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REVIEW ARTICLE

Primate tales: Memoirs from leaders in primatology

The life of a naturalist

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Abstract
This essay summarizes some of my findings while studying primates in the field from 1962 to 2018. Although I have studied primates throughout the tropics, I focused on Africa, primarily the Kibale Forest of Uganda. My research began in the early days of primate field studies when very little was known about the behavior and ecology of most species. Consequently, I was able to study nearly anything that could be observed under natural conditions. It was not necessary to specialize, and I opted to be a generalist. In much of my work I have attempted to understand the relationships between habitat quality, social organization, and population dynamics, emphasizing the great intraspecific variability that exists over time and between areas. Vocalizations have also long been of interest to me, starting with a description of predator-specific alarm calls and later showing how vocalizations among African monkeys appear to be evolutionarily stable. As my field experience progressed, I became increasingly involved with the conservation of tropical rain forests. In the last part of this essay I offer my thoughts on current trends in field primatology and some advice to the next generation of field biologists, stressing the importance of being a naturalist.

Keywords Primate behavioral ecology · Rain forest conservation · Natural history · Memoir

Introduction

I have had the good fortune to spend most of my career working in wild places as a field biologist. I was also born at the right time in the sense that when I entered graduate school the fields of primatology and behavioral ecology had only recently begun to expand. The field was young enough that upon receiving my Ph.D. in 1965 employment was not an issue. Good fortune continued to fall on me, and I landed a position that allowed me to study primates and other wildlife for many decades in Africa, South America, and South Asia. In those early days our knowledge of what wild primates do in nature was so limited that I was able to pursue nearly any subject that appealed to me. There was no need to specialize because virtually everything I saw and recorded was new to science and the western world. Times have changed.

The intent of this essay is to provide a brief description of the development of my career and to summarize some of my research. I also write about what it was like doing fieldwork 50–60 years ago in Africa, a time when there were no cell phones, there was no internet, and one communicated by letter, sometimes waiting 6–8 weeks for a reply. For urgent matters, there was always the expensive telegram or the really expensive telephone call, which at one time was $8–10 dollars per minute for a call to the USA, equivalent to about $85 per minute in 2021. I conclude this essay by putting forward some of my thoughts and opinions on the current trends in field primatology and by offering suggestions to younger generations of field biologists.

Those interested in more detailed stories (some funny, some not) about what it was like conducting field research and conservation in Africa decades ago, and during turbulent times, may like to read my memoir entitled "*I Remember Africa: A Field Biologist's Half-Century Perspective*" (2021).

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Early days

Although there are many factors that shape one's career path, my family, teachers, and mentors were key for me. My Dad, Frederick Struhsaker, was trained in forestry and worked for Michigan's state conservation commission. As secretary of this commission, he was instrumental in raising funds for the purchase of land and creation of the Porcupine Mountains Wilderness State Park in northern Michigan. Mom, Esther, conveyed her love of nature to her four kids and made sure we all completed college after Dad passed away, at the age of 49. My older brother, Paul (Fig. 1), was always interested in biology, geology, geography, and travel. He eventually became a marine fisheries biologist and worked many years with the National Marine Fisheries Service of the US government. Paul was a major influence in my career development.

I was not an outstanding student in high school, but in my final year my English teacher suggested I write an essay on the origins of the Polynesians. I have no idea how he came up with that idea, but it led me to the anthropological literature, especially the work of Thor Heyerdahl (1950) and his controversial hypothesis about people sailing from Peru on balsa rafts to Easter Island. Heyerdahl illustrated the plausibility of his hypothesis by making the journey himself. Until then, I had no idea that it was possible to be gainfully employed by combining research with the excitement of travel and exploration.

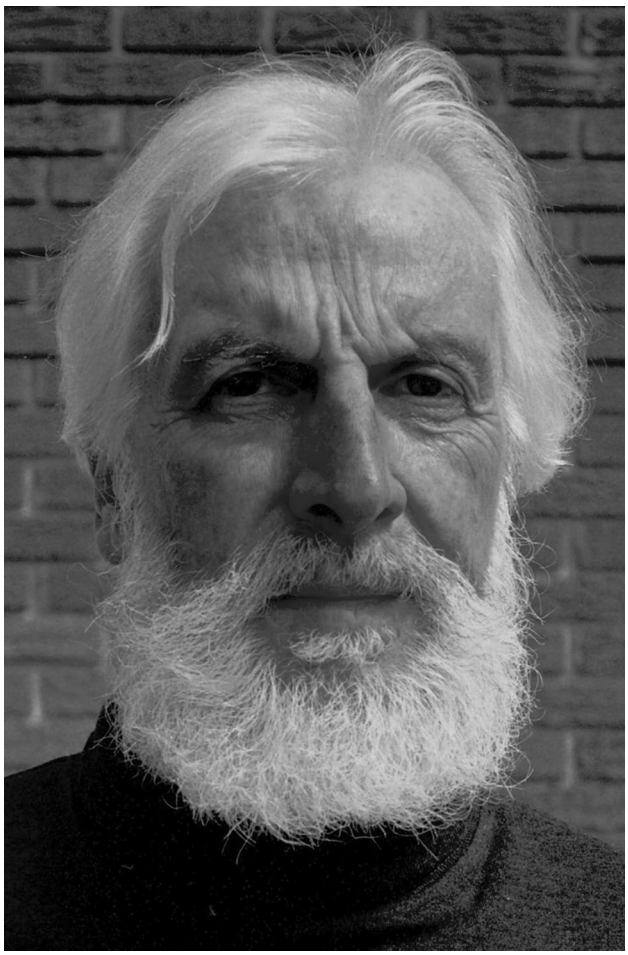

Fig. 1 Paul Struhsaker at age 66 years (photograph by Rejeanne Courcelles, all rights reserved)

During my first year at Michigan State University, I took an excellent introductory course in biology. That was another turning point that led me to major in the biological sciences. Having selected this field of study, I was permitted to take just about any course I wanted, regardless of prerequisites. In addition to courses in comparative anatomy, embryology, histology, botany, ecology, entomology, and ornithology, I was allowed to take advanced courses in physiology. In two of my three physiology courses, I was the only undergraduate. The one focusing on endocrinology was full of veterinarians seeking a Ph.D. I was clearly out of my depth, but somehow, I survived with my interest intact. The physiological basis of behavior was a topic I decided to pursue in graduate school.

Not only did I benefit from challenging and engaging courses taught by excellent professors, I gained a fabulous mentor through my part-time employment at the Michigan State University museum. I worked there all 4 years of my undergraduate studies, labelling specimens (mainly rodents and bats), and helping with the preparation of museum exhibits. The director of the museum was Rollin Baker, a mammalogist with a special interest in the deserts of southwestern USA and northern Mexico (Fig. 2). In my senior year Rollin supported my research on the morphological factors regulating flight in bats. This involved taking a variety of measurements of muscle volume and linear dimensions of wings from bats preserved in alcohol and reviewing literature on the functional anatomy of flight. I was able to publish a little paper on this study, concluding that wing aspect ratio was a major determinant of the differing flight patterns of bats (Struhsaker 1961). Functional anatomy became another strong interest of mine. After studying their anatomy, I wanted to see these different bat species in real-life flight. Added to this interest were entomology and ornithology, topics I had studied and strongly considered as fields to pursue as a profession. My interests in ornithology were further encouraged by a graduate student I met while working at the museum. I joined him on several weekends to net and band birds. While serving as a park ranger for three summers in Michigan's state parks I spent much of my spare time watching birds. A fourth summer I worked on a state funded project to study trout in several of northern Michigan's beautiful streams, the

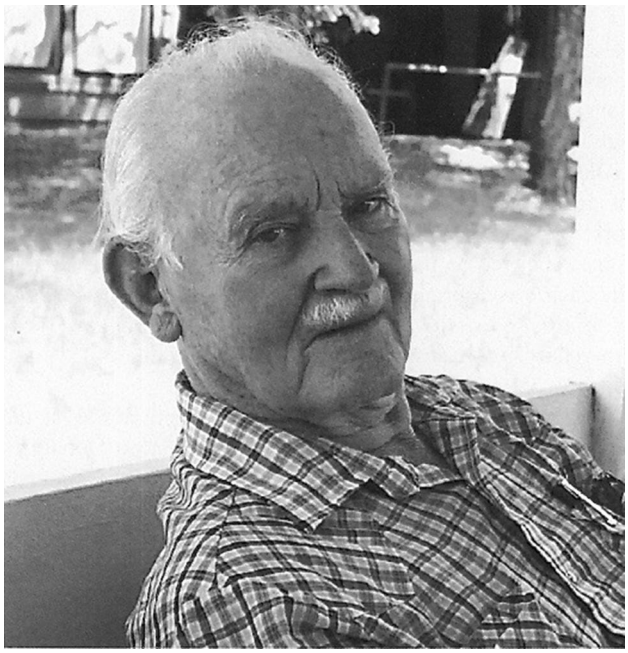

Fig. 2 Rollin Baker in his eighties (photographer unknown)

best summer job ever. It was becoming increasingly clear that virtually all of nature fascinated me.

Graduate school

Upon graduating from Michigan State University in 1960, Rollin Baker invited me to join his annual collecting expedition to northern Mexico. I was the youngest in our team of six; the others were graduate students and faculty. It was an incredible experience, and among the many things I learned, and perhaps the most important, was that I could actually earn a living having fun studying nature.

Following the trip to Mexico, I spent several weeks exploring the natural history and archaeological sites of the southwestern USA, living out of my old Ford. From there I continued on to the University of California, Berkeley to begin my graduate studies and job as a teaching assistant in the Department of Zoology. One of the first courses I was required to take was biochemistry. This course was designed for, and largely attended by, graduate students majoring in biochemistry. Once again, I was out of my league. Combined with my recent field experience in Mexico, this course caused me to rethink my idea of studying the physiological basis of behavior. It was the field, not the lab, for me. I was happiest working outdoors in nature, exploring the world, always wondering what was over the next ridge or around the next bend in the river.

