Chapter 12
The Amboseli Baboon Research Project: 40 Years of Continuity and Change

Susan C. Alberts and Jeanne Altmann

Abstract In 1963, Jeanne and Stuart Altmann traveled through Kenya and Tanzania searching for a baboon study site. They settled on the Maasai-Amboseli Game Reserve (later Amboseli National Park) and conducted a 13-month study that laid the groundwork for much future research. They returned for a short visit in 1969, and came again in July 1971 to establish a research project that has persisted for four decades. In July 1984 Susan Alberts joined the field team, later becoming a graduate student and eventually a director. Over the years, we have tackled research questions ranging from feeding ecology to behavioral endocrinology, from kin recognition to sexual selection, and from aging research to functional genetics. A number of our results have explicitly depended upon the longitudinal nature of the research. Without decades worth of individual-based data we would not have known, for instance, that the presence of fathers influenced the maturation rates of their offspring, that maternal dominance rank had pervasive effects on the physiology of sons, or that the social behavior of a female influenced her infants' survival. Here we summarize the major research themes that have characterized each of the past four decades, and our directions for the future, emphasizing the scientific insights that the longitudinal nature of the study has made possible.

S.C. Alberts
Department of Biology, Duke University, Durham, NC, USA
e-mail: alberts@duke.edu

J. Altmann (✉)
Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA
e-mail: altj@princeton.edu

P.M. Kappeler and D.P. Watts (eds.), *Long-Term Field Studies of Primates*,
DOI 10.1007/978-3-642-22514-7_12,

12.1 Introduction

In 1963, Jeanne and Stuart Altmann took a reconnaissance trip through Kenya and Tanzania, searching for the best site to study baboons, genus *Papio* (Altmann and Altmann 1970). They traveled in a Land Rover with their infant son, Michael, in the back, and they visited six national parks and reserves. One stood out to them as ideal: the Maasai-Amboseli Game Reserve, later Amboseli National Park, in southern Kenya immediately north and west of Mt. Kilimanjaro. The reserve had thousands of baboons, was dominated by an acacia tree woodland interspersed with areas of open grassland, and had a full complement of herbivores and predators. The fever tree woodlands were full of wildlife, visibility was very good (Fig. 12.1), and it was possible to drive through most of the terrain (often a problem in other parks and reserves because of thick vegetation or rocks). In addition, the yellow baboons, *Papio cynocephalus*, that inhabited the reserve neither approached nor fled from humans, as in other areas with high baboon populations. The Altmanns carried out a 13-month study, describing in detail the baboons' demographic structure, social system, ranging patterns, and feeding ecology (Altmann and Altmann 1970). With other studies of wild baboons that were being carried out in this decade, the groundwork was laid for baboons to become one of the best-studied nonhuman primates in the wild (e.g., Hall and DeVore 1965; Kummer 1968; Stoltz and Saayman 1970).

The Altmanns left Kenya in 1964, and stayed away for 5 years. When they returned for a visit in 1969, they encountered a vastly changed landscape in Amboseli, most strikingly characterized by a dramatic decline of the fever tree

Fig. 12.1 Baboons in Amboseli, Kenya. Visibility is very good in the ecosystem, and after four decades of research the animals are well habituated to the presence of neutral human observers. Photo © Susan Alberts

woodlands, a pattern that has continued since then. Several factors probably contributed to this woodland decline, possibly including natural aging of the woodlands, pastoralist grazing patterns and associated burning, rising water table with a concomitant rise in a salt layer in the soil and, increasingly, the impact of an growing elephant population that both kills trees and prevents woodland regeneration (Western and Sindiyo 1972; Struhsaker 1973; Western and van Praet 1973; Western and Maitumo 2004; Western 2007). The Altmanns described "walking around in shock" for the first several days of their return, confirming that the baboon population had decreased dramatically since 1964. They repeatedly re-censused the baboon population beginning in 1969, eventually confirming a drop in population size of more than 90% from the early 1960s (Altmann et al. 1985).

In spite of the changes, Amboseli remained a wonderful place to watch baboons. The baboon population was small, but was stabilizing in spite of the population decline (Altmann et al. 1985), the terrain was manageable, and the visibility was still excellent. In July 1971, the Altmanns and Ph.D. student Glenn Hausfater began observing Alto's Group, which consisted of 35 members, thus establishing a research project that has, against the odds, persisted for 4 decades.

Another study group (Hook's Group) was added to intensive study in 1980 with Michael Pereira's Ph.D. research, roughly doubling the size of the population under study. In 1984, in work led by Amy Samuels and by Phillip Muruthi, then a B.Sc. student at the University of Nairobi, we also began monitoring a social group living near a tourist lodge that subsisted partially on the lodge's refuse. Observations of Lodge Group lasted only 12 years (through 1996), but greatly enriched our understanding of the flexibility of baboon behavior and life history by demonstrating that baboons can substantially accelerate their life histories, growth rates, and reproductive rates when nutritional conditions are good, and can adapt behaviorally and ecologically to a wide range of environmental conditions (e.g., Altmann and Muruthi 1988; Muruthi et al. 1991; Altmann and Alberts 2005).

The subset of the Amboseli baboon population that is under intensive study (hereafter the "study population") currently consists of ~350 extant animals (with life history and behavioral data on an additional ~1,000 that have died) in six social groups. All six current study groups are either fission products of the two original groups (Alto's, which fissioned in 1990–1991, and Hook's, which fissioned in 1995) or are fission products of daughter groups of Alto's (Dotty's Group, which fissioned in 1999, or Nyayo's Group, where a fission is in process in 2011 at this writing; Fig. 12.2 and see also Altmann and Alberts 2003; Van Horn et al. 2007). All members of the study population subsist entirely on wild foods and experience no human management (Lodge Group is no longer a study group; instead, we monitor its demography opportunistically, as we do ~8 other non-study groups in the Amboseli basin).

The Amboseli study population is part of an extensive, continuous baboon population that occupies a large part of eastern Africa. From the perspective of baboons, the Amboseli basin is locally bounded on the west and the north by inhospitable stretches of land, but males move to and from social groups living to the south and to the east of the basin. Thus, the study population experiences gene

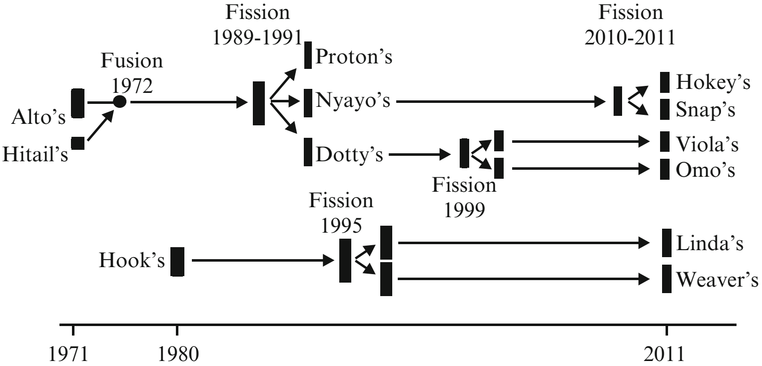

Fig.12.2 Timeline of research on wild-feeding study groups in Amboseli. Research began on Alto's Group in 1971 and on Hook's Group in 1980. Four subsequent natural group fissions produced the 2011 study groups. Proton's Group (one product of Alto's fission) was dropped from the study in 1993 for logistical reasons

flow with the surrounding local population and has a large estimated effective population size (Storz et al. 2002). The baboon population in the Amboseli basin appears to be demographically stable or moderately growing, although it still persists at a level far below that of the early 1960s (Altmann et al. 1985; Samuels and Altmann 1991).

Today the Amboseli Baboon Research Project (ABRP) is a longitudinal, coordinated series of studies of baboons in the Amboseli region with a broad range of research interests. It has supported 23 Ph.D. or M.Sc. theses, including six from Kenyan students, with another six in progress at this writing. We still rely heavily on observational techniques that have changed little since 1971, although we have also employed key technological innovations (some of which are described below) that have enriched the basic behavioral and ecological data enormously. In addition, we have invested heavily in data preservation and accessibility by developing our database, BABASE (see Sect. 12.4). This has allowed us to readily engage in multi-decade and lifespan analyses as well as shorter term cross-sectional studies.

Since the mid 1990s, the longitudinal data collection (demographic, behavioral, and ecological) has depended heavily on our dedicated and highly skilled Kenyan field team. Raphael Mututua began working for the project in 1981 as a field assistant; he developed into an outstanding observer and researcher and now fills the essential role of the project's field manager. His leadership in the field is of the highest quality. Serah Sayialel (beginning in 1989) and Kinyua Warutere (beginning in 1995) fill out our senior Kenyan research team. The project would be unimaginable without them (Fig. 12.3). Several other staff members (Gideon Marinka, Benard Ochieng Oyath, and Longida Siodi) play important roles as field assistants to Mututua, Sayialel, Warutere, and visiting researchers.

