born in May, June, and July. A female gives birth to only one baby at a time, and nurses it attentively until the next mating season, if it survives until then. The cycle puts weaning at a propitious time, when food is most likely to be abundant. A mother that has nursed a baby that long is apt to skip a year before breeding again, most likely because it takes a while to store up enough fat.

Within a group of sifakas life is reasonably peaceful: members spend a lot more time grooming each other than they do squabbling. Males within a

group get along most of the year. During the mating season, though, fights between males can be among the most aggressive in this species. There is little question that the fights are about sex, and the fact that fighters sometimes suffer injuries to their testicles may be no accident. You can tell that a threatening look, a swipe, or a bite has had an effect if you hear the intended target emit birdlike chatter, the equivalent of, "Stop picking on me! I'll leave now!"

Since the males are clearly competing with each other for access to fertile females, it is puzzling that males have not evolved to be larger than the females (or to have bigger teeth or other such endowments). According to classic behavioral ecology, when males compete, the larger or stronger males usually prevail. The larger males thus have more offspring, and those offspring carry the genes associated with being large. After several generations the repeated selection for large males should lead to males that are larger than the females. When the males and females of a species differ in such physical characteristics, the species is said to be sexually dimorphic.

Most large mammal species are sexually dimorphic. Monomorphism, where it is found, typically occurs in monogamous species, in which a single male and female pair up to raise their offspring together. To succeed evolutionarily, monogamy has to be a two-way street. The male has the genetic incentive to help feed, carry, and protect the young of a particular female only if the monogamous bond assures him the young are his. If the female needs a devoted mate to help raise her young, she has a genetic incentive of her own—to avoid mating with a male that beats up other males, because, despite winning the "right" to take many "wives," he cannot offer parental care to all his offspring. When male fighting is suppressed by such female preferences, so too is sexual dimorphism. Some lemurs such as indris (*Indri indri*) fit that pattern: they are monomorphic and monogamous. . . .

Paradoxically, though, most lemur species do not behave like indris: they mate promiscuously, and males provide little or no care for infants, which may or may not be theirs. In short, they look like monogamous species, but they act like nonmonogamous ones. The Milne-Edwards's sifaka

fits that pattern, too. But how can it be a stable arrangement?

Our observations offer part of the solution to the puzzle. First, no male, even if he is stronger than other males, can prevent a female from mating promiscuously. Nor does a larger male have the advantage of producing more sperm, because during the breeding season the testicles of all the males are roughly the same size. Thus the ejaculate of a heavy male cannot, as has been observed in some mammalian and avian species, overwhelm the ejaculate of a light male: if they both mate with a particular female, each has an equal chance to father her offspring.

Aside from the competition between males over females, serious fighting may also erupt when a new adult animal joins a group. Such transitions in group membership shed additional light on the roles of males and females—and, in particular, the dominance of females—within lemur groups.

Milne-Edwards's sifaka groups are far less predictable in composition than those of monkey and ape species. A baboon troop, for instance, characteristically includes many adult males and females. Gorilla groups are generally polygynous, consisting of one silverback male, his harem of several adult females, their young, and one or more subordinate males. By contrast, sifaka groups can be polyandrous (one female and two or more males) or polygynous (one male and two or more females). They can include multiple males and multiple females—or just one adult pair. . . .

Not only do all such combinations turn up with roughly equal frequency, but a group may change in composition from one year to the next. A new member is most likely to join a group from August until October, just before the mating season. If a new male seeks to join a group, all the animals may coexist peacefully. Sometimes, though, the resident male and the newcomer fight, and one is driven away. And sometimes a female prefers the new male, and she may help force the old male to leave.

For any dependent offspring in the group, an incoming male poses great danger: he is likely to kill them, a measure that is evolutionarily adaptive because it speeds up his chance to father offspring. Such behavior is well documented in primates.