Starker Leopold (the son of Aldo Leopold, the author of "*A Sand County Almanac: And Sketches Here and There* 1949") was my initial graduate advisor at Berkeley. His interests were in wildlife management primarily for the benefit of hunters and fishermen. In contrast, I was more interested in the behavior and ecology of animals for their own sake rather than as creatures to be killed and eaten. About this time Peter Marler took me under his wing and encouraged me to continue with my graduate studies (Fig. 3). One of the first things Peter urged me to do was to visit the San Francisco Zoo, to observe and sketch the postures and behavior of the resident spider monkeys. The idea behind this exercise was to train me to focus on the details of animal behavior. Trying to reproduce what I saw with a sketch greatly improved my observational skills.

Fig. 3 Peter Marler with a Jameson's wattle-eye, Kibale, 1971 (photograph by Art Arnold, all rights reserved)

Not long after I joined Peter's lab, our department hosted a seminar by Prof. John Emlen from the University of Wisconsin. His lecture summarized the studies of his graduate student, George Schaller, on mountain gorillas. This coincided with a time in the USA when there was an expanding interest and support of field studies of wild, free-ranging primates. Irv DeVore and his professor, Sherwood Washburn, were at Berkeley and frequently lectured about Irv's recent studies of baboons in Nairobi National Park, Kenya. Phyllis Jay Dolhinow had just returned to Berkeley from her studies of Hanuman langurs in India. She and Irv taught courses in the Department of Anthropology. All of this created an excellent atmosphere for anyone interested in pursuing a field study of primate behavior and ecology. Truth be told, it was Africa and its diversity of wildlife and habitats that I wanted to experience. A study of primates seemed a good way to raise funds that would allow me to have this experience.

One of the ideas being promoted by DeVore and Washburn was that primate social organization could be predicted in a general sense by the gross habitat a species lived in. Primates living in open savannas were predicted to live in large groups with several adult males, like the baboons of Nairobi

National Park. This is because large predators like lions and leopard are often prevalent in these habitats, where there are few trees in which primates can seek safety from them. There is safety in numbers and in groups with large males capable of deterring predators. In contrast, primates living in dense forests were expected to live in smaller groups with few or perhaps only one adult male because safety could be sought by climbing trees, where most forest primates spend most of their time, anyway. And there were fewer predators in the forest, or so it was thought. Thus large groups and many adult males would be of no particular advantage. Given DeVore and Washburn's idea, it seemed important to study other savanna-dwelling primate species in addition to baboons, to see how well this hypothesis held up. With that in mind, it seemed reasonable to propose a study of patas monkeys. Very little was known about this ground-dwelling, savanna species, but the few natural history notes available suggested that they did not live in large groups. Patas monkeys became the focal species of my Ph.D. thesis proposal. The field study would be so designed that I would learn as much as possible about the social organization, behavior, and ecology of patas monkeys. Although Peter Marler's research specialty was bird song development, he heartily endorsed my proposal. My plan was to conduct this research in Uganda, and to begin the fieldwork near the end of 1962. I had completed all but one of my obligatory courses at Berkeley. The last one was a summer field course in marine biology, which I took at Coos Bay in Oregon. The course dealt exclusively with the intertidal zone, and was another incredible experience. If I had not already committed to a study of primates, I would gladly have done a thesis on intertidal creatures.

Africa and vervet monkeys

It was December 1962 when I set off for Uganda with a skeleton budget combining a small grant from the university and personal savings from my job as a teaching assistant. Uganda had only gained independence a few months earlier, in 1962, and much of the government still had British advisors who made most of the decisions. Not long after arriving in Uganda, I was awarded grants from the National Science Foundation and the National Institute of Mental Health of the US government that were sufficient to cover essential expenses. With an old Land Rover, I spent the next several months travelling around Uganda looking for a good site to study patas.

Although I had an enjoyable time learning a tremendous amount about the wildlife, people, and geography of Uganda, it became apparent that the patas I encountered were not good subjects for study by an inexperienced graduate student. The monkeys were usually on the ground, very shy, and hidden by the very tall grass. Although it was clear that I could not collect the amount and kind of data required for a thesis, I learned that this ground-dwelling, savanna species lived in small groups usually with only one adult male, confirming early natural history observations and contradicting the prevailing hypothesis about habitat and social organization. It was time to choose another species, and vervet monkeys were the obvious choice because of their abundance and widespread distribution. After a few more months of surveys in Uganda and Kenya, I was directed to Amboseli, the perfect place for my study. Not long after setting up camp in Amboseli, Irv DeVore introduced me to Stuart and Jeanne Altmann. Stuart and Jeanne were looking for a good site to study baboons. I did everything I could to encourage them to come to Amboseli. Fortunately for me, they did. They were great companions and colleagues. We met every evening for dinner, where we exchanged ideas and our observations of the day. Stuart had already completed studies of howler monkeys on Barro Colorado Island and rhesus monkeys on Cayo Santiago, Puerto Rico, and was an outstanding mentor. It was Jeanne's first study of primates, but with her mathematical background and ability as a critical thinker, she provided a constant flow of invaluable ideas (Fig. 4).

I spent the next 12 months (June 1963–June 1964) focusing on four groups of vervets, collecting as much data as I could on everything they did (Fig. 5). Because virtually nothing had been published on the behavior and ecology of vervets, it was not possible to pose hypotheses and predictions, aside from the rather simple idea that gross habitat shaped social group composition and size. It was a time when collecting basic information and describing behavior (ethograms) were primary goals. It is this kind of information that makes possible the creation of reasonable hypotheses and predictions. My studies resulted in a number of publications on vervet behavior and ecology (Struhsaker 1967a, b, c, d, 1971a). One in particular piqued the interest of Peter Marler, the paper on vocalizations where, among other things, I described the vervet alarm calls that distinguished between three general categories of predators: mammals, birds, and snakes (Struhsaker 1967e). Peter encouraged and supported a follow-up study of my findings on these alarm calls by Dorothy Cheney and Robert Seyfarth, resulting in a series of excellent playback experiments over several years in Amboseli (e.g., Seyfarth et al. 1980) that, among other things, supported the results of my field observations. Many years later I discovered that the red colobus monkeys of Kibale also have specific alarms calls for an avian predator and poisonous snakes (Struhsaker 2010).

In terms of the idea that gross habitat is a strong correlate/predictor of group size and the number of adult males in a group, my study of vervets in Amboseli indicated that the relationship was more complex than initially thought.

Fig. 4 Jeanne and Stuart Altmann, 1963 (photographer unknown)

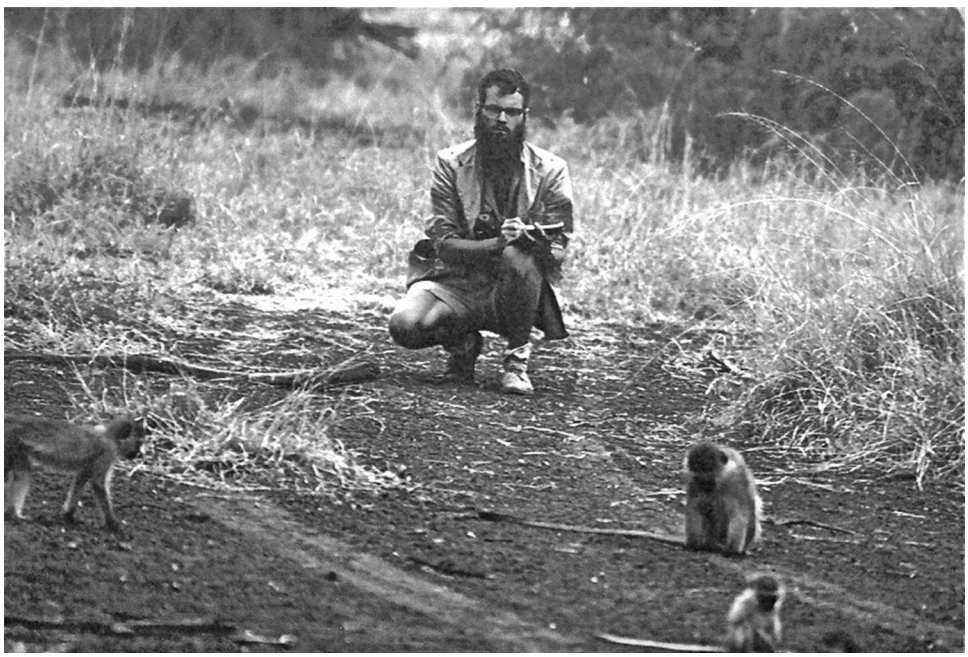

Fig. 5 Author with Amboseli vervets, 1963 (photograph by Stuart Altmann, all rights reserved)

Although baboons and vervets could be generally classified as savanna-dwelling monkeys, there were important differences in their ecologies. While baboons often foraged far from trees, vervets never did so to the same extent. This might explain in part why baboon groups were often so much larger and had more adult males than did vervet groups, at least in Amboseli. However, with more studies on vervets by Gartlan and Hall (1965) and me (1967a), and those on baboons by the Altmanns (1970), DeVore and Hall (1965), and Hall and DeVore (1965), it became apparent that there was tremendous intraspecific variation in group size and composition. Gross habitat was not an adequate predictor of social organization. I realized that, if we were to better understand the relationship between habitat and social organization, detailed studies were needed of rain forest primates because the rain forest is where the majority of primate species reside.

One of the most important consequences of my field study of vervets and other wildlife in East Africa was something that never appeared in any publication. I came to appreciate the lifestyles of other species and to develop a deep empathy for them. Spending thousands of hours

watching them engage in all their social activities and surviving from one day to the next gave me a different perspective on my own species. This was an adventurous, fulfilling, and happy time of discovery.

At the time I left Kenya to analyze my data and write my thesis, Peter Marler began his sabbatical leave to study the black-and-white colobus monkeys in the Budongo Forest, Uganda. This meant I would have no advisor back in Berkeley. Fortunately for me, the Altmanns invited me to join them at the University of Alberta in Edmonton where Stuart held an appointment. This was a great opportunity for me to continue benefitting from discussions and advice from Stuart and Jeanne.

