



My path to primatology: some stories from the field

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Abstract

In this paper, I summarize the major facets of my 50-year career as a primatologist. I briefly describe the aspects of my upbringing and early education that led me to the study of primate behavior, first in captive settings and, later, in the wild. My research on the Arashiyama West Japanese macaques and my interactions with Japanese primatologists was a formative stage in my career, and I present the background of this international project and how it led to my growing focus on female life history studies. After a couple of failed attempts to establish a long-term study of primates in their native habitats, I began the Santa Rosa Primate Project in Costa Rica in 1983, which focuses mainly on white-faced capuchins, and to some extent on howlers and spider monkeys. The Santa Rosa project has expanded over the past four decades and continues to this day, with the participation of a large team of colleagues, local field assistants and students. I present some of the major findings of our Santa Rosa monkey research in the areas of female reproduction, sexual conflict and conservation of primates in a regenerating tropical dry forest. I also briefly describe how and why I came to develop a sideline of research on gender and science.

Keywords Japanese macaques · White-faced capuchins · Female life histories · Sexual conflict · Primate conservation · Gender

Introduction

Once upon a time, I envisioned myself leading quite a different career from the primatologist I became. Being raised by an American military father and a mother who was a German-Italian war bride, I had lived in various countries and been exposed to several languages by the time I reached university. In my early teens, I was also rigorously instructed in the sciences (biology, chemistry, math) at a private school in Texas to which I was awarded a scholarship. This science-based schooling took place in the early 1960s during the Cold War between the USA and Russia. In retrospect, I realize that, as middle school students, we were receiving training to become the competitive American scientists of the future, which explains why Russian language and scholastic aptitude test (a college entrance exam) skills were also featured on the curriculum. My private schooling was interrupted when my father was once again stationed overseas.

On the military base in Germany, the high school counselors decided that, at the age of 16, I had been educated beyond what their institution had to offer. On the counselors' advice, my parents agreed that when I turned 17, I could move to France and attend the American College of Paris, with the stipulation that I live in an international dorm for young women (a *foyer*) run by an order of Polish nuns.

In my classes at the American College of Paris (1966–1968), I was immersed in the arts, the social sciences and the linguistic and cultural life of France. In my residence in the foyer, I made friends with young women from around the world. I took an introductory course in anthropology and considered the possibility that my multi-lingual training might lead to a career as a translator, or in linguistic anthropology. I was particularly taken by an ethnography of rural village life in France (Wiley 1964), which sparked my interest in how people live in small communities, in particular how women live in the social company of men. Perhaps I could be an ethnographic anthropologist?

Therefore, when I was accepted to the University of Texas at Austin for my junior and senior years (1968–1970), I majored in anthropology and took every required course, but focused especially on sociocultural anthropology. I quickly

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landed a small research assistant job on a graduate project that required me to ask women who read romance novels about their views on sex and morality. Simultaneously, I took an introductory primatology course from the newly minted Dr. Claud Bramblett (himself an early PhD student of Dr. Sherwood Washburn), for which I completed an observational project on gelada baboons at the San Antonio Zoo. That class assignment later resulted in my first publication (Fedigan 1972a). I soon realized that my introverted personality made it difficult for me to ask people questions about their private lives, which is what many sociocultural anthropologists need to do. However, my observational abilities and my love of animals made me well suited for primatology. Like many future primatologists I had grown up in an animal-friendly family. It also occurred to me that my interest in social relations between the sexes could be addressed in nonhuman as well as human primates. I switched my major to primatology, which then required me to take a wide complement of physical anthropology courses. This return to a focus on biology felt like I had circled back to my early teenage training in the sciences.

My first primatology job was as a part-time lab technician at the Balcones Research Center in Austin (1970), where Dr. Claud Bramblett maintained his groups of guenon monkeys and vervets. Dr. Bramblett had inherited his collection of monkeys from Thelma Rowell's research in Uganda and the colony included a variety of the wonderfully colorful *Cercopithecus* species (Sykes, spot-nosed, De Brazza's and blue monkeys). There was also a sizable group of vervets (*Chlorocebus pygerythrus*), to which I was especially attracted and on which I decided to conduct my master's research project (Fedigan 1972b). Simultaneously, I taught an evening course in introductory primatology, the curriculum for which included a large section on baboon social behavior as had been reported by Drs. Irven Devore and Sherwood Washburn (1963). I was struck by the contrast between DeVore and Washburn's descriptions of male-dominated baboon society and the more sexually egalitarian vervets that I was observing daily. In particular, I noted how the female vervets would respond to a male putting his hands on their hips (a sexual invitation) by either standing sturdily for a mount or by turning around and threatening away the male (even the alpha male), especially if he frightened their infants. It certainly looked to me like vervet females exercised choice and were more than a passive resource for dominant males.