Here we summarize some of the major research themes that the Amboseli Baboon Research Project has tackled since its inception. This review is by no means exhaustive; it is not possible to include all of the more than 200 publications

Fig.12.3 Raphael Mututua (*left*), field manager of the Amboseli Baboon Research Project, observing baboons with senior Kenyan team members Serah Sayialel (*center*) and Kinyua Warutere (*right*). Photo © Jeanne Altmann

on the Amboseli baboons here (see a full list of publications on the Amboseli Baboon Research Project website; http://www.princeton.edu/~baboon/). Instead, our goal is to highlight the major themes that have informed, and been informed by, the long-term and longitudinal nature of the study.

12.2 The 1970s: Foundations

Several research projects in the 1970s focused on the question of how the baboons made a living in a semi-arid environment that received only an average of ~350 mm of rain per year. The answer was: "with difficulty". These early studies showed that the baboons spent a large fraction of their time foraging – that is, moving and feeding (e.g., Altmann 1980; Post 1981). Two studies in particular suggested that the nutrition obtained by the baboons during natural foraging was minimally sufficient for growth and reproduction at a rate that would support population replacement. Specifically, Jeanne Altmann showed that mothers spent as much time feeding as they possibly could by the time their infants were 5–6 months of age, and that even when maternal feeding time was at a maximum, maintaining their own body weight would be difficult (Altmann 1980). She inferred that this constraint essentially forced the infants to begin the transition to nutritional independence at this age (Altmann 1980; see also Altmann and Samuels 1992). Further, her calculations indicated that wild baboons were subsisting on a diet that, in captivity, was considered so dangerously inadequate that experimental diets that approximated the Amboseli baboons' diet were discontinued because of health concerns for the animals (Altmann 1980). In a second, concurrent study, Stuart Altmann showed that most infants, during the transition to nutritional independence, fell well below the optimal diet that he predicted they could obtain (Altmann 1991, 1998). Decades after the infant data were collected, he was able to use the life history data that had accumulated on the female infants in his study to show that their nutritional shortfall during infancy predicted, with astonishing accuracy, their future reproductive success; such a result was only possible because of the longitudinal and long-term nature of the study (Altmann 1991, 1998). These studies of feeding ecology were important in setting the stage for future work on this population, because they framed a major component of the underlying ecological problem the baboons had to solve (the other major ecological problem, predation, provides a second, but harder to study, theme that we have not yet investigated thoroughly in Amboseli; see Alexander 1974; van Schaik 1983). Ecology provided the context in which all other aspects of behavior and life history are played out.

A second important foundation laid in the 1970s was behavioral. One of the most obvious features of baboon society, evident to any observer who spends much time watching baboons, is the agonistic interactions that regularly occur between individuals. While many less obvious features of baboon society are equally important, there is no question that the dominance relations that arise out of these agonistic interactions have a profound and pervasive influence on many aspects of baboon life. One of the first studies that the Altmanns and Hausfater carried out was a careful analysis of aggressive and submissive interactions that occurred between individuals, and the subsequent construction of dominance hierarchies based on the direction of “wins” in these interactions.

During his yearlong study, Hausfater and the Altmanns developed the system of assigning dominance ranks in Amboseli that is still used by the research project today (Hausfater 1975). With respect to male mating success, Hausfater found that higher-ranking males enjoyed greater mating success than lower ranking males, but the relationship was not perfect and the highest-ranking male in his study did not experience the highest mating success. Consequently, Hausfater’s study did not provide a definitive answer to the question “what is the importance of high rank for male primates?” This question preoccupied primate researchers for several decades to come (e.g., Strum 1982; Cowlishaw and Dunbar 1991; Kutsukake and Nunn 2006; Port and Kappeler 2010; Alberts in press). However, Hausfater’s study brought to the fore a model of dominance-based priority of access that Stuart Altmann had developed years before during research on rhesus monkeys (Altmann 1962). The priority-of-access model – which posits that dominance rank functions as a queue in which males wait for reproductive opportunities – still provides an important “null model” for how dominance rank works to enhance male reproductive success in multi-male social groups. It has provided measures of the relative importance of dominance rank in male reproductive success in numerous social systems (extending beyond primates), and departures from the predictions of the model have provided important insights about how factors other than dominance rank affect male reproductive success (e.g., Boesch et al. 2006; Kappeler and Port 2008; Ostner et al. 2011; Surbeck et al. 2011).

The 1970s also saw the publication of Jeanne's landmark 1974 paper on behavioral sampling methods (Altmann 1974). The paper provided methodological guidance for behavioral studies of all kinds, and was motivated by a longstanding recognition of the need for data collection methods suited to answering questions through quantitative, model-testing analyses. It was also, to a considerable extent, grounded in Jeanne's experience studying the Amboseli baboons.

By the end of the 1970s, a longitudinal, individual-based perspective had emerged among the Amboseli researchers (especially Jeanne, whose Ph.D. research on mothers and infants had impressed upon her the importance of a life history perspective on behavior). During this time period, the Altmanns and Hausfater formalized many aspects of data collection and wrote the first version of the standardized protocols used by the project, the Monitoring Guide for the Amboseli Baboon Research Project (Altmann and Alberts 2004). The intention was that participating researchers would contribute to the longitudinal data as well as collecting data for their own short-term projects and benefitting from the monitoring data gathered by others in previous years. The current version of the Monitoring Guide (Altmann and Alberts 2004) has this to say about the longitudinal data collection and the manner in which visiting researchers contribute to it:

> *Of the data sets described in this guide, some (i.e., demographic data) have been ongoing since 1971, while others extend back for somewhat shorter periods. Almost all data types that we currently collect extend back to at least 1980. Still other types of data were collected for shorter periods of time and are no longer a focus of our research efforts. Whatever the data set, the value of the data collected at the Project lies in its consistency and in its consistently high quality across time. This guidebook … is meant as a guide for the permanent staff in Amboseli, for short-term visitors to the Project, and for visiting researchers pursuing their own projects (Ph.D. students, post-docs and other collaborators that stay long enough to learn the baboon ID's and contribute to the long-term data). It is absolutely essential that everyone who contributes to the Project's data set collect the data in accordance with the guidelines laid out here. Visiting researchers will collect additional data for their own specific research questions, which will extend beyond the monitoring data described here; these visiting researchers will still contribute to the monitoring data collection that is described in these procedures.*
>
> *When you contribute to the data of the Amboseli Baboon Research Project, you are contributing to a data set that we believe is unique in its time depth, breadth and detail. It is important to us that you take this responsibility very seriously. Never be satisfied with your data collection; always strive for more data of higher quality.*

12.3 The 1980s: Females

When Jeanne Altmann began her landmark study on the ecology of motherhood and infancy in the mid-1970s, the topics of motherhood, and of female behavior in general, were not seen as a particularly important focus for the primate studies that were emerging at the time. Although infant development and maternal care were intensively studied among developmental psychologists in laboratory settings and a few initial descriptions were made in field studies, the questions posed were primarily about social and cognitive growth, with a view to understanding human development. However, change was in the air, and a number of scientists studying wild primates were beginning to pose important questions about females and their infants (e.g., Jay 1963; Hrdy 1977; Seyfarth 1977; Pusey 1978; Fossey 1979).

Jeanne's study of baboon mothers and infants in Amboseli (Altmann 1980) emphasized an evolutionary perspective on behavior and highlighted how important the evolutionary ecology of motherhood and infancy are for understanding a species' behavior and ecology. It also highlighted the importance of ecological constraints on social behavior, a topic of growing interest throughout the 1970s (e.g., Crook and Gartlan 1966; Clutton-Brock and Harvey 1977; Emlen and Oring 1977). In addition, the study was grounded in the notion, unusual at the time but now widespread in studies of evolutionary ecology, that viewing behavior in the context of life history is important, in particular for understanding how the things an animal does today are both shaped by and shape its reproductive and social trajectory.

Female dominance rank also came under scrutiny in Amboseli in the 1980s. Although the importance of female dominance rank for reproductive success was not yet fully understood, evidence of its importance for females of many primate species had begun to accumulate (reviewed in Silk 1987). Baboon females, like many cercopithecine primate females, typically attain a social dominance rank just below that of their mothers, with the help of both kin and unrelated females (Walters 1987). This phenomenon had been known for some time in cercopithecines (reviewed in Melnick and Pearl 1987); the Amboseli study revealed that its consequence was cross-generational, long-term consistency of dominance rank relationships in wild populations. Further, the Amboseli work identified this long-term consistency of female dominance ranks as the most important source of stability in baboon social structure, a phenomenon generalizable to other species with maternal rank inheritance (Hausfater et al. 1982).

Some years later, however, the accumulating longitudinal data provided an even richer picture of female dominance relationships, revealing that long periods of stability could be punctuated by short periods of rapid change when some matrilines permanently fell and other permanently rose in rank (Samuels et al. 1987). Indeed, some females, by targeting higher-ranking females, were able to raise the ranks of all their female family members, while in other cases entire matrilines fell in rank, and occasionally matrilines split, with one female maintaining a higher rank than the rest of her family (Samuels et al. 1987).