Postdoc study of elk

During my time in Alberta, I visited Val Geist (now an authority on North American large mammals) in Banff National Park, where he was studying bighorn sheep for his Ph.D. It was the first time that I saw bighorn sheep, mountain goats, grizzly bears, and elk in the wild. I had always thought of elk as being one of the most beautiful and stately animals in North America. This visit inspired me to find a way to return to study them. Thanks to Stuart, who had contacts in the Canadian Wildlife Service, I was given a short-term contract to study the impact of aggression between male elk during the fall mating season on mortality, and the extent to which this might explain the skewed adult sex ratio among the elk in Banff. After completing my Ph.D. thesis, I began my 2-month study on elk in late August 1965. The Cascade Valley was a paradise for me, totally closed to the public and occupied only by me and two rangers whose homes were 5 km from my cabin. Water was from the nearby stream and heat from a wood-burning stove. I did have a crank-style telephone allowing contact with the two rangers. As per my training, I took notes on everything I saw and made lots of tape recordings. Intense sparring between males was rare and only once did I see a male inflict a body blow on another (Struhsaker 1967f). Another study done in conjunction with mine concluded that the older males lost much of their body fat during the mating season (Flook 1967). This coincided with my finding that harem males and solitary males of similar age fed for only a fraction of the amount of time that all other age-sex classes fed. These males were spending much of their time defending females against other males, rather than feeding. Because these older males went into the long, bitterly cold winter with little, if any, fat reserves, they likely starved to death. Thus starvation seemed to contribute in a major way to the uneven adult sex ratio.

Cameroon and rain forest primates

Following the elk study, I returned to Berkeley for a postdoctoral fellowship with Peter Marler, during which time I published my vervet and elk research. While I was at Berkeley, Peter was offered a joint position with the Rockefeller University and New York Zoological Society (Bronx Zoo). He along with Don Griffin, who discovered bat echo location and established the field of cognitive ethology, formed the Institute for Research of Animal Behavior, a collaborative endeavor between the university and the society. Peter asked me to join this group, an opportunity critical to my future career and life style. Aside from Peter, Don, and me, others in the institute included Fernando Nottebohm (another Marler student of bird song), Roger Payne (whales), George Schaller (large mammals), and Rich Penny (penguins). Our mandate was to conduct full-time field research on wildlife of our choosing, to learn as much as we could about them, and to make conservation recommendations.

I moved to Manhattan for a few months in 1966 and successfully raised funds to commence a study of drills in Cameroon. At that time drills were thought to be closely related to baboons. A study of drills in the rain forest would yield important data on the relationship between gross habitat and primate social organization. In November 1966 I arrived in West Cameroon, where I spent the next 19 months attempting to study drills. It soon became apparent that this was going to be extremely difficult because virtually every primate in Cameroon was, and still is, hunted for food. Habituation was out of the question. And there was the incredibly heavy rainfall. My main study site was located near the Idenau oil palm plantation on the windward side of Mt Cameroon. During my time there, the annual rainfall was 10,305 mm (405.7 inches). Added to this were the inherent problems of observing rain forest primates, especially those spending time high up in the trees. It did not take me long to realize that I needed to change the direction of my research to one that was opportunistic, collecting whatever data I could on any primate species I saw. Very little was known about the behavior and ecology of any of the primates living in that part of the world, so I spent about half my time at Idenau and the other half surveying numerous forests throughout Cameroon, including two short trips to observe patas monkeys in the very hot and arid Waza National Park in the far north.

Not long after I arrived in Cameroon, I learned that Steve Gartlan was also in Cameroon to study drills. Steve and I first met in Uganda in 1962, where he studied vervets for his Ph.D. It was time to collaborate. Steve studied in the Southern Bakundu Forest Reserve near the town of Kumba, only a few hours' drive north of my study site. We met frequently to compare data and eventually published papers together.

Although I failed to achieve my goal of completing a refined study of drills, my observations in Cameroon yielded important data of relevance to theory and practice. I was able to make qualitative observations on social behavior and gain a clear idea of group size and number of adult males per group for drills, several guenon species, mangabeys, colobus, and patas. Drills, who spend most of their time on the ground, were sometimes found in groups as large as those of savanna baboons, and with several adult males. There was an indication that drills had fusion-fission societies, a conclusion more strongly supported by Gartan's study (1970). I found that the arboreal mangabeys also lived in multimale groups. In contrast, the arboreal forest guenons usually had only one adult male per group, just like the terrestrial patas monkeys of Waza (Struhsaker 1969a; Struhsaker and Gartlan 1970). It was then more obvious than ever that gross habitat type was not a good predictor of social group size or number of males per group. Nor did it matter if a species was primarily terrestrial or arboreal. Clearly, other factors were influencing group size and composition.

My Cameroon studies were the first to describe hybrids between species of guenons in the wild (Struhsaker 1970a). Gartlan and I (1972) described the very high incidence and non-randomness of polyspecific associations and niche separation, proposing that many of these associations were formed as a defense against predation. A very large part of my time in Cameroon was spent recording the vocalizations, and their context, of several species and subspecies of guenons and drills (Struhsaker 1970a). The recordings were the first ever for most of these species. I was able to show that all these species had contact calls, that there were differences in vocal repertoires between males and females, and that adult females and juveniles were the primary emitters of alarm calls, not adult males. It was also clear from my data that vocalizations were extremely stable characters from an evolutionary perspective, and good indicators of phylogenetic relationships. For example, the vocal repertoires of *Cercopithecus erythrotis* and *Cercopithecus cephus* are identical, indicating that they are the same species. This conclusion was supported by my observation of forms intermediate in facial color patterns to those of these two taxa in what was apparently a hybrid swarm in a zone of secondary contact (Struhsaker 1970a). Many years later, the idea that vocalizations among the guenons are evolutionarily stable and indicators of phylogenetic affinities was supported by Dutrillaux et al.'s (1988) chromosomal study and Gautier's (1988) analysis of vocalizations from more species and subspecies. I continued to pursue this idea with my studies of red colobus, i.e., that the vocalizations of monkeys are relatively stable characters and a better indicator of phylogenetic affinities than are the more commonly used characters of coat color and even skull morphology. Many of the similarities and differences in the vocalizations of the various red colobus taxa could be understood in terms of their distance from proposed Pleistocene forest refugia (Struhsaker 1981a, 2010).

The Cameroon experience made me aware in the clearest way possible just how threatened Africa's rain forests and their wildlife were. Shorter trips to Equatorial Guinea and Ghana during the same period only reinforced my impression that this entire biome, which was full of endemic species, was seriously under threat of extinction from human activities, such as hunting, logging and agriculture. It was critical that rain forest parks be created. Although I failed to achieve anything of relevance to conservation during this time, the seed was planted, and years later it germinated and grew.

Prior to my time in Cameroon, all of my education and training had been gleaned from those with formal education: my parents, brother, and teachers. Studies of rain forest animals, especially in forests with no established trail system or other facilities for research, require knowledge that is best gleaned from those who know the forest. In this regard, my training was mostly from Cameroonians who had little or no formal education. For me, it was on-the-job training: observe and learn. My guides all had a background in hunting. They knew how to read the signs and sounds and find their way around a forest. Ferdinand Namata was the best of these. We spent almost a year together, in the forest for many hours almost every day, travelling all over Cameroon. I could not have collected as much information as I did without his tireless and cheerful assistance and his superb knowledge of the forest and all its inhabitants (Fig. 6).

When my studies in Cameroon were completed in 1968, I spent a month in Ghana tape-recording more species and subspecies of guenons to further examine the idea about the stability of vocalizations from an evolutionary and phylogenetic perspective. Back in Manhattan at the Rockefeller University I wrote up my results from Cameroon and spent quite a bit of time next door at the Cornell Hospital's tropical medicine clinic being treated for all the parasitic infections my body had collected over the past 19 months: bilharzia, roundworms, etc. Some of the medicines made me feel sicker than did the parasites.

In addition to analyzing data and writing papers, I was asked to make a supervisory visit to Steve Green, a student of Marler, who was studying vocal communication among Japanese macaques at several sites in Japan. This was a great opportunity for me to learn about another species and another culture. Koshima Island was the best: beautiful and tourist free. Not many months later, after returning from Japan, I was once again able to escape the madness of Manhattan. Along with Peter Marler, Don Griffin, and Theodosius Dobzhansky, I helped teach a 3-month field course in animal behavior and ecology to five graduate students from the Rockefeller University, which was held in Trinidad and

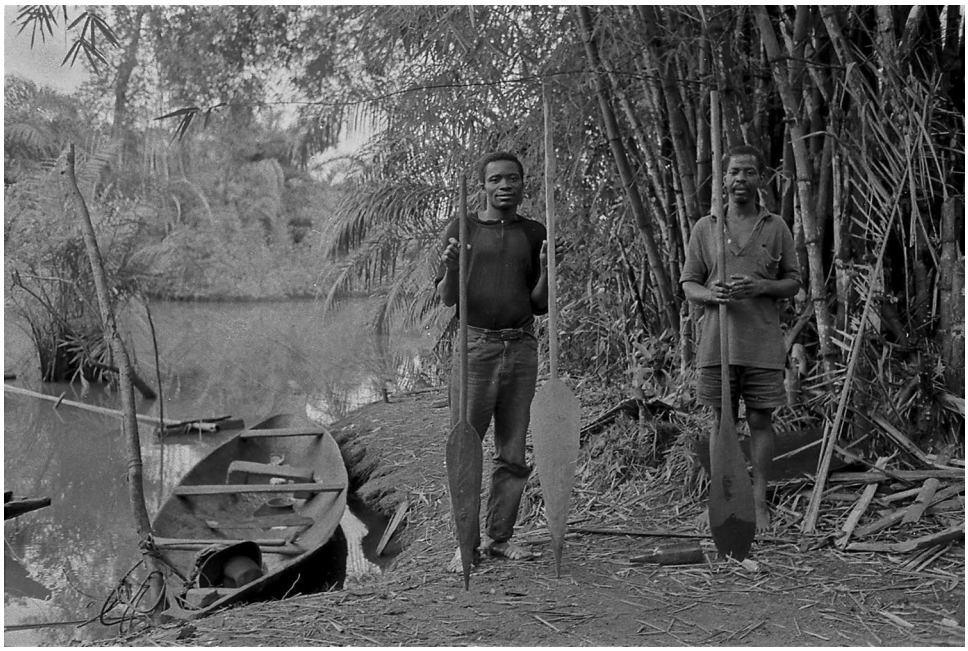

Fig. 6 Ferdinand Namata (*left*), Masore mangrove swamp, Cameroon, 1967 (photograph by the author, all rights reserved)

Barro Colorado, Panama. This course allowed me to broaden my knowledge of the tropics and primates. It also provided me with the opportunity to explore some of my other interests in biology, such as spiders (Struhsaker 1969b). More importantly, two of the students became committed to tropical studies for much of their professional life (Haven Wiley on birds and Carl Hopkins on electric fish).