The Arashiyama primate project

In 1972, as I began my PhD research project, I entered the most formative stage of my career—my long-term study of the Arashiyama West (AW) Japanese macaques. The AW

story has been told in detail elsewhere (e.g., Fedigan 1991; Huffman 1991; Huffman et al. 2012), but in brief, the distinguished ornithologist Dr. John Emlen was visiting Japan in 1966 when the equally distinguished Prof. Syunzo Kawamura suggested to Emlen that an entire group of Japanese macaques (the Arashiyama A group) might be gifted to American scientists and moved to the USA. Mr. Sonosuke Iwata, then owner of the Iwatayama Nature Park where the AW macaques ranged, seconded the invitation to Dr. Emlen. The Arashiyama macaques had recently fissioned into two groups, and while one “daughter group” maintained its home range on the mountaintop monkey park, the other group had started to range into the nearby communities, shrines, and suburbs of Kyoto, creating conflict with the human population. An important stipulation on the part of the group organizing the planned monkey move was that in their new home the monkeys would be kept together in a naturally integrated group in some type of openranging (non-cage) situation. Dr. Emlen put the word out among US scientists that he was looking for a suitable location for a large colony of Japanese macaques. So began a multi-year and countrywide search for a new home for these monkeys, which was followed by several failed attempts. Finally in 1971, a rancher in south Texas (Ed Dryden Jr.) was persuaded by his daughter (a student of Claud Bramblett) to offer some of his undeveloped brushland about 50 km northwest of Laredo, and to bear the costs of building an enormous electric fence high enough to keep the monkeys contained on the La Moca ranch. In late February 1972, almost the entire Arashiyama A group was captured in Japan (150 monkeys including a few peripheral males originally from the B group) and flown to south Texas, where they were released into their 44-ha enclosure and renamed “Arashiyama West.”

Some 6 weeks after the AW macaques were released into their La Moca home, I arrived to begin my doctoral research. My father purchased a large motor home for me that we were allowed to station immediately in front of the only gate into the monkey enclosure, and there I lived with my first husband (Larry Fedigan) for 2 years (1972–1974) and again as the AW project director from 1978 to 1979. Upon my arrival at La Moca, I experienced occurrences of what I realized in retrospect constituted amazing good fortune. A young Japanese primatologist named Tetsuzo Mano had studied the AW monkeys in Japan for several years prior to their translocation and he was on site at La Moca to coach me for 5 months. He patiently trained me to distinguish the 150 monkeys (the monkeys had a coded numerical system of tattoo marks on their faces, which helped in the beginning), and he taught me a great deal about the behavior, relationships and social system of these monkeys. As he delineated for me the matrilineal and dominance relationships among the females and the alliances between adult males and certain matrilineal lines, what had originally appeared to me like a large chaotic mass/

troop of monkeys fell into an orderly and predictable pattern. He taught me that each monkey had not only a name and number, but also a unique physical appearance, personality, history and set of close relationships. Mano-san even accurately predicted a coup among the dominant males that would only take place a few years later, after his departure.

The other Japanese primatologists who had previously studied the Arashiyama monkeys in Japan (especially Drs. Naoki Koyama and Koshi Norikoshi) had collected 18 years of life history and dominance data on these monkeys, data that they readily passed along to me. Anything I asked for and wanted to know about the monkeys (including the life history data on the other group of monkeys still resident in Japan), they gave to me without hesitation. When I was pleasantly surprised by their generosity in handing over such a treasure trove of information, Mano-san told me that this was the way it was done at Arashiyama (and presumably across Japanese primatology)—researchers mentored the next generation of observers and contributed their accumulating life history data to the project. Later, during my visits to Japan, Drs. Junichiro Itani, Yukimaru Sugiyama and Michael Huffman were also very generous in their interactions with me, and Dr. Itani emphasized to me the value of long-term life history research. This experience of generous collaboration laid the foundations for the cornerstone of my own approach to scientific research and my appreciation for the values of cooperation, mentoring, long-term research, and life history data.

Over the years that I either studied the AW monkeys directly or oversaw the collection of life history data on them (1972–1996), I focused on two major topics—female dominance and female reproduction (Fig. 1). In the early years at La Moca, Drs. Harold and Sarah Gouzoules overlapped with me in their study of the AW macaques, and we published several papers together on aspects of dominance, reproductive success and population dynamics in these monkey (e.g., Fedigan et al. 1986). I also wrote a review paper outlining the complexities of the relationships between dominance and reproductive success in primates, which is still one of my most cited papers (Fedigan 1983). During my year as AW project director (1978–1979), I wrote the first edition of my book “*Primate Paradigms: Sex Roles and Social Bonds*” (Fedigan 1982/1992) on a typewriter in the back room of the trailer we called home on the La Moca ranch. My goal in writing that book was to summarize the literature on a variety of primate patterns and behaviors (e.g., kinship, sociosexual interactions, aggression) from the female’s perspective. I was at pains to point out that some prominent assumptions at that time inherently and incorrectly viewed female animals as passive resources for males to compete over and acquire. Given the lack of personal computers and the internet in 1978/1979 I needed to make many trips on the Greyhound bus from the nearest small town in south



Fig. 1 Adult female Japanese macaque (*Macaca fuscata*) and her infant, La Moca, Texas

Texas to the University of Texas in Austin, to acquire copies of the necessary literature. My favorite memory of writing “*Primate Paradigms: Sex Roles and Social Bonds*” (Fedigan 1982/1992) was being able to look out the windows of our La Moca trailer and see the monkeys. Sometimes peripheral monkeys would escape the electric-fenced enclosure and peer into the trailer at me on the typewriter, and I hoped that what I was writing was doing justice to them.