Research on female social relationships and maternal behavior has remained a major theme in Amboseli through the years (Silk et al. 2003, 2004, 2006a, b; Van Horn et al. 2007; Gesquiere et al. 2008; Nguyen et al. 2008, 2009). A major step forward in understanding the strong and complex social relationships of female baboons came in 2003, when we discovered, with collaborator Joan Silk, that strong affiliative relationships have direct adaptive value for females: infants of more socially integrated females experienced higher survival than infants of more socially isolated females (Fig. 12.4; Silk et al. 2003). The effect of social integration on infant survival was later replicated in the long-term study of a chacma baboon

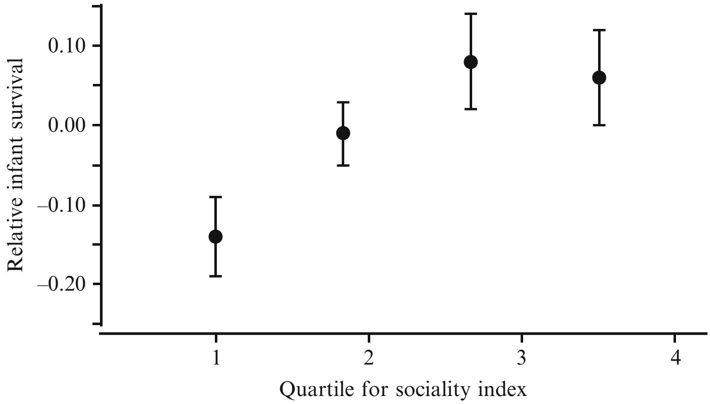

Fig.12.4 Females that were more socially integrated (females in the upper quartiles of a composite sociality index) experienced higher survival of their infants. Redrawn from Silk et al. (2003)

group in the Okavango Delta in Botswana (Silk et al. 2009), and those authors went on to demonstrate that social bonds enhanced the survival of the females themselves, not just of their infants (Silk et al. 2010). Again, without longitudinal data, these discoveries would have remained beyond our reach.

12.4 The 1990s: Males

After the first study on male dominance rank and mating behavior in the 1970s (Hausfater 1975) male social behavior took a decided back seat to female social behavior and ecological questions in the research priorities of the Amboseli team. Michael Pereira's work on the social behavior of juvenile males and females was an exception; he examined juvenile behavior in the context of the life history, and found sex differences in behavior that could be explained by the different demands made on males and females as adults (Pereira 1988a, b, 1989). Nonetheless, male social behavior was not intensively studied in Amboseli during this period, partly because of the rich vein of research on female behavior that had been tapped, and partly because some of the most interesting behavioral questions on adult males required more life history information and longitudinal data than were available in the 1970s and early 1980s.

Ronald Noë and Betty Sluijter were the first to study social behavior of adult males in Amboseli after Hausfater (Noë 1986, 1992; Noë and Sluijter 1990, 1995). They also brought a life history perspective to the study of males, in the now-growing tradition of Amboseli research, and showed that over the course of adulthood, males changed their levels of investment from an emphasis on direct male–male competition in young adulthood to a greater investment in relationships with adult females and juveniles in middle age (Noë and Sluijter 1990). These changes were associated with changes in male dominance rank, and as we amassed

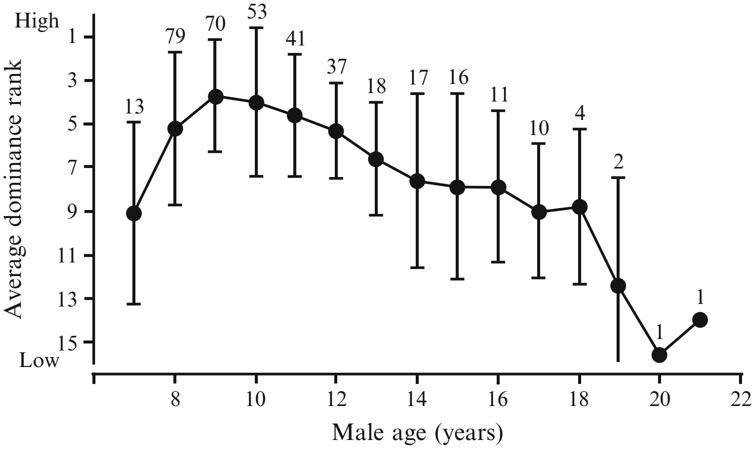

Fig.12.5 Male baboons reach their highest dominance rank in early adulthood when they are in their physical prime, and then steadily fall in rank as they age. Points show the mean (±SD) dominance rank for males in each age class, considering only males born into Amboseli study groups (i.e., males of known age); numbers above the error bars represent the number of males that contributed to the value for that age class. See also Alberts et al. (2003)

longitudinal data on known-aged individuals, it became clear how strongly age-based they were, with dominance rank peaking in young adulthood and declining steadily throughout the rest of life in a pattern very different from the relative stability of female dominance ranks (Fig. 12.5; see also Packer et al. 2000; Alberts et al. 2003).

By the late 1980s, male life history data had accumulated sufficiently for Susan Alberts to take male maturation and dispersal as the theme of her Ph.D. research. Dispersal represents an intense physical challenge at the onset of male adulthood, requiring that males leave the groups into which they were born and move into groups in which they have no prior relationships; in those groups, they must establish social relationships and obtain reproductive opportunities. Susan found that during maturation, males were subject to constraints of their mothers' dominance ranks, just as their sisters were (Alberts and Altmann 1995a). Male baboons, like most male primates, are independent of their mothers well before puberty (for an interesting primate exception to this rule see Surbeck et al. 2011); also, subadult male baboons are much larger than females and do not receive assistance from females in attaining or maintaining their dominance ranks. Indeed, analyses from another baboon population indicate that maternal dominance rank has no impact on the eventual dominance rank that sons attain (Packer et al. 2000). For these reasons, the dependence of male maturation on maternal dominance rank was surprising. However, this finding was supported by a later analysis of growth rates, which demonstrated an impact of maternal rank on growth rates for both sons and daughters (Altmann and Alberts 2005) and echoed similar findings in a few other primate species (e.g., Paul et al. 1992; Bercovitch et al. 2000; van Noordwijk and van Schaik 2001). In Amboseli, it presaged an even more profound effect of maternal dominance rank on male physiology at the onset of adulthood (Onyango et al. 2008; see Sect. 12.5).

Susan's analyses of dispersal revealed that males often spent time alone during dispersal while searching for other groups to join, and consequently both experienced elevated mortality risks (from 3 to 10 times higher than the mortality risk for males living in groups) and missed mating opportunities. However, males also appeared to experience reproductive costs if they remained in their natal group: although the sample size was small and based on observational rather than genetic estimates of paternity, the available data suggested high mortality of offspring for whom the natal males were likely fathers (Alberts and Altmann 1995b). This occurred in spite of strong evidence for close inbreeding avoidance between mothers and sons, and between maternal siblings. Finally, Susan's analysis indicated that natal males undergoing their first dispersal, and older males undergoing secondary dispersal, dispersed in response to the availability of females and to their own mating success in a given group (Alberts and Altmann 1995b; see also Altmann 2000).

By the end of the 1990s, substantial life history and behavioral data had accumulated for both males and females, and the groundwork had been laid for integrative studies of both sexes. In addition, we had begun to employ digital data loggers for collecting focal animal samples and hand-held GPS devices for collecting locational data. Among the most important advances of the 1990s was the development of BABASE, our longitudinal, individual-based database (Pinc et al. 2009). Field data are returned to the US either weekly (for digital data collected with hand-held data loggers and GPS machines) or monthly (for paper data) and are incorporated into BABASE in twice-yearly updates. BABASE is a web-based, PostgreSQL database that now houses most of our field data, including demographic, reproductive, behavioral, locational, ecological, and meteorological data. It is continually growing as we incorporate additional data sets into the original database design. These developments set the stage for the next important phase of the research, which involved getting "under the skin" with genetic and endocrine research.

12.5 The 2000s: Under the skin

In the late 1980s and early 1990s, two methodological developments occurred in genetics and physiology that had an enormous impact on primate field research, including the Amboseli baboon project. These were the development of a technique to extract DNA from feces (e.g., Höss et al. 1992; Gerloff et al. 1995) and the development of a technique to extract metabolites of steroid hormones from feces (e.g., Wasser et al. 1988). For the first time, we could study physiological responses and patterns of genetic relatedness – especially paternity – without invasive methods. This enabled us to pursue questions that were simply impossible to approach using naturalistic behavior observations alone. It would be 5–10 years after the first development of these techniques before they were perfected and applied to the Amboseli study (e.g., Khan et al. 2002; Buchan et al. 2003, 2005; Lynch et al. 2003), but once these techniques were established (with genetics analysis taking place in Susan's lab and hormonal analysis in Jeanne's), they transformed our understanding of baboon behavior and ecology (similar advances were being made in other primate field studies; e.g., Ziegler et al. 1997; Borries et al. 1999; Launhardt et al. 2001).

12.5.1 Hormones

Our hormone data have revealed several interesting surprises. In an analysis that combined endocrine data with data on male mating behavior and female reproductive states, we found that alpha males, but not males of other ranks, differentiated conceptive from non-conceptive cycles in their mate guarding (consortship) behavior, and that both the size of the sexual swelling and levels of circulating estrogen in the females provided potential cues about female fecundability (Gesquiere et al. 2007). This endocrine work nicely complemented the fecal DNA-based paternity analysis, which also revealed evidence of male mate choice (see Sect. 12.5.2 and Alberts et al. 2006).

