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REVIEW ARTICLE

Primate tales: Memoirs from leaders in primatology

Monkey business: A girl's once strange dream

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Abstract

For close to 50 years, my research has focused on social relationships and social structure, particularly in macaques, and has been marked by a gradual broadening of scope. Supported by open-minded parents, I followed a once unconventional path into field primatology largely by ignoring distinct gender-based ideas about appropriate occupations for women that were prevalent when I was a child. Later, as Robert Hinde's PhD advisee, I benefited enormously from his mentoring and from the transformative experience he provided. I began by examining infant social development in free-ranging rhesus monkeys and the integration of infants into the kinship and dominance structures of their groups. I gradually branched out to look at (1) kinship and dominance in additional age classes and macaque species, (2) additional aspects of social structure (reciprocity, agonistic support, tolerance, cooperation, conflict management), (3) mechanisms and organizing principles (e.g., attraction to kin and high rank, intergenerational transmission, demography, reciprocity, social style, time constraints) and (4) evolutionary underpinnings of social relationships and structure (e.g., parental investment, kin selection, socioecology, phylogeny, biological markets). For much of this journey, I have been accompanied by talented PhD students who have enriched my experience and whom I am now proud to call colleagues and friends. It is gratifying to realize that my career choice is no longer considered as unconventional as it once was.

Keywords Social relationships · Social structure · Social development · Macaques · *Macaca mulatta* · *Macaca thibetana*

Introduction

Like most baby boomers born in the USA, I began life at a time when gender roles were quite distinct. Girls typically aspired to be teachers, nurses, or secretaries, and women were often expected to work outside the home only until they had children of their own. Fortunately, I blithely assumed that none of that applied to me, and I began down a path that most people thought quite strange.

I was fascinated with all things biological from as early as I can remember, and never doubted I would have a lifelong career. My parents never discouraged this goal, and when I was a preschooler, they allowed me to bring all sorts of worms, tadpoles, and insects into the house. (It took me a while to figure out why the creatures soon vanished, and why my mother was not concerned that they may be loose in the house). Beginning at about age 10, my parents actively encouraged me as I carried out a variety of science projects at home, with them sometimes serving as lab assistants. I will always be grateful to them for this.

Fortunately, societal attitudes began changing as I grew up, opening up opportunities for me to pursue a dream that had begun to take shape in middle childhood. My interest in animal behavior was sparked by a short book by Vance Packard called "Animal Intelligence". It fascinated me, taught me that animal behavior was an actual area of scientific inquiry, and put me on the road to seeking a career in that area. For my 16th birthday, a family friend gave me a subscription to National Geographic magazine. The second issue I received had Jane Goodall's first publication on her work with wild chimpanzees (*Pan troglodytes*). I was captivated by her descriptions of chimpanzee behavior, and excited that there appeared to be opportunities for people, and particularly young women, to do this kind of work in the field.

At about this age, I began to pursue summer jobs in animal behavior laboratories, and a National Science

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Foundation program for high school students placed me in experimental/comparative psychology labs at the University of Maryland and other labs in the Washington, DC area where I lived. I learned a tremendous amount in these settings, but also realized that the approach these labs took was not what I was looking for. They used stimulus–response paradigms with individually housed captive animals, asking whether the animals could perform highly artificial tasks in Skinner boxes in an effort to reduce our understanding of complex behavior to simple principles based purely on learning through reward and punishment. They were also highly anthropocentric in their goals; in an attempt to explain human behavior using these principles, they aimed to produce behavior in their subjects that resembled human behavior rather than to understand how and why animals behave in the wild. When I went to Brandeis University and majored in psychology, I found that this approach dominated the courses and research opportunities there too. Fortunately, Brandeis had a study abroad program that allowed students to spend their junior year at Sussex University in England. I signed up to take several courses in developmental psychology there as well as my first course in ethology taught by Lesley Rodgers, then a PhD student studying brain development and behavior in chickens. She was inspirational, and although I was thousands of miles from where I grew up, I felt like I had just found a home.

It was not until I graduated from Brandeis in 1971, however, that I got to know a wider community of researchers interested in understanding the natural behavior of animals in their own habitats by systematically observing animals going about their lives in the wild. As I worked as a lab assistant for the US Food and Drug Administration for the next 2 years, I dug into the wider literature on ethology and on primate ethology in particular. I wrote to researchers whose research grabbed me, asking about graduate programs. One of these people was Robert Hinde at the University of Cambridge in England. After about a year of correspondence about my interests and opportunities in his lab at Madingley, he suggested that I apply to their PhD program to pursue dissertation research on the social development of free-ranging rhesus monkeys (*Macaca mulatta*) on Cayo Santiago, an island off the coast of Puerto Rico. This was the start of the career I dreamed about. I was thrilled and terrified at the same time. My family and friends were proud and happy for me, if not a bit bewildered by what seemed to them a very strange path to follow.

Robert Hinde was already a giant in the field of animal behavior having written 'the bible' that synthesized American Comparative Psychology and European Classical Ethology (Hinde 1970). His lab at Madingley was also a focal point and home base for field studies of nonhuman primates. Hinde had advised Jane Goodall's dissertation on the chimpanzees of the Gombe Stream Reserve and was doing the same for several other PhD students doing research on wild chimpanzees, baboons (*Papio* sp.) and mountain gorillas (*Gorilla beringei*). We all felt that it was a 'Golden Age' at Madingley in this regard. Hinde's own research focused on understanding mother–infant relationships in small captive social groups of rhesus monkeys as a way to test John Bowlby's attachment theory of social bonding (Bowlby 1969) and to develop a science of social relationships. With Hinde's guidance, I designed a study of free-ranging rhesus monkeys on Cayo Santiago to test whether some of his findings on mother–infant relationships could be generalized to a larger, naturally formed, and species-typically organized social group of the same species. My aim was also to expand our understanding of the ways in which rhesus infants become fully integrated members of their societies in this more natural setting. I set out in December 1973 with a pre-doctoral fellowship from the US National Institutes of Mental Health (NIMH) and several smaller research grants in hand—still thrilled and still terrified!

Cayo Santiago has been home to a free-ranging population of rhesus monkeys since 1938. The monkeys are all descendants of 409 individuals that were brought from India in that year. They have formed species-typical, although often large, social groups composed of a core of adult females and their immature offspring, and a more transient set of adult males. Like all macaques, the females are typically philopatric, remaining in their natal groups for life, whereas males disperse generally around puberty and join other groups periodically throughout their lives. They are seasonal breeders with distinct birth and mating seasons. Although they forage on natural vegetation and drink from natural ponds, they are also provisioned daily with commercial monkey chow and fresh rainwater collected and distributed over the island. With plentiful food and no predators, reproductive rates have been high and mortality relatively low, producing social groups with as many as four generations present at once and social bonds that are embedded in extended matrilines. These matrilines have been the key to much research there, including mine.