After I started my tenure track position at the University of Alberta in the 1970s, my graduate mentees also began to study the AW monkeys and produced theses and many publications on the macaques. One PhD student at the time (Dr. Mary Pavelka) was interested in female old age and end of life reproduction, so we initiated a series of ten papers on reproductive senescence in Japanese macaques and how reproductive termination differs in female nonhuman primates from menopause in human females (e.g., Fedigan and Pavelka 2010). A review paper on this topic (Pavelka and Fedigan 1991) is one of our more oft-cited publications.

In 1984, I became acquainted with Dr. Pamela Asquith and learned that she specialized in the comparative study of the science of primatology as conducted in Japan versus the West. Pam Asquith and I began a collaboration that resulted in a conference in Banff, Alberta in 1987 that was sponsored by the Wenner-Gren Foundation. We invited primatologists from both Japan and Canada/USA, all of whom had studied the Arashiyama macaques and, with the help of a couple of translators, we shared our knowledge of these monkeys. It was a very productive meeting (Fig. 2) that led to an edited volume of papers on the Arashiyama monkeys (Fedigan and Asquith 1991).



Fig. 2 Arashiyama conference in Banff, Alberta, 1987. First row (left to right): Jean Kitahara-Frisch, Naoki Koyama, Linda Fedigan, Nobuo Asaba, Larry Fedigan, Caroline Lanigan. Second row (left to right): Pam Asquith, Masami Iwasaki, Yukio Takahata, Hisayo Suzuki, Meredith Platt, Mary Pavelka. Third row (left to right): Takamasa Koyama, Carolyn Ehardt, Ben Blount. Back row (left to right): Yukio Yasutake, Masayuki Nakamichi, Michiko Inoue, Mona El Hadad

Mr. Dryden, the Texas monkey benefactor, died 2 years after the monkeys arrived at La Moca, and although his widow kept the monkey colony going financially for another 6 years, her heart was not in it. In 1980, once again thanks to the efforts of Dr. Bramblett and one of his former students, Dr. Louise Griffin, the entire AW group was moved to a ranch near Dilley, Texas, about 37 km north of La Moca. There the monkeys remained and the population continued to increase to the extent that they began fissioning into daughter groups, and one or more subgroups were constantly attempting to range outside of their enclosure (analogous to what had happened nearly 20 years earlier in Japan). Added to the population growth issues were financial ones—although the non-profit organization known as the Arashiyama West Institute, spearheaded by Bramblett and Griffin, did apply for and receive some grant funding, it was increasingly difficult to obtain enough funds to support the colony. Finally, in 1999, control of the AW colony was taken over by the Animal Protection Institute (a national, non-profit animal advocacy organization). They purchased the land near Dilley on which the monkeys resided and took over supervision and care of the animals, which included instituting universal forms of population control. The first attempts at birth control began in 1996 and marked the end of our life history research on these monkeys. In addition, the 1999 takeover by the Animal Protection Institute (now called “Born Free USA”) meant that the facility became a sanctuary rather than a place of scientific objectives and did not encourage visits by outsiders. Over the many years that our scientific work

at AW was taking place, a number of Western researchers visited the Arashiyama monkeys in Japan and several Japanese primatologists visited the AW group in Texas to carry out small projects (see Fedigan 1991; Huffman et al. 2012). Fortunately, the research in Japan on the Arashiyama monkeys has continued (e.g., Gunst et al. 2020; Leca et al. 2012) and has now been ongoing for more than 70 years.

My search for a stable primate field site in a native habitat

Even as I was collecting and overseeing the collection of life history data on the Japanese macaques at AW, I started to look for a field site where the primates would be completely free-ranging and living in their native habitats with only minimal human interference. If possible, I wanted to continue studying monkeys living in multi-male, multi-female social groups. I also wanted to establish a stable and safe long-term site where my students and I could start the collection of life history data similar to what had been collected on the Arashiyama macaques. In this endeavor, I experienced several false starts that I have described elsewhere (Fedigan 2020). I first tried to initiate a spider and howler monkey study in Tikal, Guatemala in 1977. Although this attempt did result in theses and publications for two of my graduate advisees, there was a great deal of political turmoil in Guatemala at that time and I terminated the project when I felt that it would not be safe for graduate students from the University of Alberta to spend time there. I next spent a year attempting to set up a long-term study of vervets on the island of St. Kitts (1981–1982). In this case, the country was politically stable and friendly to visitors, so the students and I would be safe, but the monkeys were not. Although one thesis and several publications on the St. Kitts vervets resulted, I soon realized that my attempt to habituate the vervets to observations was rendering them vulnerable to capture and harassment from the local human population, which largely regarded the monkeys as a nuisance if not vermin. In fairness, some of the vervets did raid their crops.

During the year that I was on St. Kitts, I corresponded with Dr. Ken Glander (a fellow former Bramblett mentee) about my search for a field site in a politically stable country, and he suggested that I survey Costa Rica for possibilities, where he already had a long-running howler research site at La Pacifica in the province of Guanacaste. Therefore, in the spring of 1982, Larry Fedigan and I made a reconnaissance trip to Costa Rica. We were very impressed by the natural beauty and the abundance of reserves and parks in that country, and after examining several possible sites for research, we settled on Santa Rosa National Park in the province of Guanacaste. It was a fortuitous choice, not only because it met my objective of doing research and training students in

a stable and safe environment for the primates and humans alike, but also because we have been able to work for the past 39 years in a situation/habitat/environment where a world-renowned experiment in tropical forest regeneration has been taking place.

