

Robert W. Sussman (1941–2016)

Peter S. Ungar

Department of Anthropology, University of Arkansas, Fayetteville, Arkansas, USA

When I was a graduate student at Stony Brook back in the mid-1980s, there was a section of our doctoral qualifying examination asking us to identify key researchers in biological anthropology. One of the names was “R. Sussman.” I figured that it was intended to trip up the budding functional morphologists and paleontologists among us, since Randall Susman was on the faculty of our graduate program. But it didn’t trip me up. Bob Sussman’s work was an inspiration to me. I wrote of his species-specific dietary adaptations model, which argued that primates seek out and eat the sorts of foods to which their digestive anatomy was adapted—those that their species had evolved to eat. He had championed the idea since the early days of field primatology, developed in part from his work on the Indian Ocean islands of Madagascar and Mauritius.

*I was fortunate to chat with Bob shortly before he passed away about his early career for a recently published book, *Evolution’s Bite: A Story of Teeth, Diet, and Human Evolution*. The editor at Princeton University Press, Alison Kalett, kindly granted permission for me to share the passage about Bob’s contributions to the story here, to honor him and the work that inspired me all those years ago.*

Bob Sussman and the concept of species-specific dietary adaptations

From Madagascar to Mauritius¹

Bob Sussman was a graduate student in search of a project at Duke University back in the late 1960s. Those were exciting times in Durham, North Carolina. John Buettner-Janusch had just moved his colony of about 90 captive primates, mostly lemurs, from Yale to a large research sanctuary in the Duke Forest. What was lacking though, was basic information on the ecology of most lemur species in their natural habitats—how they used the forest to earn a living. Buettner-Janusch encouraged Sussman to go to Madagascar and help discover the details. Sussman first visited the island back in 1969, and spent much of the remainder of his career studying the behaviors of its lemurs. Much of this early work is described in Bob’s own words in *Primate Ethnographies*, edited by Karen Strier (Pearson Publishers, 2014).

Madagascar is to primates as the Galapagos are to finches. The island provides an amazing example of niche differentiation and speciation, with more than one hundred species of lemurs today—up to a dozen found in any one place. This fact created a conundrum for early primatologists. How could two or more species competing for the same resources coexist? According to evolutionary theory, the best-adapted one should have outcompeted the others, forcing less “fit” species to turn to alternative resources or face extinction. So how could so many closely-related, similar primate species live together in the same place at the same time? Bob Sussman wanted the answer, and Madagascar was a great place to find it. This was an important and relevant question to address at the time for biological anthropologists. Milford Wolpoff had just proposed the single-species hypothesis, which argued that two closely-related hominins could not have coexisted given competitive exclusion.

Alison Jolly, who had studied Buettner-Janusch’s captive primates when they were still at Yale, was among the first to document the ecology of lemurs on Madagascar. She began her work in the Berenty Private Reserve at the south end of the island in 1963, and had already published an influential book, *Lemur Behavior; a Madagascar Field Study*, when Sussman started. In it she described a group of ring-tailed lemurs that had adopted a solitary brown lemur. Brown lemurs were not endemic to Berenty. This one had been captured about fifty miles away, was brought to the area, and then escaped from captivity to join his ring-tailed cousins. The brown lemur slept with the ringtails, moved with them, ate with them. Did this mean that the two species might use

¹Reprinted with permission from *Evolutions’ Bite: A Story of Teeth, Diet and Human Origins* by Peter S. Ungar. Princeton University Press, Princeton, NJ. 2017. ISBN 9780691160535.

the same resources where their ranges overlapped? No one had yet documented the diets of brown lemurs in the wild in detail, let alone the effects of competition on coexistence with ringtails. Sussman seized the opportunity to add to the growing body of knowledge on lemur ecology and, at the same time, learn how two closely-related primate species of similar size and shape might divvy up forest resources to live together in peace.

