THE EVOLUTION OF A PHYSICAL ANTHROPOLOGIST

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CHOOSING A CAREER

Until recently, no one had to wonder what they would do when they grew up because the answer was simple: individuals fortunate enough to survive to adulthood typically did whatever their mother or father had done and that was that. Today conditions are different. Now almost everyone must face the question of what career to pursue. Though a fortunate few seem born knowing they want to be brain surgeons or fashion designers, for most of us the question is not so simple. And indeed for some of us, the question of what career to pursue continues to preoccupy us for some years into adulthood. I was one of these rather slow starters. That is to say, I stumbled in and out of several different career trajectories before I finally fell backwards into the right choice. I guess I represent a classical example of the fact that many of the best things in life aren't planned—at least not initially.

EARLY ATTEMPTS

When I was growing up in Alabama, though good grades were emphatically encouraged, never once was the idea presented to me that one might study something just for fun—that it might be a real kick to use one's mind. Nor did anyone ever suggest entering a field such as biology, mathematics or physics—anything in the sciences was neither mentioned nor conceived. Ditto for business. The notion of a "career" in terms of itself, of the joy and happiness that might come from one's work, simply wasn't an issue. Perhaps my parents thought it was obvious and I always have been slow at realizations. I do remember that at one

point my father did say I should become a lawyer because I loved to argue. But that was about it for suggestions regarding my future career.

When I occasionally discussed the subject of college with my mother (my father being too busy to engage is such conversations), I dimly realized that while at college one was supposed to acquire a degree in "something"—from my mother's point of view, some practical thing that, "will help you earn a living if you lose your husband in an accident and have to support your children." That certainly didn't sound like much fun; in fact it sounded like something to avoid.

In any case, off I went to a college in Virginia, Sweet Briar, which far from being as saccharine as its name implies, turned out to be the most intellectually rewarding of all my by now extensive encounters with higher education. The professors at Sweet Briar were terrific, they loved their subjects, they loved to teach and I loved learning from them. It was only at this point that I began to realize that thinking was fun. Toward the close of my senior year, the fun turned to nervousness. I had taken considerable coursework in English literature prior to the twentieth century but hadn't managed to get to my own century, which I found of particular interest. My professors recommended graduate schools with good programs in twentieth century English literature. I made application to several of these programs, went through my graduation ceremony at Sweet Briar and returned home to Alabama. That summer I just sat around in a daze—I didn't know what to do, what I would do, what day of the week it was. It was a shock to suddenly be out of college, the arena where my life had been totally focused for the past four years. I was a graduate, I had a B.A., I was supposed to be doing something but that something was not manifesting itself with any clarity.

I was saved by a phone call. The University of Iowa rang up to say that yes they would take me as a graduate student and yes they even had a job for me so that I could earn my tuition and living expenses. So off I went to graduate school in Iowa City, once again suffused with purpose, to study modern English literature and prepare for a career as a literary critic. I got my M.A. and moved to New York to seek a position as a literary crit-

ic. This was not so easy as such jobs seemed in remarkably short supply. I took a position at Time Inc. as an editorial assistant while I pondered my future—was journalism the answer to my career concerns?

During this period, I also got married and my husband's job required that we move to Argentina. Buenos Aires was beautiful and sophisticated and once I got settled in, my life was perfect in every way except for just one little thing—I was bored to death within only a few weeks. There were no jobs for women in Buenos Aires for which I was qualified and I had very little to do. I worked at numerous small jobs—occasionally writing for the English language newspaper and such but basically these were stop-gap activities and realizing this, they only made me sad. In frustration, I began reading books in the English language library near my house. They had a biology section with books on animal behavior and I read through the entire shelf. Much of the work was ecological and I gradually decided that being a behavioral or ecological scientist would be an ideal thing to aspire to because then I would never again find myself with nothing to do. The literary careers I'd initially been fumbling toward were always ones that required a formal setting and other people—their presence, their books, a formal working infrastructure— in order to be active. Being a scientist doesn't necessarily require a formal setting or the presence of other people in any type of routinized environment. You can do many types of science wherever, whenever—if there are no cats, monkey, or earthworms around to observe, you can study plants or your fellow humans. The trick, or so it seemed to me, was to learn what problems were worth studying and how one would go about compiling information on these problems in a scientific manner.

So that is how I got into my career as a scientist—pure desperation, a handy library, a fortuitous shelf of books—and the idea that science would save me from boredom for the rest of my life. I hated being bored, I couldn't stand having nothing of real interest to do and I would have done anything to escape this boredom. People, particularly women raised in a conventional setting, often don't realize that they may have a mind that requires more than the daily routine and an occasional newspaper or magazine to be happy. I was lucky—being bored in

Argentina while I was still quite young made this crystal clear and so off I went, back to the United States and back to school once more but this time to get my scientific education.