The Santa Rosa Primate Project

The fascinating history of what was formerly called “Santa Rosa National Park” (SRNP; 1971–1989) and then became the Área de Conservación Guanacaste (ACG; 1989 to present) has been published in detail elsewhere (Allan 2001; Evans 1999). In brief, a project spearheaded by Dr. Daniel Janzen and a team of Costa Rican conservationists led to the creation of a “megapark” of which Santa Rosa is now one sector within the much larger ACG (www.acguanacaste.cr). Dr. Janzen convinced the Costa Rican National Park Service to merge SRNP with several nearby small parks and reserves and then created the non-profit Guanacaste Dry Forest Conservation Fund (<http://gdfcf.org/>), which raised funds to purchase almost all the ranches that surrounded the original park and later large tracts of land on the neighboring mountains and beyond. In 1999, the ACG was declared a United Nations Educational, Scientific and Cultural Organization World Heritage Site, and it now extends from the lowland forests along the west coast of Guanacaste, up through the dry forests of Santa Rosa, and further up and over the neighboring volcanic mountains through the cloud forest and Atlantic rainforest on the eastern slopes.

I have written earlier about the history of my own involvement with SRNP (Fedigan 2014). After my reconnaissance trip to Guanacaste in 1982, I applied for and received permission from the National Park Service of Costa Rica to carry out research on the primates of Santa Rosa starting in 1983. Along with the behavioral and life history research that I was given permission to conduct on the monkeys, the National Park Service requested that I census the three species of monkeys in the park (*Cebus olivaceus*, *Alouatta palliata*, *Ateles geoffroyi*). Because Santa Rosa had been only recently established as a protected area on former ranch lands, the park service wanted to know how the primate populations were faring. Thus, I agreed to add “park-wide census” to my job list, not quite realizing what a large task it would be, nor the rewarding findings that would result.

At the level of tracking individuals and groups of monkeys, I had the lofty goal to replicate the rich long-term dataset of the Arashiyama research project, but I needed to start pretty much from scratch. Although all three primate species in Santa Rosa live in the multi-female, multi-male (polygynandrous) social systems about which I wanted to learn more, I soon came to concentrate my behavioral ecology and life history studies on the female-philopatric

white-faced capuchins, about which very little was known at the time. With the help of Dr. Ken Glander and permission from the park, we tried darting, marking and releasing some individuals of all three monkey species, but soon abandoned that attempt for a number of reasons. The capuchins were so reactive and so agitated by any human disturbance that they were nearly impossible to capture safely. We quickly realized that capture of the capuchins was not necessary because, fortunately, they were relatively easy to tell apart. Nonetheless, the process of simply locating, following and habituating the capuchins to being observed required a couple of years (1983–1985) and as the project developed, I began to hire local Costa Rican field assistants to help, in particular Rodrigo Morera and Saul Cheves, our long-term project managers (Fig. 3). Additionally, over the four decades of the study, many students and graduate advisees came to Santa Rosa from the University of Alberta and later from the University of Calgary to conduct their own theses projects and to contribute data to the overall project.

In 1985, I selected five study groups of capuchins within easy walking distance of our park housing and began the systematic collection of life history data on them. In 1997, Dr. Kathy Jack first came to Santa Rosa to conduct her doctoral research and in 2004, I invited her to become a co-director of the project. She and I agreed that her research would mainly focus on male capuchins (e.g., Jack and Fedigan 2018), while I continued to focus primarily on the females. In 2004, Dr. Amanda Melin began her thesis research on the capuchins and, in 2011, Kathy Jack and I invited her to join us as a co-director on the project, with Dr. Melin’s main areas



Fig. 3 Saul Cheves Hernandez, project manager, Santa Rosa Primate Project

of expertise being behavioral and sensory ecology (Fig. 4). In 2009, Kathy Jack and I raised funds for, and were given permission to build in Sector Santa Rosa, our own research house, a facility which is owned by the park, but managed by our project (Fig. 5a, b).

I should add that the success of long-term projects of the type I am describing here is greatly facilitated by funding that continues steadily over many years. In addition to the Canada Foundation for Innovation grant that supported the development of the Primate Adaptations to Changing Environments (PACE) database (see below) and many smaller grants that funded student projects, my long-term research has been continuously supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) for the past 39 years, starting in 1983. Uninterrupted funding is pretty much a prerequisite for the collection of life history data in long-lived species like primates. The other factor in my career that greatly facilitated the success of our Santa

Rosa project was that, in 2001, I was recruited to the University of Calgary to hold a Tier I Canada Research Chair. The chair came with research funding and a reduced teaching and administrative load, which allowed me to focus more of my time on the Santa Rosa project. Canada Research Chair and NSERC funding also enabled me to work on the comprehensive and collaborative “*The Complete Capuchin: the Biology of the Genus Cebus*” (Fragaszy et al. 2004) that I co-wrote sitting side-by-side with Drs. Dorothy Fragaszy and Elisabetta Visalberghi (Fig. 6) during three consecutive months of May in a beautiful beach house on Long Island. Finally, and not least, the Canada Research Chair, being based at the University of Calgary, also allowed me to become part of a vibrant and productive team of like-minded primatologists in Calgary, each of whom was carrying out their own long-term primate field projects in Africa and Central America.



