



The off-the-record stories primatologists tell each other

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Talking about them and about us

Early one morning in the winter of 2000, I found Vera sitting on the ground, hunched over with her head down, having probably spent the night outside. Thirty years old, she was the matriarch of the group of Tonkean macaques that lived in a wooded park at the Center of Primatology in Strasbourg, France. She urgently needed to be caught for treatment. I fetched Pierre Uhlrich, our caretaker, and we went back to the park. In Vera's condition it would have been dangerous to sedate her, so I decided to seize her directly. She was so weak that I managed to pick her up without getting bitten, but the whole group was in uproar: they were furious, screaming and charging at us. Pierre and I retreated to the park gate and left with Vera.

It turned out that Vera's body temperature had dropped to 23 °C, which meant that she should have been dead. We put her in an incubator. Pierre kept an eye on her all day, and miraculously, degree by degree, her temperature slowly returned to normal by the end of the day. We found that she was in a state of septic shock due to an ulcer in her left eye. Vera had been one-eyed for a long time, and now the cornea of her remaining eye was badly perforated and purulent. The prognosis was grim, and the entire research team was in anguish. One of the first things that students were surprised to learn when they joined our team was that Vera was older than they were. That day we realized just how important she was to everyone. We treated her by placing an antibiotic insert under her lower eyelid and suturing the upper and lower eyelids together. The treatment worked: when the stitches were removed 12 days later, the eye had healed. But a white veil had developed in the cornea, which prevented

Vera from seeing. We returned her to the group, and she was able to communicate and interact with her groupmates. She could also move around, but she probably only saw shadows, and she regularly bumped into obstacles. As the months passed, though, those mishaps became less frequent, and I noticed that, as if by a second miracle, Vera's eye was clearing up. After a year, quite remarkably, her cornea had completely regained its transparency.

When writing scientific articles, it is our practice to use an impersonal tone to convey objectivity. Here, however, I am going to take advantage of the liberty afforded by an editorial to go behind the scenes and talk about things primatologists may say about their study subjects when they are confident that those things will not be formally reported. Almost every experienced primatologist has stories like the one I have just told. We like to tell them to each other during team breaks, over meals at conferences, or in the evenings at a field station. These are unofficial accounts, most of which will never make it into published works because they are anecdotal or open to interpretation. Young people are often eager to hear these stories and cannot wait to experience similar events. Of course, we are careful not to share these stories with colleagues who study other kinds of animals, to avoid worsening our reputation for empathizing too much with our subjects.

As a scientist, I have a tendency to divide the universe into categories, so I cannot resist proposing a little classification of the different kinds of stories we tell in private. I will illustrate this with examples, most of which involve Tonkean macaques, the species with which I have the most experience. Like many other primatologists, I have followed the same social groups for years. This makes us chroniclers of the dramas that unfold before our eyes as the demographics change and the individuals evolve, with their perpetual fate of births, deaths, accidents, departures, arrivals, encounters, overthrows, and the various other events of their life. We are particularly fond of relating this kind of story. I have chosen to write about Vera, but I could just as well have described how Dilie, a female from a subordinate matriline, managed to achieve a high social position by winning the support

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of some of the highest-ranking members of the dominant matriline; or how Gaston, an adult male, was twice betrayed by his own body while fighting for group dominance with another male. Indeed, Gaston was involved in two takeover events, 5 years apart, and each time acute stress caused him to fall seriously ill after a few days of fighting, preventing him from being able to stay in the competition. In the past, some of these stories might have found their way into monographs or popular science books, but with today's emphasis on focused scientific articles, we are content to share them informally with our colleagues.