Red colobus monkeys, other primates, and Kibale Forest

It was while at the Rockefeller that Peter Marler told me about a 2-day visit that he had made to the Kibale Forest during his 1964 sabbatical in Uganda. Peter was struck by the extreme differences in social organization of the two colobus species living there. The black-and-white colobus lived in small groups, whereas the red colobus groups were much larger. At that time, both species were considered as belonging to the same genus, which made the idea of a study comparing them in the same area all the more appealing. The situation in Kibale provided an opportunity to further examine how habitat affected social organization. With that in mind I raised funds for a study of red colobus monkeys, species about which we knew very little.

In December 1969, I began a 5-month search for a long-term study site of red colobus. This survey took me first to Senegal and Gambia, then to the Tai Forest Reserve of Ivory Coast. While searching for monkeys in Tai I was able to collect indirect evidence that chimpanzees were using stones and sticks to smash open nuts (Struhsaker and Hunkeler 1971), something already well known by my tracker and other hunters and gatherers using the forest. One consequence of these observations and publication was the long-term research project of Christophe Boesch and his colleagues on the chimpanzees of Tai, thanks to the collegial efforts of the late Prof. François Bourlière (Boesch and Boesch-Achermann 2000). From Tai I surveyed the Korup Forest Reserve in Cameroon, and finally the Kibale Forest Reserve of Uganda. Although these surveys lasted only a few weeks in each country, they were very productive in terms of the new basic information I was able to collect on red colobus, such as the presence of large sexual swellings in some species and not others. The tape recordings I made and analyzed remain the only ones of these red colobus species that have been published, and the first to describe the copulation calls of females and males of some, but not all, species (Struhsaker 1975a, 2010). In addition to these discoveries, this survey further reinforced my fears over the future of Africa's rain forests and the potential loss of an entire biome due to overhunting, logging, and agriculture (Struhsaker 1972).

I chose Kibale as a major study site for many reasons. Firstly, the monkeys were not hunted, unlike in the sites in Ivory Coast and Cameroon. Secondly, Kibale was a relatively large forest compared to the forests in Senegal and Gambia. Finally, the local people were friendly and receptive to the idea of research, and the climate was near perfect.

My survey of the Kibale Forest began in May 1970, and after a month or so, I started creating a trail system in the forest adjacent to the Kanyawara Forest station, under the administration of the Uganda Forestry Department. Later in 1970 I was joined by John Oates, who studied the black-and-white colobus for our comparison of the two colobus species

in Kibale (Oates 1977; Fig. 7). Among the many findings of our comparative study were that these two colobine monkeys, although both largely folivorous, differed to some extent with regard to the plant species and stages of development of the leaves they consumed. Furthermore, the red colobus in Kibale were not territorial, whereas the black-and-white colobus defended a core area within their home range. The red colobus groups were larger, with several adult males, while the smaller black-and-white groups usually had only one adult male (Struhsaker and Oates 1975; Fig. 8). Little did I realize at the time that I would remain in Kibale for the next 18 years as a full-time resident of Uganda. During these 18 years my living conditions remained rustic: a tin, one-room hut without electricity or running water, and no cell phones or computers. It was marvelous simplicity.

In January 1971, not long after John arrived, Idi Amin staged a coup d'état, overthrowing Milton Obote. The negative impacts of this coup on Uganda were not immediate and it seemed reasonable to host another field course for Rockefeller graduate students, this time in Kibale and Queen Elizabeth National Park. Once again, this was Peter Marler's idea, and he raised the funds for this incredible experience. The 13-week course began in April 1971 when five students along with Marler, Karen Minkowski (our camp manager) and Steve Green (graduate student assistant) arrived in Uganda. A tented camp was established at Kanyawara and after a week or two of a general introduction to forest ecology, including bird banding, tree enumeration, and soil analysis, the students selected their own research projects, working in pairs or alone. One of these students was Peter Waser, who did his project on mangabey behavior and ecology. Peter became so enthusiastic about this study that he returned the following year to continue observing the mangabeys for his Ph.D. thesis (Waser 1977; Fig. 9). In 1972 we were joined by Rudy Rudran, a Ph.D. student of John Eisenberg at the University of Maryland. Rudy studied the behavioral ecology of blue monkeys (Rudran 1978). The following year I expanded my research to redtail monkeys, while continuing with my studies of red colobus. We were now accumulating a solid set of baseline data on the behavioral ecology of five species of sympatric monkeys, leading, among other things, to a better understanding of

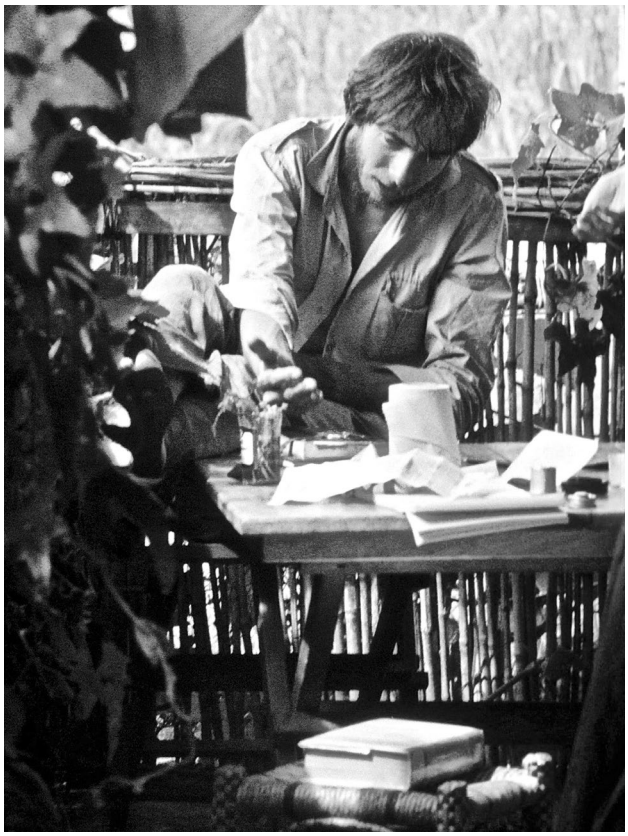

Fig. 7 John Oates identifying plants, Kanyawara, Kibale, 1974 (photograph by Peter Waser, all rights reserved)

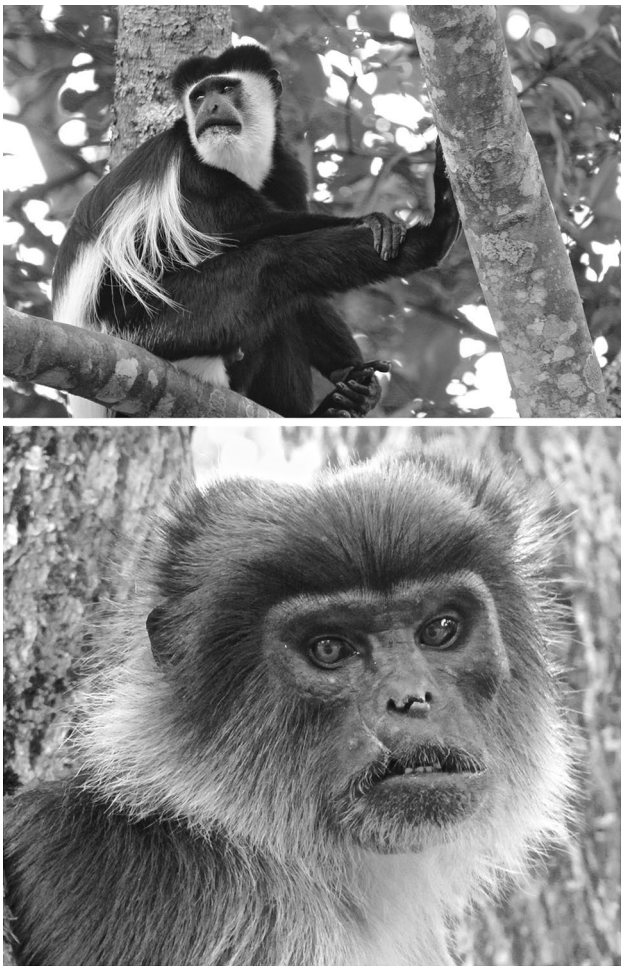

Fig. 8 Adult male black-and-white colobus (*top*), adult male red colobus (*bottom*), Kanyawara, Kibale (photographs by the author, all rights reserved)

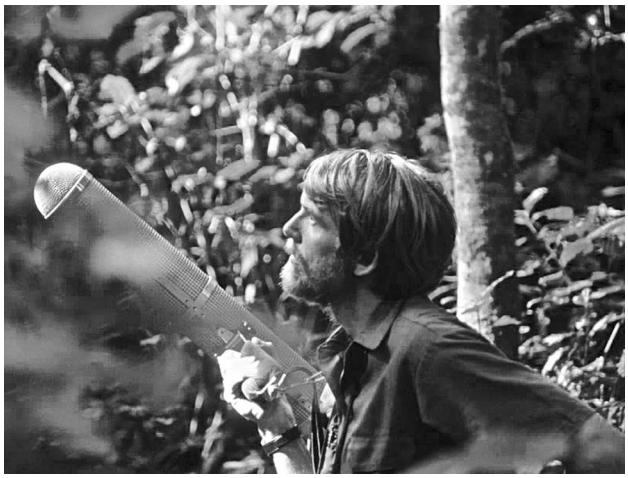

Fig. 9 Peter Waser tape-recording mangabeys, Kibale, 1972 (photograph by Mary Sue Waser, all rights reserved)

the relationship between habitat and social organization and social behavior, and interspecific dietary overlap and potential competition. One of the discoveries I found most interesting was that dispersal by red colobus from their natal group was primarily by females, in contrast to all the other monkey species in Kibale, where it is the males who are the primary, if not only, dispersers. In this way red colobus resemble chimpanzees and mountain gorillas (Struhsaker and Leland 1979).