When I arrived on Cayo Santiago, Donald Stone Sade, the Scientist-in-Charge, encouraged me and facilitated my work while I was there (Fig. 1). Sade had already completed seminal studies on the kinship and dominance structures of the social groups (Sade 1965, 1967), which were consistent with pioneering research on free-ranging Japanese macaques (*M. fuscata*) (Koyama 1967; Yamada 1963). Together, their classic work established that rhesus and Japanese macaque groups were spatially and socially structured around the lineages of maternally related females, and that female dominance was closely linked to these kin-based affiliative structures; daughters consistently took on ranks in the adult female hierarchy that were immediately below their mothers and in reverse order of age. No one had tackled a

Fig. 1 Carol Berman as a graduate student in 1975 on Cayo Santiago, Puerto Rico. Photo by Sam Libber with permission

detailed quantitative study of the course of development of mother–infant relationships on free-ranging or wild rhesus monkeys or asked how infants become integrated into the kin-based affiliative and dominance structures of the group, although Jeanne Altmann was in the process of doing so in wild baboons in the Amboseli Reserve in Kenya (Altmann 1980). Nor had anyone used focal-animal sampling on Cayo Santiago, a time-sampling method recently introduced to primatologists in a classic article by Jeanne (Altmann 1974). Focal-animal sampling, which requires researchers to follow monkeys individually, is a highly accurate and straightforward method to collect behavioral data that allows researchers to calculate comparable rates of interaction between focal animals and each individual they interacted with–data that I needed to quantitively describe changes in infant relationships as they developed.

Habituation

Cayo Santiago monkeys were not accustomed to being followed individually. So, in order to do focal-animal sampling, my first task was to habituate the monkeys in my study group (group I) to this way of following them. I began with pregnant females, attempting to stay far enough behind them to avoid fear responses. I moved slowly at an angle oblique to their paths and avoided looking directly at them. Over time, I hoped to gradually decrease the distance between them and me until I could stay near enough to comfortably observe details of their interactions without eliciting signs of wariness from them or other group members. I was largely successful within about 10–12 weeks when the first infants of the 1974 birth season began to appear, but my endeavor to habituate my group to being followed individually was not without its challenges. More than once during the process, I inadvertently overstepped the invisible boundary between apparently being tolerated and provoking fear or aggression in my focal subject, and on a few occasions, I ended up being screamed at, threatened, and lunged at not only by my focal female, but also by her male associates and a large proportion of her matriline–all at once! Out of necessity, I quickly learned how to better avoid such confrontations and how to protect myself while calming the monkeys down after they began. My techniques varied from lipsmacking, to backing away slowly, to stepping toward the monkeys or banging on my metal clipboard, depending on the intensity of the attack, the ranks and the personalities of the participants, but I'll never forget how my knees quivered the first time I was mobbed like that!

A few particularly calm and bold monkeys also appeared to use this newcomer to further their social goals. One young adult female had recently lost her mother and had no other close maternal kin to support her within the group. Probably as a result, she lost rank among the females in her matriline. However, she found a way to elicit support from powerful adult males. As I sat quietly observing another female, she would approach, sit calmly by my side, and sometimes even attempt to groom me. However, when a powerful male came by, her demeanor changed on a dime; she screamed, threatened, and fear-grinned at me while soliciting aid (and perhaps future support) from the male. I soon learned to avoid this 'faux friend'.

The course of mother–infant relationships

Despite these initial challenges, I managed to collect data over two birth seasons (1974 and 1975) recording infant interaction with mothers and with other group members for 20 infants from birth to at least 30 weeks of age. At that time, researchers recognized that, in most primate species, an infant's relationship with its mother is its first, most intense, and in many cases, its most enduring social relationship. Among cercopithecines, mothers and infants initially spend nearly all their time in ventro-ventral contact and on the nipple, but gradually over time, they spend less time in contact, as the infant begins to leave the mother for short periods of time to explore its environment and interact with other group members. Early views, which were derived from studies of mother–infant pairs in severely restricted social environments viewed the relationship as an isolated system of interaction, governed primarily by the changing needs and propensities of the infant. The infant used a largely passive mother as a secure emotional base as it regulated its interaction with her and gradually achieved independence by seeking stimulation from the environment (e.g., Harlow and Harlow 1965). However, a different view emerged from Hinde's studies at Madingley and other captive socially living colonies (e.g., Hinde and Spencer-Booth 1967; Jensen et al. 1968); this research demonstrated that the mother plays an active role in promoting the infant's independence from her by gradually rejecting its attempts to suckle and to remain in contact (Fig. 2), and by actively and selectively regulating its interactions with other group members. In this view, the mother's relationships with her infant and with other group members and the infant's relationships with other group members develop in an interdependent manner. Although a handful of quantitative field studies on other primate species were in harmony with this general view (e.g., Altmann 1978), no systematic comparisons had been made for the same species living in the field and in captivity. So, my first analysis directly compared several measures of mother–infant interaction among my subjects with those at Madingley in 1974. Whereas Cayo Santiago mothers raised their infants on a lush 15-ha island in free-ranging groups with several extended matrilines, Madingley mothers lived in small concrete and wire outdoor enclosures and raised their infants in stable groups composed of a single adult male, a few adult females, and their offspring. Such a comparison had the potential not only to generalize Hinde's findings in a more natural setting, but also to shed light on the effects of varying physical and social environments on these relationships.

I found that the general course of mother–infant relationships among the two populations was remarkably similar both qualitatively and quantitatively (Berman 1980a). Nevertheless, there were small, but consistent quantitative differences: mothers and infants at Madingley spent somewhat less time out of contact with one another, mothers rejected their attempts to get on the nipple at lower rates, and mothers played a relatively larger role in maintaining proximity to their infants than mothers on Cayo Santiago. This pattern of differences suggested that differences in mother–infant relationships between the two populations were due primarily to differences between mothers rather than differences between their infants; the Madingley mothers had more protective maternal styles than the Cayo Santiago mothers. The data also suggested that Madingley mothers were changing over time. When I compared data from Madingley recorded in 1968 and 1974, I found that the earlier mothers were even more protective than those in 1974.

Fig. 2 A rhesus mother on Cayo Santiago, Puerto Rico, rejects her infant's attempt to make nipple contact while her yearling sits nearby. Photo by C. Berman

This latter finding focused my attention on factors that may have changed over the years at Madingley. Physical and social conditions at Madingley had remained more or less stable between 1968 and 1974 with one major exception. In 1968, only a few Madingley mothers raised their infants in the presence of close maternal kin, but by 1974 most mothers did so. In contrast, Cayo Santiago mothers nearly all raised their infants among several maternal kin. Did the presence of close kin encourage otherwise more protective mothers to relax and encourage more independence in their infants? I could only speculate at this point, but this question prompted me to think more about the role of maternal kin in infant social development in general, and particularly on the possible role of mothers and maternal kin in the integration of infants into the social structure of their groups.

The integration of infants into group structure

To approach these issues, I analyzed infants' developing social networks within their groups (Berman 1982a). I found that infants' social networks were shaped by similar factors as those of their mothers (maternal degree of relatedness, and companion's age, sex and rank), and in this sense, infant social networks appeared to mirror those of their mothers: most strikingly, from birth to 30 weeks of age, infants spent more time near and had more friendly interactions with group members that were more closely related to them, even when controlling for companions' age, rank, and sex (Fig. 3). Among equally related and similarly ranked companions, they interacted more with female companions than male companions and more with younger companions than older ones. Similarities between maternal and infant social networks during the first few weeks of life were not surprising. At this age, mothers exert almost total control over the infant's interactions. From the beginning, mothers introduce their infants to their own close associates (who

Fig. 3 Kin-based clusters of rhesus monkeys grooming on Cayo Santiago, Puerto Rico. Photo by C. Berman

tend to be their own close maternal kin), and they are more tolerant of close kin than others when they attempt to handle or interact in other ways with infants. In this sense, infants appear to function as members of their matriline from the beginning. However, the persistence of these maternal patterns in infants as old as 30 weeks suggests that the mothers' early influence has long-term consequences for the development of offspring social networks. By 30 weeks, infants are considerably more independent from their mothers, spending about half their time more than 5 m from their mothers, and some of it out of her sight. Moreover, by this time, it is the infant rather than the mother that takes primary responsibility for maintaining contact and proximity to her. Nevertheless, the infant continues to distribute its affiliative interactions largely according to maternal patterns. In this sense, the mother transmits her network to her infant. Infants come to not only associate with close kin more than others, they also favor them in all kinds of friendly and cooperative interaction and support them in conflicts with other families that are less closely related. Nevertheless, their relationships with group companions gradually change in nature over time. They become more independent in that they are sustained primarily through interactions between the infant and the companion, and they may have different qualities (e.g., warmth, playfulness) from those of the mother with the same companion. In this sense, they differentiate from those of the mother with the same companion (see also Berman 1982b, 2004).