Unpublishable results provide a second category of stories. A single example of this will suffice. On 11 August 1999, a total solar eclipse occurred in Europe and was fully visible in Strasbourg. Stories have always circulated about the reaction of animals to such an event and their ability to make sense of it. Reputedly, many of them go silent when darkness falls, which only deepens the mystery. To find out for sure, my students and I organized the surveillance of our two study groups of Tonkean macaques, one at the Primate Center and the other at the city's Orangerie Zoo, to record their reactions. The eclipse took place in the middle of the day, and the period of total darkness lasted only a few minutes. It does not take many words to describe what we saw. In both places, when darkness fell, the individuals in each group started to gather in their usual sleeping areas. However, daylight soon returned and they left again. Information about other groups of monkeys—and a variety of other animal species in different locations—pointed to the same effect: many of them went to their night quarters as “twilight” fell. What struck me about the Tonkean macaques was their behavior when daylight returned: they simply resumed their activities as if nothing had happened, seemingly unfazed by the brief period of unexpected darkness. The great mystery of animal muteness had been solved. The discovery that only humans care about the meaning of night, day and cosmic events was hardly a major breakthrough, and the story of the eclipse was sent to the purgatory of unpublished results, where it remains, ready to pop up whenever it suits a conversation.

Highlighting their performances

A third kind of anecdote, which we particularly enjoy, is about the quirks and inventions of our primate subjects. Recounting these anecdotes often leads to rambling chats in which participants do their best to vaunt the exploits of their favorite species and surprise each other with reports of unusual behavior. Here are some of these exchanges:

- I knew a young female Tonkean macaque who, in order to interact with the newborns of other females, offered

her tongue for suckling. She's the only monkey I've ever seen do this. I leave it to you to decide the significance of this behavior.

- I'd say I remember a female rhesus macaque who kept pebbles in her cheek pouches and sucked them regularly. When she moved, you could hear the pebbles clattering together. Hardly a useful habit. After once being deprived of her pebbles during a health check, she replenished her pebble stock within a few weeks!
- If you're interested in really pointless behavior, here's what one female Tonkean macaque did. Whenever she saw an earthworm near her, she would pick it up and throw it away as if in disgust. Don't ask me why she did it. She just seemed to dislike earthworms.
- Yes, there's no guarantee that any particular action will provide some benefit. Personally, I've seen curious forms of grooming in my study groups that remind me of some reports from long ago. One long-tailed female macaque used to groom her infant's eye area with a leaf, a flower or even a piece of wood. I also observed a similar practice in a female rhesus macaque, but in this case the mother would sometimes strip the leaves off, leaving just the stem, which she then used to groom her offspring's eye area. The infant didn't seem to approve of this and often pushed her mother's hand away. In both cases, the use of a grooming tool by the mother did not seem to be particularly effective.
- Okay, but you see, we may not always understand the goals of individuals. And some can develop pretty impressive abilities. I worked for a long time with a male Tonkean macaque who was able to unscrew bolts. He's still alive. It was probably rewarding for him to do this because such a skill requires stubbornness. The caretakers always kept an eye on him.
- What's more, a new pattern of behavior can really help an individual cope better. Listen to this: in our study group of brown capuchin monkeys, there is a female who had her right leg amputated after a fracture. Don't pity her, because she has learned to use her prehensile tail as a fourth limb. Her gait is so fluid that anyone unfamiliar with her story would be slow to notice that she is missing a leg. It's fair to say that she has made up for her handicap through her own rehabilitation.

We can photograph some idiosyncratic behaviors (Fig. 1) because they are exhibited over and over again. However, there are other behaviors that are too rare to record, and we may be reluctant to talk about them with anyone for fear of not being believed. Consider this dialogue:

- Have you ever heard a male make an estrus call?
- You're joking! Only females go through estrus.