In 1972 I was given an honorary appointment in the Department of Zoology at Makerere University, Kampala. Among other things, this allowed me to supervise Ugandan graduate students. The first of these was Deborah Baranga, who studied the chemistry of black-and-white colobus diets in Kibale from 1974 to 1975, making a significant contribution to our understanding of this species' ecology. After completing her master's degree in Kibale, Deborah went on to complete her Ph.D. with a study of redtail monkeys near Kampala. Following that she had a long career teaching at Makerere. In 1976 Isabirye Gil Basuta joined our project to study the impact of selective logging on rodent populations for his master's degree. This was the first of a long and important series of studies on the impact of selective logging on species other than primates. Gil went on to study the chimpanzees at Kanyawara for his Ph.D. John Kasenene joined us in 1978, studying the impacts of selective logging and rodent populations on forest regeneration for both his M.Sc. and Ph.D. Basuta and Kasenene jointly served as the administrators of the Kibale field station for a number of years, as well as having long careers teaching at Makerere University. The last Ugandan student I supervised was Jerry Lwanga. Jerry began his studies in 1984, focusing on group fission in blue monkeys for his M.Sc. (Lwanga 1987), and on seed and seedling predation of key tree species for his Ph.D. (Lwanga 1994). Jerry went on to teach at Makerere University and to become director of the field station at Kanyawara and manager of the long-term chimpanzee studies at Ngogo, the latter in collaboration with John Mitani and David Watts. During my 18 years in Kibale a total of 12 Ph.D. and five M. Sc. degrees were completed.

With my long-standing interest in ornithology, the begging calls of a nestling led to the discovery of a crowned hawk-eagle nest in the center of my main study area at Kanyawara. Examination of the bones found underneath this nest allowed us to estimate prey selectivity by this species, the most important predator of monkeys in Kibale (Struhsaker and Leakey 1990).

The Kibale project created a methodology for studying rain forest primates, such as establishing a marked and measured trail system, a sampling regime for behavioral ecology, and a standard for estimating primate abundance through line transect censuses (Struhsaker 1975a, 1981b). Our experience with line transect censusing of primates demonstrated why the Distance method, commonly used elsewhere, was inappropriate for estimating densities of rain forest, group-living primates, and often overestimated true densities when compared with those based on focal group studies. Reasons for rejecting the Distance method are detailed in Struhsaker (1997, 2010).

My 18 years of study in Kibale expanded our understanding of the biology of red colobus (Struhsaker 1974, 1975a, 1978, 2010; Struhsaker and Pope 1991) and redtail monkeys (Struhsaker 1977, 1980, 1988, 2017a; Struhsaker and Leland 1988), by demonstrating, among other things, the great variability and dynamics of social group size (including group fission) and composition and temporal variation of diet. One obvious conclusion from these results is that a thorough understanding of intraspecific variation is essential before meaningful interspecific comparisons can be made. These were also the first studies to document infanticide in rain forest monkeys (redtail monkeys and red colobus), providing data supporting the idea that infanticide has reproductive advantages to the infanticidal male (Struhsaker 1977; Struhsaker and Leland 1985; Leland et al. 1984).

In 1974 a second research camp was established at Ngogo, in the middle of the Kibale Forest and about 10 km from our main base at Kanyawara. Initially, we camped at this site for 7–10 days each month, but eventually, a few small mud wattle huts were constructed. The forest at Ngogo differed from that at Kanyawara in terms of tree species and proportional composition of the primate community. Blue monkeys, for example, had much lower densities of groups and adult females but higher densities of solitary adult males at Ngogo than at Kanyawara. This meant a shortage of mates for males and may have been one of the reasons for a higher incidence of infanticide by blue monkeys and hybridization between blue monkeys and redtail monkeys at Ngogo

compared to Kanyawara (Butynski 1990; Struhsaker et al. 1988).

Long-term monitoring at both the Kanyawara and Ngogo sites demonstrated the great temporal variability in tree phenology and species composition of primate, rodent, and tree communities (Struhsaker et al. 1989; Struhsaker 1997; Lwanga et al. 2000, 2011). These results clearly demonstrated the importance of long-term monitoring in terms of describing forest community dynamics, and the limitations of using data based on only a few years' study to make generalizations regarding ecological correlates, such as the relation between tree species composition and primate diversity and density. It was, for example, the long-term censusing at Ngogo that revealed the massive decline in red colobus monkeys due to predation by chimpanzees (Mitani et al. 2000; Teelen 2008; Lwanga et al. 2011). Kibale was an ideal place for this kind of long-term research because our study sites were reasonably well protected, and the primates there were not targets of hunters.

Being able to habituate the monkeys in Kibale meant that I was able to make more refined and detailed observations of interspecific associations and social interactions, much more so than in Cameroon where I first became interested in these subjects. Virtually every conceivable social interaction that occurred within a monkey species also occurred between different species in Kibale, even reproduction (Struhsaker 1981c, 2010). I was fortunate to be able to follow and observe hybrids and backcrosses between redtail and blue monkeys for many years (Struhsaker et al. 1988). The high incidence of polyspecific associations in Kibale and elsewhere in Africa led to a series of papers discussing likely causes, which ranged from pure chance (Waser 1982), similar diets, to predator avoidance (Gautier and Gautier-Hion 1969; Struhsaker 1981c). My field experience in Colombia, Surinam, Malaysia, and Sumatra, albeit limited, along with the studies of others, clearly indicated that monkeys in those countries were less likely to form interspecific associations than those in Africa, likely due to the absence or paucity of large avian predators. Only the smaller monkey species in Colombia and Surinam were often seen in polyspecific associations, perhaps because they were prone to more predation by several smaller species of raptors (Struhsaker 1981c). When I conducted studies on the islands of Zanzibar and Bioko, I was immediately struck by the paucity of polyspecific primate associations when compared to their mainland counterparts. Raptor predators and leopards were absent from both islands, and this gave further support to the idea that these associations are, to a very large extent, a means of reducing the risk of predation (Struhsaker 2000). These results are but some examples of the many insights to be gained by visiting other sites.

It was the detailed observations of social interactions between redtail, blue, hybrid, and red colobus monkeys I made in Kibale, however, that led me to wonder whether or not individuals of one species might not have "friendships" with individuals of other species with whom they frequently associate. Individuals of different species groom one another, play together, and even reproduce (Struhsaker 1981c, 2010; Struhsaker et al. 1988). There was, for example, a case of an adult male blue monkey who spent many years with a group of redtail monkeys that included an adult female hybrid and backcross (Struhsaker et al. 1988). This blue male moved with the redtail group and occasionally even helped defend its territory against neighboring redtail groups. Should we broaden our definition of the primate social group to include associations between different species, especially when these associations are common and affiliative behavior occurs between them? Do non-human primates also have "the urge to affiliate with other forms of life," as expressed by Erich Fromm in his concept of biophilia (1964)?

Conservation in Kibale

When I arrived in Kibale, selective logging was ongoing and rapidly approaching my study area at Kanyawara. Kibale was a forest reserve that was meant to supply timber for domestic markets and export to neighboring countries. A short walk through logged areas revealed the devastation. Far too many trees had been removed and many more were killed during the process of felling and extraction of the species sought by the loggers. In addition, in some areas, tree species considered of no commercial value were poisoned with an arboricide. These practices led me to take three actions. The first was to approach the Uganda Forest Department's research department and request that the area where I was studying primates be declared a research site and off-limits to logging. It took a while, but in March 1973 compartments K14 and K30 were officially declared research plot 703, thanks primarily to Tony Stuart-Smith, who was senior conservator of research. Logging would not occur where we were conducting our research. This was not appreciated by some of the Ugandan foresters who, at that time, seemed to have little interest in basic ecological research or conservation of the natural forest.

The second course of action was to begin studies of the impact of logging on the flora and fauna. Results from such studies would help us to develop a stronger case for forest conservation and recommendations for timber harvest methods that would minimize the negative impacts of logging on forest regeneration and wildlife. This led to a series of long-term studies by many students and postdocs, which explored the impacts of varying degrees of logging intensity on vegetation, forest regeneration, and populations of primates, rodents, birds, insects, and elephants

(Struhsaker 1997). Some of the more important conclusions were that the then current levels of logging were having a negative impact on tree regeneration, populations of most primate species, and were altering the avian species composition. Rodent populations increased in heavily logged forest and were likely one of the reasons forest regeneration there was poor, due to their consumption of seeds and seedlings. Elephants used heavily logged forest more than unlogged forest, probably because of the dense growth of herbaceous vegetation that developed after heavy logging had allowed in more sunlight, resulting in a "salad bar" for the elephants (Struhsaker et al. 1996; Struhsaker 1997). Elephants not only trampled tree seedlings in the heavily logged areas, but also pulled up the smaller, young trees of several canopy tree species to eat the cambium. The dense herbaceous vegetation that developed after heavy logging also had a direct negative impact on tree seedling survival, through competition for resources. As a consequence of these studies, a number of recommendations were made regarding the management of tropical forests, with an emphasis on their conservation and non-extractive uses (Struhsaker 1987, 1990, 1997).