In a study of pregnant females, we found evidence of a hormonal signature of impending fetal losses among pregnant females. This signature was evident for up to 2 months before the loss itself occurred (losses occurred in 91 of 656 pregnancies), ~14% (Beehner et al. 2006). In an additional instance of longitudinal data use, we discovered that maturing males whose mothers had been low-ranking when the males were born had higher fecal glucocorticoid levels than males whose mothers had been high-ranking, even when the glucocorticoid levels were measured 6–8 years after the males' births, years after males were independent of their mothers and in many cases years after the mothers had died (Fig. 12.6; Onyango

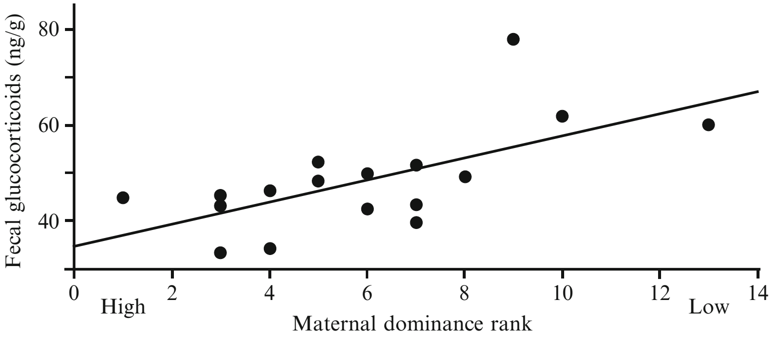

Fig.12.6 Subadult males born to higher ranking mothers had lower levels of fecal glucocorticoids than males born to lower ranking mothers, even when the fecal glucocorticoids were measured years after the period of offspring dependence on the mother. $R^2 = 0.421$, $P = 0.005$. Redrawn from Onyango et al. (2008)

et al. 2008). Glucocorticoids are products of the hypothalamic-pituitary axis (HPA) and are important in regulating the stress response and in mobilizing metabolic activity (Nelson 2005); our results indicated a long-term effect of maternal dominance rank on offspring physiology. Fecal glucocorticoid levels also predicted the peri-parturitional behavior of new mothers (specifically their responsiveness to their new infants), confirming findings that had previously only been documented in captive animals (Nguyen et al. 2008). Finally, we identified physiological effects of Amboseli's harsh dry seasons on both adult males and adult females (Gesquiere et al. 2008, 2011).

Most recently, we identified a surprising relationship between male dominance rank and endocrine profiles (Fig. 12.7; Gesquiere et al. in press). While fecal testosterone (fT) levels declined as a function of dominance rank (with high-ranking males having the highest fT and low-ranking males the lowest), fecal glucocorticoids (fGC) presented a different and unexpected relationship with male dominance rank. Alpha males exhibited the highest fGC levels, and beta

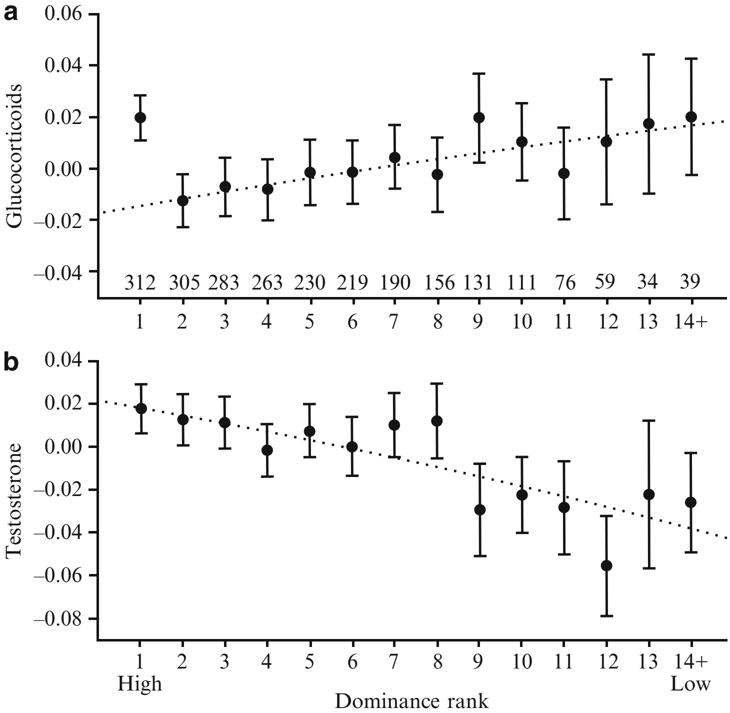

Fig.12.7 Highest ranking (alpha) males had very high glucocorticoids, much higher than second-ranking males and a striking departure from the pattern for glucocorticoids to increase (**a**) and testosterone to decrease (**b**) as dominance rank declined. Values (mean ± SE across male monthly averages) represent the residuals obtained from a statistical model of log-transformed hormone concentrations that accounted for age, environmental factors, and hierarchy stability as fixed factors, male identity as a random factor. After Gesquiere et al. (in press)

(second-ranking) males exhibited the lowest fGC levels, with a monotonic increase in fGC below rank 2. This striking difference between alpha and beta males has not been described before, possibly because researchers often group these males together as "high ranking males." Moreover, despite predictions in the literature that alpha males should experience elevated glucocorticoids only when the dominance hierarchy is unstable, we found no effect of hierarchy stability on the relative endocrine levels of alpha and beta males although overall levels of stress hormones were higher during instability. Thus, regardless of how stable male rank relationships are, being at the very top of a social hierarchy may be more stressful than being immediately below, probably because of energetic costs associated with mating and with male–male competitive interactions (Gesquiere et al. in press).

12.5.2 Paternity

The first problem we tackled using DNA extracted from feces was the problem of paternity and its impact on social relationships. The question of whether male dominance rank mattered for male reproductive success had been a vexing one for decades; different primate studies produced different answers to this question and a resolution to the contradictions was slow to emerge (see reviews in Kutsukake and Nunn 2006; Port and Kappeler 2010; Alberts in press). Using 32 group-years of behavioral data on mating success in Amboseli, we had shown that the apparent contradictions across different studies were probably explained by real variance in the importance of male dominance rank over time for many if not most primates (Fig. 12.8; see also Strum 1982 for an early prediction of this sort). Both male

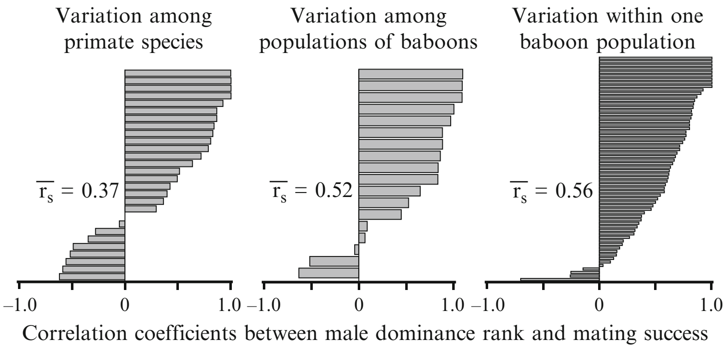

Fig.12.8 The relationship between male dominance rank and mating success shows similar variance at all levels of analysis; among primate species (*left panel*, data from Cowlishaw and Dunbar 1991), among populations of a single species, baboons (*center panel*, data from Bulger 1993), and within a single population of baboons, Amboseli (*right panel*, data from Alberts et al. 2003). Each graph shows the rank-ordered distribution of Spearman correlation coefficients for the relationship between male rank and mating success across studies (*left and center panels*) or across time periods in Amboseli (*right panel*). Redrawn from Altmann and Alberts (2003)

density and the distribution of male competitive abilities within groups affected the relationship between male dominance rank and mating success in Amboseli (Alberts et al. 2003; see also Cowlishaw and Dunbar 1991, Kutsukake and Nunn 2006; Port and Kappeler 2010).

However, an important question remained: what would the data look like if we were able to measure reproductive success using actual paternity data instead of just mating success? Our first paternity analysis, focusing on Lodge Group (the food-supplemented group that we studied from 1984 to 1996) and using DNA extracted from blood obtained during a darting project (see Sect. 12.6.4), had indicated that genetic paternity results were nicely predicted from behavioral data (Altmann et al. 1996). Would the same hold true in the wild-feeding groups? Using fecal DNA, we assigned paternity to 208 offspring conceived across a range of demographic conditions in wild-feeding groups. We found that male reproductive success, like mating success, depended on dominance rank but in a density-dependent manner and also depended on relative male competitive ability. In addition, we found little evidence for successful surreptitious mating (although subadult males occasionally produced offspring using this strategy), and no evidence for differential sperm success or sperm depletion. Most strikingly, we found clear evidence that alpha males fathered more offspring than expected based on their mating behavior, and that this excess of offspring resulted from male mate choice for female experiencing conceptive rather than non-conceptive cycles (Alberts et al. 2006). These results supported behavioral evidence of male mate choice in other baboons (Bulger 1993; Weingrill et al. 2003) and complemented our work on male mate choice based on female endocrine profiles and sexual swellings (Gesquiere et al. 2007).