Fig. 4 Left to right Kathy Jack, Linda Fedigan, Amanda Melin, American Society of Primatologists conference in Atlanta, Georgia, 2015 (photograph by John Addicott, all rights reserved)



Fig. 6 Left to right Elisabetta Visalberghi, Linda Fedigan, Dorothy Fragaszy, Peconic Bay, Long Island, 2000 (photograph by Dorothy Fragaszy, all rights reserved)



Fig. 5 a Newly constructed research house in Sector Santa Rosa, Área de Conservación Guanacaste (ACG), 2011. **b** Left to right Linda Fedigan, Marvin Jimenez Salas (contractor/builder), Roger Blanco

Segura (program director, ACG), Alejandro Masis Cuevillas (director, ACG) in front of the newly constructed research house in Santa Rosa, 2011 (photograph by John Addicott, all rights reserved)

By 2001, our accumulated data had resulted in far too many Excel files, and my husband, Dr. John Addicott, generously created an Access database for the capuchin data. Several of my colleagues at the University of Calgary were collecting their own long-term field data on primates at other international sites, so in 2008, I applied for and received a Canada Foundation for Innovation grant to design and develop a multi-project, relational database for us all. Creating the database, which has the acronym PACE (see above), was a very complex and time-consuming endeavor and, once again, Dr. Addicott oversaw the design of the database, and in its early years, its maintenance. PACE is now the repository for many different forms of data (e.g., demographic, behavioral, phenological, weather, life history, hormonal, genetic, and more) and the PACE database manager (Jeremy Hogan) regularly uploads new data and provides data upon request to researchers associated with the PACE project. Similarly, but on a larger scale, in 2007, Karen Strier and Susan Alberts initiated a collaboration among seven researchers who have each collected more than 30 years of continuous life history data on a variety of species. We established the Primate Life History Working Group, and developed an integrated database, the Primate Life Histories Database (PLHDB), which includes literally thousands of life history records on individual primates from around the world (Strier et al. 2010). The PLHDB collaborative endeavor has resulted in a series of influential papers addressing larger, more inter-specific issues with more fulsome data than any of us could have generated alone (e.g., Campos et al. 2022).

Over the years of my research at Santa Rosa, very clear themes emerged despite the variety of interests expressed by project members and in the papers we published together. As sufficient amounts and years of data accumulated, I was able to turn my attention more and more to the fundamental life history questions that have always intrigued me—how and why do some females reproduce better than others over time? And how do females successfully carry out their lives in the social company of males?

Female reproductive success

Our Santa Rosa life history records document tremendous variation in adult female capuchin lifetime reproductive success: females produce anywhere from zero to 11 offspring during their reproductive years, and their infants survive to 1 year of age (which is the period of highest mortality risk) for 0–100% of the time (Fedigan et al. 2008). Over the years, we have examined many predictors or sources of female reproductive success (Fig. 7). We turned to the most obvious predictor first—dominance rank. Female capuchins in a social group do exhibit strong



Fig. 7 An adult female white-faced capuchin (*Cebus olivaceus*) and her infant, Sector Santa Rosa, ACG, Costa Rica (photograph by Fernando Campos, all rights reserved)



Fig. 8 Amanda Melin (*left*) and Shoji Kawamura (*right*), International Primatological Society conference, Edinburgh, 2018 (photograph by John Addicott, all rights reserved)

and linear dominance hierarchies; however, neither fecundity rates nor infant survival are predicted by dominance rank. To take this to its extreme, the alpha and the omega females in a social group do not differ noticeably in the number of infants they produce and that survive. As part of the capuchin color vision research project led by Dr. Amanda Melin and Dr. Shoji Kawamura (Fig. 8), we also tested and found that dichromat (color blind) females do not experience lower reproductive success than do trichromat females (Fedigan et al. 2014). However, some factors do appear to predict better success: (1) giving birth in a group that includes a greater adult male to female ratio, particularly with stable male membership (presumably because the resident males protect the infants); (2) giving birth in a group where the mother has a larger number of close matrilineal kin with whom to form alliances

and exchange allonursing favors; (3) giving birth in a year where there has been abundant rainfall (versus a drought year) to ensure a good supply of food and water; (4) living a long life (although there is limited evidence of age-specific fecundity or reproductive senescence) (Campos et al. 2020; Fedigan and Jack 2011; Fedigan et al. 2008, 2021).

We puzzled long and hard over the lack of a relationship between dominance rank and female reproductive success. It is possible, indeed likely, that because capuchins are opportunistic omnivores whose group members forage in a dispersed manner, that subordinate females can work around their lower status by pursuing alternative food resources as the group forages across its daily range. Furthermore, we know that a female's rank can sometimes change over her lifetime when members of her matriline come and go, and thus it may be that in the short-term, dominance rank is important to success, but not when examined over a lifetime.

