Kin-Directed Behavior in Primates

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Abstract

Kinship was one of the first foundational principles of primate social organization to be recognized and to be viewed within an explicit evolutionary framework, specifically kin selection theory. Over time we have come to appreciate how much kinship structures and kin preferences vary between and within species, and how they are constrained by demography, life history characteristics, ecology, and mechanisms for recognizing kin. We have only recently discovered that many species are able to recognize paternal kin and to express preferences for them, but we have much to learn about how individuals do this, and how they make choices among different classes of kin and nonkin. Many potential benefits of close kin relationships have been uncovered, and some have been firmly linked to fitness benefits. Questions about kin selection versus mutualism or reciprocity as an explanation for kin preferences continue to pose challenges. Recent empirical studies support the operation of kin selection, but suggest that it may extend only within fairly narrow limits of relatedness. Much current theoretical research focuses on modeling the ways in which kinship interacts with dispersal patterns, reproductive skew, habitat saturation, and other ecological and life history patterns to produce various selective regimes related to cooperation. Some recent promising theoretical models of the origins of human social systems also rely in part on principles of kin selection and on a greatly expanded understanding of kin-related behavior in nonhuman primates.

INTRODUCTION

The 1960s marked a pivotal advance in our understanding of primate social structure from both empirical and theoretical perspectives. During this time, field workers began to appreciate the importance of kinship as a central organizing principle of primate social organization, along with age, sex, and dominance. This was significant from an anthropological perspective, because kinship had long been considered a unique and central organizing principle for human societies. The 1960s also coincided with the formal development by W. D. Hamilton (1964) of kin selection theory, an evolutionary framework to explain the origin and maintenance of altruistic behavior among

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related individuals. Because kin are likely to share genes, including genes that might influence altruistic behavior, helping kin reproduce can increase one's own representation of genes in the next generation. Hamilton formalized this idea in what is now called *Hamilton's Rule* which posits that altruism with kin could evolve and would be expected when the cost to the actor was less than the benefit to the receiver, discounted by their degree of relatedness. This idea dovetailed nicely with the observations that group-living primates showed strong preferences for their kin. Despite the subsequent abandonment of the kinship concept by many cultural anthropologists, these developments opened the way for biological anthropologists to construct plausible evolutionary hypotheses that link kin-related behavior in nonhuman primates and humans.

Early studies of kinship focused primarily on provisioned groups of macaques and other species with matrilineal social organizations. In many of these species, one can predict female bonds and dominance relationships with high accuracy by knowing matrilineal kin relationships. Both high rank and close maternal kin relationships have been linked to higher survival rates for females and for their offspring, suggesting that kin preferences are adaptive, and more specifically that kin selection is likely to be an important adaptive process driving strong affiliative and supportive relationships among maternal kin.

Over the years, studies of additional species have both strengthened and complicated this perspective. Researchers have discovered more varied social/kinship structures among primates, some of which show divergent and/or less intense patterns of kin preferences. Given this wide variation, explanatory models currently focus on ways in which ecological, life history, and demographic factors interact to produce both diverse kinship structures and diverse combinations of selective pressures governing social interaction among related and unrelated group members. Recently, the case for kin selection has been both boosted by accumulating evidence of paternal kin recognition and favoritism and challenged by demonstrations that some examples of kin-biased behavior in primates and other animals might be better explained in terms of mutualism, reciprocity, or nonadaptive processes. Nevertheless, current studies support the operation of kin selection, albeit within narrower limits than previously thought. Some recent promising models of the possible origins of human family systems also rely at least in part on principles of kin selection as well as on a greatly expanded understanding of kin-related behavior in nonhuman primates. Below is a brief review of primate kinship. For more detail and specific citations, see the reviews listed in Further Readings.

FOUNDATIONAL RESEARCH

Diversity and Constraints on Kin Preferences

Patterns of kin-related behavior vary widely both between and within primate species and are constrained by factors that determine the kin composition of groups (e.g., dispersal patterns and reproductive rates) and the mechanisms available for recognizing kin. Nevertheless, kin preferences appear to be reoccurring themes throughout the primate order, seemingly surfacing repeatedly when circumstances allow. Since many recent reviews document the widespread nature and diversity of kin-related behavior among nonhuman primates, only two contrasting examples are given here. Briefly, many female macaques and baboons display strong tendencies to affiliate, cofeed, tolerate, and/or support their close maternal kin (typically in direct proportion to their degree of relatedness to them). Many also show matrilineally based dominance hierarchies in which females inherit their ranks socially from their mothers largely through strong tendencies for mothers and other close female kin to support them in conflicts with other individuals. Strong, enduring, matrilineal bonds are probable given that females remain in their natal groups for life and continue to associate closely with their mothers, bringing them in contact with their mothers' close associates (primarily siblings and other close maternal kin). They form bonds with them through a combination of familiarity, maternal control, and independent learning. Males, however, disperse to other social groups around puberty and reside with few maternal kin. Hence, they have more limited opportunities to form relationships with kin.

