Part I Introduction

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Trudy R. Turner , Christopher A. Schmitt , Jennifer Danzy Cramer
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1 Introduction

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and Jennifer Danzy Cramer

Savanna monkeys – the ubiquitous, medium-sized animal known as the vervet monkey in East and South Africa, African green monkey in West Africa, and several other local names in other parts of Africa – were one of the first primates studied by contemporary primatologists. The initial studies of savanna monkey behavior took place in East Africa in the 1960s (Jackson & Gartlan, 1965; Gartlan & Brain, 1968; Gartlan, 1969; Struhsaker, 1967a, 1967b, 1967c, 1967d, 1969; Lancaster, 1971; Dunbar & Dunbar, 1974), South Africa (Basckin & Krige, 1973; Krige & Lucas, 1974), and West Africa (Dunbar, 1974) in the 1970s. In the 1980s, these early studies were supplemented by more intensive work on animals at Amboseli and Samburu in Kenya (Cheney et al., 1981; Wrangham, 1981; Cheney & Seyfarth, 1983; Whitten, 1983; Lee, 1984; Isbell et al., 1990), Cameroon (Kavanagh, 1978), Senegal (Harrison, 1983), and South Africa (Henzi & Lucas, 1980; Henzi, 1985). Studies were also conducted on the Caribbean islands of St. Kitts, Nevis, and Barbados, where savanna monkeys have lived for over 300 years after having been transported there from West Africa on ships (Sade & Hildrech, 1965; Poirier, 1972; Horrocks & Hunte, 1983a, 1983b, 1986; Chapman & Fedigan, 1984; Fedigan et al., 1984; Fairbanks & McGuire, 1985; Hunte & Horrocks, 1987; Fedigan & Fedigan, 1988; Boulton et al., 1995). Nonetheless, compared to other widely distributed primate species, like macaques and baboons, savanna monkeys were not so well studied. In the landmark volume, *A Primate Radiation: Evolutionary Biology of the African Guenons* (Gautier-Hion et al., 1988), which both summarized and set the stage for further research, there is only a single chapter devoted to savanna monkeys (Fedigan & Fedigan, 1988). In a follow-up volume, *The Guenons: Diversity and Adaptation in African Monkeys* (Glenn

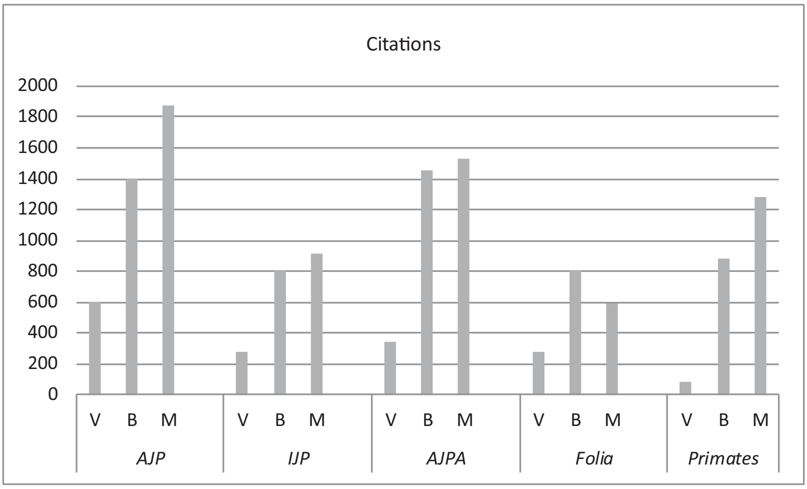

FIGURE 1.1 Number of articles that discuss vervets (V), baboons (B), and macaques (M) in the *American Journal of Primatology* (*AJP*), *International Journal of Primatology* (*IJP*), *American Journal of Physical Anthropology* (*AJPA*) *Folia Primatologica* (*Folia*), and *Primates*.