I also found that maternal kinship plays a major role in the integration of the infant into the dominance structure of its group (Berman 1980b). Like many nonhuman primates with stable female dominance hierarchies, rhesus monkeys cannot be ranked within a hierarchy of their peers for the first few months of life. However, by 1 year, a stable linear dominance order is apparent that correlates with the order among their mothers (Sade 1967). By adolescence or adulthood, females typically attain ranks in the adult female hierarchy immediately below their mothers (Sade 1972). At the time, there was evidence that rank acquisition at both stages involves the active intervention and support of offspring by mothers in their offspring's disputes (e.g., Cheney 1977; Kawai 1958). When mothers intervene, offspring are able to win disputes against individuals that their mothers dominate, but not against those that dominate the mother. However, in some cases, young monkeys also attain these 'expected' ranks in the absence of their mothers (e.g., Sade 1972; Walters 1980), suggesting that other factors, including agonistic support from other group members, may also be important. During a postdoctoral fellowship at Northwestern University (funded by the US National Science Foundation), I found that several aspects of early agonistic experience, including support from close female kin, may play important roles in the infant's immediate protection and its later rank acquisition. Even before infants are fully integrated into a peer–peer hierarchy, infants of high-ranking mothers receive fewer threats than infants of low-ranking mothers, and they are less likely to be threatened by unrelated and unfamiliar individuals. When threatened, mothers of high-ranking infants are just as likely to intervene on their behalf as mothers of low-ranking infants. What differs are the chances of being supported by other close female kin; infants of high-ranking mothers are more likely to receive protection from them and their protectors are less likely to display fearful gestures when doing so (see also Chapais and Gauthier 1993). These differences may be due in part to tendencies for high-ranking infants to have more close female kin who are also high-ranking, and to spend more time with each of them. Eventually, Bernard Chapais and colleagues (1995) confirmed the critical role for interventions by close female kin in rank acquisition in experimental studies of Japanese macaques.

The consistency and transmission of maternal style

After my postdoc, I continued my research on Cayo Santiago as a faculty member in the Department of Anthropology at the State University of New York at Buffalo. Thanks to funding from NIMH, I increased my sample of mother–infant pairs to 124 between 1980 and 1986, a number that enabled me to examine the factors shaping maternal style and their implications in much more detail. At the time, maternal style was often conceived of as a characteristic of individual mother–infant pairs; mothers in the same social group varied greatly in their styles of mothering at any one time, but individual mothers displayed consistent styles with particular infants as they matured. When I examined the maternal styles of mothers that had raised infants in multiple years, I found that their styles were also reasonably consistent across the multiple infants that they raised, thus expanding the concept of maternal style to individual mothers over years (Berman 1990a). Indeed, some aspects of maternal style appeared to be transmitted intergenerationally from mothers to their adult daughters; nipple rejection rates for individual mothers were both reasonably consistent from infant to infant and similar to those of their own mothers (Berman 1990b; see also Chauvin and Berman 2004; Fairbanks 1989). This was noteworthy because maternal style in general and rejection styles in particular had been associated with a number of possible fitness-related outcomes for infants and mothers. The absence of rejections had been associated with delays in the infant's development of independence (Hinde 1974), whereas high rejection rates had been associated with increased infant mortality and morbidity (Altmann 1980), decreased mother–infant contact (Berman 1978; Hinde and Spencer-Booth 1967), increased interaction with other group members (Altmann 1980) and indications of insecure attachment (Hinde 1974; Stevenson-Hinde and Simpson 1981). Moreover, the rate and temporal patterning of rejections had also been shown to influence the timing of weaning (Altmann et al. 1978; Simpson et al. 1981), the mothers' resumption of mating and interbirth intervals (e.g., Berman et al. 1993; Fairbanks and McGuire 1987; Malik et al. 1992). Thus, any fitness-related consequences of a maternal style could also be consistent over multiple infants, affecting not only the mother's cumulative lifetime reproductive success but also that of her adult daughters.

Mothers' resumption of mating

In 1990, I began a collaborative project with Kathlyn Rasmussen and Stephen Suomi, funded by the US National Institute of Child Health and Human Development, examining 24 mother–infant pairs on Cayo Santiago born that year. Having only recently published about the consistency of maternal styles, we ironically found one point in the development of infants when mothers abruptly changed their maternal styles (Berman et al. 1994)! That point was when mothers resumed mating and often appeared to be too preoccupied with ardent males to be particularly responsive to their infants. The nature of the change in maternal behavior (mothers abruptly sought less proximity and rejected more attempts to suckle) and infants' responses to it (agitation, distress calling, increased attempts to suckle) were reminiscent of experimental studies at Madingley in which infants of about the same age experienced abrupt, short forced separations from their mothers (e.g., Hinde and McGinnis 1977). The Madingley studies were key model tests of Bowlby's attachment theory; the separated infants showed striking similarities to responses of human children when separated from primary caregivers. Now there also appeared to be parallels with the responses of free-ranging infant rhesus monkeys to a more natural form of disruption of their relationships with their mothers, broadening the biological validity of Bowlby's separation paradigm; forced separations of infant rhesus monkeys in captivity also modeled species-normative developmental processes in rhesus monkeys in the field. See also DeVinney et al. (2001, 2003) for similar investigations of responses to the birth of a new sibling (Fig. 4).

We also asked whether these abrupt changes in maternal behavior on Cayo Santiago had reproductive consequences for mothers (Berman et al. 1993). In most primates, ovulation is inhibited after giving birth and while infants suckle intensely. What was not clear at this time was the extent to which nonhuman primate mothers could influence their chances of reproducing a new infant by regulating their current infant's suckling. Parent–offspring theory (Trivers 1972) posited that mothers make 'decisions' about when and how much to invest in current offspring vs. future offspring, weighing the prospects that current offspring will thrive against the prospects for future offspring. There was some evidence that rhesus mothers that rejected infants at high rates were able to return to estrus earlier than others (Johnson et al. 1993; Malik et al. 1992). Whether they could also influence their chances of conceiving a new infant after resuming mating was unclear. Although most mothers in our sample (70%) conceived by the end of the mating season, only about 40% conceived during their first estrous period, and 30% did not conceive at all. Differences between these outcomes were not related to maternal styles before mothers resumed mating. Nor were they related to the mother's rank or the current infant's sex. Rather mothers that conceived during their first estrous periods rejected their infants attempts to suckle more, initiated nursing less than

Fig. 4 Barb DeVinney and Carol Berman on Cayo Santiago, Puerto Rico in 1990. Photo by Kathlyn Rasmussen Robbins with permission

the other mothers and rarely responded positively to their infant's distress during their first estrus. This suggests that cycling mothers could indeed 'decide' whether to curtail investing heavily in their current infant, thereby increasing their chances of conceiving a new infant. Alternatively, they could continue to invest heavily in their current infant, postponing conceiving until the next mating season. Mothers that 'chose' to continue investing heavily tended to be those whose infants were the most vulnerable; their infants were among the youngest when the mother resumed mating and perhaps most in need of further investment.