Notably, not all female philopatry/male dispersal species conform to this classic matrilineal model. Some macaques, guenons, langurs, and capuchins display more moderate and less consistent tendencies to favor and support kin. As a result, female hierarchies may be based relatively more on individual competitive abilities than on maternal kin alliances.

In a few female philopatric species, there is also evidence that adult and/or juvenile paternal sisters affiliate more with one another than with unrelated adult females. Males also favor their own offspring in some cases. For example, male baboons preferentially intervene on behalf of their own juvenile offspring when they get into fights with other youngsters, possibly facilitating their earlier maturation. Putative fathers may also attempt to protect their own offspring from infanticide by other males.

Kin-related behavior is more limited in chimpanzees, a species in which males are philopatric and females generally disperse. Adults females reside with only a few categories of adult matrilineal kin—sons and the occasional undispersed daughter. Accordingly, chimpanzee mothers are able to positively influence their son's dominance ranks and spend substantial amounts

of time with undispersed daughters. Adult males also affiliate and cooperate preferentially with maternal brothers, but most strong relationships are with other males. Slow female reproductive rates may limit the benefits of cooperation among maternal brothers; brothers that are widely spaced in age may be too unevenly matched to provide substantial mutual benefits. Males also potentially reside with several categories of male paternal kin (fathers, sons, grandfathers, grandsons, brothers, etc.). Although males appear to recognize and favor their offspring in limited ways, there is no evidence of preferential relationships between paternal brothers. Lack of recognition among paternal brothers may be due to low levels of reproductive skew among males, making age similarity a poor cue for paternal relatedness.

Reproductive Benefits

While examples of kin favoritism and cooperation are abundant, evidence that strong affiliative and supportive relationships with kin yield reproductive benefits are still sparse, partly because it is difficult to quantify the costs and benefits of particular behaviors over a lifetime. For brevity's sake, only one example is given here: adult female chacma baboons that form strong, enduring bonds with mothers and daughters have longer-lived offspring than those with weaker bonds. When females have no mothers or daughters within their group, offspring survival is enhanced for those with relatively strong relationships with maternal sisters. While these benefits are independent of rank effects on fitness, support from kin is nevertheless important in attaining high rank (Silk *et al.,* 2010).

Evolutionary Processes

Links between kin favoritism and increased fitness are necessary to infer kin selection, but are not sufficient. Theoretically, kin preferences could also be the result of nonadaptive processes or kin-based mutualism/reciprocity. In many species, close kin are of similar age or rank. Thus, kin preferences could be nonadaptive artifacts of processes that bring individuals of similar age or rank into close association and cooperation. However, rank and age effects are not sufficient to explain kin preferences; strong kinship effects are sustained when rank and age are controlled statistically in several species. Indeed, kinship effects are often stronger than age and rank effects and evident in species in which rank is not correlated with kinship. The arguments that kin preferences are nonadaptive outcomes of persistent mother–offspring relationships or artifacts of common proximity with the mother rather than independent relationships have also been refuted. Finally,

the existence of preferential relationships among paternal kin suggests that kin preferences cannot be explained as a byproduct of extended maternal ties.

Another possibility is that kinship bonds are outcomes of mutualism or reciprocity rather than kin selection. In mutualism and reciprocity, both cooperating individuals receive immediate or delayed direct benefits from their interaction. In kin selection, individuals derive indirect benefits by augmenting the reproduction of genetic relatives. In reality, kin interaction often yields both direct and indirect benefits, and it is difficult to determine which are primary. For example, young adult tamarins that help parents rear younger siblings may receive indirect benefits from helping kin as well as direct benefits from remaining on their parent's territory. Indeed, some helpers are unrelated to the parents and offspring, and help is distributed without regard to kinship in some cases, suggesting that direct benefits may be sufficient to explain helping behavior. However, other findings suggest a role for indirect benefits: in other cases, both the amount of help given and the probability that a dominant female shares reproduction with a subordinate are correlated with degree of relatedness (Griffin & West, 2003).