Bob Sussman and his wife Linda headed to the uncharted lowland forest in the southwest to establish their own research camp. They found two forest patches, Tongobato, which had brown lemurs but no ringtails, and Antserananomby, which had both. The plan came together. He would study brown lemurs at both sites and compare their diets to determine the effects of competition with ringtails. He would also study ringtails at Berenty, which again, had no groups of brown lemurs, to see how they differed there. The three forests were very similar, especially Tongobato and Antserananomby, which were separated by just a few miles of cultivated fields and degraded wild vegetation. Berenty had a few species of large trees not found to the west, but the forest canopies at all three sites were dominated by tamarind trees. These trees produce pod-like fruits used in cuisines throughout the World today. You might know it from the distinctive flavor of Worcestershire sauce. Lemurs also eat tamarind fruits, along with their leaves, flowers, and bark, depending on the season. The study design was completed by planning to work at Antserananomby in the dry season, and Tongobato and Berenty in the rainy season. That way, Sussman could compare diets of each species between seasons as well as between sites where they lived together and separately.

After months of study in 1969 and 1970, he had his results. The two species did overlap in their diets—both ate fruits, leaves, flowers, and bark. But the brown lemurs concentrated more on leaves, and ringtails consumed more fruits, and ate a greater number of plant species. The ringtails moved about half a mile each day, and ranged in height from the tops of the trees to the ground. The brown lemurs in contrast, moved only about 100 yards and stayed in the main canopy. These differences made sense in terms of their diets, and were consistent between sites and between seasons, whether the same exact foods were available

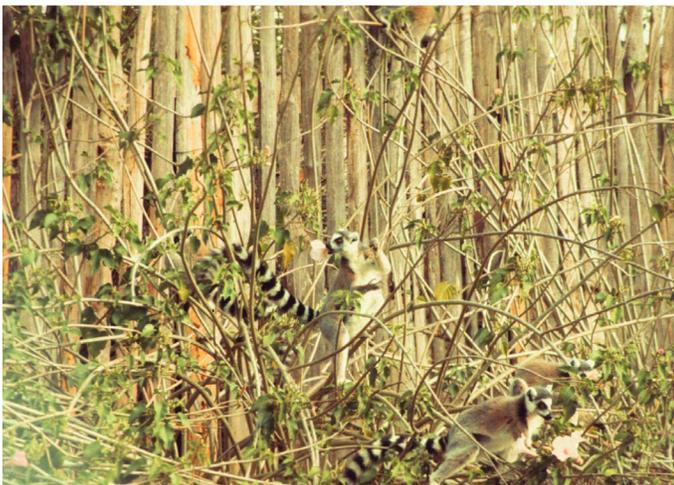


Figure 1. Photographs of lemurs taken by Bob Sussman during his early work on Madagascar.



Figure 2. Bob with likely his most prolific academic son in terms of graduate students, Paul Garber (second from the left), and two of his academic grandsons, Bernardo Urbani (left) and Martin Kowalewski (right). At the Second Midwest Primate Interest Group (MPIG) Meeting. Saint Louis, USA, October 2005. Courtesy of Bernardo Urbani.

at a given time and place or not. In other words, the lemurs sought out and ate the variety of foods to which they were adapted regardless of where, when, or with whom they were eating. This allowed them to split the forest's resources where they coexisted.

But what about primates living in radically different environments? Would they still seek out and eat particular types of food? Sussman followed up his lemur study with macaque monkeys on the idyllic tropical island of Mauritius, about 450 miles to the east of Madagascar. He hadn't intended to work there. He was actually en route to Madagascar in 1977 when his flight from Paris to the capital city, Antananarivo was cancelled. Sussman, along with his wife and his colleague Ian Tattersall, an anthropologist from the American Museum of Natural History, managed to get rerouted to Mauritius in the hopes that they could catch a flight on to Antananarivo from there. But Madagascar was still reeling from the assassination of President Ratsimandrava and the effects of the military coup that had established a new socialist government. Demonstrations erupted in Antananarivo because of shortages of food and other commodities. There was simply no way to get there.