MONKEY BUSINESS AS A CAREER

Suffice it to say that it was very difficult for an English major to get into graduate school to study biological subject matter. Finally, I managed to get accepted into the newly created Anthropology Department at New York University to study physical anthropology—as it was a new program, it is likely that few students initially applied, giving me a better chance. In a program in physical anthropology, I would be able to study the ecology and behavior of non-human primates—prosimians, monkeys, and apes—as well as that of my own species and this seemed to offer sufficient scope for my scientific aspirations. Further, the city of New York, with its many colleges, universities, and museums gave me the opportunity to delve into a number of other courses and programs while enrolled in the Ph.D. program at NYU.

By 1973, I had managed to leap through all of the sticky academic hoops required for what is termed *advancement to candidacy*. This meant that now all that stood between me and the Ph.D. was my dissertation research—in other words, course work, exams, boring professors, and the like were behind me forever. But now, I needed a research topic for my thesis. In the early 1970s, most field studies of wild primates were strongly focused on aspects of sociality. In particular, as primates were known to have a large number of different patterns of social organization, there was considerable interest in determining the factors that might underlie all of this variability. But at the time, relatively little attention was being paid to features of the environment—that is, to aspects of the ecology of the primates rather than only to aspects of their sociality. It seemed to me that this was trying to understand the cherry on the top of the sundae without looking at the composition of the sundae itself. Since most individuals then interested in primate behavior were, like me, in depart-

ments of anthropology, which tend to be dominated by social scientists, it is easy to see why they were pondering social behaviors rather than features of the environment. Perhaps they felt that examining patterns of food distribution, dietary quality, predator pressures, and the like would produce a type of environmental determinism at the monkey level. But I suspected that more attention needed to be paid to factors impinging on the monkeys from the outside rather than just determining that monkey A was dominant over monkey B or noting that some primate species lived in large groups and others in small ones.

I somehow had decided that a detailed examination of diet was likely to provide me with a key to understanding most aspects of primate behavior but it is difficult for me to be certain of just how I arrived at this dietary focus. Perhaps it was due, at least in part, to an article I had read in *American Anthropologist* in which Bartholomew and Birdsell gave a strikingly original, *ecological* overview of early human evolution in which they focused on potential environmental pressures placed on the earliest humans as a means of understanding key features of human morphology and behavior.[1] Too, some primatologists were beginning to explore aspects of diet in their fieldwork which must have indicated to me that "this was what one was supposed to be doing." But I also knew, probably because even then I did not confine my reading to journals and books only about primates but rather read widely in the general ecological and evolutionary literature, that to understand diet, one had to do more than just describe what the monkeys were eating—make dietary laundry lists. Rather, one had to be able to document what foods were available in the forest and then determine why the monkeys were choosing certain foods rather than others. Thus from my earliest days as a researcher, I also had an interest in plants.

I came up with several dissertation topics that didn't work out. For example, first I wanted to study the ruffed lemur, *Varecia variegatas*, in Madagascar—it had an unusual loud call, gave birth to twins rather than a single infant and had other striking characteristics that I felt must relate in some manner to dietary energetics, but political conditions in Madagascar made such research impossible. I then thought about studying a New World

monkey, *Cebus apella*, unusual because it had such a wide geographical distribution relative to other members of its genus. I suspected its dentition (and therefore its diet) might explain its distribution—but there were so little data available in the early 1970s on members of the genus *Cebus* that even if I had obtained information on the diet of *C. apella*, I would have had almost nothing to compare it with—leaving me with a problem in a vacuum. If you want to understand how something is similar to or different from something else, you need information on the something else to compare with the material you compile.

OFF TO PANAMA

Finally, Alison Richard, a primatologist at Yale, suggested I go to Panama and work in the tropical forest there to gain some practical experience. I decided to focus my attention on mantled howler monkeys (*Alouatta palliata*). In fact, these howler monkeys had been the first primates studied in the natural environment—in the early 1930s. C. Ray Carpenter had observed howlers for a period of months and published an excellent monograph on features of their social organization, diet, and behavior.[2] Various other well known primatologists had also examined aspects of howler behavior in the ensuing years but generally for only short periods of time. Thus I would be following in the footsteps of illustrious predecessors and could build on their earlier observations. The question was, what was it about howler monkeys that I was going to research? I felt that some aspect of the howler diet would be appropriate but in March of 1974 when I flew to Panama, I was still very uncertain as to what my study actually would consist of. It is clear, however, that my interests were always focused on diet, for in reading over an old letter I wrote in 1973 to request permission to come to Panama to begin my preliminary research, I state that one of my reasons for wanting to work on howler monkeys at a field station called Barro Colorado Island was the fact that the island had a *herbarium* (formal plant collection) that would permit me to identify the plant foods the monkeys were eating and learn the scientific names of the tree species.