Collaborative work with Rodney Johnson and Iqbal Malik around the same time focused on the lactational and environmental factors that shape seasonal mating behavior in female rhesus monkeys. Using my data from Cayo Santiago, Rodney and Iqbal's data from Tughlaqabad, India (funded by Rodney's US National Child Health and Human Development postdoctoral fellowship), and published data from Madingley (Gomendio 1989), we examined suckling rates, dates that mothers resumed mating, and the age of the infant when mothers resumed mating (Fig. 5). The results pointed to a dynamic model that postulates an initially rising and then falling threshold for the disinhibition of mating in females over the course of the mating season that is presumably shaped by environmental factors (Johnson et al. 1993). When a female begins mating depends on the suckling intensity of her infant in relation to this moving threshold. Suckling intensity is influenced in turn by the infant's age and the mother's behavior regulating the infant's suckling. Thus mothers whose infants are relatively young when the mating season begins will resume mating later than mothers of older infants. Moreover, if two mothers have infants of the same age, the one that restricts suckling more will begin mating earlier than the less restrictive one.

Fig. 5 Rodney Johnson collecting data on rhesus monkeys in 1985 at Tughlaqabad, India, as a man makes offerings to the monkeys. Photo by C. Berman

Kin bias–adult females

During the 1990s, I turned my attention increasingly to questions concerning kin bias, i.e., tendencies among rhesus monkeys to favor their maternal kin. By this time, my interest in kin bias had expanded to include adults as well as hypotheses about the evolutionary underpinnings of social structure in general. Thus, I was delighted to work with Ellen (Eleni) Kapsalis as she completed her dissertation on the relative importance of current hypothesized organizing principles of affiliative relationships, including kin bias, among adult female rhesus on Cayo Santiago (Fig. 6). To do so, she first needed to resolve some methodological issues that made it difficult to interpret past studies. In Kapsalis and Berman (1996a), she used recently introduced matrix regression methods (an improved way to correct for the lack of independence inherent in dyadic analysis) to determine the most appropriate way to characterize kin and to examine the relative importance of two related variables, maternal kinship vs. rank, in shaping female affiliative patterns. Did the monkeys' behavior suggest that they perceived two discrete categories (kin vs. nonkin) or finer-graded degrees of relatedness? How closely related did a female need to be to be treated as kin? She constructed competing models with different criteria for kinship: discrete categories with a short cutoff ($r=0.125$; aunts, nieces), graded categories with the same short cutoff, and graded categories with a long cut off ($r=0.0005$; 4th cousins once removed). In each model, Eleni examined the independent relationships of several measures of affiliation with kinship and with rank distance among females separately for four years (1983–1986). She found that affiliative interaction was strongly correlated with kinship for all measures, all years and all models, whereas significant correlations with rank distance were much

Fig. 6 Ellen (Eleni) Kapsalis waiting for the boat to Cayo Santiago, Puerto Rico, in 1986. Photo by C. Berman

less consistent. Overall, the discrete model (kin vs. nonkin) explained less variation than either graded model, suggesting that females appear to recognize different levels of relatedness. Finally, the two graded models explained similar amounts of variation, suggesting that females apparently treat kin more distantly related than aunts and nieces as nonkin. At around the same time, Bernard Chapais' lab found a similar cut-off for kin bias in experimental studies of agonistic support among captive Japanese macaques (Chapais et al. 1997).

Having established that both maternal kin and rank distance were important correlates of affiliative interaction among rhesus females, Eleni noted that both were consistent with three current, nonexclusive hypothesized organizing principles of female affiliative relationships. Kin-based attractiveness, a presumed outcome of kin selection theory, posited that females are directly attracted to their close female kin (e.g., Hamilton 1964; Sade 1972). Attraction to high rank posited that females are attracted to high-ranking females, but experience competition for access to high-ranking females. Because competition limits lower-ranking females more than others, females end up interacting most with similarly ranked females (who tend to be their close kin) (Seyfarth 1977). This principle was hypothesized to be an outcome of individual selection and/or reciprocity-based mutualism. Finally, the similarity principle suggested that females are attracted to other females that resemble them in rank, relatedness, and age (de Waal and Luttrell 1986). Such attractions were also presumed to be an outcome of mutualism, based on the premise that individuals with similar needs and resources could most effectively exchange benefits. In Kapsalis and Berman (1996b), Eleni tested several predictions of the three hypotheses, examining the independent relationships of kinship and rank with aspects of support, tolerance and reciprocity. There was strong support for kin-based attractiveness as the primary organizing principle within the group; kin were more likely to support one another in aggressive conflicts and to exchange grooming with support and access to resources. Nevertheless, she also found evidence that attraction to high rank may operate in concert with attraction to kin to some extent; low-ranking females were attracted to high-ranking females in some, but not all years of the study, and high-ranking females exchanged access to resources for grooming by low-ranking females. Age did not emerge as an important factor; hence there was little support for the similarity principle.

Kin bias—development and demography

Combining data on infants and adult females, Eleni and I next took a closer look at the development of kin bias in infants, asking whether maternal transmission was really the whole story. This time we focused not simply on whether infants preferred the same individuals as their mothers, but also whether they displayed the same degree of preference for them over nonkin (Berman and Kapsalis 1999). When infants were no longer under the tight control of their mothers, to what extent did they learn to favor kin from their own experiences with kin and nonkin? It was already established that from birth, kin are more likely than nonkin to initiate friendly interaction, aid infants when threatened or attacked and tolerate infants around limited resources (Berman 1980b; de Waal 1993; Spencer-Booth 1968). We focused on infants that were 25–30 weeks of age, the first age period when infant kin relationships appear to exist independently from those of the mother (Berman 1982b; de Waal 1996). We also examined the infant's exposure to social risk, i.e., its chances of being threatened or attacked by group members, which we could estimate as the mean number of group members near the infant at any one time (Mull and Berman, unpublished data). We found that infants that spent relatively more time near the mother developed relatively high degrees of kin bias, confirming a role for maternal transmission. However, high kin bias was also independently associated with social risk, suggesting that infants and other kin likely also learned to seek out one another directly when social risk was high. On the other hand, time near the mother did not appear to lead to similar degrees of kin bias between mothers and infants. Here only social risk emerged as important; mothers and infants appeared to respond to levels of social risk independently, suggesting that infants relied on their own perceptions of social risk and sought out kin accordingly. As a result, mothers and infants that experienced different levels of social risk tended to display different degrees of kin bias, whereas those that experienced similar levels of social risk tended to display similar degrees of kin bias. We suggested that infants develop a basic preference for kin through maternal transmission, but then adjust their degrees of kin bias based on their own experiences with other group members.