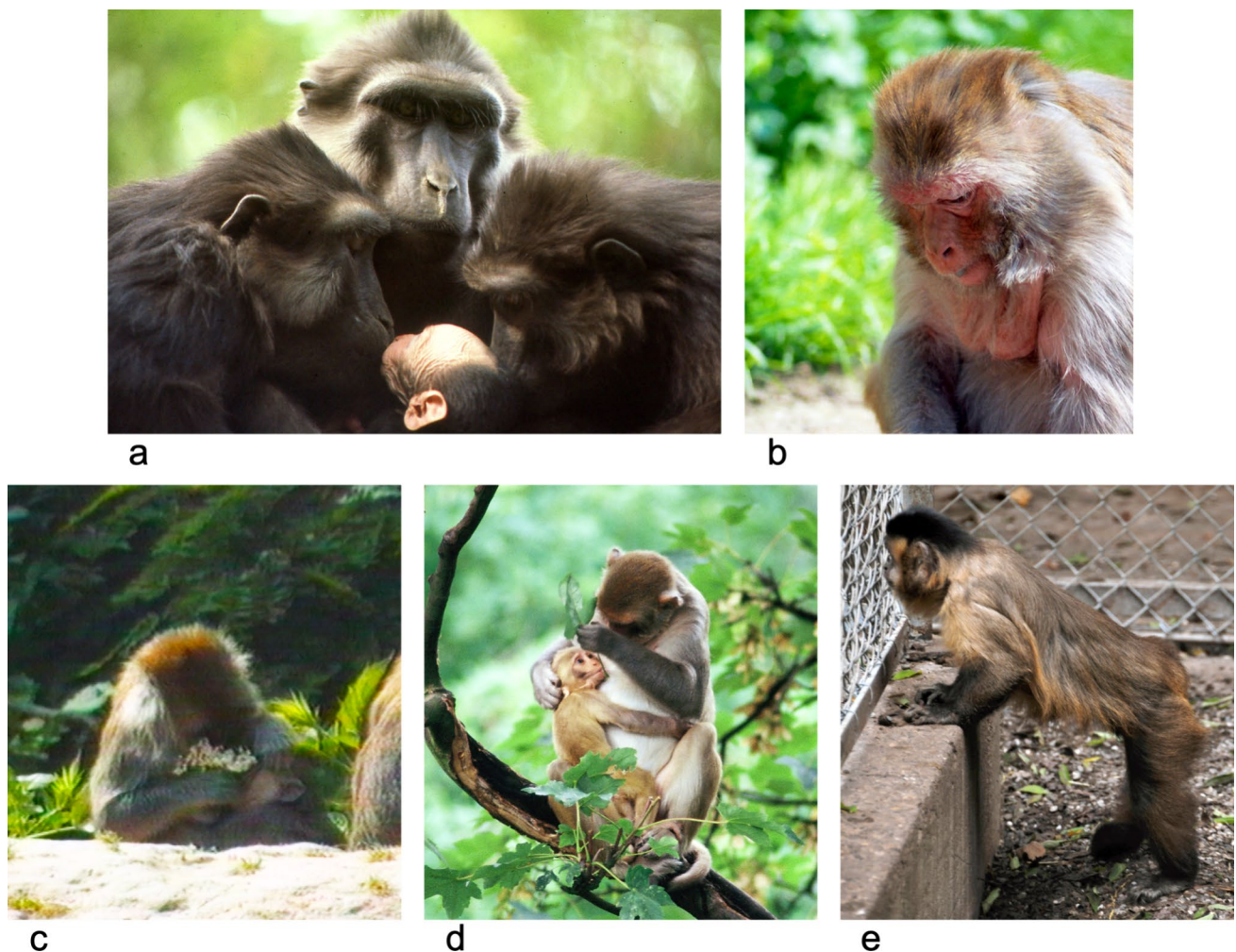


Fig. 1a–e Idiosyncratic behaviors in female monkeys. **a** Valentine (Tonkean macaque *Macaca tonkeana*) offering her tongue to a newborn for suckling; **b** Greta (rhesus macaque *Macaca mulatta*) sucking a pebble, her cheek pouches weighed down by the pebbles inside; **c** Crinoline (long-tailed macaque *Macaca fascicularis*) grooming her

infant's eye area with a flower; **d** Année (rhesus macaque) grooming her infant's eye area with a leaf; **e** Rosy (brown capuchin *Sapajus apella*) standing on three limbs and her tail [photos taken by the author (Center of Primatology, Strasbourg)]

- Well, I saw and heard a young male Tonkean macaque making estrus calls. He probably only did this for a few days in his life. His name was Janek. He was almost 4 years old at the time, so he was entering puberty. Perhaps this behavior was caused by his first surge of sex hormones, the effects of which were still not properly targeted at that age. Janek's calls consisted of a short series of the repeated units that are typical of female estrus calls. There was no specific context of occurrence, as is often the case with females of his species. However, Janek only vocalized this way during two periods of a few days within a 6-week interval, each corresponding to the days on which females in his group were in estrus.
- Wow! Could this be an X-chromosome effect?
- I don't know anything about the genes involved, but to me it shows that both sexes share the same potential

repertoire, right? It could also be that a male is capable of experiencing an emotional state similar to that of a female when vocalizing.