My third course of action begin in 1970 when I started lobbying for Kibale to become a national park. This was part of a broader attempt to protect more of Africa's rain forest from west to east (Oates et al. 1987, 2000; Struhsaker 1972, 1987, 2005, 2010). Over the following decades many others joined in this effort, and after 23 years of lobbying, through civil wars, political unrest, corruption, and economic chaos, Kibale was eventually declared a national park in 1993.

When I began studying in Kibale there was no effective protection against the theft of timber and the poaching of animals. Hunting was not allowed without a permit. The only permit I knew of was one granted to the forest department, allowing them, in cooperation with the game department, to kill a certain number of elephants every year. Elephants were considered detrimental to timber production because of the damage they caused to some tree species. Most of the illegal hunting focused on duikers, bushbuck, bush pigs, and buffalo, and was done with snares, nets, and dogs, and to a much lesser extent with guns for buffalo and elephant. Initially I attempted to deter poachers from my study area by removing snares and destroying the spears and nets that I confiscated from them. It soon became apparent that illegal activities were so widespread in Kibale that I needed help. I asked the Game Department for assistance and they assigned two, and eventually three, game guards to work with me. The Game Department paid the salaries of the guards, while I supervised them, assisted them with logistical support, and paid them bonuses for the spears, snares, nets, crosscut saws, sawn boards, and pangas (machetes) they confiscated, and for every poacher that was convicted in court (Struhsaker 1997, 2002).

Dealing with illegal encroachment by farmers in the southern part of Kibale was more difficult because they were often encouraged by politicians and corrupt high-ranking forest department officials. The best I could do was to lobby even higher-ranking officials. Given the political and economic chaos, the corruption and the lack of professionalism during the despotic reigns of Idi Amin and later Milton Obote, this approach was not very effective (Struhsaker 1997, 2002). Each of these regimes was estimated to have been responsible for the death of at least 300,000 Ugandans (Lamb 1987; Mutibwa 1992). Corruption proliferated during these times due, in large part, to the economic collapse, and because government employees' salaries were grossly inadequate and paid at infrequent intervals. This encouraged poaching of animals and timber and illegal agricultural encroachment into the forest reserves by the very employees meant to protect these resources. Achieving effective conservation was challenging to say the least. Our efforts at protecting Kibale met with resistance from some of the foresters. The worst case of this occurred when the Tanzanian army invaded Uganda to overthrow Idi Amin. One of the forest officers at Kanyawara organized and accompanied a small group of soldiers (Tanzanian and Ugandan) who came to my home and robbed me at gunpoint, stealing many items from my home, including my Land Rover. With the assistance of higher-ranking Tanzanian officers, we were able to recover the Land Rover and some of my personal items. The forester was eventually arrested and imprisoned for a short time, but then released [see Struhsaker (2021) for details].

The economic collapse of Uganda meant that even the most basic items, such as rice, sugar, salt, soap, and fuel, were in short supply and could only be obtained by trips to Kampala, if you knew someone there with connections. Sometimes we had to drive to Kenya to get these basic items. These trips were particularly tiresome and long because the road to Kampala was largely unpaved and in a terrible condition. Along with this were the many roadblocks, up to 18, manned by soldiers who were often drunk. Getting through these required patience and imagination, how to convince these guys to let us pass.

Dealing with government officials during the Amin years was particularly challenging because many, if not most, of them were semi-literate at best. There was great suspicion that Obote or someone else was preparing to stage a coup. After all, Obote had attempted one in 1972. One consequence of this paranoia was that Peter Waser (at that time studying mangabeys in Kibale for his Ph.D.) and I were once arrested as spies. We were only held for a few hours, but for a while our fate seemed uncertain, particularly so when an army officer waving an AK-47 stormed into the room and began yelling and shouting that our passports were forgeries and that we were spies. Fortunately, this was at a time when there were still some educated Ugandans in government who

had not yet fled the country. They knew how to deal with these guys and managed our release [see Struhsaker (2021) for details].

In addition to our research on primates and forest ecology and our lobbying and anti-poaching efforts, we worked with local schools and the Wildlife Clubs of Uganda to promote education relevant to conservation. These latter activities included field trips and lectures at Kanyawara for schoolteachers and their students and providing native tree seedlings from our tree nursery to schools for woodlots. As mentioned earlier, the training of graduate students was a major focus of my activity in Kibale and elsewhere (Struhsaker 1997a; Fig. 10).

Studies elsewhere (a busman's holidays)

During my 18-year residency in Kibale, I had the opportunity to conduct surveys and to visit the research projects of colleagues throughout the tropics. These trips broadened my understanding of tropical forest ecology, primate behavior, and conservation issues. With the financial support of my employer, the New York Zoological Society, I was able to fund, initiate, and supervise Clive Marsh's Ph.D. study of the Tana River (Kenya) red colobus in 1973 and, along with Steve Gartlan, Doyle McKey's Ph.D. study of the black colobus in the Douala-Edea Forest Reserve of Cameroon in 1974. Both of these studies made important contributions to our understanding of the variability in colobine biology. The Tana River effort led to the creation of a national primate reserve (largely due to the efforts of Clive) and many more studies of the endemic primates and forest ecology of this reserve. This was part of a broader objective of mine to study and conserve the four endemic red colobus taxa in East Africa, all of whom were considered to be threatened or endangered.

Doyle McKey was a student of Dan Janzen, then at the University of Michigan. Janzen was particularly interested in the role of plant secondary compounds as defense mechanisms and, not surprisingly, so was Doyle. This interest in turn rubbed off on Steve Gartlan and me, resulting in comparative studies of plant secondary compounds and nutrients in tree leaves of forests growing on different soil types (Douala-Edea vs Kibale) and how this correlated with the abundance of colobines (McKey et al. 1978; Gartlan et al. 1980). The phytochemistry of leaves from individual trees that had been initially sampled in Kibale during the 1970s and were again sampled 30 years later showed a decline in nutritional quality (protein-to-fiber ratio), possibly reflecting an impact of climate change (Rothman et al. 2015).

In 1974 I was invited to serve as a consultant to the Pan American Health Organization as part of a team that conducted a 2-month survey of northern Colombia. The objective of this survey was to evaluate the population status of the cotton-topped marmoset and the night monkey, both of which were used in biomedical research. Our team was headed by Norm Scott, and it was not long before we realized that the habitats of both the cotton-topped marmoset and the night monkey were under threat and that these species faced extinction (Scott et al. 1976). Following this

Fig. 10 The author with Ph.D. students John Kasenene, Gil Isabirye Basuta, and Jerry Lwanga (photograph by Lysa Leland, all rights reserved)

survey, I headed south to explore Parque National La Macarena with Lysa Leland. We spent 3.5 weeks conducting wildlife censuses in the vicinity of cabana El Duda. The area was full of wildlife at that time, and it was there that we discovered *Cebus apella* hammering palm nuts against tree trunks and branches to open them for access to the edible parts (Struhsaker and Leland 1977). We also discovered the difficulties of protecting this marvelous and remote park, where poaching and illegal agricultural encroachment were rampant (Struhsaker 1976a). Not long after our brief study at La Macarena, Lysa joined me in Kibale, where she collaborated with me on virtually all aspects of my research and conservation efforts there.

Declines in the Amboseli vervet monkey population were documented during my 1971 visit there (Struhsaker 1973). This study was done while on my way to the Tana River, where I conducted a survey for the endemic red colobus and mangabey, which eventually resulted in the studies referred to above. In 1975 I once again censused the Amboseli vervets, demonstrating an even further decline in the population, which I attributed to a natural decline in fever trees, one of their main food resources (Struhsaker 1976b).

Return visits to Cameroon were made in 1972, to survey wildlife in the Douala-Edea Reserve and along the Sanaga River with Steve Gartlan and Ferdinand Namata. In 1974 I was again back in Cameroon to supervise Doyle McKey's Ph.D. research and for the two of us to conduct more wildlife surveys along the Sanaga River. A 1976 visit to Cameroon was to survey the Korup Forest Reserve with Steve and Sue Gartlan, Doyle, and Ferdinand. It was during this visit that Steve and I refined a proposal for the creation of the Korup National Park. Steve took the lead on this effort and joined forces with colleagues in Yaounde to make this a reality.

As part of my broader effort to conserve the red colobus of East Africa, Lysa Leland and I made the initial primate survey of the Magombera Forest Reserve, Tanzania in 1977. This was at the invitation and efforts of Alan Rodgers. We discovered a reasonable population of the endemic Udzungwa red colobus, which at that time, in the absence of information on its status, was considered nearly extinct. Upon completing this survey, on the way back to Dar es Salaam, we made a short stop at the edge of the Mwanihana sector of the Udzungwa Forest Reserve, where we were led to a relatively well-habituated group of Udzungwa red colobus. Following this we proceeded to Zanzibar, where we conducted another brief survey of the endemic red colobus living there. Both of these studies yielded basic information on the ecology and behavior (especially vocalizations) of these two red colobus species, and demonstrated the need and possibilities for more study and conservation action (Struhsaker and Leland 1980).

The Ituri Forest in the Democratic Republic of Congo is vast and its human population relatively low. Many of the primates there are different from those in Kibale. It is a place I always wanted to explore, not only because of my fundamental interest in exploration and in seeing new places and new species, but also because so little was known about the primates living there. In 1983, and again in 1988, we were able to visit John and Terese Hart, who were conducting research on okapi, duikers, and vegetation in the Ituri, based at Epulu. I was able to tape record the red colobus of the Ituri and another taxon of red colobus on the western lower slopes of the Ruwenzori Mountains. Comparison of these recordings with those I had collected across Africa supported the idea that these two red colobus taxa of eastern Democratic Republic of Congo are very closely related to the Kibale and Tana River taxa (Struhsaker 1975a, 1981a, 2010).

The longest break I took from my residence in Kibale was the 9 months I spent at the Center for Advanced Study in the Behavioral Sciences at Stanford University in California (1983–1984). We were a group of five (Barbara Smuts, Dorothy Cheney, Robert Seyfarth, and Richard Wrangham, and me), and together we contributed chapters and edited the multi-authored volume "*Primate Societies*" (Smuts et al. 1987) that summarized and synthesized what was then known about wild primates worldwide.