& Cords, 2002), there is again only a single chapter devoted to savanna monkeys, despite the fact that they are the most numerous and most widespread of all the cercopithecines. An examination of the five major journals that publish work on primates – *American Journal of Primatology*, *International Journal of Primatology*, *American Journal of Physical Anthropology*, *Folia Primatologica*, and *Primates* – clearly documents this lack of focus. Figure 1.1 shows all citations to savanna monkeys, baboons, and macaques in a search of the journals' online content. Savanna monkeys have less than a third of the number of citations compared to baboons and less than a quarter compared to macaques. When viewed over time, the same trend is observed. In Figure 1.2, only articles where the name of the species is found in the title are considered. Again, the number of articles about savanna monkeys is only a fraction of what there is for baboons and macaques.

Why has comparatively little attention been paid to these animals? Some reasons may be that they are smaller in body size than

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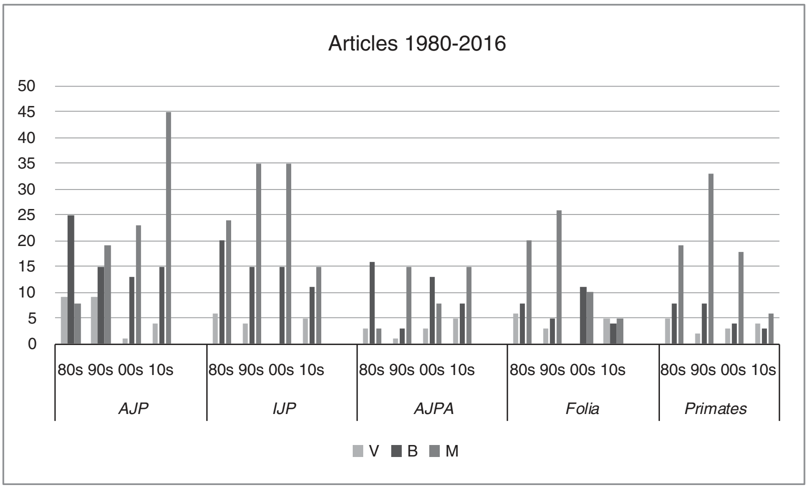

FIGURE 1.2 Number of articles in the decades of the 1980s, 1990s, 2000s, and 2010s that list vervets (V), baboons (B), and macaques (M) in their titles in the *American Journal of Primatology* (*AJP*), *International Journal of Primatology* (*IJP*), *American Journal of Physical Anthropology* (*AJPA*), *Folia Primatologica* (*Folia*), and *Primates*.

baboons and macaques, they have more subtle behavioral signals and smaller group sizes, and they rely more on cryptic behavior to avoid predators. There has been the assumption that they are somehow less interesting than either the forest-dwelling guenons or the larger, savanna-dwelling baboons and macaques. An examination of the articles found in Figure 1.2 may provide some clues – there are a limited number of authors who have published on savanna monkeys, and these articles come from a limited number of sites. Many of those who published on savanna monkeys early in their careers have moved on to other species. Only rarely do you find a researcher continuing at the same field site. This is paired with a downward trend in the number of locations reported on in publications over time – the exact opposite of what has happened for baboons and macaques.

This is beginning to change. In the last few years, more publications from a greater number of locations have begun to emerge. There is a growing recognition that their widespread distribution and concomitant adaptability to a wide array of environments make savanna monkeys a fascinating and useful study subject for a number of questions. Researchers now recognize that savanna monkeys display remarkable differences in group composition (Whitten & Turner, 2004), hormonal profile (Whitten & Turner, 2004), and body type and proportion (Turner, 1997). At the same time, the taxonomy of savanna monkeys has been continually revised, recognizing not only their separation from the rest of the guenons by placing them in a separate genus (Groves, 2001), but also the rich taxonomic variability that can be found within the genus *Chlorocebus.*

Savanna monkeys are widely distributed across sub-Saharan Africa, ranging from the forest/scrubland mosaics of West Africa to the dry, semidesert habitats of northern Kenya and Ethiopia to the snowy heights of the South African Highveld. They are flexible, rapid reproducers, making use of environments as diverse as pristine national parks and reserves and rapidly changing suburban landscapes. The great adaptability of this genus is manifest in these diverse environments through observable changes in body size, social organization, and life history. They are the great opportunists. Although not often used as a model for human evolution, like humans, they appear able to adapt to nearly every environment they encounter. Also like humans, they carry viruses like simian immunodeficiency virus (SIV) – the simian analogue of HIV – that are transmitted sexually and can mutate quickly.