- Hmm, that sounds a bit far-fetched to me.
- Keep this to yourself, but I actually witnessed another event of the same kind, this time involving a sexually mature male. I remember it as if it were yesterday. The male was Belphegor, a 6-year-old long-tailed macaque. He was watching a mating between a male and a female in his group, about 10 m in front of him. The female gave the copulation call typical of her species, then the male dismounted and the female began to groom him. It was at this point, just after the mating, that Belphegor himself made a call, a little hesitantly, but that was clearly identifiable as the female copulation call.
- Incredible!

– I know...I haven't seen anything like it since.

Assessing their personalities and motivations

Have I covered all the stories we share behind the scenes? Far from it. Let me now turn to the personalities of the individuals we follow. Again, we could go on endlessly about them, comparing their characters, their skills, even their strengths and weaknesses. As social primates ourselves, we are well equipped to assess the personalities of our peers, and it is hard to ignore those of our subjects when we are constantly in contact with them. Of course, we are on a slippery slope here. Not so long ago, any reference to animal personality was considered suspect, but now it has become a subject of study in its own right. Still, without quantitative measures, do we have the right to invoke it? Not really, especially because we use common language to describe individuals in rather vague ways: so-and-so is irritable, so-and-so is mischievous, so-and-so is timid or gentle.

Nevertheless, I can talk about Donald, a young Tonkean macaque from the Orangerie group, who showed himself to be quite reckless and regularly sought to tease me when I entered the group's enclosure to collect urine from the ground as part of a hormone study. At 4 years of age, he was sent with half of his group to a partner Italian zoo, and I saw him again 6 years later, during a visit there. To my amazement, Donald turned out to be one of the most sensitive individuals in the group. When I approached the enclosure fence, he ran towards me and put both hands through the wire mesh to grasp my fingers, all the while emitting intense affiliative grunts as he looked at me and did not let go of my fingers. The annoying adolescent had matured into an affectionate adult who had not forgotten me. I also remember Darwin, who for a long time was the highest-ranking male in the Orangerie group. I think of him as one of the most headstrong monkeys I have ever met. He was once challenged by the second-ranking male, who headed an alliance of four adult males. Darwin withstood the attacks of his opponents for several weeks. It was winter, and no matter how close the temperature got to zero, Darwin refused to go into the shelter, where he would surely have been forced into submission. By using all his strategic abilities to ensure that he was never surrounded, he survived the challenge and maintained his position at the top for a long time to come. This attitude was proof of great strength of character, I think you will agree.

At this point in our gossip, there is no more cold beer at the field station, but that is okay—we will move on to warm beer. Now that we have had a chance to show off all of our scars from field accidents and bites from our kind subjects, what else can we say? As in fact no one else is listening to us, we can move on to the most awkward topic: our

opinions about the emotions and intentions of non-human primates. In a word, the great sin of our discipline: anthropomorphism. This issue has often been in the background of the aforementioned stories, and having sufficiently compromised myself in several of them, I will not go into too much detail. I have to remind myself that this is a scientific journal. However, I will mention the case of the “frustration call” of Marie and other Tonkean macaques. This female, Marie, displayed this call more often than the others. When she was in trouble, for instance because she had lost a dispute with another individual, she would rush to hug Vera, and make a special vocalization, for which I have coined the term, for lack of a better one, “the like-Mamie frustration call.” Mamie was Marie's mother, and it was with her that I first identified this particular screeching call, which to the human ear sounded like a mixture of protest and complaint. Mamie made this vocalization when she was moving away from a troublemaker. As for Marie, others would say that she came to Vera for consolation, but I am one of those who are not convinced that consolation exists in monkeys. Vera responded to Marie with vigorous lip-smacking and a mutual embrace. Nancy Rebout (unpublished results) later found, in her acoustic analyses for her PhD, that the frustration call consisted of two overlapping parts, a scream followed by a grunt. It seemed to me that Marie was seeking comfort through her display, claiming that no one should harm her in this way. Of course, I never wrote any such thing in a scientific paper. It was only in confidential conversations that I could express my own frustration at not being able to objectivize what Marie was feeling at those moments.