While direct benefits may be sufficient to explain some forms of cooperation, individuals that form mutualistic or reciprocal relationships preferentially with kin should theoretically be at an advantage over those who cooperate with nonkin, because they are able to reap both direct and indirect benefits. Support for kin-biased reciprocity or mutualism comes from studies of female grooming that found independent effects of kinship and reciprocity across several primate species, more equitable grooming relationships among closely related female baboons, and kin-biased alliance patterns used against low-ranking targets. When both partners rank above the target, the costs of aggression are low, and each alliance partner is likely to benefit directly by reinforcing its rank over the target and by obtaining resources it holds. On the other hand, other factors, including competition, may offset some or all of the benefits of cooperating with kin. Also cooperation with kin may be less beneficial than cooperation with nonkin when the task requires skills that kin lack.

One class of behavior, unilateral altruism, can be used to rule out the effects of mutualism/reciprocity, because it involves behavior that increases the fitness of another individual at a cost to the actor and is directed only from the altruist to the recipient. Agonistic support on behalf of a youngster involved in a fight with an individual that ranks above the supporter is an example. Not only is it risky for the supporter, the youngster is incapable of reciprocating effectively. Several observational and experimental studies indicate that such support is highly kin-biased. Another form of unilateral altruism involves allowing a subordinate access to monopolizable food. Observational studies support the idea that passive cofeeding and active food

sharing are highly kin-biased. Similar results were found in an experimental study of Japanese macaques that controlled for variations in motivation (e.g., hunger) and costs of defending food (e.g., injury, loss of efficiency). However, when the costs of defending food were minimal, females extended feeding tolerance only to daughters. Thus, while these results support the notion of kin selection in unilateral altruism, they also suggest that unilateral altruism may extend only to one's closest kin (Chapais & Belisle, 2004).

CUTTING EDGE RESEARCH

Kin Recognition

Since group-living individuals are expected to favor kin only if they can distinguish them from nonkin, there is considerable interest in understanding whether they can, and if so, what mechanisms are involved. Most researchers agree that maternal kin recognize each other primarily through familiarity (see above), but much less is known about kin recognition among paternal kin, particularly in groups with multiple males. Some hypotheses focus on reproductive skew; if only a few high ranking males sire most infants in a given year, the probability is high that any care they provide is directed toward kin. High reproductive skew also leads to the production of similarly aged paternal siblings. Thus, offspring can potentially use age similarity as a cue for paternal relatedness with an accuracy approximating the degree of reproductive skew. Recent studies are beginning to find evidence for other cues as well. For example, both mandrills (Setchell *et al.,* 2011) and ring-tailed lemurs (Charpentier, Crawford, Boulet, & Drea, 2010) produce scents that contain information about relatedness. Lemurs in particular appear to moderate their responses to these odors in ways that may increase their chances of avoiding incest and favoring male kin. Chimpanzees and rhesus monkeys have some abilities to match unfamiliar parents and offspring using photos of faces (Bower, Suomi, & Paukner, 2012; Parr, Heintz, Lonsdorf, & Wroblewskiet, 2010), although how much this aids them in identifying their own kin is unclear. Finally, mate advertisement calls of male mouse lemurs contain information about their patrilineage membership (Kessler, Scheumann, Nash, & Zimmerman, 2011). The extent to which individuals use this information is unknown.

Close Kin Relationships: Benefits, Physiological Underpinnings, Allocation Issues

Recent findings enhance our understanding of some of the benefits of strong bonds with kin. Extending findings of increased survival and reduced infant mortality for female chacma baboons with strong kin bonds (see above), Charpentier *et al*. (2012) found that mandrill females that enjoy strong

bonds with kin as juveniles begin to reproduce about a year earlier than others. Recent studies also support the idea that social networks that are focused on a few strong, enduring relationships yield benefits at least in part by reducing levels of stress (e.g., Brent, Semple, Dubuc, Heistermann, & MacLarnon, 2011), and that both oxytocin (e.g., Fairbanks, Jorgensen, & Bales, 2012) and endogenous opioids (Machin & Dunbar, 2011) may mediate the formation and reinforcement of strong bonds with kin and nonkin, as they are thought to do in humans and other mammals.