As recognition of savanna monkeys' adaptability has increased, so too has the recognition that much can be learned from this widely distributed group of organisms. It is through the study of differences in localized populations in widespread taxa – where plasticity and adaptive responses to differing environments cause subtle shifts in phenotype – that inferences on the processes of evolution can best be ascertained. The recent resurgence of work on the behavior and biology of vervets (Van de Waal & Bshary, 2011; Pasternak et al., 2013; McFarland et al., 2014; Teichroeb et al., 2015; Henzi et al., 2017), as well as on their genetics and morphology (Turner et al., 2016), is a reflection of this realization.

BRINGING IT TOGETHER: GENETICS, GENOMICS, AND MORPHOLOGY

We have participated in a series of studies on savanna monkeys for several decades (TRT), as well as more recently (JDC and CAS). Over time, our studies have expanded in scope and across the distribution range of the species. The original focus of our work was population genetics, but our work now includes the collection of a wide range of data that are crucial for understanding the life history of savanna monkeys. Our first study of these animals was in Ethiopia in 1973. One of us (TRT) trapped and sampled 125 monkeys from seven troops living in the hot, dry savanna along the Awash River in central Ethiopia (Turner, 1981). Savanna monkeys lived exclusively in the riverine forests and did not venture far from the trees. This study was contemporaneous with the well-known Awash baboon study. Aside from blood for genetic information, the only other biological parameter collected during this study was body weight. Genetic markers were used to determine genetic distance between troops and the rate of migration between troops.

The second study, conducted by TRT, took place in Kenya. As opposed to the close focus of the Awash River study, this Kenya study expanded the scope by sampling at four different sites in Kenya. Each site differed from the others in altitude, rainfall, availability of food, and human presence. While the study was primarily to determine the genetic distances between populations and to track migration between local and more distant groups, greater amounts of biological data were collected on the animals. A series of measures, which we now call "classic" measures, were taken on each animal, along with tooth casts and blood dots to assess parasite infection. We looked at four sites and a total of over 30 groups. Our sampling method in Kenya had two goals: to sample deeply at each site, but also to get a representative sample over the broad distribution of animals in Kenya.

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Sites were located between 80 and 300 km apart, and at a single location we sampled anywhere between 5 and 8 groups of animals; each of the groups had between 8 and 25 members. By using this method, we hoped both not to miss any common genetic variants and to really get a sense of the full range of variation in the biological parameters sampled at each location. This strategy of range-extensive and locally intensive sampling has remained our strategy throughout future studies.

An unexpected benefit to one of our sites in Kenya was the presence of a field researcher, Patricia Whitten, who was studying the behavior of vervets in Samburu National Park and agreed to allow us to trap the animals she was observing. While such collaborations may not sound unusual today, it was a radical step forward in the late 1970s. While behavioral ecologists would certainly have been interested in our conclusions, they were not anxious to have their study animals handled in any way, primarily for fear of upsetting their natural behavior. Pat was the exception, and her willingness to allow this led to a three-decade-long collaboration with TRT. Over the course of those decades, new technologies developed that allowed us to examine hormonal variation from serum samples collected from the animals. This led to a multifaceted sample at Samburu, where we had access to behavioral, morphological, hormonal, and genetic data, developing into a rich series of publications that are discussed in this volume.