The most surprising result from our paternity analyses was the discovery that male baboons differentiated their own offspring from the offspring of other males, and supported them disproportionately during agonistic interactions (Buchan et al. 2003). A number of previous researchers had hypothesized that paternal care occurred in baboons, and some had provided strong circumstantial evidence for its occurrence (Ransom and Ransom 1971; Altmann 1980; Stein 1984; Palombit et al. 1997). In addition to our confirmation of paternal care in baboons, we later discovered that offspring who resided with their fathers longer during their juvenile periods reached maturity earlier than offspring whose fathers dispersed or died earlier in their juvenile periods (Charpentier et al. 2008a). Neither of these results on paternal effects would have been discovered without longitudinal data; the implication was that paternal presence had an impact not only on the juvenile's daily interactions, but on an important life history component (see Altmann et al. 1988; Altmann and Alberts 2003 for data on the importance of age at maturity in this population). However, much remains to be done before we fully understand male–juvenile interactions in multi-male primate species. Some care by male baboons cannot be explained as paternal investment (Smuts 1985; Buchan et al. 2003; Moscovice et al. 2009; Nguyen et al. 2009), raising the possibility that males are engaged in mating effort when they care for young (incentivizing future mating with the mother; e.g., Smuts 1985; van Schaik and Paul 1996). Furthermore, the extent of paternal care in most other multi-male primate species remains an open question, with few data either refuting or confirming its occurrence (but see Paul et al. 1996; Ménard et al. 2001; Lehmann et al. 2006; Wroblewski 2010).

The paternal care that male baboons provide had an important corollary in our research; female baboons differentiated paternal sisters from non-kin, and formed preferential relationships with them (Smith et al. 2003; Silk et al. 2006a), supporting Jeanne's early predictions about paternal kin selection in primate groups (Altmann 1979). These relationships between paternal sisters were typically not as strong as relationships between maternal sisters, but were measurably stronger than relationships among non-kin, and sometimes played a role in patterns of permanent group fission (Van Horn et al. 2007). Significant relationships between paternal sisters were first documented in rhesus macaques (Widdig et al. 2001), suggesting that paternal kin networks may be a robust phenomenon in many primates (see, e.g., Watts 1997 for data on relationships among paternal siblings in gorillas, but see Langergraber et al. 2007 for different results in chimpanzees). The genesis of relationships between paternal sisters in baboons remains obscure, and fathers may well play a role in establishing them when they provide care to their offspring.

12.6 2010 Forward: New directions

At the start of this decade our energy and interest will be focused on four areas involving major new collaborations with Elizabeth Archie and Jenny Tung. These areas are aging, disease transmission, hybridization, and functional genetics and genomics. These investigations expand the multidisciplinary nature of our program in ways that explicitly allow us to capitalize on the longitudinal, long-term nature of our study.

12.6.1 Aging

With 40 years of demographic, behavioral, and ecological data accumulated, we are in a position to examine not only mortality patterns, but also behavioral and health correlates of aging that contribute to mortality; this represents a long-time goal that is finally within sight. To our knowledge, the work we have recently initiated is the first systematic study of how health and behavior change with age in a natural primate population, and of whether genetic and social predictors of these changes can explain individual differences in survival and longevity. Sex differences in health and survival during aging are major topics of interest in medicine, epidemiology, demography, and evolutionary biology. Despite this pervasive interest, and despite a wealth of data on aging in humans and a few well-studied model organisms, patterns of aging in wild animals remain largely undescribed. Not only are there large gaps in our knowledge of age-related changes in survival in wild animals, but virtually nothing is known about age-related changes in physiology, behavior, or other aspects of health and functioning for animals in the wild (Brunet-Rossinni and Austad 2006). We argue that studies of aging in wild animal populations, especially in our primate relatives, can provide a comparative perspective on human aging (Bronikowski et al. 2011), generate new questions, produce insights into the answers to old ones, and identify opportunities for alleviating the adverse consequences of aging. The longitudinal nature of our data will allow us to analyze not only declines in survival with age (demographic senescence; Bronikowski et al. 2002, 2011) but to produce a systematic description of how multiple indicators of health and functioning ability change with age in a wild primate (e.g., Altmann et al. 2010; Galbany et al. 2010, 2011).

12.6.2 Disease Transmission

Biologists currently have a poor empirical understanding of how infectious agents spread within and between social groups of wild animals, because of the logistical challenges of directly tracking the movements of infectious agents in the wild. Our parasite research, led by Elizabeth Archie, is designed to map the movements of common infectious agents onto the social landscape of the Amboseli baboons, using tools from social network analysis and population genetics.

One of our key hypotheses involves whether the transmission of nematodes or bacteria is socially structured at the level of social groups (i.e., whether baboons are most likely to be infected by group members for some or all parasites), a rarely tested but critical assumption of most research on the disease-related costs of group living (Altizer et al. 2003; Nunn and Altizer 2006). We will also test whether social networks predict the movements of infectious organisms within social group, and whether and how infection risk varies among individuals. Finally, we will examine the ecological correlates of between-group parasite transmission. This research will employ fecal samples that were collected during the past 15 years, as well as new samples, to provide a unique longitudinal perspective on parasite transmission in this population.

The result will be a picture of how different infectious agents, with a variety of transmission modes and fitness effects, move between and within social groups. This in turn will enhance our ability to understand individual differences in the risk of infection in more detail than has been possible before in natural primate populations. Socially structured disease transmission has important implications for understanding the evolution of sociality – a basic feature of our primate lineage – because exposure to disease is thought to be a major evolutionary cost of group-living (Alexander 1974; Altizer et al. 2003). Also, current models of disease transmission tend to be highly sensitive to variation in transmission patterns; hence, to predict the dynamics of an epidemic in social wildlife, biologists need accurate information on how disease spreads in natural populations of social animals.

12.6.3 Hybridization

The Amboseli baboon population comprises primarily yellow baboons (*P. cynocephalus*), specifically the "ibean" morphotype of yellow baboons. This morphotype shares some morphological similarities with anubis (olive) baboons, possibly because of anubis admixture in the ibean lineage over the course of evolutionary history (Jolly 1993). Further, Amboseli is situated on the boundary between the ranges of yellow and anubis baboons, with yellow baboons to the south and east and anubis baboons to the north and west (Jolly 1993; Kingdon 1997; Newman et al. 2004). Six anubis males have immigrated into Amboseli study groups over the course of the study, and one small (ca. 18) mixed-sex group of anubis baboons also entered the basin in the early 1980s (Samuels and Altmann 1986; Tung et al. 2008). Hybrids now occur both in study and non-study groups in Amboseli, resulting both from the anubis immigrations we have detected (and probably other, undetected anubis immigrants into non-study groups) and from the movement of hybrid males between study and non-study groups and successful reproduction by these males. In Amboseli, as in all baboon hybrid zones studied thus far, mating occurs freely and results in viable and fertile offspring; little or no evidence of hybrid dysgenesis has been found (reviewed in Tung et al. 2008).

Strikingly, in Amboseli, both males and females with a higher proportion of genetic admixture from anubis baboons (measured via a genetic "hybrid score"; see (Tung et al. 2008)) reached physical maturity earlier than animals with a yellow baboon genetic background (another result that depended on longitudinal data). Males showed a particularly pronounced effect of admixture, especially for age at natal dispersal (Fig. 12.9; Charpentier et al. 2008b). We are now poised to examine

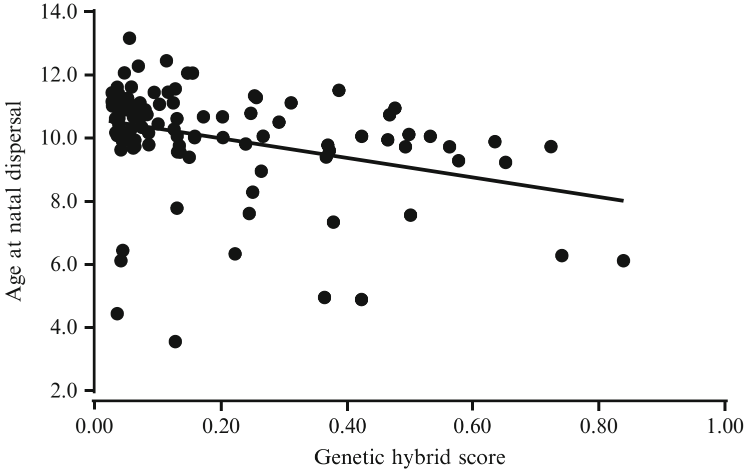

Fig.12.9 Male baboons in Amboseli with higher genetic hybrid scores (more anubis ancestry) are likely to disperse at a younger age than males with lower genetic hybrid scores (less anubis ancestry). $R^2 = 0.216$, $P < 0.0001$. After Charpentier et al. (2008a, b)

the consequences of hybridization further, considering both life history traits and behavioral traits that are associated with life history (specifically dominance, mating, and dispersal) as a function of hybridity.