When I arrived in Panama, I must have presented an amusing and unpromising sight. I was rather plump and stuffed into somewhat inappropriate field clothes. I knew nothing about keeping off the myriad hoards of ticks and red bugs that make the researcher's life in this tropical forest a perpetual living hell and in fact during my first week on the island I actually went on a picnic and *sat on the ground*—tantamount to committing suicide in this bug-infested environment. I had little idea how one was supposed to carry out real field research and toward this end, I was burdened down with an old blue American Tourister suitcase, giant sized, that must have weighed over 100 pounds as it was crammed with every scientific article I owned to aid in planning my research assault. I was so out of shape that for first few weeks when walking on the trails, I had to stop and rest every twenty or thirty feet. Barro Colorado Island was created in the early part of this century by damming the nearby Chagras River to form a waterway for the Panama Canal. The rising water flooded most of the region, leaving only the steeper hilltops sticking up out of the new lake. Barro Colorado is a six-square mile island composed of these rolling hilltops and walking about on the island typically involves a considerable amount of climbing up and down steep trails in the hot muggy climate.

Back in the early 1970s, tropical ecology had not yet become the popular research field it is today. There were few other scientists on the island my first months there and often I was the only person eating dinner in the large dining hall. But frankly, I didn't notice or care, a personality trait that has stood me in good stead over the course of my career—because I had an entire island full of exotic animals as my companions. The forest was loaded with howler monkeys, cebus monkeys, spider monkeys, tapirs, wild pigs, deer, coatis, sloths, agoutis, weird bugs, and neon-blue butterflies the size of dinner plates. I kept a little notebook and recorded all the animals that I saw, particularly noting information on where I saw howler monkeys and various details of their behavior as well as collecting samples of the plants they were eating.

I've always devoted considerable time to the observation of plants as well as animals. Understanding what trees are doing helps me to understand the behavior of the monkeys and vice versa. Plants face most of the same problems animals do—name-

ly, how to obtain adequate nutrition, how to find the best mate, how to do the best one can for one's offspring and how to avoid danger and illness. And they've had to solve these critical problems while rooted in one place in the ground. Working with trees and their fruits, seeds, flowers, and leaves has been an education in itself, since many of their solutions to these problems are subtle ones that can involve exotic chemicals, elaborate genetic mechanisms, and the like.

You might assume that a fruit is a fruit is a fruit. But scientists believe that the first primitive fruits were elaborated millions of years ago to help plants disperse their seeds, thereby improving their prospects for colonization and growth. The sweet juicy pulp surrounding the seeds is the plant's way of luring seed dispersal agents such as monkeys, bats, or birds into eating the fruit, simultaneously scattering or swallowing the seeds, which may then be defecated some distance from the parent tree. The solutions plants have evolved to their problems often in turn become primate problems; certainly we can assume that over evolutionary time natural selection has favored plant defenses that help them avoid the loss of their new leaves, nectar-filled flowers, unripe fruits, and edible seeds to hungry primates. How primates get around these plant defenses and solve their dietary problems are, in essence, what has made primates primates. The old adage, you are what you eat, is absolutely true. As Darwin noted, living matter possesses an almost infinite capacity to replicate itself. Yet at the same time, dietary resources available on the planet at any one time are always limited and always far lower than the potential mouths seeking to devour them. Thus selective processes have produced myriad ways of securing some portion of these always finite essential resources—and these different dietary battle plans in essence are the diverse array of living life forms present on the planet. With our overly well-stocked supermarkets and endless food at our fingertips, we often forget that obtaining adequate food and water is generally the single most compelling daily activity of most other living organisms. Indeed, even human societies that live in remote regions and lack our technological means of food preservation typically devote the greatest percentage of their daylight hours to activities directly involved in obtaining, cleaning, and preparing the food they eat.

HOWLER MONKEY ECONOMICS

I wasn't on Barro Colorado Island very long before finding a dissertation topic. I decided to study the interface between the components of the howler diet, howler digestive processes, and howler food acquisition activities (where and when different foods were available)—because what I observed in my first few weeks on the island did not tally with what I had expected from reading the literature. Howler monkeys were known to be arboreal herbivores—that is, they lived in the trees not on the ground and they obtained all of their foods from plant parts. But I could quickly see that howler monkeys were not just some type of arboreal cows that sat around stuffing themselves with the most convenient leafy foods all day—rather the monkeys were traveling all over the forest, eating many different species of leaves as well as considerable amounts of fruits and flowers—ten, twenty or more species in some days. Clearly making a living as an arboreal herbivore was a far trickier business than I'd been led to believe. I wanted to figure out what was going on.

My viewpoint—the reality I saw in 1973—was simultaneously both the same and different from that seen by my scientific predecessors who'd carried out earlier observations on howler monkeys in this same forest. As scientific knowledge is always advancing, many new things had been learned since these earlier howler monkey studies—new information about the chemical constituents of wild plants, about the often subtle mechanisms involved in food selection and, most importantly, about the deceptive nature of reality—the fact that though tropical forests looked as if they could provide an endless food supply for plant eaters, in truth most of this lush greenery was not of a quality to sustain life for mammals the size of howler monkeys. *Optimal foraging theory*[3] had also emerged, a theory which presented models which made predictions about how a given animal should behave when faced with different types of dietary situations. I had read all of this ecological literature and thus when I began to examine howler monkey behavior in 1974, though their behavor probably differed little if at all from that observed by my predecessors, I was mentally primed to view their foraging

activities somewhat differently. In this way, each new generation of scientists builds on the scientific resource base passed on to them by their predecessors.