In another study, this time with Kathlyn Rasmussen and Stephen Suomi (Berman et al. 1997), we found evidence to support a major current hypothesis about causal links between demography, infant development and social structure in primates (e.g., Altmann and Altmann 1979). Specifically, we asked whether changes in group size might influence the development of kin bias, and conversely whether such changes in kin bias might lead to progressive changes in social structure. My original study group (I) on Cayo Santiago grew steadily in size between 1974 and 1984 from 53 to 321 individuals. In 1985 and 1986, it went through a series of fissions. All but the top-ranking lineage split off, reducing its size to less than 200. After that it grew again, as did its four smaller daughter groups (Q, T, R, S). These changes set up a natural experiment in which we could examine changes in the development of infant kin bias as the groups grew in size, then decreased and then grew again. We found that as groups expanded, infants were surrounded by more group members, but a smaller proportion of them were familiar close kin, posing more social risk. At the same time, mothers appeared to become more protective, spending more time near their infants and taking larger roles in maintaining proximity to them. Likely as a result, infants developed progressively higher degrees of kin bias. Notably, these trends reversed after fissionings both in the main group and in the smaller daughter groups; infants were surrounded by fewer group members, mothers became less protective, and infants developed lower degrees of kin bias. Maternal behavior clearly had a role in these changes, but we also found evidence that infants and other kin apparently adjusted how much they sought one another out in accordance with changes in their social surroundings. Since amounts of food available per monkey and other resources on Cayo Santiago remained constant over these years, these results could not have been due to changes in resource availability. Given the long-term nature of mothers' influences on offspring social networks, we suggested that group growth could indeed lead to progressive changes in social structure via progressive increases in kin bias and resulting kin-based factionalism. Such factionalism could eventually result (and probably already played a role in) the group's fissionings along kinship lines.

Tibetan Macaques in Huangshan, China

As much as I loved the monkeys and island of Cayo Santiago, by the late 1990s, I was itching to work on a less well studied macaque in a habitat country. By coincidence, I received an email from a new PhD and faculty member at Anhui University in China who was looking for a Western collaborator. Jinhua Li had already spent several years observing a population of Tibetan macaques (*M. thibetana*) living in Huangshan. Huangshan is a beautiful mountainous area in Anhui Province and a popular tourist destination. Each year millions of tourists climb the tall mountains, stay overnight, and watch the sun rise over the clouds. Jinhua and his colleagues had monitored one social group (YA1) at Huangshan since 1986, developed a basic ethogram, recorded maternal kinship and dominance relationships and analyzed aspects of feeding and ranging behavior, male dominance relationships, and maternal and reproductive behavior (Li 1999). This sounded to me like a wonderful opportunity to delve more deeply into the social structure of this understudied species. The population of Tibetan macaques at Huangshan also offered an opportunity to look into issues of conservation and management. So, after making an initial month long visit in 1999 to scope out the field site and collect preliminary data (funded by the Margot Marsh Biodiversity Foundation and Primate Conservation Inc.), I applied for grants from the National Geographic Society, the Wenner-Gren Foundation and the Leakey Foundation to carry out a 2-year project in which I focused on aspects of both social structure and the effects of management for tourism. Both the research and my experience living with a wonderful Chinese family in a tiny rural village that had only recently gotten electricity proved to be highly rewarding and uniquely memorable (Fig. 7).

Management for tourism: provisioning, range restriction and tourists

When I began my study at Huangshan, primate tourism was (and still is) a growing trend in primate habitat countries. Many primate tourism operations aimed to achieve conservation goals as well as provide financial and educational benefits for local communities. However, little work had been done to evaluate the effects of these operations on the welfare of primate groups. This was in spite of indications that close contact with humans, including tourists, could contribute to disease transmission (e.g., Wallis and Lee 1999), habitat destruction (e.g., Wrangham 2001) and changes in behavior (e.g., de la Torre et al. 2000). In most cases, it had not been possible to specify particular aspects of management for tourism that were and were not harmful to primates. So, my hope was to do this at Huangshan

Fig. 7 Carol Berman collecting preliminary data on Tibetan macaques on Huangshan, China, in 1999. Photo by Jinhua Li with permission

in order to help designers of tourism operations minimize detrimental effects on primate populations.

Between 1986 and 1992, Jinhua and his colleagues observed group YA1 when it was virtually unmanaged and living in its natural home range. However, in 1992, the local government drove the group about 1 km out of its home range to an unoccupied area where it could be viewed easily by tourists. Staff provisioned the group regularly and restricted its movement away from the new provisioning area, reducing its home range from 7.75 km^2 to less than 3 km^2. Shortly thereafter, tourists began to view the monkeys from a newly constructed pavilion. In 2002, its range was further restricted to about 1 km^2. However, tourism and range restriction were suspended in 2003 due to the SARS epidemic. This allowed us to ask questions about the effects of provisioning, range restriction and tourism by comparing the demography and behavior of the monkeys before, during, and after these management practices were used.

Shortly after relocation, Li and colleagues (1996) noted that the group began to show signs of disturbance, including apparently increased aggression and infant loss. Jinhua and I first asked whether demographic data from the 6 years before management and from 6 years after relocation suggested serious problems associated with management practices (Berman and Li 2002). We found no differences in birth rates before management and following relocation. However, infant mortality rates increased dramatically, apparently due at least in part to wounding by adult males. As a result, there were proportionally fewer juveniles in the group after relocation than before, and fewer than in another unmanaged group (TT). We also found suggestive evidence that these changes may have been related to increased within-group competition for food compared to an unmanaged group; although mean assessments of body leanness/fatness (Berman and Schwartz 1988) did not differ, those for YA1 members varied more widely than those in an unmanaged group.

By the end of 2003, we were better able examine possible causes of high infant mortality in our study group. In Berman et al. (2007a), we found that infant mortality not only increased after the group was relocated and managed for tourism, it decreased to pre-management levels during the suspension of tourism and range restriction in 2003. We also found that aggression rates among adults did indeed increase steadily during the period of tourism and range restriction. After management began, deadly attacks on infants occurred shortly before they were found dead, and many infant corpses had bite wounds. Notably, infants did not appear to be primary targets. Rather they sustained wounds after aggression broke out among adults in the provisioning area used for tourist viewing. Of the many possible causal factors we examined (numbers of tourists, regularity of provisioning, degree of range restriction, changes in alpha males, group size, numbers of adults, male-to-female sex ratios, presence or absence of group fissioning), we found range restriction to be the factor most closely associated with both infant mortality and adult aggression. We suggested that range restriction, which was done by herding, may lead to aggression by increasing within-group competition for/dependence on clumped provisioned food and/or by raising levels of fear-induced stress. As such, range restriction and herding appear to be harmful tourism management practices. In a follow-up study, Megan Matheson and her colleagues found that the monkeys did indeed display stress-related behaviors and threats in response to being herded or subjected to specific human behaviors, e.g., pointing, making noise (review in Berman et al. 2014). Clearly tourism operators and visitors should avoid these practices (Fig. 8).

