RESEARCH INTERESTS

Study populations

The research in my lab focuses on two populations of large mammals. For both populations, detailed life histories are available and observation conditions are very good. The savannah baboon population in Amboseli National Park, southern Kenya, has been the subject of ongoing research for over 30 years by the Amboseli Baboon Research Project. The elephant population in Amboseli has also been the subject of intensive behavioral and demographic research for 25 years, by the Amboseli Elephant Research Project. These two populations are among the best-studied mammal populations in the world and provide truly exceptional opportunities for understanding the relationships between social behavior, relatedness, and population genetic structure. My own work focuses mainly on the baboon population (I co-direct the Amboseli Baboon Research Project with Jeanne Altmann at Princeton University), and most of the work described below is done in collaboration with my baboon research collaborators (visit the baboon project website for more information).

Laboratory methods for DNA extraction

The work in my lab depends on having study animals that are well habituated to the presence of observers. Obtaining tissue samples (blood or skin) can affect habituation in both study species. Because of this, we depend to a great extent on DNA extracted from dung for the gentic work in my lab. Extracting an analyzing DNA from fecal material is labor intensive and challenging but microsatellite markers can be reliably amplified from fecal material if the right techniques are used (3,8,9).

Major research questions

Three of the major research questions that we are working on include understanding the importance of expression of kin relationshps in our studiy species, understanding the importance of dominance relationships, and understanding behavioral responses to environmental change.

1. Kin relationships and kin recognition.
Like many mammal species, savannah baboons and elephants live in matrilineal societies. Older females, their mature daughters, and their immature offspring of both sexes live in close proximity, and maternal relatedness is known (in the case of baboons) or hypothesized (in the case of elephants) to be a major predictor of social interactions within groups.

In studies of large mammals, research on kin relationships is almost entirely restricted to relationships among materal kin – animals related through their mothers. However, selection should act with equal force on relationships with paternal kin – animals related through their father. Although this fact is widely recognized, most researchers have ignored the issue of paternal kinship in studies of the role of kinship, particularly in large mammals. This is partly because paternal kin relationships have been difficult for observers to detect in species where both sexes mate with multiple partners. Maternal identity is obvious in mammals but paternal identity is rarely as clear. This has led many researchers to believe that paternal relatives in multiply mating species are unable to identify each other. However, in a series of papers on paternal kind relationships we have demonstrated that baboons clearly differentitate their paternal relatives from other conspecifics. Paternal brother-sister pairs show evidence of reduced sexual attractiveness to each other compared to nonrelatives (1). Paternal sisters form close affiliative bonds of the same nature and intensity as those of maternal sisters (2). And male baboons differentiate their own offspring from the offspring of other males and preferentially support them during social disputes (3).

Because of the strong affiliative bonds that kin (including, now, paternal kin) exhibit, researchers have inferred that close affiliative bonds, especially with relatives, confer fitness advantage – i.e., that they enhance survival or reproduction. Empirical evidence in support of this hypothesis is very limited, because the data needed to demonstrate this are difficult to obtain. Increasingly, researchers have proposed that associations between maternal relatives arise as a non-adaptive byproduct of phyiscal proximity to the mother. These criticisms have thrown down the gauntlet for proponents of the adaptive argument. We have recently demonstrated that sociality per se confers fitness advantages in baboons – females that are more socially integrated have higher survival among their infants (4). We have not yet identified the mechanism by which this occurs, and we have not identified the specific role of kin relationships in this phenomenon. This is a major goal of our current research, in order to answer the question, “Does natural selection shape kin relationships?” Our ability to combine genetic with behavioral and demographic data from the long-term baboon study gives us unusual power in addressing these questions.