The approaches that I employed in the fieldwork and the results I obtained are presented in detail in my book on howler monkeys, which was my doctoral dissertation.[4] I spent approximately fourteen months carrying out my study, using two different groups of howler monkeys and collecting data in a systematic manner that made it highly amenable to statistical analyses. I carried out simple feeding trials to examine howler food choices and digestive processes. I also carried out work on different aspects of the forest, determining the density of different tree species, their spatial patterns, the production patterns of new leaves and fruits and so on. I was able to integrate these botanical data successfully with the feeding and physiological data on the monkeys and come up with a novel synthesis—what I termed a study of *monkey economics*—that took food availability, food locations, dietary quality, howler energetics, and howler digestive abilities and integrated them into a solid overview of howler monkey dietary behavior. These same data also permitted me to understand a considerable amount about howler monkey social behavior. During these months of fieldwork, it was often hard for me to get up at 4 A.M. and walk out into the dark, frequently rainy forest for twelve hours of monkey observations, but I kept at it, confident that my results would make the momentary discomfort well worth the effort. And I believe that they were. Often researchers state that they are never satisfied with their research—indeed, some never publish anything because it isn't perfect. Well, nature isn't interested in perfection and neither am I. I'm interested in doing the best job possible with the facts known at the moment—and this is what I believe I did in my book. I've since moved on and learned considerably more and now of course I'd change some things to reflect what I've since learned; but at the time, I believe my book was state of the art and I was thrilled with my synthesis. My favorite story about my dissertation work and the book that resulted from it is one that was told to me by a colleague from Duke who was flying out to the west coast. He noticed that the young woman sitting next to him was intently reading a book. On inspection it turned out not to be a hot new best seller but rather my howler monkey book, being read by a

prospective graduate student coming to visit the Berkeley campus. My friend was very impressed and of course once I heard that story, I thought the prospective student seemed unusually promising.

After obtaining the Ph.D. in Physical Anthropology, I went on to spend two more years on Barro Colorado Island working on questions my dissertation work had raised. In fact even now, twenty years later, I still travel to Panama each year to continue my research on howler monkeys. These visits, which generally occur around Christmas or during summer vacation, used to drive my parents in Alabama absolutely crazy. They could not believe that in a few years I hadn't answered every question worth asking about those pesky monkeys. But as I've tried to explain, scientific work generally leads from one question to another and one could spend several lifetimes studying howler monkeys on Barro Colorado Island and still have an eternity of interesting questions left over. Why, for example, over the past fifty years has average troop size for howler monkeys on this island remained at around nineteen individuals? Why, too, are there so few juvenile monkeys in the population when so many cute new babies are born every year? Clearly most of these baby monkeys must not make it to adulthood but why is this? Are predators eating them? Are they dying of disease? Are their mothers abandoning them and, if so, why? Or am I just off in my censusing work? I imagine I'll be working on questions like these until I'm too old to climb those steep hills. Then I'll probably sit in my laboratory at Berkeley and fiddle with my years of data on the computer. Few of my colleagues work on demographic questions—censusing monkeys at the same times year after year is tedious, there are many confounding variables and often years can pass before any population shifts occur to give insight into critical factors that warrant investigation. Right now, for example, I am studying the parasites of howler monkeys, trying to determine how parasites affect the health of an infested monkey and what the critical parasite load may be for monkeys of different ages. Examining these questions will take me four or five years—and as I go along, I will add new questions. I'm not frustrated by the long time this type of population study takes, because I know that finding answers to complex questions about

longlived animals such as monkeys generally takes many years. Too, I have other research interests that provide me with more immediate feedback and intellectual gratification.

MORE MONKEY BUSINESS

Howler monkeys are my first love but I've also given away a large piece of my heart to another monkey, the woolly spider monkey *Brachyteles arachnoides*, a rare geographic isolate found only in one small area of southeastern Brazil. Woolly spider monkeys have long been almost mythical creatures to primatologists—they seem always to be described in terms of superlatives—the largest monkey in the New World, the most endangered monkey, the least known and little studied monkey and so on. Even when I was in graduate school I dreamed about studying woolly spider monkeys. But because they were so rare there were few potential study sites and further, I thought that a Brazilian primatologist would certainly want to carry out the first study of their ecology since this species occurs only in Brazil. Years passed and yet no one had managed to get a study of this fabulous monkey under way. Given its highly endangered status, this was absurd. We needed to obtain all of the information we could on their ecology to try and implement an intelligent conservation program. But it never occurred to me that the someone who might do this would be me. I'd obtained my position at Berkeley and was busily trying to master the intricacies of teaching huge courses with five hundred or more students and handle all of my other new responsibilities. Any thoughts of monkey business were on hold for the moment when out of the blue I received a remarkable invitation. A private landowner in Brazil wrote to me inviting me to come and carry out a study of the woolly spider monkeys living in the forests on his ranch. As he'd heard I liked to live close to the monkeys I was studying, he offered to build me a small house in the forest and cut me a series of trails to facilitate my work.