Reflecting on their abilities

Scientific inquiry is a human endeavor dedicated to the methodical pursuit of knowledge. However, most epistemologists and historians of science currently agree that scientists do not differ from their fellow humans in their logics of reasoning. While we may aspire to an ideal of rationality and objective truth, we are first and foremost human beings, and as such, primate animals. Our subjects remind us of this every day. It would be unproductive to deny that there is a gray area between scientific and non-scientific issues. As scientists, we have an obligation to consider all relevant facts and possible explanations. The stories we tell each other, with all their subjectivity, are part of that process. How can we achieve accurate knowledge if we do not discuss the issues in which we need to make progress toward greater objectivity? Sure, we take the liberty of saying things that may need confirmation, but we are speaking to trained colleagues, and we know that they are capable of weighing up what we say. Our stories are testimony to the richness of the behavioral repertoire of non-human primates. Not only do

we enjoy talking about the individuals we study, but these informal exchanges can serve as brainstorming sessions that have the potential to lead to new insights and studies. I will illustrate this point with two final examples, again in Tonkean macaques.

One behavior that has always impressed me is cheek pouch emptying. Let me first explain the context in which this behavior occurs. An individual has just eaten monkey chow and their cheek pouches are now swollen with half-chewed food. At that moment, a caretaker arrives to begin distributing fruit to the group. The individual then runs up to the caretaker and presses their cheek pouches with the back of their hands to spit out the chow. Over the course of several decades, I have observed this cheek pouch emptying behavior half a dozen times in different individuals, and once in three individuals simultaneously. The point is that the individuals that perform this action must anticipate the fact that they will not be able to store fruit quickly in the upcoming competition, while at the same time accepting that they have to give up a low-value food in order to acquire one of a higher value. Of course, these events alone are not sufficient to prove that individuals make conscious calculations about what they are losing and what they are gaining. However, they do suggest that we could gain insight into the intentional capacities of monkeys by conducting experimental studies of the cognitive mechanisms involved in their cheek pouch emptying behavior.

I will end this editorial with the most trivial anecdote I can think of, which I like to tell even though I am not sure anyone cares to hear it. An individual is sitting on a low branch or other support less than 1 m above the other members of their group. At some point, the individual urinates on some of their groupmates below, with apparent disregard for them. Let us focus on cases where the peeing individual is

of a lower dominance rank than the ones below. What do the latter do? They abruptly move away to avoid being sprayed again. I have seen this happen many times, and always with the same reaction, even when the highest-ranking male in the group is being sprayed. Those hit often look in the direction of the urinator, but they never show aggression or any sign of annoyance. This outcome can be compared with those of other situations, such as when an individual accidentally bumps into a higher-ranking groupmate; here, the individual responsible for the disturbance is usually vocally threatened, or even punished by being grabbed if it is a juvenile. Nothing similar happens when one monkey urinates on another. The perpetrator does not refrain from urinating, nor does the victim blame the former for the disturbance. Compare this with the behavior of male chimpanzees in captivity, who are able to target and urinate on humans from a distance: they seem fully aware that their action will be considered hostile by the recipient (Valérie Dufour, private communication). I cannot help but think that such contrasting behaviors between Tonkean macaques and chimpanzees are related to the latter's ability to attribute intentions to others, an ability that macaques lack. Admittedly, such observations do not constitute hard evidence. They are not on a par with the results of decades of experimental research on theory of mind. Yet they have allowed me to make an assessment of an issue which, despite all the experiments that have been conducted, still divides colleagues considering the performance gap between monkeys and great apes. By the way, are you convinced by what I am telling you right now? Yes? No? Don't worry, this is off the record...

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