Could they somehow salvage the trip? Mauritius had no lemurs or other endemic primates to study, but there was one invasive species of monkey, the long-tailed macaque. Macaques had been brought to the island from Indonesia by European sailors around four hundred and fifty years ago, and their population had exploded to tens of thousands. This could be the start of an interesting project. Sussman spent that summer surveying macaque populations, and returned a couple of years later to compare the diets of groups living in degraded savannah habitat to those in undisturbed forest.

Just like the brown lemurs and ringtails, macaque populations living in different sites had similar diets, both in terms of diversity of plant species and proportions of different plant parts eaten. In this case though, the primates lived in very different settings, with access to very different sorts of foods. In fact, the Mauritius macaques even had similar diets to those living thousands of miles away in their native forests of Southeast Asia.

This study, together with his earlier work in Madagascar, led Sussman to conclude that primates have what he called *species-specific dietary adaptations*. Their food preferences depend on the teeth and guts that gave their ancestors an advantage in

acquiring and processing the sorts of things they had evolved to eat. This is why different primate species living together had different diets despite access to the same foods. This is why populations of the same species living in different settings sought out similar foods despite having access to different resources. To Sussman, diet was related, first and foremost, to adaptations of the teeth and digestive tract inherited from ones ancestors. It was a matter of evolutionary legacy.

Bob Sussman's results were like music to a paleontologist's ears. They gave extra credibility to reconstructions of diet based on fossil teeth. We can't infer all the details of the foods available to past primates, or exactly how competitors forced them to share the resources of their forests. But if Sussman's lemurs and macaques were anything to go by, teeth should give a pretty good indication of diet regardless. This also made sense in light of Rich Kay's studies of molar shearing crest length and crushing area. Remember that primates classified as leaf eaters tend to have longer crests and smaller crushing areas than do fruit eaters.

Nature is anything but simple

That said, it is one thing to demonstrate that living primates with a given tooth shape tend to eat specific types of food, but quite another to be confident that the form-function relationship is strong enough to be used to reconstruct the diet of a given fossil species. As Richard Preston wrote in *The Hot Zone*, "In biology, nothing is clear, everything is too complicated, everything is a mess, and just when you think you understand something, you peel off a layer and find deeper complications beneath." To be sure, folivorous primates tend to have longer shearing crests than do closely-related frugivores today. But how do we know that the connection is sufficiently tight to use crest length to determine whether a fossil species ate fruits or leaves?

One approach involves pretending specific living primates are fossils, inferring their diets based on tooth shape, and seeing how closely the "reconstructed" diets match actual ones. We can look, for example, at brown lemurs and ringtails. Rich Kay, Bob Sussman, and Ian Tattersall did just that back in the late 1970s. Surprisingly, the two species have remarkably similar teeth. If we found them in the fossil record, we'd infer that they had the same diet. I guess they just don't realize that they should eat the same foods. Brown lemurs consume more leaves and ringtails take more fruit despite the fact that their shearing crests are the same length.

So the relationships between teeth and diet are not so simple after all. Truth be told, the two lemur species do eat mostly the same sorts of foods – fruits, leaves, flowers, and bark – just in different proportions. Kay, Sussman, and Tattersall speculated that perhaps tooth shape is more about the *types* of foods a species eats than the frequencies in which they are eaten. In other words, maybe shearing crest length doesn't reflect how many leaves you eat but, rather, whether you need to be able to eat them at all. Kay, Sussman, and Tattersall evidently didn't realize it at the time, but they had hit on a profound new idea. It would take a couple of decades, and work on very different primates to bring it to the forefront, but Bob Sussman's early studies presaged today's theories of dental ecology, and the importance of fallback adaptations to primate evolutionary biology.

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