Well, few people, I imagine, are fortunate enough to get invitations like this. I went to my department chair and told him

about the letter. And he agreed that it was an amazing research opportunity and that I should take full advantage of it. One nice thing about my department at Berkeley is the fact that it both expects and encourages its professors to carry out original research and does not penalize them if they take a leave of absence for this purpose. No one pays my salary while I'm gone but at least when I return, my job is waiting for me. So I wrote back and said I was coming, obtained a small grant to cover a few expenses and off I went.

In this case, I had no central hypothesis to test—rather, since there had never been any long-term studies of this monkey species, anything I could learn about its ecology and behavior would be a benefit. Thus my objectives were to count the number of woolly spider monkeys on the ranch and to obtain as complete and detailed an account of their diet, ranging patterns, and social behavior as was possible. But interestingly enough, this study turned out to involve some dramatic and totally unexpected new insights. Some see what they think they should see—luckily, my formal academic training was so spotty that I've never suffered from a bad case of preconception. Perhaps just for this reason, I saw something very unexpected when I studied woolly spider monkeys, so unexpected in fact that it's taken a number of years for my point of view to be fully accepted.

Woolly spider monkeys are related to spider monkeys (genus *Ateles*) and closely resemble them in general appearance. In fact, to me woolly spider monkeys look like a blown-up version of spider monkeys and they even have the same type of whinnying call. There have been a number of excellent studies of wild spider monkeys at various sites in Central and South America and all of these studies have shown that spider monkeys take their diet almost exclusively from ripe fruit. In fact, spider monkeys are one of the most extreme examples of ripe fruit specialists in the primate order. I guess because of the close physical similarity between spider monkeys and woolly spider monkeys, people thought that fruit would also figure heavily in the woolly spider monkey diet. This "common sense" view was so prevalent that whenever woolly spider monkeys were captured and put in zoos, they were fed fruit. Apparently no one ever connected the short life span of captive woolly spider mon-

keys with the fact that perhaps, just perhaps, they were being fed the wrong food.

But there were some indications that woolly spider monkeys might not be all that frugivorous. For one thing, woolly spider monkeys were larger than spider monkeys. For reasons as yet imperfectly understood, in mammals larger body size results in lower energetic costs per unit of body weight. This relationship permits the larger animal to utilize foods lower in energy than those tolerated by their smaller counterparts. Large body size in woolly spider monkeys to me indicated lower quality foods—in other words, fibrous leaves, not sugary fruits. In addition, the teeth of woolly spider monkeys showed differences from those of spider monkeys and at least one expert in primate dentition had predicted that when woolly spider monkeys were studied, they would be found to eat large quantities of leaves. But given the striking similarity of spider and woolly spider monkeys in most other traits, these more subtle observations on their body size and dentition were generally ignored and fruit was regarded as the probable dietary foundation.

To make a long story short, my field study of woolly spider monkeys was a dream study in which everything went right. The monkeys seemed to realize that this was their chance to tell their story and though I'm not the sentimental type, it often seemed as if the monkeys were going out of their way to make sure I saw and understood what they were doing, even waiting at times for me to get my camera ready or repeating an action two or three times as if to say, "do you think she's finally figured out what's going on?" I believe that, ultimately, I did, though initially many behaviors of woolly spider monkeys were difficult for me to understand. First, my data showed that leaves, not fruit, made up the overwhelming percentage of the annual diet of woolly spider monkeys. Inspection of another group of woolly spider monkeys in a nearby forest likewise showed precisely the same leaf-eating pattern. At first I thought, well, maybe this is just a seasonal thing that will change in a few weeks. But it prevailed over all sample months but one, leaving no doubt that the foundation of the woolly spider monkey diet is leafy matter and that fruits (and flowers) are more limited, generally seasonal delicacies. Zoos, listen up—if you are ever fortunate enough to obtain a woolly spider monkey or two, be sure to give them

leafy matter as their major dietary component, not ripe sugary fruits!

For a long time, too, I was totally puzzled by the fact that woolly spider monkeys didn't seem to have any type of permanent social grouping. Each female appeared to have a home range or core area in which she would generally be found. But various females often would come together at different points during the day or from day to day and forage for one or more hours as a group. I could find no consistent pattern to their fusioning and fissioning. Males were the oddest of all. Immature males often showed up alone and hung around with a particular female for days or even weeks. Then at other times smaller or larger groups of males would appear, foraging and associating with one or more of the females I was observing for a period of time and then off they would go, not to be seen again for days. In addition, these woolly spider monkey males had some very striking attributes in the form of the largest testes (and penis) I'd ever seen on a monkey. Indeed, when I first saw the testes of a fully adult male woolly spider monkey, I thought the animal had elephantiasis or was deformed. Why on earth, I thought, would an arboreal monkey, swinging through the trees with all those sharp sticks, branches, and thorns, need with those megatestes?