Charpentier *et al*. also examined questions concerning associations with maternal versus paternal kin. Although kin selection theory predicts equal degrees of favoritism toward each, several studies have found much lower levels of association with paternal than maternal siblings. Hypotheses include constraints on paternal kin recognition, due perhaps to low levels of reproductive skew, and/or differential availability of paternal versus maternal kin: female baboons appear to prefer close maternal kin, but form strong social bonds with paternal kin when maternal kin are absent. Similarly, juvenile mandrills living in groups with high reproductive skew prefer mothers and maternal siblings over others. Relationships with paternal siblings are common, but those with less closely related maternal kin are constrained by the availability paternal siblings. Why maternal siblings are preferred, however, when paternal siblings are available and recognizable remains unclear.

Explaining Diversity

While demographic and life history processes constrain the potential for kin preferences, and kin selection, reciprocity, and mutualism help explain its broad adaptive nature, these processes still leave much to explain about why kin-related behavior varies across and within primate species. Several ecologically based models are under consideration. Three are briefly described here. Sterck, Watts, and van Schaik (1997) views kin preferences among group-living females as adaptations to direct forms of competition for food resources. The degree of preference should depend on levels of within-group competition (WGC) and between-group competition (BGC). For example, females that experience high WGC and low BGC should benefit by forming matrilineal hierarchies and within-group alliances with kin to increase their access to food. Kin are favored based on their long-term familiarity and potential indirect fitness gains. Conversely, kin preferences are expected to be weaker or absent under different competitive regimes. Unfortunately, studies investigating links between competitive regimes and tendencies for females to affiliate and ally with one another have produced inconsistent results, and none have found direct links between levels of WGC and

intensities of kin preferences. Hence, recent reviews have recommended the construction of less comprehensive models.

Dunbar's (1992) time constraints model posits that as groups increase in size, WGC intensifies, increasing the need for strong female affiliative relationships and large within-group alliances. However, social time is likely to be limited, and at some point, females may not have enough time to maintain strong relationships with all other females in the group. Under these circumstances, the model suggests that females should benefit by focusing their affiliative interaction on a small proportion of group members, that is, one's closest kin. Recent studies of rhesus, Tibetan and Tonkean macaques, and capuchin monkeys support several predictions of this model.

The phylogenetic model (Thierry, Iwaniuk, & Pellis, 2000) posits that the tendency to favor kin is a species characteristic that is integral to its social style. The social style concept is based on the observation that a suite of characteristics, including kin preferences, tend to covary among primate species. Social style is viewed as lying along a continuum from despotic to relaxed. Species with relatively despotic styles generally display strong kin preferences in affiliation, support, and reconciliation; highly asymmetric and intense aggression; little social tolerance; and weak conciliatory tendencies. Those with more relaxed styles display the opposite tendencies. According to this view, social style is largely inherent, and it depends primarily on the species' phylogenetic history. As such, this model hypothesizes that female kin preferences in macaques are part of a highly integrated, self-organized, tightly constrained set of social characteristics that have evolved in tandem and have been conserved over their evolutionary histories. Advocates hypothesize that ecologically based costs and benefits shaped social styles in the distant past, but that subsequent evolutionary constraints have decoupled social style from current ecological conditions. Recently, several core social style characteristics have been found to have strong phylogenetic signals, but kin preferences *per se* display only weak evidence for a phylogenetic signal.

Human Origins

During the mid-twentieth century, many cultural anthropologists saw kinship as central to understanding the structure of human societies, and nonhuman primates as important tools for tracing the origins of human kinship. However, by the 1980s, interest in human kinship and its origins was virtually abandoned due partly to the realization that kinship labels, concepts, and behavior varied widely among societies and often deviated from expected based on genetic relatedness. Nevertheless, kinship ties are viewed as important (as "mutuality of being") within virtually all societies

(Sahlins, 2011), and as Robin Fox states, "…actual or putative genetic connexion, according to the local definition of 'genetic' or 'consanguineous', is usually the basis of kinship relations" (Fox, 1967, p. 34). On the basis of this latter view and on a greatly expanded knowledge of nonhuman primate behavior, two recent models for the origins of human kinship behavior from primate origins have appeared. They can only be very briefly and superficially summarized here. Chapais' (2008) pair-bonding model begins with Levi-Strauss' notion of reciprocal exogamy as a uniquely human, universal structural feature of society that represents "the atom of kinship." However, unlike Levi-Strauss, Chapais argues that reciprocal exogamy is not a purely cultural invention. Rather, common biological principles tie it to its primate origins. To illustrate this, Chapais breaks down reciprocal exogamy into twelve component parts, some but not all of which are found separately in a variety of nonhuman primate species. He then applies the logic of phylogenetic reconstruction to trace their separate origins and stepwise configuration into its uniquely human form. Some components represent homologies, some convergences, and some emergent properties of combinations that preceded them. The pivotal event was the evolution of pair-bonding within a chimp/bonobo-like social structure. Pair-bonding subsequently opened the way to the recognition of many more categories of kin than were previously possible, including paternal kin and "affines," expanding opportunities for kin-biased favoritism and cooperation. This in turn led to the formation of bonds between groups that exchange mates and ultimately to larger, segmented tribal structures.