However, to my mind, the most likely explanation is that male capuchins disrupt what would be the causal link between female dominance rank and differential female reproductive success (Kalbitzer et al. 2017). Capuchin males change groups multiple times throughout their lifetimes, and newly arrived males are very aggressive to resident males. During the process of a male “takeover,” resident females attempt to flee the scene of the fighting with their infants and to avoid the new males that are attempting to join the group. However, resident females do get wounded during these social upheavals, as do their infants (Fedigan 2003). This brings us to my second research theme, which is: how are females and their reproductive success affected by the males with which they live (Fig. 9)?



Fig. 9 Adult male and adult female capuchin, an instance of “double threat,” Sector Santa Rosa, ACG, Costa Rica (photograph by Fernando Campos, all rights reserved)

Sexual conflict

The interactions of adult capuchin males with infants range from impressively protective to extremely aggressive. An adult male may confront a predator to protect and then physically rescue an infant, or conversely, may fatally puncture an infant with his canines. The former (the protective male) is almost always the resident alpha male, the likely sire of the infant (Wikberg et al. 2017), and the latter (the aggressive male) is typically a newly arrived male who has not mated with the infant's mother. Dr. Kathy Jack and I published a series of studies demonstrating that over the course of their lives, male capuchins move from group to group in search of better reproductive opportunities, and when they enter a new group aggressively not only are resident males injured and expelled due to the resultant fighting, but the females and infants may also be wounded (e.g., Fedigan and Jack 2004; Jack and Fedigan 2006). Infanticide in white-faced capuchins is a major cause of infant deaths and a major disruptor of the pattern of female reproductive success (Fedigan et al. 2021). When males are in the process of entering a new group, they seek out the center of the group, where the highest-ranking females can usually be found. With Dr. Urs Kalbitzer, we demonstrated that during times of resident male stability in groups, the infants of high-ranking females exhibit high survivorship, whereas during periods of aggressive incursions of outside males, the infants of these same high-ranking females fare worse than do infants of the more peripheral, low-ranking females (Kalbitzer et al. 2017). This differential success based on group social dynamics is likely why dominance rank alone does not predict long-term reproductive success in female capuchins.

Thus, the complexities of understanding female reproductive success led me to a second major topic: an examination of sexual conflict, a topic that has gained more interest and coverage in the past couple of decades (Fedigan and Jack 2013). Since males compete for reproductive success, it is possible that part of that competition involves the elimination of their rivals' offspring. In the case of white-faced capuchins, males do not harass or sequester females or coerce mating; however, newly arrived males may suddenly wound an infant whose mother they have been grooming. We have sometimes witnessed such attacks, and from these direct observations, we know that infanticide is a very swift event and thus difficult to observe. We cannot say exactly what proximate cue triggers an attack on an infant, but in all the cases for which we have paternity data, the perpetrator is not the father of the infant, and is almost invariably a recently arrived male.

Unlike males, female monkeys can be certain that a given infant is their own offspring, and they invest much

energy in keeping their infants alive. They also exhibit many patterns that act as “counterstrategies” to male aggression (reviewed in Fedigan and Jack 2013). For example: (1) they mate with multiple males and do so even when they are already pregnant and not cycling, thus further confusing paternity; (2) kin-related females form reliable alliances and defend one another and their infants from male aggression; (3) many adult females form alliances with the resident males, particularly the alpha male, to the extent that they will sometimes emigrate with the former alpha male to another group after a takeover; (4) during (and for some days after) a male takeover, females of the group avoid the newly arrived males and they fail to answer male “lost calls” once they manage to put distance between themselves and the newly immigrated males. Nonetheless, change in adult male group membership is inevitable in capuchins, and most females will experience alpha male replacement while rearing an infant during their reproductive lifetime. It is during this period of time that infants sired by the former resident males are at their peak vulnerability (55% of infants perish in their first year of life after a male takeover versus only 18% infant mortality during stability). We have recently published a study (Fedigan et al. 2021) that documents the very high costs of male infanticide to female reproductive success, and the risks to Santa Rosa capuchin population viability overall should the rate of infanticides increase any further.

Primate populations return to regenerating forests in Santa Rosa

As noted earlier, when I first received a permit from the Costa Rican National Park Service to study the monkeys in Santa Rosa National Park in 1983, the administrators asked me to monitor how the monkey populations were faring in the park. No censuses of the monkeys had been conducted in Santa Rosa since a partial count in 1972, one year after the area came under protection in 1971. Prior to the creation of the park in 1971, this area of the province of Guanacaste had been subjected to hundreds of years of human activities (e.g., cattle ranching, logging, agriculture, hunting) that had resulted in a mosaic of forest fragments of different ages, sizes and composition. The park service’s hope was that after the park was created in 1971, the monkey and other animal populations would recover in conjunction with the regeneration of the native tropical dry forest.

Therefore, along with my intensive studies of the life histories and behavioral ecology of selected groups of monkeys, in 1983 I began to conduct censuses of the howler and capuchin monkey populations in the 100-km² area of tropical dry forest that was originally Santa Rosa National Park but is now known as “Sector Santa Rosa” in the ACG

(Fedigan and Jack 2012). Because spider monkeys live in fission–fusion social systems and are much harder to census, we have only occasionally estimated spider monkey population density via transect studies in particular fragments of the ACG forests (Chapman et al. 1988; Sorenson and Fedigan 2000; DeGama and Fedigan 2006).