Well, woolly spider monkeys, ever the cooperative study subjects, were not long in letting me know why such testes might prove useful. One of my females became sexually receptive. She generally foraged only in the company of her juvenile offspring. Suddenly one day she increased her day range from the normal 400 or so meters to almost a full kilometer (1000 meters). Shortly thereafter, I noticed that male woolly spider monkeys suddenly began appearing out of nowhere in large numbers. These males showed up in groups of two or three until there were some nine or ten males clustered around her. The coy female acted as if she didn't even see the males, moving about and attempting to feed but, at the same time, she emitted a ridiculous twittering vocalization I'd not heard before and that I later termed the "mating twitter." The males obviously found her twitter absolutely irresistible and one after another each male would attempt to copulate with her. Unlike many male primates, these males didn't fight or act aggressive toward one

another in terms of gaining access to the female; rather, each waited until the one before had moved away from the female before approaching her. This lack of aggression was all the more impressive because it was obvious that the males were intensely excited, so much so that at times they almost fell out of the trees, often hugging one another in their enthusiasm. I decided the males must have a type of dominance hierarchy, perhaps worked out in their daily activities, that let them know more or less the correct order in the copulatory scheme and thus keep quarreling to a minimum. But where do the huge testes fit in? In my view, the arena for reproductive success in this monkey species has moved from overt fighting between the males for sexual access to receptive females into the interior of the female's reproductive tract. I speculate that the huge testes of the males provide copious quantities of sperm at each ejaculation and that males compete for reproductive success at least in part through sperm competition in which each male tries to wash out and dilute the sperm deposited by his predecessors and in this way father the infant.

To understand why selection may have favored sperm competition in this species, we need to consider its diet. Unlike fruits, leaves do not offer a rich source of readily digestible energy. As woolly spider monkeys eat diets composed largely of leaves, I would imagine that excess energy is generally in short supply. The fluid grouping patterns of the females appear to force males to travel extensively to monitor their reproductive condition. Such travel activities may leave little excess energy for male-male combat, favoring a less dramatic form of male competition. Perhaps in this species, owing to its generally limited energetic substrate, selection has favored sperm competition rather than energetically expensive and dangerous fighting between males for possession of a sexually receptive female. Too, many males in a mating aggregation may also be closely related, which would also tend to lower intermale aggression. If you don't father the infant, perhaps your brother will, passing on many of your own genes in the process.

Sperm competition may explain the huge testes in woolly spider monkey males, but there is still the huge penis to explain. Most primates are not noted for penis size. In fact the erect penis

of the gorilla, the largest living primate, is only around one and a quarter inches in length while the human male has one of the largest penises in the primate order.[5] A scientist named William Eberhard has speculated that in many mammals, penis size may often relate to female choice—that is, to pleasing the female rather than to specific features related to sperm deposition.[6] In the case of woolly spider monkeys, the large penis may aid in depositing a large amount of sperm high in the female's reproductive tract, but its size is so large relative to the penis size in most other primates that I believe some further selective pressures are involved. Chimpanzees, for example, have unusually large testes and multi-male mating behavior, and sperm competition is also believed to occur in this species. But the erect penis of a male chimpanzee is only around three inches long, indicating that a large penis is not essential in sperm competition. Thus it may well be that penis size in woolly spider monkeys relates in some way to pleasing the female and to female choice—that is, it may be the female who has the ultimate say as to which male in the crowd will father her infant. Copulation in this species is unusually prolonged, lasting for four to eight minutes rather than the thirty seconds or less typical of most primates. This suggests that in some manner, female woolly spider monkeys may be judging individual males through features of penis size and copulatory competence, though this remains to be demonstrated.

All in all, with the leafy diet, the fluid pattern of social organization, and the dramatic and unexpected features of mating behavior, woolly spider monkeys gave me one surprise after another but finally I believe that I was able to make sense of what initially had seemed to be a totally confusing set of behaviors and morphological features. In terms of the contributions of my study to woolly spider monkey conservation, sad to say but even now, some ten years later, very little has been done to facilitate the conservation of this fabulous monkey. Indeed, conservation organizations have more or less ignored my findings and seem disinterested in factual information about the species. Due to this apparent disinterest, I am wary of large conservation foundations and their professed concern with "saving" particular species.

ed. I further determined, through travel, questioning, and interviews with Brazilian anthropologists, that there still were various indigenous groups deep in the rain forest that as yet had been largely unaffected by exposure to outside influences. Thus I decided that I would carry out a series of studies on indigenous peoples of the Brazilian rain forest to document features of their ecology before western technology intervened.