A second model posits that many derived characteristics of human societies stem from the evolution of cooperative breeding by early hominids (Hrdy, 2009; van Schaik & Burkart, 2010). *Cooperative breeding* in humans refers to the extensive investment by individuals (in addition to the mother) in the rearing of offspring. In most societies, these allomothers are close kin. Their energetic contributions directly or indirectly supplement the mother, allowing her to reproduce more frequently and more successfully than otherwise possible, and allowing offspring to mature more slowly and grow larger brains. The social tolerance and prosocial tendencies engendered by cooperative breeding also allow increased opportunities for social learning of complex technical and interpersonal skills that are needed both to procure care as a child and participate later in joint problem solving. How cooperative breeding arose is less clear. Van Schaik and Burkart suggest that it appeared at a time when dispersal from natal groups was very difficult, but when helping had a large effect on the fitness of related immatures. These conditions would not only facilitate helping, but also drive changes in female reproductive patterns (including the evolution of menopause), making helping by kin even more productive and specialized. They suggest

that cooperative breeding likely arose in *Homo erectus* around 1.8 Ma, based on evidence of the appearance of larger brains, complex foraging methods, and cooperative hunting/defense of large carcasses. The skills needed for these activities probably were beyond the abilities of juveniles, yet they likely yielded more resources than necessary to sustain skilled adult practitioners, a situation that could have been sustained only through supplementation of immatures and/or their mothers.

FUTURE ISSUES

Views of primate kinship began to take shape about 50 years ago and were influenced almost exclusively by studies of matrilineal societies. Over the years, studies of a diverse range of species have greatly expanded that perspective. Nevertheless, theoretical work still relies heavily on matrilineally organized species, partly because they remain the most thoroughly studied. Thus, one critical task for the future is to continue to expand our knowledge of a variety of primate species, preferably over multiple generations, and to apply it to theoretical models. The continued development and application of noninvasive molecular genetics methods to wild populations will greatly facilitate efforts to understand the factors that determine both kinship structures and any reproductive advantages of kinship. Behavioral and genetic studies in pristine ecological contexts are often considered ideal, but those in provisioned, free-ranging, disturbed, or marginal conditions can also be crucial for understanding the environmental influences on kinship structures and kin-related behavior. Similarly, studies of multiple groups and populations of the same species, along with those in different species, should produce opportunities for analysis on a variety of levels: within groups, populations, species, and higher taxonomic categories. Such studies are particularly urgent, given the endangered status of many species and the disappearance of undisturbed populations.

Continued studies are also needed of the behavioral, physiological, and reproductive consequences of kin relationships. These provide means to test predictions of kin selection theory and other adaptive and nonadaptive explanations for kin preferences. Topics of particular interest include proximate mechanisms by which strong kin relationships lead to reproductive benefits at various points of the life cycle. Several studies point to the importance of strong relationships in lowering levels of physiological stress, but it is still unclear precisely how kin do this. Does their mere proximity engender feelings of security, or does proximity provide real protection from predation or other risks? Do benefits derive from specific services rendered (e.g., grooming, agonistic support)? Related to this is the question of the extent to which relationships with nonkin can compensate for the absence

of kin relationships. Indications are that nonkin relationships can provide many of the same benefits as those with kin, but it is still unclear whether they do so as efficiently or reliably.

Studies of paternal kin recognition and its mechanisms have made significant strides in recent years, but much remains unclear. To date, paternal kin recognition and favoritism has been examined in only a small number of species. Possible visual, vocal, and olfactory cues to paternal relatedness are beginning to be uncovered, but studies about whether and how individuals make use of these cues are still in their infancy. Another intriguing question concerns the reasons why patrilineal kinship appears to be less important than maternal kinship in shaping relationships even when paternal kin are recognizable. Issues of availability are being investigated, but do not appear to be the whole story.