12.6.4 Functional Genetics and Genomics

By combining the detailed behavioral and ecological data available for the Amboseli baboons with genetic and genomic research, we have the opportunity to place genetic inferences in the context of a well-understood natural primate system. Indeed, we have argued that as genomic resources for primate species accumulate, natural populations of primates should increasingly be targets of research on evolutionary and functional genetics and genomics because they offer the prospect of identifying functional genetic variation that influences traits of known ecological and adaptive significance (Tung et al. 2010). While work on captive populations can identify genetic systems of suspected significance, only field studies can confirm whether and how the systems in question are variable or relevant in nature (e.g., Keele et al. 2009; Tung et al. 2009); this in turn can have important implications for understanding both primate and human evolution.

In 1989, we learned from Robert Sapolsky how to temporarily anesthetize and immobilize baboons for drawing blood and taking morphometric measurements. We employed the technique at the time for both endocrine and genetic analyses, darting ~150 animals in a 3-year period (e.g., Sapolsky and Altmann 1991; Altmann et al. 1996; Sapolsky et al. 1997). We have continued to employ this technique occasionally over the years to affix radio collars to single females in each group. Beginning in 2006, we resumed a more extensive darting effort in order to obtain high quality DNA and RNA samples for as many adults as we could in the population. Because our research depends heavily on not affecting the behavior, health, survival, or reproductive success of the study animals, we have invested considerable effort in our time- and labor-intensive approach, which is focused on safety and on maintaining habituation in our study animals.

We dart individual baboons, one at a time, with an anesthetic-bearing dart, using a hand-held blowpipe. We dart no more than two animals per day, and no study group is darted more than once per week. On the day of a planned darting, the target animal (an adult male or an adult female that is not carrying a dependent infant and not past early pregnancy) is followed, often for many hours, until an appropriate opportunity arises. This occurs when the air is still, when neither the target animal nor other baboons will witness the darting, and when the animal is seated, standing still, or walking slowly. After the animal is darted and falls asleep (within 3–10 min), we wait for the other group members to move on (only rarely do other group members take any interest in the sleeping individual) and then quickly pick up the sleeping animal and move it to a shady processing site. We weigh the animal, carry out various other body measurements, and collect blood and skin samples in DNA- and RNA-preserving buffers. After the protocol is complete, the animal is allowed to recover in a holding cage in the back of our pickup truck until fully awake (after 3–4 h), when it is released at some distance from its social group but within sight. We have darted over 100 animals since 2006 in this manner, with no injuries and no untoward incidents. Blood and tissue samples remain in Amboseli for up to 48 h in an evaporatively-cooled hut before we send them to Nairobi (via air) for temporary freezing, and then transport them to the US (Tung et al. 2011).

Our functional genetics and genomics research, which uses the blood and skin samples that we collect during darting, has already begun to bear fruit even though it is in its early stages. For instance, in research led by Jenny Tung we identified variation in the *cis*-regulatory region of the baboon *FY* (Duffy) gene that was associated with variation in susceptibility to *Hepatocystis*, a malaria-like pathogen common in baboons (Tung et al. 2009). We also found evidence, in several genes involved in immunity, of allele-specific gene expression patterns (i.e., cases in which segregating genetic variants cause differences in the levels of expression of particular genes), and in one of these genes (*CCL5*) we identified an influence of maternal dominance rank on the extent to which a given *cis*-regulatory variant affected gene expression (Tung et al. 2011). Much of our effort in functional genetic analyses going forward is focused on early life effects on adult gene expression patterns.

12.7 Conclusions

The Amboseli Baboon Research Project, like the other long-term primate studies described in this volume, represents a labor of love. The researchers who have worked on the Amboseli project, particularly its directors, have made enormous personal sacrifices to keep the project going over the long term. Funding for the project has invariably come in grants of short duration, typically 2–3 years but occasionally, when we have been very lucky, 5 years. We have no NGO or endowment, and the intellectual growth of the project depends on us being able to convince grant reviewers that we really do have something new to study every few years (we have fielded questions of the sort “haven’t you studied this species enough yet? Couldn’t this be done more cheaply on captive rodents?”; other authors in this volume have surely had similar experiences). Yet, as Clutton-Brock and Sheldon (2010) have noted, long-term studies of primates and other animals offer our best opportunity for novel and innovative research on behavioral ecology. Our study provides ample evidence of this. The novel maternal and paternal effects we have described, our evidence for the functional importance of female social relationships, the patterns of continuity and change in dominance ranks that we have documented for both sexes and their implications for lifetime fitness, and a range of other results described here, have helped to shape current research in evolutionary ecology in ways that simply would not have been possible for a comparably long series of independent short-term studies. The same is true for the other longitudinal studies described in this volume. And, as we have argued elsewhere, longitudinal studies also offer our best opportunity for understanding the evolution of important traits by combining genetic, phenotypic, and environmental data on the same individuals (Tung et al. 2010). Surely, a challenge for the twenty-first century involves raising the profile of long-term primate studies and ushering in an era in which the value of such studies, as evidenced by the chapters in this volume, are more widely acknowledged.

Acknowledgments We gratefully acknowledge the National Science Foundation for generous support over the years, most recently through DEB 0846286 and DEB 0919200 to S.C. Alberts, DEB 0846532 to J. Altmann, and IOS 1053461 to E. Archie. We are also very grateful for support from the National Institute of Aging (R01AG034513-01 and P01AG031719). We also thank the Princeton Center for the Demography of Aging (funded through P30AG024361), the Chicago Zoological Society, the Max Planck Institute for Demographic Research, the L.S.B. Leakey Foundation and the National Geographic Society for support at various times over the years.

We thank the Kenya Wildlife Services, Institute of Primate Research, National Museums of Kenya, and members of the Amboseli-Longido pastoralist communities for their cooperation and assistance in Kenya. A number of people, too numerous to list here, have contributed to the long-term data collection over the years, and we are grateful to all of them for their dedication and contributions. Particular thanks go to Stuart Altmann, the late Amy Samuels, and the Amboseli Baboon Project long-term field team (Raphael S. Mututua, Serah N. Sayialel, and J. Kinyua Warutere), as well as to Vera Somen and Tim Wango for their untiring assistance in Nairobi.

Karl Pinc has provided expertise in database design and management for many years and we are grateful for his seminal contributions to the development of BABASE. We also thank the database technicians who have provided assistance with BABASE over the years, most recently D. Onderdonk, C. Markham, T. Fenn, N. Learn, and L. Maryott. Our Amboseli research is approved by the IACUC at Princeton University and at Duke University and has adhered to all the laws and guidelines of Kenya.

References

Alberts SC (in press) Magnitude and sources of variation in male reproductive performance. In: Mitani J, Call J, Kappeler PM, Palombit R, Silk JB (eds) The evolution of primate societies. University of Chicago Press, Chicago

Alberts SC, Altmann J (1995a) Preparation and activation: determinants of age at reproductive maturity in male baboons. Behav Ecol Sociobiol 36:397–406

Alberts SC, Altmann J (1995b) Balancing costs and opportunities: dispersal in male baboons. Am Nat 145:279–306

Alberts SC, Watts HE, Altmann J (2003) Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. Anim Behav 65:821–840

Alberts SC, Buchan JC, Altmann J (2006) Sexual selection in wild baboons: from mating opportunities to paternity success. Anim Behav 72:1177–1196

Alexander RD (1974) The evolution of social behavior. Annu Rev Ecol Syst 5:325–383

Altizer S, Nunn CL, Thrall PH, Gittleman JL, Antonovics J, Cunningham AA, Dobson AP, Ezenwa V, Jones KE, Pedersen AB, Poss M, Pulliam JRC (2003) Social organization and parasite risk in mammals: integrating theory and empirical studies. Annu Rev Ecol Syst 34:517–547

Altmann SA (1962) A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. Ann NY Acad Sci 102:338–435

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–266

Altmann J (1979) Age cohorts as paternal sibships. Behav Ecol Sociobiol 6:161–164

Altmann J (1980) Baboon mothers and infants. Harvard University Press, Cambridge, MA

Altmann SA (1991) Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. Proc Natl Acad Sci USA 88:420–423

Altmann SA (1998) Foraging for survival: yearling baboons in Africa. University of Chicago Press, Chicago

Altmann J (2000) Models of outcome and process: predicting the number of males in primate groups. In: Kappeler PM (ed) Primate males: causes and consequences of variation in group composition. Cambridge University Press, Cambridge, pp 236–247

Altmann J, Alberts SC (2003) Intraspecific variability in fertility and offspring survival in a nonhuman primate: behavioral control of ecological and social sources. In: Wachter KW, Bulatao RA (eds) Offspring: human fertility behavior in biodemographic perspective. National Academies Press, Washington, DC, pp 140–169

Altmann J, Alberts SC (2004) Monitoring guide for the Amboseli baboon research project: protocols for long-term monitoring and data collection. http://www.princeton.edu/~baboon/monitoring_guide.htm

Altmann J, Alberts SC (2005) Growth rates in a wild primate population: ecological influences and maternal effects. Behav Ecol Sociobiol 57:490–501

Altmann SA, Altmann J (1970) Baboon ecology: African field research. University of Chicago Press, Chicago