The third major vervet project of our group began in South Africa as a collaboration between TRT and J. Paul Grobler of the University of the Free State, South Africa. Grobler is a conservation geneticist who was asked by the Department of Environmental Affairs in Limpopo, South Africa, to help solve the vervet "crisis" in the country. Each year, hundreds, perhaps thousands, of vervets are killed in South Africa by cars and people. Vervets are notorious crop and garden raiders and can sometimes make the difference between profit and loss for small farmers. For years, they were considered vermin in South Africa and could be killed at will. But, for as many people who hated vervets, there were those who loved them and wanted to protect and save them. Many of these people set up sanctuaries on their farmland – even in their homes – that would quickly become crowded with injured or orphaned animals. Far from amateurs, these sanctuary owners showed remarkable skill in helping vervets form troops from these unrelated groups animals. Using the vervets' predisposition to allocare, they assigned young, orphaned animals to bond with seasoned mothers, and in that way they slowly integrate into a troop structure – a remarkable feat that has been studied by several research groups (Wimberger et al., 2010; Guy et al., 2011). However, these sanctuaries quickly became overcrowded. Owners wanted to release recovered animals back to the wild and worked hard to find locations where the troops could thrive. At the time, wildlife authorities would not allow releases of animals into areas where they might represent a different subspecies, as defined by some of the older taxonomists. Grobler was enlisted to help solve this dilemma, and TRT joined him as part of a collaboration with the Coriell Institute, which was working to establish a biobank of nonhuman primate tissue samples. Grobler discusses the results of this in this volume. As a result of their work, Grobler and Turner were well positioned to expand their studies.

The Kenya samples were collected at the beginning of what was to become the AIDS epidemic in the early 1980s. Vervets were found to carry SIV, the simian analogue of HIV. Vervets from both Kenya and Ethiopia were found to have the virus, but in very different frequencies (Dracopoli et al., 1983). Vervets became a topic of keen interest as a potential model for HIV, since their own version of the virus appeared to be transmitted sexually. Savanna monkeys had, of course, been used in medical laboratories (where they are usually called African green monkeys) for decades, providing the vector for polio vaccines and as models for human diseases. Their use as an HIV analogue ultimately led to the formation of the fourth major project in which we all (TRT, CAS, and JDC) have participated. This collaborative endeavor ultimately became known as the International

Vervet Research Consortium (IVRC) and has added enormously to our knowledge of vervets across their known range.

Although the IVRC was founded to study the distribution of SIV among savanna monkeys, specifically (see the work of Apetrei and colleagues, this volume), its driving theoretical focus has always been the relationship between genetic/genomic and phenotypic traits, as detailed by Jasinska in this volume. Over the years, the ethics of trapping animals in the wild changed. We have consistently worked on the principle that the trapping and release of animals brings with it the obligation to collect as much information on that animal as possible. In part, it was our goal in this project to ensure that a large-scale trap-and-release study of this kind would not have to be done again. That the tissue we collected could be transformed into immortal cell lines saved in a public repository was part of this goal, providing an ever-ready source of biological information that could be used in conjunction with the phenotypes we worked so hard to collect while trapping.

As a part of the IVRC, we launched major expeditions in South Africa, The Gambia, and St. Kitts and Nevis, along with minor collections in Botswana, Zambia, Ethiopia, and Ghana. We have samples from every taxon of savanna monkey (with the notable exception being the elusive *Chlorocebus djamdjamensis*) and finally have the data to answer some of the major questions about savanna monkeys' adaptations to changing environments and climates. Figure 1.3 presents a comprehensive map of all of the locations we have surveyed. As an expansion of this research, CAS continues trapping and collecting samples from the South African vervet monkeys initially trapped in the IVRC collections in order to gain a better sense of anthropogenic and climate impacts on population processes and evolution in these groups. JDC has continued similar work in The Gambia.

EXPANDING THE SCOPE: RECENT RESEARCH ON SAVANNA MONKEYS

Of course, we are not the only group conducting research on savanna monkeys. Behavioral studies have proliferated in South Africa over