For the first 6 years of my studies in Santa Rosa, starting in 1983, we conducted annual censuses of the howlers and capuchins during the dry season and then we moderated to less frequent censuses being conducted every 2 to 4 years. Over the past 38 years, my colleagues, students, field assistants and I have conducted 15 park-wide censuses of the capuchins and howlers. Our most recent census has been delayed by COVID-19-related restrictions and concerns; however, our 16th census is occurring as I write this article, during the dry season of 2022.

What have we found? The capuchin population of Santa Rosa increased rapidly during the 1980s and 1990s, likely because suitable habitat was also increasing due to forest regeneration in the protected park. After the initial period of rapid sustained growth, the capuchin population began to stabilize around the year 2000, with small perturbations associated with drought years (Campos et al. 2015, 2020), and has remained roughly three times as large as the original 1983 population (717 compared to 226 individuals). It is possible that the capuchins have reached the carrying capacity of the available habitat and will only continue to grow slowly as the forest continues to regenerate. During the 1980s and 1990s the howler population at first grew more rapidly than did the capuchin population, likely because howlers have a faster life history pattern (they give birth at an earlier age and more often). However, the howlers then experienced a sharp population decline, possibly either due to disease cycles that are typical of howlers elsewhere or because of increased use of pesticides that were sprayed on the crops of farms neighboring Santa Rosa. Once those farms were purchased by the ACG and agriculture ceased, the howler population began to increase again. Overall, the howler population size has fluctuated more often and more strongly than that of the capuchins.

We also found that the two species “grew” their populations via two different mechanisms. Over the first decades of our study, we repeatedly saw lone howler males move into a small unoccupied forest fragment and begin to howl until eventually one or more females joined them and they then formed a new, small group and produced offspring. And with each park-wide census we counted more and more small howler groups. This pattern of creating new groups is feasible for howlers because both males and females disperse. In comparison, the mechanism of capuchin population growth was by an increase in group size and group range. In each consecutive park-wide census, we found that the average capuchin group size had increased. We also found

that capuchin groups began to range into newly regenerating forest patches that had been pasture only 25 years earlier. Capuchins were particularly prone to move through and forage in a young forest patch if the previous pastureland included a large fruit tree. A typical pattern of land clearing by local ranchers was to leave one or more large fruit trees in the pasture to provide shade for cattle, which proved “fruitful” for capuchins upon their return! No capuchin group restricted itself to such a young forest patch, rather they simply extended their home range to incorporate it.

With the help of local botanists and park historians, we estimated the ages of the forest fragments in Santa Rosa, and we also estimated and monitored the density of each of the three monkey species in these forest patches. We found that capuchin groups can use forest patches that are as young as 25 years, but are usually found in older forest with a water source that remains available during the dry season. They range in such a way as to have access to a water source for drinking at least once a day. Howlers seldom drink water, rarely occupy forest fragments under 60 years of age, and are more common in riverine forest patches with large trees that are 100–150 years old. Spider monkeys in Santa Rosa are only rarely seen in forest fragments less than 100–200 years old and prefer larger patches of forest, presumably to accommodate their trap line pattern of foraging on fruit (DeGama and Fedigan 2006; Fedigan and Jack 2012; Sorenson and Fedigan 2000).

What lessons can we draw from our park-wide censuses in addition to our major finding that capuchin and howler populations can substantially recover in tandem with forest regeneration and habitat protection? From our long-term study of the ranging and population patterns of the three primate species in the tropical dry forests of Guanacaste, we concluded that the fundamental requirement for capuchins is a year-round water source, whereas howlers need large trees of species with leaves and fruit that have low levels of secondary compounds, while spider monkeys do best in large tracts of old growth forest in order to maintain their fission–fusion system and frugivorous diet. These are all noteworthy points of information for conservationists working to return Neotropical monkey species to recovering habitats. For an excellent recent summary of the many contributions to science and conservation of our long-term primate research in Sector Santa Rosa of the ACG, see Melin et al (2020).

Gender and science studies

“*Primate Paradigms: Sex Roles and Social Bonds*” (Fedigan 1982/1992), which was first published in the early 1980s, was my first attempt to redress the neglected role of females in the scientific literature as being significant players in the

social life of their groups and in the evolution of their species. The book was widely and positively reviewed, and I was invited to produce a second edition in 1992. It is an extensive book, summarizing a great deal of literature and covering many aspects of primate behavior. It was also a goodly amount of work, and I have been sometimes asked why I undertook such a large writing project so early in my career. Looking back, I feel that the ways that the female monkeys that I was observing managed to live their lives in the constant presence of males that often had conflicting reproductive agendas was an issue, a topic, that simply resonated for me. At the same time, some of the literature, terminology and explanations prevalent during that stage of primatology as a science did not correspond with my own observations. For example, hamadryas baboons were originally described as living in “harems” where females were “owned” by the males. Hamadryas males do indeed attempt to mate guard the females in their group, but they do not own them. And dominant males in several primate species were said to have greater reproductive success due to their “priority of access to receptive females,” as though the latter were passive resources. The female monkeys that I was observing were neither owned nor passive. Similarly, females were usually portrayed as playing minor roles in evolutionary models of early human social life, despite lack of corroborating evidence from our primate relatives and from non-industrial human societies. The exceptions to these male-biased models were representations of human evolution that were developed by women anthropologists. These were models of human social evolution in which early women were hypothesized to have played significant parts. I wrote a paper on this topic (Fedigan 1986) that is still one of my more cited gender essays.