Fig. 8 Carol Berman in 2000 in front of newly installed signage intended to enhance tourists' knowledge about Tibetan macaques and their value. Photo by Jinhua Li with permission

The social structure of Tibetan macaques

Social style

My first investigation of social structure in Tibetan macaques focused on their social style (Fig. 9). The social style concept is based on the observation that several aspects of social structure appear to covary along a continuum (later simplified to 4-grade scale) among primate species, and particularly macaque species (de Waal 1989; Thierry 2000). At one end, despotic species, such as rhesus macaques, have strict dominance hierarchies; dominants consistently enforce their ranks and show little tolerance for subordinates around resources. In addition, aggression is highly asymmetric and may be intense, conflicts are rarely reconciled, kin bias is high, and mothers discourage other group members, particularly nonkin, from handling their infants. At the other end of the scale, tolerant species, such as the Sulawesi

Fig. 9 Huddling Tibetan macaques on Huangshan, China. Photo by C. Berman

macaques, show all the opposite tendencies: rank is less rigidly enforced, dominants are more tolerant around resources, aggression is more symmetric and mild, conflicts are often reconciled, kin bias is mild and mothers are tolerant when other group members handle their infants. At the time, the social style concept was relatively new, and the styles of many macaque species, including Tibetan macaques, had not been examined in detail. So it was not yet possible to evaluate the general usefulness of the concept. Our research eventually revealed a number of complexities to its use.

Thierry (2000) tentatively described Tibetan macaques as moderately tolerant based on their close phylogenetic relatedness to other tolerant macaque species and reports about ritualized affiliation among males and maternal tolerance of infant handling by males (e.g., Deng 1993; Ogawa 1995). Thus, we expected to confirm that Tibetan macaques were indeed a tolerant species. However, to my surprise, our findings for most core social style indicators (Berman et al. 2004, 2006) supported a despotic social style; aggression was highly asymmetric and there was very little counter-aggression among both males and females. Conciliatory tendencies were moderate for males, but very low for females. Finally, female affiliative relationships and social tolerance were consistently kin biased. Nevertheless, males in particular indeed displayed the tolerant characteristics cited by Thierry. Some not only showed ritualized affiliative behavior, but also frequently supported one another in agonistic conflicts and peacefully consumed provisioned food side by side.

The evolutionary origin of this mix of mostly extreme despotic characteristics and a few moderately tolerant characteristics was difficult to explain based on contemporary hypotheses. Thierry's (2000) phylogenetic hypothesis predicted a tolerant social style based on the species' membership in the generally tolerant sinica-arctoides lineage, as did the socioecological explanation by Sterck et al. (1997) based on the species' historically highly folivorous diet and low predation risk. Finally, the systematic variation hypothesis (Castles et al. 1996), an early corollary of the phylogenetic hypothesis, predicted uniformly moderate or uniformly despotic characteristics. Since none of these hypotheses were supported, we speculated that some or all of the despotic behaviors in our group may have arisen recently due to human activity; aspects of tourism, particularly range restriction, herding, and food provisioning elevated levels of intragroup aggression and competition (Berman and Li 2002) leading to a largely despotic social style in a species that might otherwise show more social tolerance. It may be that evolved tendencies for traits to covary and conform to phylogenetic lines or ecologically derived adaptations may be somewhat flexible, allowing individuals to cope with contemporary pressures posed by human management (Balasubramaniam et al. 2020).

Male tolerance and cooperation

The peculiar mix of despotic, supportive, and tolerant characteristics displayed by Tibetan macaque males in particular intrigued me. Generally, males in multi-male, multi-female groups are not expected to show tolerance and cooperation, because they primarily compete to fertilize females, and fertilizations cannot be shared like food patches or other resources (Schülke and Ostner 2008; Sterck et al. 1997). Li and Wang (1996) had already described evidence that Tibetan macaque males experienced high levels of competition for matings. Indeed, Li (1999) estimated that the alpha, beta, and gamma males account for an average of about 64, 21, and 8% of the matings within the group, respectively, leaving only about 7% for all lower-ranking males combined. So I wondered why males also regularly tolerated one another when feeding and supported one another in agonistic conflicts. Could these males tolerate and cooperate with some males in order to cope with intense conflict and competition from other males? Could cooperation with some males against others actually enhance a male's competitive abilities within his group (cf. Ogawa 1995; Preuschoft and Paul 2000)?

Consistent with a despotic social style, Tibetan macaque males form rigid hierarchies within their groups. Alpha males tend to have short tenures (mean = 10.4 months) after which they are replaced by beta males or by young adult males who rise rapidly from the low ranks they occupy as sub-adults or new immigrants (Li 1999). Between rank changes, the alpha, beta, and gamma males appear to display unusually high levels of tolerance (in terms of co-feeding and low rates of aggression), ritualized affiliation and agonistic support with one another. Moreover, during the mating season, the beta male, and to a lesser extent the gamma male, appear to be the only males able to mate regularly in the presence of the alpha (Fig. 10). Nevertheless, the beta and gamma males occasionally form rank-changing coalitions against the alpha. These observations prompted us to ask whether increased tolerance in predominantly despotic males may occur when high-ranking males need support from other males to maintain their positions.

We found strong evidence that high-ranking males do indeed use tolerance in a highly targeted manner to garner support (Berman et al. 2007b). High-ranking males were able to prevent most males from successfully challenging their rank positions by engaging in conservative coalitions (i.e., agonistic conflicts in which two higher-ranking males jointly challenge a lower-ranking opponent). These served to reinforce the existing hierarchy and prevent most revolutionary coalitions (i.e., conflicts in which two lower-ranking males jointly challenge a higher-ranking male). However, the alpha male could not prevent revolutionary coalitions by the beta and gamma males because there were no other males that out ranked them. We found that high-ranking males displayed tolerance in the form of co-feeding specifically toward lower ranking males that supported them, presumably helping to maintain their support. In particular, alpha males actually supported and cooperated most with the beta and gamma males, the very males most capable of jointly usurping them in a revolutionary coalition. Thus, it appears that high-ranking males discourage revolutionary alliances by using two strategies; they primarily rely on conservative alliances, but also offer tolerance to potential rivals in cases in which conservative coalitions are less effective (Berman et al. 2007b). Such targeted tolerant behavior among these largely despotic males, may indeed be an adaptive modification of despotism that allows them to enhance their competitive abilities within their group (cf. Balasubramaniam 2020; Kaburu & Newton-Fisher 2015).

Fig. 10 The alpha Tibetan macaque male observes as the beta male mates openly with a female. Photo by C. Berman

Variation in kin bias: a matter of time constraints

Focusing once again on female macaques, I turned my attention back to maternal kin bias. By the early 2000s, it was well established that the intensity of kin bias varies markedly among macaque species. However, there was still little known about how much it varies within single species or groups, and if so, what factors shape it. Examining within group variation had the potential to provide key tests of several major hypothesis about the origins of social structure among primates, particularly macaques. For example, Thierry's phylogenetic hypothesis (2000) viewed kin bias as a tightly constrained inherent species characteristic that is linked to a species' social style and that responds little to current environmental or social circumstances. Hence it predicted little variation in kin bias within species. In contrast, Sterck et al.'s (1997) socioecological hypothesis and Dunbar's (1992) time constraints hypothesis saw kin bias as responsive to current conditions. Briefly, the socio-ecological hypothesis posited that high levels of affiliative kin bias in females are shaped by high within group competition for food and the resulting need for female alliances to cope with that competition. The time constraints hypothesis linked high affiliative kin bias to constraints on females' time available to maintain strong social bonds through social grooming. Finally, my previous work with rhesus monkey infants (Berman et al. 1997) suggested that kin bias in proximity relationships increased as a response to increases in social risk. So I set out to test predictions for each of these hypotheses, beginning by examining grooming kin bias among female Tibetan macaques in our study group.