Altmann J, Muruthi P (1988) Differences in daily life between semiprovisioned and wild-feeding baboons. Am J Primatol 15:213–221

Altmann J, Samuels A (1992) Costs of maternal care: infant carrying in baboons. Behav Ecol Sociobiol 29:391–398

Altmann J, Hausfater G, Altmann SA (1985) Demography of Amboseli baboons, 1963-1983. Am J Primatol 8:113–125

Altmann J, Altmann SA, Hausfater G (1988) Determinants of reproductive success in savannah baboons, *Papio cynocephalus*. In: Clutton-Brock TH (ed) Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, pp 403–418

Altmann J, Alberts SC, Haines SA, Dubach J, Muruthi P, Coote T, Geffen E, Cheesman DJ, Mututua RS, Saiyalel SN, Wayne RK, Lacy RC, Bruford MW (1996) Behavior predicts genetic structure in a wild primate group. Proc Natl Acad Sci USA 93:5797–5801

Altmann J, Gesquiere L, Galbany J, Onyango PO, Alberts SC (2010) Life history context of reproductive aging in a wild primate model. Ann NY Acad Sci 1204:27–138

Beehner JC, Nguyen N, Wango EO, Alberts SC, Altmann J (2006) The endocrinology of pregnancy and fetal loss in wild baboons. Horm Behav 49:688–699

Bercovitch FB, Widdig A, Nürnberg P (2000) Maternal investment in rhesus macaques (*Macaca mulatta*): reproductive costs and consequences of raising sons. Behav Ecol Sociobiol 48:1–11

Boesch C, Kohou G, Néné H, Vigilant L (2006) Male competition and paternity in wild chimpanzees of the Taï forest. Am J Phys Anthropol 130:103–115

Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P (1999) DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. Proc R Soc Lond B 266:901–904

Bronikowski AM, Alberts SC, Altmann J, Packer C, Carey KD, Tatar M (2002) The aging baboon: comparative demography in a non-human primate. Proc Natl Acad Sci USA 99:9591–9595

Bronikowski AM, Altmann J, Brockman DK, Cords M, Fedigan LM, Pusey AE, Stoinski T, Morris WF, Strier KB, Alberts SC (2011) Aging in the natural world: comparative data reveal similar mortality patterns across primates. Science 331:1325–1328

Brunet-Rossinni AK, Austad SN (2006) Senescence in wild populations of mammals and birds. In: Masoro EJ, Austad SN (eds) Handbook of the biology of aging. Elsevier, Amsterdam, pp 243–266

Buchan JC, Alberts SC, Silk JB, Altmann J (2003) True paternal care in a multi-male primate society. Nature 425:179–181

Buchan JC, Archie EA, Van Horn RC, Moss CJ, Alberts SC (2005) Locus effects and sources of error in noninvasive genotyping. Mol Ecol Notes 5:680–683

Bulger JB (1993) Dominance rank and access to estrous females in male savanna baboons. Behaviour 127:67–103

Charpentier MJE, Van Horn RC, Altmann J, Alberts SC (2008a) Paternal effects on offspring fitness in a multimale primate society. Proc Natl Acad Sci USA 105:1988–1992

Charpentier MJE, Tung J, Altmann J, Alberts SC (2008b) Age at maturity in wild baboons: genetic, environmental and demographic influences. Mol Ecol 17:2026–2040

Clutton-Brock TH, Harvey PH (1977) Primate ecology and social organization. J Zool Lond 183:1–39

Clutton-Brock TH, Sheldon BC (2010) The seven ages of *Pan*. Science 327:1207–1208

Cowlishaw G, Dunbar RIM (1991) Dominance rank and mating success in male primates. Anim Behav 41:1045–1056

Crook JH, Gartlan JS (1966) Evolution of primate societies. Nature 210:1200–1203

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223

Fossey D (1979) Development of the mountain gorilla (*Gorilla gorilla beringei*): the first thirty-six months. In: Hamburg DA, McCown E (eds) Perspectives on human evolution, vol 5, The great apes. Benjamin, Cummings, Menlo Park, CA, pp 139–184

Galbany J, Dotras L, Alberts SC, Pérez-Pérez A (2010) Tooth size variation related to age in Amboseli baboons. Folia Primatol 81:348–359

Galbany J, Altmann J, Pérez-Pérez A, Alberts SC (2011) Age and individual foraging behavior predict tooth wear in Amboseli baboons. Am J Phys Anthropol 144:51–59

Gerloff U, Schlötterer C, Rassmann K, Rambold I, Hohmann G, Fruth B, Tautz D (1995) Amplification of hypervariable simple sequence repeats (microsatellites) from excremental DNA of wild living bonobos (*Pan paniscus*). Mol Ecol 4:515–518

Gesquiere LR, Wango EO, Alberts SC, Altmann J (2007) Mechanisms of sexual selection: sexual swellings and estrogen concentrations as fertility indicators and cues for male consort decisions in wild baboons. Horm Behav 51:114–125

Gesquiere LR, Khan M, Shek L, Wango TL, Wango EO, Alberts SC, Altmann J (2008) Coping with a challenging environment: effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons (*Papio cynocephalus*). Horm Behav 54:410–416

Gesquiere LR, Onyango PO, Alberts SC, Altmann J (2011) Endocrinology of year-round reproduction in a highly seasonal habitat: environmental variability in testosterone and glucocorticoids in baboon males. Am J Phys Anthropol 144:169–176

Gesquiere LR, Learn NH, Simao MCM, Onyango PO, Alberts SC, Altmann J (2011) Life at the top: Rank and stress in wild male baboons. Science 333:357–360

Hall KRL, DeVore I (1965) Baboon social behavior. In: DeVore I (ed) Primate behavior: field studies of monkeys and apes. Holt, Rinehardt, and Winston, New York, pp 53–110

Hausfater G (1975) Dominance and reproduction in baboons (*Papio cynocephalus*): a quantitative analysis. Karger, Basel

Hausfater G, Altmann J, Altmann SA (1982) Long-term consistency of dominance relations among female baboons (*Papio cynocephalus*). Science 217:752–755

Höss M, Kohn M, Pääbo S, Knauer F, Schröder W (1992) Excrement analysis by PCR. Nature 359:199

Hrdy SB (1977) The langurs of Abu: female and male strategies of reproduction. Harvard University Press, Cambridge, MA

Jay P (1963) Mother-infant relations in langurs. In: Rheingold HL (ed) Maternal behavior in mammals. Wiley, New York, pp 282–304

Jolly CJ (1993) Species, subspecies, and baboon systematics. In: Kimbel WH, Martin LB (eds) Species, species concepts, and primate evolution. Plenum Press, New York, pp 67–107

Kappeler PM, Port M (2008) Mutual tolerance or reproductive competition? Patterns of reproductive skew among male redfronted lemurs (*Eulemur fulvus rufus*). Behav Ecol Sociobiol 62:1477–1488

Keele BF, Jones JH, Terio KA, Estes JD, Rudicell RS, Wilson ML, Li Y, Learn GH, Beasley TM, Schumacher-Stankey JC, Wroblewski EE, Mosser A, Raphael J, Kamenya S, Lonsdorf EV, Travis DA, Mlengeya T, Kinsel MJ, Else JG, Silvestri G, Goodall J, Sharp PM, Shaw GM, Pusey AE, Hahn BH (2009) Increased mortality and AIDS-like immunopathology in wild chimpanzees infected with SIVcpz. Nature 460:515–519

Khan MZ, Altmann J, Isani SS, Yu J (2002) A matter of time: evaluating the storage of fecal samples fo steroid analysis. Gen Comp Endocrinol 128:57–64

Kingdon J (1997) The Kingdon field guide to African mammals. Academic, London

Kummer H (1968) Social organization of hamadryas baboons: a field study. University of Chicago Press, Chicago

Kutsukake N, Nunn CL (2006) Comparative tests of reproductive skew in male primates: the roles of demographic factors and incomplete control. Behav Ecol Sociobiol 60:695–706

Langergraber KE, Mitani JC, Vigilant L (2007) The limited impact of kinship on cooperation in wild chimpanzees. Proc Natl Acad Sci USA 104:7786–7790

Launhardt K, Borries C, Hardt C, Epplen JT, Winkler P (2001) Paternity analysis of alternative male reproductive routes among the langurs (*Semnopithecus entellus*) of Ramnagar. Anim Behav 61:53–64

Lehmann J, Fickenscher G, Boesch C (2006) Kin biased investment in wild chimpanzees. Behaviour 143:931–955

Lynch JW, Khan MZ, Altmann J, Njahira MN, Rubenstein N (2003) Concentrations of four fecal steroids in wild baboons: short-term storage conditions and consequences for data interpretation. Gen Comp Endocrinol 132:264–271

Melnick DJ, Pearl MC (1987) Cercopithecines in multimale groups: genetic diversity and population structure. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 121–134

Ménard N, von Segesser F, Scheffrahn W, Pastorini J, Vallet D, Gaci B, Martin RD, Gautier-Hion A (2001) Is male-infant caretaking related to paternity and/or mating activities in wild barbary macaques (*Macaca sylvanus*)? Neurosciences 324:601–610