Kin selection continues to pose intriguing questions and challenges. Approaches are needed to probe increasingly more precise predictions of Hamilton's rule and to rule out alternative explanations. Particularly promising approaches include carefully controlled experimental studies such as those of Chapais and colleagues on unilateral altruism and long-term field-based studies relating mother–daughter rank reversal in baboons to reproductive value. Long-term field-based studies have also made it possible to examine predictions of reproductive benefits for baboons with strong, enduring kin bonds.

Quantitative genetic approaches to understanding the heritability of social propensities may also prove useful in understanding the potential selective value of kin preferences in various ecological and demographic contexts, although studies in naturally organized social groups are currently unable to distinguish the extent to which propensities to form particular types of relationships, including bonds with kin, are inherited genetically or socially through mothers. Individuals may prefer kin to varying degrees because of their genetic profiles, because the mother modeled or controlled her offspring's earlier interaction, and/or because both respond to contextual factors that are ecological in nature or due to genetically influenced behavior patterns displayed by other group members (e.g., levels and intensities of aggression). Cross-fostering studies show promise to sort out these possibilities.

Recent debates over the relative importance of kin selection and ecology in the evolution of cooperation (e.g., Abbott *et al.,* 2011; Nowak, Tarnita, & Wilson, 2010) have reinforced efforts to view variation in kin-related behavior among primates within an ecological framework. Quantitative models of the interaction of dispersal patterns, reproductive skew, habitat saturation, and patch quality are offering more explicit predictions for local patterns of relatedness than previously available, along with implications for diverse

patterns of kin selected cooperation (e.g., Rodrigues & Gardner, 2012). Among other things, these models have helped identify the conditions under which local concentrations of kin will or will not lead to the cancelation of selective advantages of kin cooperation by the disadvantages of competition among kin. While it is uncertain whether these particular models can be applied directly to primate populations, efforts in these directions promise to sharpen theoretical thinking among primate researchers and stimulate new empirical research on the interaction of life history, phylogeny, ecology, and kinship.

A related issue is that there is currently no consensus over the relative importance of current conditions versus past selection in shaping kin-related behavior in primates; studies generally examine one or the other rather than both. One exception found evidence that variation in grooming kin preferences among macaques was associated with both current demographic conditions within groups and phylogenetically related species differences (Berman & Thierry, 2010). There is also disagreement about the role of complex adaptive systems versus self-organizing systems driven by a few initial conditions. Future studies should profit from the application of both ecological and phylogenetic analysis, and should ultimately aim to encompass a wide range of species in order to correct a historically narrow concentration on matrilineal social structures.

In the early days of primate behavior research, primate ethologists could work in relative isolation, and aim for basic descriptions of behavior patterns, social relationships, and social organization of a given species. However, most current research questions require the collaborative efforts by a team of experts from a wide range of specialties: ethologists, ecologists, quantitative and population geneticists, demographers, bioinformatics specialists, quantitative modelers, endocrinologists, neurobiologists, and so on. For those interested in the evolution of human societies, the expertise of paleoanthropologists, bioarchaeologists, human biologists, evolutionary medicine specialists, climate specialists, and cultural anthropologists are also essential. This trend will no doubt continue into the future, as predictions become more precise, models become more complex, and analytical methods become more technical. Such efforts tend to involve more coordination, better communication across disciplines, as well as more expense. To accomplish this, training of new researchers also needs to be increasingly collaborative and interdisciplinary. Problems of funding for primate behavioral ecology research in particular are becoming increasingly serious in difficult economic times, and yet increasingly urgent given the poor conservation prospects of many species. As such, academically oriented researchers must also devote their efforts and support to conservation initiatives around the world, to educate the broad population in habitat

countries as well as in first world Western countries, and particularly to train and recruit scientists in habitat countries to develop research programs and conservation initiatives themselves.

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Carol M. Berman received a B.A. in Psychology from Brandeis University and a PhD in Animal Behavior from the University of Cambridge University, UK. She is currently a professor in the Department of Anthropology and in the Graduate Program in Evolution, Ecology and Behavior at the University at Buffalo. Her research has focused on the social behavior of free-ranging rhesus macaques on the island of Cayo Santiago, Puerto Rico, on wild rhesus macaques in India and on wild Tibetan macaques in China. Her early work examined parent–offspring relationships and the ways in which they are both influenced by and impact social structure. More recently, she has been examining various other aspects of social structure, including conflict management, social style, and kinship. In particular, she is focusing factors that influence variation in the intensity of kin preferences within groups over time and across species. A secondary interest concerns the effects of tourism on the behavior and fitness of targeted macaque species. See http://www.anthropology.buffalo.edu/people/faculty/berman/.

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