Tibetan Macaques

Hideshi Ogawa had examined grooming among adult females in our study group in 1991–1992, before the group was managed for tourism. Curiously, he found little or no evidence of kin bias in grooming, huddling or other affiliative interaction (Ogawa 2006), whereas between 2000 and 2002, I found consistent evidence that females favored their close kin in grooming, proximity, and tolerance (Berman et al. 2004). So we decided to combine our data to see if we could make sense of this apparent discrepancy. We were also able to add grooming data from 2004 gathered by Huabao Yin. Our results (Berman et al. 2008) strongly supported the time constraints hypothesis. The intensity of grooming kin bias did indeed vary markedly at different time periods, increasing in years when the group was large and contained many potential female grooming partners. Conversely it decreased when the group became smaller and contained fewer potential female partners. Hence, contrary to the phylogenetic hypothesis, our findings did not support the view of kin bias as highly constrained within species. Moreover, contrary to the socioecological hypothesis, grooming kin bias was not related to measures of within-group competition or kin bias in agonistic support. Nor was it related to measures of risk such as human presence, intensity of herding/range restriction, or rates of aggression within the group. Rather females behaved as if they had a limited amount of time to devote to grooming and relationship maintenance; the total time they spent grooming remained roughly constant rather than increasing with the numbers of potential female grooming partners. The number of partners actually groomed also remained roughly constant, as expected if females needed to spend at least a certain minimum amount of time grooming individual females in order to maintain strong social bonds with them. As such when the group was small, they were likely to be able to maintain strong bonds with most or all other females, but when the group was large, they did not appear to have time to groom all other females sufficiently to maintain strong bonds. Rather than grooming each female for an insufficient amount of time, they groomed a smaller proportion of the females when the group was large, focusing more of their limited grooming time on close female kin and less on other females.

Cayo Santiago rhesus macaques

I next looked at Cayo Santiago female rhesus, a despotic species that appears to show kin bias more consistently and often more intensely than Tibetan macaques. The results were remarkably similar (Berman and Kapsalis 2012). When group size/numbers of potential grooming partners increased, females did not appear to have time to groom all other females sufficiently to maintain strong bonds, and they responded by focusing increasingly on a limited number of close kin. Notably, the intensity of kin bias was similar for rhesus and Tibetan macaques when group sizes/numbers of potential partners were controlled, suggesting that differences *between* these two species could also be explained by group size/numbers of potential partners rather than inherent differences.

Tonkean macaques

Although time constraints appeared to best explain patterns of grooming kin bias both within groups and between despotic Tibetan and rhesus macaques, I wondered whether time constraints may play a role within groups of tolerant species that show little or no kin bias. Could they also explain differences between despotic and tolerant macaque species? I collaborated with Bernard Thierry to examine grooming kin bias in his corral-living study group of extremely tolerant Tonkean macaques (Berman and Thierry 2010). We used data recorded between 1987 and 2002, when group size and numbers of potential female grooming partners varied markedly. After testing predictions for time constraints, we compared the data for all three species. We reasoned that if differences between all three species could be attributed largely to differences in numbers of potential partners, the results would further argue against inherent differences and the phylogenetic hypothesis. However, if differences between species were sustained when numbers of potential partners were controlled and were related to species social style, there could be a role for inherent species differences and the phylogenetic hypothesis.

Our results (Berman and Thierry 2010) confirmed a role for time constraints within the Tonkean macaque group, suggesting that time constraints can shape grooming kin bias within groups regardless of whether they typically show intense or weak kin bias. However, kin bias was consistently weaker for Tonkean macaques than for both rhesus monkeys and Tibetan macaques when the number of potential partners was controlled, suggesting a role for inherent differences between despotic and tolerant species, as predicted by the phylogenetic model. We suggested that tolerant Tonkean females may display different social reaction norms (cf. Kappeler and van Schaik 2002) from despotic rhesus and Tibetan macaques, i.e., qualitatively similar, but inherently different ranges of responses to social and demographic conditions. Perhaps more than any other project, this one drove home to me the idea that similar principles of behavior apply to diverse macaque species even those living in diverse conditions (wild, free-ranging, corral-living).

Origins of social structure: phylogenetic signals and socioecology

With my interests turning more and more to the origins of social structure, in 2007 I was delighted to begin working with a new graduate student, Krishna Balasubramaniam and evolutionary geneticist Katharina Dittmar. For his dissertation, Krishna asked whether the core social style indicators, counteraggression and hierarchical steepness (a measure of aggressive success between adjacently ranked individuals) display phylogenetic signals. He used a dataset of 14 social groups representing nine macaque species, and found that both measures varied significantly between species, but only inconsistently within species. Moreover, state of the art phylogenetic analysis methods revealed strong evidence for phylogenetic signals (Balasubramaniam et al. 2012a). Using the same datasets, he next asked how well these measures mapped onto Thierry's four grade social style scale (Balasubramaniam et al. 2012b; Thierry 2000). Both measures correlated with the placement of their species on the scale, although there were several inconsistencies for species in intermediate grades. When he mapped the behavioral measures onto phylogenetic trees, he found that correlations with the scale could be largely attributed to species' phylogenetic relationships. Taken together, these findings strongly support the idea that between-species variation in these core aspects of macaque social structure and social style are indeed shaped by species' phylogenetic relationships.

Conversely, Krishna found little support for some key predictions of Sterck et al.'s (1997) socioecological hypothesis in a study of three social groups of rhesus macaques on Cayo Santiago (Balasubramaniam et al., 2014). In this population, he was able to examine relationships between group size, contest competition and aspects of social structure in a way that controlled for variation in predation (it was absent) and the monopolizability of resources (all groups fed from identical hog feeders and drank from identical water stations). As predicted by the socioecological hypothesis, the largest group experienced more within group competition than the smaller groups for these resources, but the smaller group experienced more between group competition than the larger groups. However, aspects of social structure (dominance asymmetry, intensity of aggression and reconciliation) did not vary across groups in the directions predicted by the socioecological hypothesis. It may be that socioecological principles are applicable only at the species level (or above) or to other aspects of social structure, e.g., grooming.

After Krishna completed his PhD, he continued to examine questions concerning phylogenetic origins vs. adaptation to current conditions. Using a social network approach and dataset of 38 macaque groups representing ten species (Balasubramaniam et al. 2017), he asked whether network traits related to female dominance and grooming show phylogenetic signals and covary with each other, with species-typical social style grades, and/or with current sociodemographic characteristics (group size, sex ratio). He found moderate-strong phylogenetic signals for dominance traits, but only moderate–weak signals for grooming traits. Moreover, grooming traits did not covary with dominance traits or social style grade. Reminiscent of earlier findings of higher kin bias in larger groups (Berman et al. 1997; Berman and Thierry 2010), larger groups had more modular grooming networks. He concluded that female dominance networks were more phylogenetically conserved across macaque species than grooming networks, whereas grooming networks responded more to current demographic factors.

Biological markets theory and infant handling

Another graduate student, Erica Dunayer and I shared an interest in a relatively recent explanatory hypothesis for patterns of social exchange within primate groups—biological markets theory (BMT). Briefly, BMT (Noë and Hammerstein 1994) views animal societies as economic systems in which multiple individuals exchange services (e.g., grooming, tolerance around resources, agonistic support), based on economic laws such as supply and demand. Services that are rare, highly valuable, or controlled by a limited number of individuals should be in greater demand than others, such that 'sellers' can demand higher prices for them, but potential 'buyers' can shop for better deals from alternative sellers. Erica initially catapulted herself into an ongoing discussion between Sanchez-Amaro and Amici (2015, 2016) and Kaburu and Newton-Fisher (2016) over many theoretical issues and complexities associated with the application of BMT to primate exchanges. When the discussion appeared to be at an impasse, she clarified key theoretical aspects of BMT and offered practical approaches to resolve disagreements over such issues as the proper timeframes of exchanges, testing possible alternative explanations (e.g., stress, social bonding) and various methodological pitfalls (Dunayer and Berman 2016). Treading a middle ground, we fully expected an attack by each set of authors, but were pleasantly surprised to receive agreement and kudos from both!