After Kibale

In 1988 I raised substantial funds from the European Economic Commission and the United States Agency for International Development to expand and improve the field station at Kanyawara. Later that year my employer ordered me to leave Kibale and Uganda [see Chap. 12, Struhsaker (2021) for details]. I then moved to Kenya for a year where I focused on supervising students studying the endemic mangabey and red colobus and vegetation at the Tana River Primate Reserve. The research camp there was administered by the National Museums of Kenya, in collaboration with the Kenya Institute of Primate Research where I was based. In addition to my activities on the Tana, I was asked to head a survey team of scientists (two foresters, a botanist, and a sociologist) to evaluate the status of forest conservation and management issues in the Ngorongoro Conservation Area of Tanzania. We concentrated on the Northern Highland Forest where we found thousands of Maasai cattle using the area, which were causing considerable damage to the habitat. This survey was sponsored and completed under the auspices of the International Union for the Conservation of Nature who, 9 years after our survey and receipt of our report, published a collection of studies, including our results and recommendations (Struhsaker et al. 1997b, a), which to the best of my knowledge were never implemented.

I left Kenya in 1989 and took up residence in Gainesville, Florida where I was given an honorary appointment in the Department of Wildlife and Range Sciences at the University of Florida. From there I was able to recruit graduate students, including Jerry Lwanga who, as mentioned earlier, studied the impact of rodents, duikers, and elephants on forest regeneration in Kibale for his Ph.D. (Fig. 11) Other students included Jessica McCoy (M.Sc.) who compared the abundance of Kibale duikers in logged and unlogged forest (McCoy 1995); Margaret Kinnaird (Ph.D.), who studied the ecology of the endemic and endangered Tana River mangabeys (Kinnaird 1990); Paula Kahumbu (M.Sc.), who evaluated the impact of tree harvesting for canoes on the food resources of the Tana primates (Kahumbu 1992); and Kirstin Siex (M.Sc.), who studied the ecology of the endangered and endemic Zanzibar red colobus (Siex 1995). I always enjoyed working with these students in the field and preferred this form of teaching to giving lectures and exams.

While at the University of Florida I collaborated with Theresa Pope, Rosa Lemos, Ken Glander, and Karen Strier to conduct a short study of muriqui monkeys (*Brachyteles*). The objective was to collect blood samples and to make physical measurements of these endangered monkeys from their northern and southern populations to better understand their taxonomic relationships to one another. Based on morphological and genetic differences, we concluded that these two populations were distinct enough to be considered at least two subspecies, and urged the conservation of both populations (Lemos de Sa et al. 1993; Pope 1998). A more recent study with a larger sample supports our conclusions, but treats them as two sister species (Chaves et al. 2019).

I also had the privilege of serving as a field assistant to Theresa Pope in her field study of the genetics, ecology, and social behavior of red howler monkeys in the Llanos of Venezuela. For me this involved relatively short trips between 1991 and 1994, when I learned more about the techniques of darting and catching falling monkeys, collecting blood from them, and taking their vital measurements. It was a great opportunity for me to learn more about an entirely different ecosystem and primate species. For example, I discovered that, contrary to popular belief, red howlers are incredibly interesting in terms of their behavior, such as juvenile males carrying orphaned infants and adult males playing with infants. It just took a lot more time and patience to learn this, and the heat, humidity, hordes of mosquitoes, ticks, and chiggers at Theresa's sites did not make this any easier.

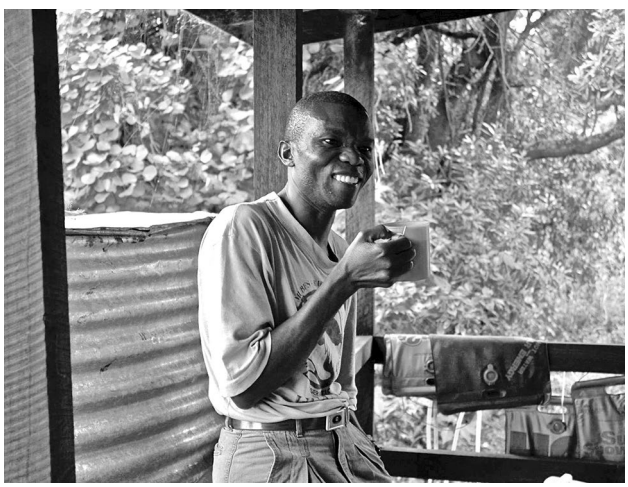

Fig. 11 Jerry Lwanga (1960–2015) at Ngogo, Kibale (photograph by Sholly Gunter, all rights reserved)

In 1992 I was invited to join Gail Hearn and Dietrich Schaaf in a primate survey on the southwest coast of Bioko, Equatorial Guinea. Our goal was to evaluate the status of primate populations and the conservation issues they faced. This area is rich in primate diversity and endemic species and subspecies. I was able to make important observations on behavior and to make tape recordings, particularly of the red colobus endemic to this island, revealing how truly distinct it is from mainland red colobus taxa (Struhsaker 2010). The data on polyspecific associations that I discussed earlier were collected during this survey (Struhsaker 2000).

At the end of 1992 I moved to Durham, North Carolina, where I was given an honorary position in what is now the Department of Evolutionary Anthropology at Duke University. I continued to supervise my students from the University of Florida who were working in Kibale and on Zanzibar. In 1993 I conducted two surveys on primates and other wildlife in the Kakum and Bia National Parks of Ghana as part of a collaborative effort between the Ghana Wildlife Department, Conservation International, and the United States Agency for International Development. These forests had been severely degraded by logging and hunting. The most disturbing finding was in Bia, where three monkey species that had been studied or documented there less than 15 years earlier were now extinct there, namely Miss Waldron's red colobus (*Procolobus badius waldroni*), Diana (*Cercopithecus diana roloway*), and the white-naped mangabey (*Cercocebus atys lunulatus*) (Oates et al 2000; Struhsaker 1999, 2005, 2008). None of the park rangers or the warden had even heard of these species. Two other species, the ursine colobus (*Colobus vellerosus*) and the olive colobus (*Procolobus verus*), were either extirpated or extremely rare.

Kirstin Siex joined me at Duke in 1996 to pursue her Ph.D. on the Zanzibar red colobus, focusing on the effects of population compression on demography, ecology, and behavior (Siex and Struhsaker 1999a, b; Siex 2003). Working together, Siex and I found that dispersal between social groups of the Zanzibar red colobus was quite different from what I found with the Kibale red colobus. On Zanzibar, both

sexes transferred between groups, although adult males did so more frequently. We concluded that some of this difference between the two species was the result of environmental differences. On Zanzibar, red colobus habitat was being rapidly destroyed by humans for cultivation. The monkeys were forced to find suitable habitat elsewhere and Jozani, our study area, was one of the very few places that was protected. Habitat loss resulted in a compression of the red colobus population into our study area, leading to an increased and unusually high population density (784 monkeys per km^2). There was also a pronounced decrease in the number of adult females per adult male. I suggested that this was due to the possibility that habitat loss led to greater nutritional stress in females than males due to the demands of pregnancy and lactation, resulting in higher female mortality (Struhsaker 2010).

Siex and I also addressed the complaints of coconut farmers, who claimed that the colobus were adversely affecting their harvest. We showed that these claims were unwarranted. Consumption of immature coconuts by the colobus actually resulted in a larger harvest of mature nuts, likely due to a pruning effect (Siex and Struhsaker 1999a, b).

It was while studying the Zanzibar red colobus that I became fascinated by their habit of eating charcoal. Working with a chemist who specialized in the uses of charcoal, we concluded that they were likely eating charcoal to adsorb secondary compounds present in some of their foods (e.g., leaves of mango, Indian almond, and cassava) that might be potentially toxic or at least act as antifeedants (Cooney and Struhsaker 1997; Struhsaker et al. 1997b, a).

Jozani was, and probably still is, the prime habitat of the Zanzibar red colobus. When the road through Jozani was improved, vehicles were able to drive faster, resulting in a significant number of colobus being killed. Most drivers had no appreciation or concern whatever for the welfare of the monkeys. Siex and I lobbied the Zanzibar government for several years to install speed breaks along 2 km of road to reduce the number of road-killed colobus. Nothing seemed to work until the government officials were shown the issue of National Geographic magazine with my photo of a dead and bloody red colobus lying in the middle of the road. This negative publicity in a country heavily reliant on tourism had an immediate effect. Speed breaks were installed within months and the incidence of road kills declined dramatically.

As a continuation of my efforts to study and protect the East African red colobus species, I joined forces with Carolyn Ehardt and Tom Butynski in 1998 to begin surveys and detailed studies of the endemic Udzungwa red colobus (*Procolobus gordonorum*) and the Sanje mangabey (*Cercocebus galeritus sanjei*). These two taxa are restricted to the Udzungwa Mountains, with the red colobus also occupying a few forest remnants in the Kilombero Valley of Tanzania. After the initial surveys, I focused on how red colobus demography varied in relation to gross ecological parameters (Struhsaker et al. 2004; Rovero et al. 2006; Rovero and Struhsaker 2007), and supervised two Ph.D. studies of red colobus ecology (Marshall 2007; Steel 2012). While we learned a great deal about how habitat quality affected group size, composition, and fusion-fission, I think one of the most important consequences of our efforts in the Udzungwa Mountains was the creation of a research station there, primarily through the efforts of Francesco Rovero.

Central research theme

Aside from focusing on primates and especially red colobus, if there was a central theme to my research it was to learn as much as I could about the natural world. This interest in a wide range of topics seems only logical to me. How can one fully understand why animals do what they do if we do not try to observe and collect information on everything they do in the wild and what is happening around them? Working with the museum at Michigan State University under Rollin Baker taught me the importance of taking detailed notes on whatever I observed, date, time, and location being critical. I began my studies by collecting data on group size and composition of monkey groups in relation to gross habitat types. Much of my early training at Berkeley, under the tutelage of Peter Marler, focused on vocalizations. Trying to understand vocal communication has always been central to my research.