When an adult female tries to join a group, friction with the resident female seems inevitable. The two sometimes bite, slap, and chase each other. The resident female generally leaves, probably an indication that the incoming female has shrewdly judged her chances before attempting to gain entry. Just as males do, an incoming female may kill any dependent young. In other primates, at least, it is less common—and less easily explained as adaptive behavior—for the female to kill the young than it is for the male. The murderous action of the incoming female seems to hasten the departure of the resident female. When two adult females live together peaceably in a group, we suspect that they are closely related. Genetic studies currently under way should clarify this.

To investigate why the sifaka's social arrangements vary so widely, we compared sifaka survivorship and fertility patterns with those of some other primates. For example, tamarins and marmosets, both New World monkeys, suffer high mortality in their early years; sensibly, then, they reach sexual maturity and begin reproducing at an early age. By contrast, many Old World monkeys, such as baboons and macaques, live longer, start to reproduce later, and have more time between babies.

The mortality pattern of the Milne-Edwards's sifaka closely resembles that of the tamarins and marmosets: many die in their first few years of life. In fertility, however, Milne-Edwards's sifakas resemble baboons and macaques: the sifakas that do survive reach sexual maturity fairly late (about three and a half years for females, and four and a half years for males), and they reproduce at a slow rate over a span approaching thirty years. It is almost as if sifakas have deliberately chosen the most difficult of all the primate patterns ever observed: high mortality coupled with slow reproduction. By the end of her life, a female tamarin or marmoset will have three or four daughters; a baboon or macaque will have two or three. But by the end of her lifespan, a female sifaka will rarely have more than one daughter that survives to reproduce. The constraints on reproduction may be responsible for encouraging the sifakas' highly flexible group structures.

The sifaka's lifespan is unusual for a mammal its size. On average, the larger the species, the longer it lives. As we noted earlier, Milne-Edwards's sifakas weigh about thirteen pounds, yet they live nearly thirty years in the wild. Such longevity may have evolved in response to unpredictable environmental conditions. After all, a longer life gives the animals a better chance of reproducing during the years when conditions are most favorable. It is hard to imagine that food could ever be scarce in a place such as Ranomafana National Park, where greenery covers every surface. Yet the availability of food varies seasonally, with the rain. Furthermore, Madagascar is prone to cyclones and droughts, which can also lead to shortages.

Perhaps here too is part of the solution to our original question about lemurs: why are females the dominant sex? The behavioral pattern, in which males cede food to females, appears essential for balancing female and male reproductive needs. For females, fertility, pregnancy, and nursing all depend on sufficient body weight. Weight is less important for males, because their reproductive role is limited to copulation and, as we mentioned earlier, during the breeding season, the testes of small-bodied males are the same size as those of larger-bodied males. If

the males did grow larger overall, Madagascar's unpredictable environment might prove fatal to them. In sum, neither having a small body size nor relinquishing high-calorie foods to females seems to compromise the fertility of males.

In the past few years we have considered a number of ways to account for these observations. Because the females mate promiscuously, perhaps each male simply defers to all females, on the grounds that there is always some chance that one of them will bear his offspring. Or a male may yield food to a female only when he has some good reasons for thinking he will sire her offspring. Or a male may defer to a close female relative (mother, sister, daughter), whose offspring would indirectly share some of his genes. Or maybe the reality is some combination of all those factors. . . .

One way to learn more about what is going on is to test offspring for paternity. Toni Lyn Morelli, one of Wright's graduate students, has been sampling blood of these sifakas and analyzing it genetically. In a species where the average number of adults in a group is three, however, discerning a statistically significant pattern may take some time. And—who knows?—the results may lead us to some new lemur mystery.

DISCUSSION QUESTIONS

1. How do relationships among males and females in Milne-Edwards's sifakas differ from those in other primate groups?
2. What kinds of social group structures have been observed among Milne-Edwards's sifakas?
3. How might environmental factors influence relationships among the sexes and variation in social groups among Milne-Edwards's sifakas?
4. What are some unusual behavioral and anatomical traits that have been seen among lemurs as compared to most other nonhuman primates such as monkeys and apes?



INTERNET RESOURCES

You can find additional information about primate species by searching for "animal diversity" on the web or visiting the website of the University of

Wisconsin's National Primate Research Center at <http://pin.primate.wisc.edu>.