Erica's dissertation then aimed to carry out some of the 'fixes' she identified in Dunayer and Berman (2016). After tackling a methodological issue related to the question of whether reciprocating grooming partners match the time spent grooming one another and whether they do so on a short- or long-term basis (Dunayer et al. 2019), Erica examined exchanges in which females apparently groom mothers of young infants in order to be allowed to handle the infant, asking whether these exchanges conform to supply and demand (S&D) principles (Dunayer 2020) (Fig. 11). Do mothers demand more grooming when there are fewer infants in the group? If so, are exchanges mediated by stress responses from the mother? While increases in grooming when infant availability is low may indicate S&D, they may also reflect increased needs for grooming to calm protective mothers whose infants, as rare commodities, attract increased attention from others. Were mothers' emotional stress-related responses a viable alternative explanation to market effects? Did they function as proximate mechanisms that tied grooming durations to infant availability? She found that grooming for infant handling interchanges did indeed conform to S&D: as infant availability increased, grooming by would-be handlers decreased. However, she found no relationships between maternal stress-related responses (either behavioral or physiological) with infant availability, infant age, or rank distance. Taken together, her results provide support for biological market effects, but not stress effects, in shaping grooming for infant handling exchanges. See also Balasubramaniam and Berman (2017) for an assessment of BMT principles with regard to exchanges of grooming for access to water among females on Cayo Santiago.

Delving deeper, Erica reviewed the literature (Dunayer and Berman 2018), asking why infant handling should be subject to market forces at all? Why are primates motivated to handle infants that are not their own? How has handling evolved and what function(s), if any, does it serve? Among primates, infant handling takes a variety of forms. Some provide infant care, others are merely affiliative and some appear to be deliberately abusive. These variations seem to reflect the separate propensities and interests of each interactor (handler, mother, and infant). Consequently, selective forces driving the behaviors of each interactor do not necessarily align. Hence, most functional explanations focus on the benefits for only one type of interactor (see also Maestripieri 2004). The most promising hypotheses related to short- or medium-term benefits for particular species vary with breeding system, reproductive biology, socioecological factors, and life-history characteristics. Explanations based on life history variables (e.g., reproductive rates) or long-term evolutionary processes related to cooperation (e.g., kin selection) appear to have broader applications, but nevertheless fail to explain infant handling in all its manifestations. The review concluded with support for the idea that handling may have initially evolved as a nonadaptive byproduct of maternal responsiveness, ensuring that mothers provide appropriate care to their own infants (e.g., Silk et al. 2003a). Infant characteristics that evoke maternal responsiveness subsequently ‘spilled over’, eliciting care from others. However, once handling became widespread in a species, opportunities for new adaptive functions, (e.g., learning to mother, socializing infants, freeing up mothers’ foraging time) likely emerged, particularly in species in which handling posed few risks for mothers and infants. As a result, handling became a heterogeneous phenomenon, serving multiple functions in different species and contexts.

Fig. 11 Infant handling by nonmothers among Cayo Santiago rhesus monkeys. Photo by C. Berman

Finally, Erica analyzed data from my dissertation research on Cayo Santiago rhesus infants to test a hypothesized function of handling that has received little attention in the literature: handling may facilitate the formation and maintenance of social bonds between the handler and both the mother and infant (Dunayer and Berman 2017). If so, handling could benefit all three interactors (mother, infant, handler). In the short term, friendly touching is thought to promote the release of oxytocin and/or endorphins that in turn promote positive social emotions and attachments (Dunbar 2010). Longer-term benefits of strong social bonds, which are often initially formed in infancy, appear to promote longevity and future offspring survival in adult female baboons, macaques, and humans (e.g., Brent et al. 2017; Holt-Lunstad et al. 2010; Silk et al. 2003b, 2010). So Erica asked whether handling rates in early infancy (≤ 14 weeks) predict enhanced social bonds months later (25–30 weeks) when infant relationships are more independent of those of their mothers (Berman 1982a, b). Her findings provided the first evidence that early handling is indeed associated with later social bonds that are stronger than would be expected based on kinship, rank, and age/sex class. Given the adaptive benefits of strong social bonds among adult primates, we are now developing a longitudinal database to investigate whether early infant handling may have longer-term social and fitness effects.

Continued branching out with graduate students

In many of the research projects described above, I have been fortunate enough to work with talented and enthusiastic PhD students (Fig. 12). One of my greatest pleasures has been to watch them develop from bright beginners into exceptional researchers, colleagues, and friends. What a joy it has been seeing them reach the point when they can challenge and teach me as much as vice-versa! In recent years, my research has continued to expand in scope, thanks primarily to them. For example, Laura Labarge completed a stellar dissertation and published several papers on social aspects of perceived predation risk among

Fig. 12 Erica Dunayer, Carol Berman, Katharine Burke, and Krishna Balasubramaniam visiting Cayo Santiago during the 75th anniversary of its founding. Photographer unknown

wild samango monkeys (Labarge et al. 2020a, b; 2021, 2022). Erin Weigel and Akie Yanagi completed excellent dissertations on play and play signaling in captive gorillas and free-ranging rhesus monkeys, respectively. They found a plethora of new play signals (Weigel and Berman 2018; Yanagi and Berman 2013) and made headway into understanding the possible theoretical implications and functions associated with having multiple play signals (Weigel 2020; Yanagi and Berman 2014, 2017, 2018). Maura Tyrrell's dissertation describes social relationships among wild crested macaque males. Unlike extremely tolerant and affiliative females, males show an avoidant social style, i.e., a mix of extremely despotic and extremely tolerant social style traits, and apparent avoidance of both affiliative and agonistic interaction with one another (Tyrrell et al. 2020). Although males engage in post conflict affiliation, this behavior does not appear to restore tolerance in the short term, but it may facilitate future coalitionary behavior and eventual increases in rank (Tyrrell 2021). Katharine Burke examined relationships between stress-related hormones and social relationships in juvenile rhesus monkeys on Cayo Santiago and found evidence, that unlike adults, but like many human adolescents, strong bonds with peers may be sources of physiological stress rather than buffers (Burke 2021). Finally, Dominique Bertrand is completing a dissertation on the effects of tourism and crop defense on wild crested macaques. So far she has found graded behavioral responses to tourists similar to the graded responses of other primates to varying degrees of predation risk (Bertrand et al. in press).

Conclusions

Looking back over the years, a career in primate behavioral field research is no longer considered as unconventional for a young woman as it once did. There is even a primatologist Barbie doll available to little girls with dreams like mine. The field has grown enormously, and for some time it has been well represented by talented women as well as by theoretical frameworks that seriously consider both sexes. That is tremendously gratifying. It is also gratifying to think that my example, along with that of other established primatologists, male and female, may have encouraged younger women to follow similar dreams. I personally was incredibly fortunate to be born when and where I was, and to open-minded parents who were able to support my choice. Being gently and patiently mentored by the late Robert Hinde was also a great gift. I will be forever grateful to all those who helped me realize my once strange dream.

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