The monkeys soon taught me that I needed to learn a lot about botany, not only identification, but phenological patterns, phytochemistry, factors affecting seed and seedling survivorship, population structure of food species and habitat variation in relation to disturbance patterns and soil type. By visiting and surveying a wide variety of forests throughout the tropics, the value of the comparative method became ever more apparent to me. Combined with my long-term studies in Kibale, these comparisons revealed the tremendous variation that occurs over time, within a species, within a social group, within a deme, within a forest, between forests, habitats, and regions. All of this variation complicates interspecific comparisons, emphasizing the importance of taking a population perspective rather than a typological one (Struhsaker 1999, 2000, 2008). No condition is permanent. Long-term monitoring of populations and habitats is critical to understanding variation and change.

Equally important in the study of free-ranging, wild populations is the need to be observant of things beyond the primary focus of one's study. I never seemed to have trouble looking at things that, at the time, did not seem relevant to my study objectives. I observed and took notes. This is the essence of being a naturalist. For me, this approach led to a number of publications on interesting discoveries, such

as diseases in red colobus (Struhsaker 2010) and baboons (Struhsaker et al. 2011, 2019), potential causes of tree mortality and regeneration of species important to primate and avian diets (Struhsaker et al. 1989), interactions between forest mambas and mongoose (Struhsaker and McKey 1975), ground python diet (Gartlan and Struhsaker 1971), ecological and behavioral notes on bushbabies (Struhsaker 1970b), the geographical distribution of mangabeys (Struhsaker 1971b), a golden mole altitudinal record (Struhsaker 1975b), robin chats imitating the antiphonal duet of rufous warblers (Struhsaker 2017b), bushpig polychromatism and ecology (Ghiglieri et al. 1982), elephant diets and their impact on forest regeneration (Struhsaker et al. 1996), the sun squirrel's diet (Struhsaker 2019), and growth rates of giant rosette plants on the Ruwenzori Mountains (Struhsaker 2020a, b). Natural history observation is where it all starts.

Conservation efforts

Once I began studying rain forest primates, I became acutely aware of how rapidly their populations and forests were being degraded and destroyed due to hunting, logging, and agriculture, driven primarily by unsustainable growth in human populations and their ever-increasing needs and wants for material things, some necessary, many not. Humans never have enough. My response to this realization was to become more engaged in conservation activities to the point where it seemed like I was putting at least as much effort into conservation as I was into research. Fortunately, I was not employed by an academic institution where conservation efforts by faculty are not often rewarded with promotions or tenure. Part of my mandate with the New York Zoological Society was to try and protect wild areas.

Although I have published books (Struhsaker 1997, 2010) and a number of articles advocating conservation actions (Oates et al. 1987, 2000; Struhsaker 1972, 1976a, b, 1978, 1981d, 1987, 1990, 2005; Struhsaker et al. 2005), I am not sure how effective these were. For example, I have seen no evidence that any of my recommendations, or those of many others, have influenced logging operations in the tropics. Logging in the tropics is still largely a pillage and plunder operation for short-term profits with no concern for long-term sustainability or for the animals that live there. As a consequence, it seems to me that the most effective way to conserve tropical forests and their wildlife is through the creation of national parks. I believe my most effective conservation work resulted from my lobbying efforts and support of anti-poaching activities. No single person creates a national park. It took 23 years of lobbying by me and many others to have Kibale declared a national park. There are a number of reasons it took so long. Our efforts occurred during the chaotic years in Uganda, with civil wars, economic collapse, and many changes in government. In addition, there was opposition to granting Kibale park status from the Uganda Forestry Department, who wanted to retain control of this resource. Once political and social stability had been reestablished, foreign aid began flowing into Uganda, including funds from the US government to assist with the development of new national parks. These new parks included five former forest reserves: Kibale, Semuliki, Ruwenzori Mountains, Bwindi, and Mgahinga. It is likely that this financial incentive was crucial to the formation of these parks, but I emphasize that this incentive was strongly, if not primarily, the result of lobbying efforts by scientists.

During my first visit to Zanzibar in 1977 to observe the endemic red colobus, I met with an official in the forestry department that managed the Jozani Forest Reserve. I suggested that Jozani be converted into a national park. The official responded by saying something to the effect of: "But where would we get the zebra and giraffe to put in the park?" Aside from wondering how these savanna species would fair in a groundwater forest, I realized how little this official knew about his island's endemic monkey species and other wildlife, and wondered how prevalent this lack of knowledge was on Zanzibar. It was not until 1992, when Kirstin Siex and I started a longer-term research project focusing on the Zanzibar red colobus, that we began lobbying for the creation of a national park to protect this endangered species. Finally, in 2004 the Jozani-Chwaka Bay National Park was established, Zanzibar's first and only national park. No zebras or giraffes were involved.

Gaining the political support for the creation of national parks is typically a slow process. Persistence is imperative. Effectively managed and protected national parks conserve biodiversity and ecosystems better than any other form of land use. In my experience, natural resource extraction, no matter the scale, is incompatible with conservation. Even something as simple as firewood extraction has a negative impact. For example, the threatened Sanje mangabeys of the Udzungwa Mountains National Park rely heavily on insects that reside in dead wood that lies on the ground. Firewood collection from this national park was allowed for many years, resulting in the virtual absence of fallen dead wood for hundreds of meters inside the park boundary. It was rare to see a mangabey in areas devoid of dead wood. Furthermore, any excuse that allows neighboring communities to freely enter a national park, whether for firewood or even water, provides the opportunity for abuse, such as setting snares.

In my opinion, anyone who studies and/or is interested in wildlife should do what they can to preserve these natural systems. Failing to do so, will, of course, increase the chances of losing these systems, which we study and enjoy. I am not suggesting that every field biologist/primatologist get involved in law enforcement to protect wildlife, but they can serve as scientific watchdogs reporting illegal activities

to the appropriate authorities and writing reports and letters advocating conservation action. Getting to know the local authorities is crucial to receiving their support when it comes to implementing conservation action.

Thoughts on current trends in field primatology

In the past 10–30 years there have been a number of outstanding developments in technology allowing for studies of wild, free-ranging primates that would have been extremely difficult, if not impossible, in earlier times. I am thinking in particular of the kinds of genetic and hormonal data that can be derived from feces, the improvements in radio telemetry, Global Positioning System accuracy, and camera traps, and the computer programs that allow for the rapid and complex analyses of large data sets, including analyses of sound recordings.

On the downside, professors all too often rely on inexperienced students and locally recruited field assistants to collect most, and sometimes all of the data. When the majority of data are collected by someone else, the principal investigator lacks the firsthand knowledge of what the study subjects have done and a feeling for the animals. Most importantly, the data lack context. Typically, local field assistants and inexperienced students are instructed to collect data in a rigid and formatted manner, e.g., on data sheets or data recorders with predetermined categories. Although this methodology is essential for quantifying behavior, qualitative information may well be ignored, never described or tallied. Important events that at first seem irrelevant are not recorded, but may well be critical in interpreting the quantitative results and in shaping future and productive avenues of research, hypotheses, and predictions. I always interrupted my scan or focal samples whenever I recognized important contexts or behaviors that I had not anticipated. For example, that is how I discovered that vervet alarm calls are predator specific, and why I dropped everything to pursue the source of an alarm call that I did not recognize and discovered my first hybrid redtail/blue monkey in Kibale.

While I appreciate that professors have teaching responsibilities that limit their field time, when they are in the field it seems to me they should spend as much time observing their study subjects as possible. Similarly, graduate students are also too frequently overly dependant on field assistants to collect their data. In my opinion, graduate students should be in the field collecting their own data with limited assistance from field assistants. To do otherwise results in a graduate student, soon to become a professor, with little firsthand experience of his/her study subjects. Furthermore, while there are many excellent field assistants, not all of them are, and they usually lack the professional training and motivation of a highly trained biologist who is conducting their own research and understands the importance of high-quality data. This trend raises questions of data quality and reliability. One way to deal with this potential problem is to conduct regular inter-observer reliability checks. For example, I once had a field assistant who collected monthly phenological data on marked trees. It was easy to check the reliability of his data with periodic and random checks on a subsample of trees. His work was excellent for about 1 year, then in one of my checks I discovered that he was recording leaves and fruit on trees that had been dead for many years and still were dead. I have heard similar stories from colleagues working elsewhere, indicating that my experience was not an isolated one.

Descriptive and exploratory studies are being replaced by hypothesis-driven studies. While these latter studies are important and the natural consequence of the initial descriptive studies, there is always a need for detailed description. The same concern applies to exploratory studies, where there are usually no hypotheses or predictions because we simply do not know what is out there. Funding for exploratory and descriptive research is becoming increasingly scarce. Publishing the results of this type of research is also difficult. Natural history notes and opportunistic observations were routinely published 20–30 years ago. It is now almost impossible to find a scientific journal that will accept articles of this sort. To repeat myself, this trend ignores the fact that it is precisely these natural history observations that provide the basis for more detailed studies and the eventual development of hypotheses, predictions and experimental study. A personal example of this concerns my research on vervet monkeys where I described the different types of predator alarm calls. Without these observations, there would have been no basis for the excellent experimental studies that followed. Natural history is where it all starts. Think of Alfred Russel Wallace, Charles Darwin, and Alexander von Humboldt, explorers and naturalists interested in just about everything. Think of the mountains of research that have resulted as a consequence of their descriptive and exploratory work.

My advice to the new generation of field primatologists is to watch your animals, describe in detail what they do, and photograph and sketch what they do. Do not let hypotheses and predictions influence what you see. Objectivity is key. Observe not just your study subjects but everything that is around them and what might be affecting them, whether biotic or abiotic. If you want to know how your study subjects interact with other and shyer species, then move as quietly as a hunter. No shouting back and forth between your fellow observers. I urge visiting other areas, other populations, and other species for comparisons and insights, which are critical to understanding variability. Most importantly, enjoy the animals and their homes while you can.

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