Soon after the publication of “*Primate Paradigms: Sex Roles and Social Bonds*” (Fedigan 1982/1992), I became acquainted with two researchers, Drs. Shirley Strum and Pamela Asquith, who were very interested in the science of primatology itself as an object of study. I met Shirley Strum during the 1984 International Primatology Congress in Nairobi and became aware of Pam Asquith’s research at the same conference. Both of these women scholars were destined to become important collaborators in my research, and they crystalized my interest in science studies. Pam Asquith (Fig. 10) helped me to fully appreciate that Japanese primatologists, at least in the earlier decades of their history, had unique methodological and conceptual approaches to primate studies. The approach of Japanese primatologists eventually proved to be as equally insightful as the approaches of the European and American researchers. Indeed, aspects of Japanese primatology were later adopted by Western scientists (e.g., collaborative, long-term, life history studies). For her part, Shirley Strum (Fig. 11) introduced me to some leading figures in the field of science studies, and together



Fig. 10 Linda Fedigan (*right*) with Pamela Asquith (*left*), Edmonton, Alberta, 1990 (photograph by John Addicott, all rights reserved)



Fig. 11 Linda Fedigan (*left*) with Shirley Strum (*right*), Teresopolis, Brazil, 1996 (photograph by Laurie Obbink, all rights reserved)

she and I wrote a history of changing views of primate society (Fedigan and Strum 1999; Strum and Fedigan 2000a). Also, in 1996, Shirley and I co-hosted a Wenner-Gren Foundation-sponsored conference in Brazil to address the question of how and why ideas about primate society have changed over time. We invited 23 scientists and scholars of different disciplines, generations and national traditions to address the roles of theory, method, gender and culture in changing our ideas about primate societies. Set in Teresopolis, Brazil, this Wenner-Gren conference took place during a period when the “science wars” were particularly active between a group of scientists who considered themselves fully external to their study systems and those scholars who viewed the scientists themselves and their scientific work as objects of study. These so-called science wars took place mainly in the 1990s and comprised a complex set of antagonistic exchanges between scientists and those scholars who study science itself as a sociocultural enterprise. Thus, the

conversations and presentations during our Teresopolis conference were highly spirited as we attempted to convince the participants to exchange ideas rather than hostilities. Later, we published an edited volume of our conversations and the conclusions we drew from them (Strum and Fedigan 2000b).

As far back as the 1980s, colleagues, friends, my family and popular science journalists had begun to ask me variants of this question: “why are there so many women primatologists?” For quite a while I dismissed this repeated question as being based on the mistaken assumption that there *are* so many women primatologists. In my mind, I labeled this as “the National Geographic effect,” referencing the extensive and popular media coverage of Jane Goodall, Dian Fossey and Birute Galdikas that led people to assume that all primatologists are women. However, the thrumming background recurrence of this question being put to me slowly made its way forward in my mind until one day I realized that I was being asked about the coexistence of women with men. What an irony. I had been dismissing a question that was right up my alley, even though in this case, the question was about how human females and males coexist in a scientific “society.”

After this realization, I conducted a small study of the proportions of women and men in various scientific subdisciplines, using data from professional directories (Fedigan 1994). From that analysis, I found that there were indeed higher proportions of professional women in primatology compared to other organism-focused sciences (e.g., ornithology, entomology, etc.). Furthermore, there were increasing proportions of women listed in primatology directories in 1992 as compared to 1982. Although at that time there were not more women in the primatological societies than in the “parental” disciplines of anthropology, psychology and animal behavior, my preliminary data analysis set me on a new path of inquiries about why primatology developed into an especially welcoming field for women scientists. Thus, I began a series of papers addressing this topic (e.g., Fedigan 2001). Because my grant funds were all designated as being for studies of the monkeys themselves, I thought of my analyses and papers on gender and science as “moonlighting,” as research that I did on the side during my spare time. Nonetheless, my essays on the ways in which women scientists themselves have strongly affected the depiction of female roles in primate society, and how females are depicted in models of human evolution, continue to be widely cited (see Asquith 2018).

In my examination of gender and primatology (as was also the case with my studies of how monkey populations recover in regenerating tropical forest), it has been my experience that it is wise to keep an open mind as to which research questions are worthy of pursuit. Along with the questions that we set out to pursue, questions are sometimes brought to us because we are the right person to address

them, and by doing so, we may achieve valuable scientific insights.

Conclusions

Elsewhere, I have published a list of “lessons learned” from my 50-year career (Fedigan 2020). Here I will simply conclude by saying that there are many paths to a career in primatology and it is important to follow your own pathway, that is, to recognize and address the issues that are important to you. I feel very fortunate to have spent much time in the company of my primate relatives and in beautiful tropical habitats. And I am grateful to have had a wide network of support from my funders, family, research assistants, colleagues and collaborators. I wish all readers, especially younger ones, an equally rewarding career.

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