2. Fighting ability and dominance rank.
Elephants and baboons exhibit linear dominance hierarchies in both sexes – animals can be ranked linearly according to their patterns of wins and losses in social conflicts. Among female baboons, daughters typically “inherit” their mother’s dominance rank (that is, they attain adulat ranks just below their mothers). Further, the relative ranking of families tends to be stable across multiple generations. Among male baboons, dominance rank is independent of maternal rank, and changes markedly with age; males reach their highest rank between 8 and 10 years of age (in their prime), and fall in rank steadily as they age. Baboons are typical among Old World primates in these patterns. We have just recently documented that elephant females also exhibit linear dominance hierarchies (work in progress); we are still analyzing our data with respect to mother-daughter rank inheritance in elephants and rank stability over time. Rank relationships among male elephants are well understood to be size- and state-dependent. That is, the largest males hold the highest rank positions (elephants grow throughout their lives and males reach their largest size and their highest rank in their 50’s and 60’s). However, males in the state of heightened sexual and aggressive behavior known as musth can outrank larger males. Musth appears to be a very energetically costly state to maintain, and only large, older males can maintain it for extended periods (up to several months).

In contrast to the functional significance of kin relationships, the functional significance of dominance rank has been much studied, but with conflicting results. For instance, many primate studies have reported that high-ranking animals have fitness advantages (higher fertility or survival), but many others have reported that rank does not confer such advantages. These differences across studies have been the subject of debate for several decades. We contributed to the resolution of this debate (5) by demonstrating that, in Amboseli, the extent to which dominance rank predicts mating success for male baboons varies substantially over the long term, even though on average high ranking males have an advantage. By partitioning our long-term data into six-month blocks of time, we demonstrated that during some time periods the dominance hierarchy functions as a queue in which males wait for mating opportunities – when only one female is in estrous (the most common situation), only the highest ranking male mates with her; when two females are in estrous, the two highest ranking males will mate, and so on. The consequence is that the highest-ranking male obtains the vast majority of mating opportunities. During other blocks of time, lower-ranking males engage in extensive “queue-jumping”, primarily by forming coalitions with other males and attacking high-ranking males higher up in the queue. Queue jumping predominates when there are many males in the group, when older males (who more frequently form male-male coalitions) are well represented in the group, and when the highest ranking male is relatively new in his position of highest rank. Our results (5) provide strong support for the propositions that (1) males experience natural selection on fighting ability (it influences mating success through its effects on dominance rank), but that (2) there is variance over time in the extent to which high-ranking males monopolize access to females, and hence variance in the strength of selection on fighting ability.

3. Life in a changing environment.
Amboseli has undergone dramatic habitat and climate change in the past 30 years, with daily high temperatures increasing by more than 7º C and large areas of the Amboseli basin experiencing extensive tree die-off (6). An important goal of our recent and current research involves analyzing the baboons’ responses to these changes.

We have found dramatic effects of this habitat change on the baboons’ behavior (7). During periods of habitat decline, baboons dramatically increase their time spent foraging (from a low of 50% to more than 80% of waking time) and significantly reduce their time spent socializing. In spite of these striking behavioral changes, our standard deterministic model of population growth indicates that the Amboseli baboon population is growing at a moderate rate. That is, the baboons successfully mitigate the detrimental effects of habitat change. How they do this remains unclear, but we have shown that, in response to habitat change, the Amboseli baboons have actively sought out areas of intact habitat. This suggests that behavior – the flexibility to move to new areas and seek new resources to exploit – may play a major role in this mitigation.

Although our deterministic model of population dynamics indicates moderate growth, we are developing stochastic models that indicate that the population has experienced successive episodes of shrinkage and growth, and that the repeated episodes of shrinkage may actually threaten the long-term survival of the population. Our preliminary analyses indicate that shrinkage has occurred as an immediate consequence of habitat degradation, and that growth has occurred as an immediate consequence of home range shifts to intact habitat. This result is an important example of how animal behavior – seeking and moving to new habitats – has important consequences for population-level processes. This work is of particular interest in light of a recent influential theory of human evolution, which posits that our uniquely human characteristics, particularly our behavioral flexibility, evolved in response to continual habitat change during the Pleistocene. We aim to use baboons as a model to test some of the assumptions and predictions of this recent theory.

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