My reading of the literature showed that the behavior of forest-based peoples in Amazonia had been the object of considerable anthropological speculation in spite of the lack of ecological information. In particular, single-factor hypotheses related to diet had been used to try and explain many features of these forest-based cultures such as settlement size (generally small), nomadic and semi-nomadic behaviors (tropical forest peoples are reported to move about a great deal), lack of social stratification (such societies are often described as egalitarian and appear to largely lack stratification), and even behavioral traits such as aggression (some scholars had speculated that tropical forest peoples were aggressive and engaged in frequent warfare because protein dietary sources in the tropical forest were in short supply). Tropical forest peoples frequently were denigrated in these writings by being referred to as "marginal" peoples or "refugees"—terms suggesting that they would not want to live in the tropical forest if they hadn't been forced to. One especially insensitive paper actually compared them to street people, implying, I guess, that they were dysfunctional misfits in the modern world! Others referred to forest peoples as if they were relics of the Pleistocene, peoples without a history, whose customs never altered. Finally, there were views that ranged from the noble savage in the Garden of Eden to the other end of the spectrum in which tropical forest peoples were portrayed as cannibals and headhunters. Clearly there was a lot of work to be done if all of these often contradictory and confusing portrayals were ever to be reconciled into a coherent and factual account of the real lives of forest dwellers. And, as I've noted, the time remaining to actually gather information on peoples of the forest who were still living without shotguns, machetes, and the like was fast running out.

I wrote a grant proposal to test one of the hypotheses about Amazonian forest peoples then in the anthropological literature

—namely, that forest dwellers living in upland regions well away from major rivers would suffer more from these postulated protein shortages than indigenous societies living near large rivers—ostensibly because the deep forest dwellers would lack access to fish, turtles, and other riverine protein sources. I selected an indigenous group called the Maku for this dietary work, who were ideal because they lived in upland forest regions with poor, sandy soil, regions noted for their paucity of game animals. I felt that if I could find no evidence of protein shortage in this extreme situation, the possibility of it occurring in richer areas of Amazonia would be even more improbable. After eighteen months of petitioning for permission to do my study from various Brazilian agencies, permission was granted and with a grant from the National Geographic Society in hand, I set off for Brazil to study the dietary ecology of the Maku and test the protein limitation hypothesis.

After various delays and setbacks, I managed to get to a small town called Sao Gabriel de Cachoeira, located in the northwest of the Brazilian state of Amazonas on the bank of the Rio Negro. I could then find no means of transport to go further into the region where the Maku were reported to live. I went around looking for anyone with a canoe who might be willing to take me for some weeks along smaller rivers into the Maku area but could find no one. Finally, the Brazilian air force agreed to fly me in as they had to take supplies to a remote Catholic mission in the area They flew me in an old cargo plane dating from World War II. The plane landed on a dirt runway, sending up a huge dust cloud; the soldiers quickly threw the cargo, including all of my supplies for six months, into the dirt, they helped me out of the plane, waved goodby and off they flew—leaving me standing alone in the middle of the forest on a dirt runway with a large crowd of people racing toward me. This was truly a moment of intense fear on my part. I spoke not a word of any indigenous language, I was in the middle of the Amazon Basin totally out of contact with anyone or anything familiar to me, I had no idea what would transpire, and I was afraid. Immediately I was surrounded. These were not the Maku but rather were Tukanoans, riverine people who would know how I might find the forest-dwelling Maku. By sign language and using some words of Portuguese they let me know

that I could stay in the headman's house and they helped me carry all my goods there. I rigged up my hammock in one corner of the mud house and stacked my goods along a wall, covering them with a large sheet of plastic to keep off falling dirt, palm thatch, and bugs. That night the Tukanoans had a huge ceremony which involved the drinking of much manioc beer and considerable noise and intoxication. Again, I was frightened, especially as small groups of very inebriated Tukanoans kept staggering into the hut to try and converse. All of this was totally strange—I longed for the tranquillity and relative simplicity of my monkey studies and rued the day I'd foolishly decided to try and work with members of my own species—scary, strange, and all too human.

Eventually I adjusted, eventually I did meet some Maku who let me accompany them, back to the forest and live with them, and eventually I did compile the data required to test the protein-limitation hypothesis. I came to know many of the Maku and feel at home in their forest environment and eventually to understand some relatively rudimentary aspects of their ecology and their relationship with the Tukanoans. Suffice it to say that the Maku appeared to have less of a problem with protein resources than the Tukanoans—suggesting that the view of protein shortages in the upland forests may be inaccurate. Indeed, my data suggested that the main dietary problem of forest-based peoples such as the Maku may relate more to locating sufficient amounts of energy-rich carbohydrate foods than it does to protein.

Following this initial study, I've had the good fortune to live with four other indigenous groups in the Brazilian Amazon (the Arara, Parakana, Arawete, and Mayoruna) as well as the so-called "lost tribe" (the Hagahai) in Papua New Guinea, and have been able to collect the same data on dietary ecology and uses of the forest environment in each case. My strategy in terms of these human studies has been to try and document the ecological practices of as many different forest-based indigenous societies as possible, as soon all such societies will be brought into contact with the outside world on a more routine basis and many features of their ecology will be rapidly altered. Thus, I'm attempting to maximize the size of my data base while I can.

In the future, I hope to be able to visit several other recently contacted or as yet uncontacted indigenous groups in the

Amazonian forests to collect similar data and, in addition, I also have a wealth of new questions about the societies among whom I've already had the privilege of living. The careful study of forest-based human ecology has been much neglected and I believe it is essential to gain a better understanding of human behavior and human management practices in this unique and complex ecosystem. Such studies offer insights into dietary practices and activity patterns that promote human health and well being, they offer us the chance to learn more about the myriad useful plants and animals which inhabit the forest environment and, by observing the ecological practices of the indigenous inhabitants, we can learn more about indigenous management practices that preserve rather than destroy the forest.

SATISFIED WITH SCIENCE

All in all then, it would appear that my decision to become a physical anthropologist has more than fulfilled my every expectation. Indeed, being a physical anthropologist, to my way of thinking, is one of the most wonderful things imaginable because, in essence, it means that you can look at, examine, and speculate on just about anything you find of interest in the natural world. By definition, physical anthropologists deal with any subject matter having to do with human evolution, human adaptation, human biology, and human behavior. There is little that, in one way or another, does not impinge in some manner on our own existence as a species and thus, in effect, my career has been a liberating experience that has set me free to explore wherever my thoughts lead and, at the same time, offers me excitement and discovery, continuous mental stimulation, interesting students and colleagues and, best of all, the opportunity to advance our understanding and appreciation of the myriad complexities and beauty of the natural world. Isn't that just about as close to having your cake and eating it too as anyone could ever hope? I think so!

NOTES

1. G.A. Bartholomew Jr. and J.B. Birdsell, "Ecology and the Protohominids," *American Anthropologist* 55 (1953): 481–498.
2. C.R. Carpenter, "A Field Study of the Behavior and Social Relations of Howling Monkeys," *Comparative Psychological Monographs* 10 (1934): 1–168.
3. T.W. Schoener, "Theory of Feeding Strategies," *Annual Review of Ecology and Systematics* 2 (1971): 369–403.
4. K. Milton, *The Foraging Strategy of Howler Monkeys: A Study in Primate Economics* (New York: Columbia University Press, 1981.
5. R.J. Short, "Sexual Selection in Man and the Great Apes," in C.E. Graham, ed., *Reproductive Biology of the Great Apes* (New York: Academic Press, 1981), pp. 319–341.
6. W.G. Eberhard, *Sexual Selection and Animal Genitalia* (Cambridge: Harvard University Press, 1985).

SUGGESTED READINGS

Milton, K., "Protein and Carbohydrate Resources of the Maku Indians of Northwestern Amazonia," *American Anthropologist* 86 (1984): 7–27. This paper discusses the study I carried out of the Maku diet and goes into detail about protein limitation and other factors involved in the ecology of forest dwellers in Amazonia.

——. "Habitat, Diet and Activity Patterns of Free-ranging Woolly Spider Monkeys (*Brachyteles arachnoides*, E. Geoffroy 1806)," *International Journal of Primatology* 5 (1984): 491–514. For those interested in further information on the behavior of this fabulous monkey, this paper discusses in detail my study site, the diet of the monkey, and its ranging behavior.

——. "Mating Patterns of Woolly Spider Monkeys, *Brachyteles arachnoides:* Implications for Female Choice," *Behavioral Ecology and Sociobiology* 17 (1985): 53–59. A more scientific accounting of the incredible sexual activities of woolly spider monkeys.

——. "Primate Diets and Gut Morphology: Implications for Human Evolution," in M. Harris and E.B. Ross, eds., *Food and Evolution: Toward a Theory of Human Food Habits.* Philadelphia: Temple

University Press, 1987, pp. 93–116. Why is the digestive tract important in understanding the food choices of an animal? Once you read this paper, the answer will be clear and the role played by diet in shaping the evolution of a given lineage, including our own, should be much easier to appreciate.

——. "Foraging Behavior and the Evolution of Primate Cognition," in A. Whiten and R. Byrne, eds., *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. Oxford: Oxford University Press, 1988, pp. 285–305. This paper evaluates results of an earlier paper in which I first discussed the role played by diet in terms of the brain size of different primate lineages. I find my initial paper still relevant and update many earlier comments in terms of more recent research on aspects of brain size in mammals.

——. "Comparative Aspects of Diet in Amazonian Forest Dwellers," *Philosophical Transactions of the Royal Society, Series B*. 334 (1991): 253–263. My study of four indigenous groups in the Brazilian Amazon proved surprising. Not only did each group have its own distinctive dietary focus, but different groups often appeared to taboo the foods most favored by their closest neighbors.