Moscovice LR, Heesen M, Di Fiore A, Seyfarth RM, Cheney DL (2009) Paternity alone does not predict long-term investment in juveniles by male baboons. Behav Ecol Sociobiol 63:1471–1482

Muruthi P, Altmann J, Altmann SA (1991) Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. Oecologia 87:467–472

Nelson RJ (2005) An introduction to behavioral endocrinology. Sinauer Associates, New York

Newman TK, Jolly CJ, Rogers J (2004) Mitochondrial phylogeny and systematics of baboons (*Papio*). Am J Phys Anthropol 124:17–27

Nguyen N, Gesquiere LR, Wango EO, Alberts SC, Altmann J (2008) Late pregnancy glucocorticoid levels predict responsiveness in wild baboon mothers (*Papio cynocephalus*). Anim Behav 75:1747–1756

Nguyen N, Van Horn RC, Alberts SC, Altmann J (2009) "Friendships" between new mothers and adult males: adaptive benefits and determinants in wild baboons (*Papio cynocephalus*). Behav Ecol Sociobiol 63:1331–1344

Noë R (1986) Lasting alliances among adult male savannah baboons. In: Else JG, Lee PC (eds) Primate ontogeny, cognition and social behaviour. Cambridge University Press, Cambridge, pp 381–392

Noë R (1992) Alliance formation among male baboons: shopping for profitable partners. In: Harcourt AH, de Waal FBM (eds) Coalitions and alliances in humans and other animals. Oxford University Press, Oxford, pp 285–321

Noë R, Sluijter AA (1990) Reproductive tactics of male savanna baboons. Behaviour 113:117–170

Noë R, Sluijter AA (1995) Which adult male savanna baboons form coalitions? Int J Primatol 16:77–105

Nunn CL, Altizer S (2006) Infectious disease and primate social systems. In: Nunn CL, Altizer S (eds) Infectious diseases in primates: behavior, ecology, and evolution. Oxford University Press, New York, pp 176–213

Onyango PO, Gesquiere LR, Wango EO, Alberts SC, Altmann J (2008) Persistence of maternal effects in baboons: mother's dominance rank at son's conception predicts stress hormone levels in subadult males. Horm Behav 54:319–324

Ostner J, Heistermann M, Schülke O (2011) Male competition and its hormonal correlates in Assamese macaques (*Macaca assamensis*). Horm Behav 59:105–113

Packer C, Collins DA, Eberly LE (2000) Problems with primate sex ratios. Philos Trans R Soc Lond B 355:1627–1635

Palombit RA, Seyfarth RM, Cheney DL (1997) The adaptive value of 'friendships' to female baboons: experimental and observational evidence. Anim Behav 54:599–614

Paul A, Kuester J, Arnemann J (1992) Maternal rank affects reproductive success of male Barbary macaques (*Macaca sylvanus*): evidence from DNA fingerprinting. Behav Ecol Sociobiol 30:337–341

Paul A, Kuester J, Arnemann J (1996) The sociobiology of male-infant interactions in Barbary macaques, *Macaca sylvanus*. Anim Behav 51:155–170

Pereira ME (1988a) Agonistic interactions of juvenile savanna baboons. I. Fundamental features. Ethology 79:195–217

Pereira ME (1988b) Effects of age and sex on intra-group spacing behaviour in juvenile savannah baboons, *Papio cynocephalus cynocephalus*. Anim Behav 36:184–204

Pereira ME (1989) Agonistic interactions of juvenile savanna baboons. II. Agonistic support and rank acquisition. Ethology 80:152–171

Pinc KO, Altmann J, Alberts SC (2009) BABASE: Technical specifications for the Amboseli Baboon Project Data Management System. http://papio.biology.duke.edu/babase_system.html

Port M, Kappeler PM (2010) The utility of reproductive skew models in the study of male primates, a critical evaluation. Evol Anthropol 19:46–56

Post DG (1981) Activity patterns of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. Anim Behav 29:357–374

Pusey AE (1978) Age-changes in the mother-offspring association of wild chimpanzees. In: Chivers DJ, Herbert J (eds) Recent advances in primatology. Academic, London, pp 119–123

Ransom TW, Ransom BS (1971) Adult male-infant relations among baboons (*Papio anubis*). Folia Primatol 16:179–195

Samuels A, Altmann J (1986) Immigration of a *Papio anubis* male into a group of *Papio cynocephalus* baboons and evidence for an *anubis-cynocephalus* hybrid zone in Amboseli, Kenya. Int J Primatol 7:131–138

Samuels A, Altmann J (1991) Baboons of the Amboseli basin: demographic stability and change. Int J Primatol 12:1–19

Samuels A, Silk JB, Altmann J (1987) Continuity and change in dominance relations among female baboons. Anim Behav 35:785–793

Sapolsky RM, Altmann J (1991) Incidence of hypercortisolism and dexamethasone resistance increases with age among wild baboons. Biol Psychiatr 30:1008–1016

Sapolsky RM, Alberts SC, Altmann J (1997) Hypercortisolism associated with social subordinance or social isolation among wild baboons. Arch Gen Psychiatr 54:1137–1143

Seyfarth RM (1977) A model of social grooming among adult female monkeys. J Theor Biol 65:671–698

Silk JB (1987) Social behavior in evolutionary perspective. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 318–329

Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. Science 302:1231–1234

Silk JB, Alberts SC, Altmann J (2004) Patterns of coalition formation by adult female baboons in Amboseli, Kenya. Anim Behav 67:573–582

Silk JB, Altmann J, Alberts SC (2006a) Social relationships among adult female baboons (*Papio cynocephalus*). I. Variation in the strength of social bonds. Behav Ecol Sociobiol 61:183–195

Silk JB, Altmann J, Alberts SC (2006b) Social relationships among adult female baboons (*Papio cynocephalus*). II. Variation in the quality and stability of social bonds. Behav Ecol Sociobiol 61:197–204

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2009) The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc R Soc Lond B 276:3099–3104

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2010) Strong and consistent social bonds enhance the longevity of female baboons. Curr Biol 20:1359–1361

Smith K, Alberts SC, Altmann J (2003) Wild female baboons bias their social behaviour towards paternal half-sisters. Proc R Soc Lond B 270:503–510

Smuts BB (1985) Sex and friendship in baboons. Aldine, Hawthorne, NY

Stein DM (1984) The sociobiology of infant and adult male baboons. Ablex, Norwood, NJ

Stoltz LP, Saayman GS (1970) Ecology and behaviour of baboons in the northern Transvaal. Ann Transvaal Mus 26:99–143

Storz JF, Beaumont MA, Alberts SC (2002) Genetic evidence for long-term population decline in a savannah-dwelling primate: inferences from a hierarchical Bayesian model. Mol Biol Evol 19:1981–1990

Struhsaker TT (1973) A recensus of vervet monkeys in the Masai-Amboseli Game Reserve, Kenya. Ecology 54:930–932

Strum SC (1982) Agonistic dominance in male baboons: an alternative view. Int J Primatol 3:175–202

Surbeck M, Mundry R, Hohmann G (2011) Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). Proc R Soc Lond B 278:590–598

Tung J, Charpentier MJE, Garfield DA, Altmann J, Alberts SC (2008) Genetic evidence reveals temporal change in hybridization patterns in a wild baboon population. Mol Ecol 17:1998–2011

Tung J, Primus A, Bouley AJ, Severson TF, Alberts SC, Wray GA (2009) Evolution of a malaria resistance gene in wild primates. Nature 460:388–391

Tung J, Alberts SC, Wray GA (2010) Evolutionary genetics in wild primates: combining genetic approaches with field studies of natural populations. Trends Genet 26:353–362

Tung J, Akinyi MY, Mutura S, Altmann J, Wray GA, Alberts SC (2011) Allele-specific gene expression in a wild nonhuman primate population. Mol Ecol 20:725–739

Van Horn RC, Buchan JC, Altmann J, Alberts SC (2007) Divided destinies: group choice by female savannah baboons during social group fission. Behav Ecol Sociobiol 61:1823–1837

van Noordwijk MA, van Schaik CP (2001) Career moves: transfer and rank challenge decisions by male long-tailed macaques. Behaviour 138:359–395

van Schaik CP (1983) Why are diurnal primates living in groups? Behaviour 87:120–144

van Schaik CP, Paul A (1996) Male care in primates: does it ever reflect paternity? Evol Anthropol 5:152–156

Walters JR (1987) Transition to adulthood. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate societies. University of Chicago Press, Chicago, pp 358–369

Wasser SK, Risler L, Steiner RA (1988) Excreted steroids in primate feces over the menstrual cycle and pregnancy. Biol Reprod 39:862–872

Watts DP (1997) Agonistic interventions in wild mountain gorilla groups. Behaviour 134:23–57

Weingrill T, Lycett JE, Barrett L, Hill RA, Henzi SP (2003) Male consortship behaviour in chacma baboons: the role of demographic factors and female conceptive probabilities. Behaviour 140:405–427

Western D (2007) A half a century of habitat change in Amboseli National Park, Kenya. Afr J Ecol 45:302–310

Western D, Maitumo D (2004) Woodland loss and restoration in a savanna park: a 20-year experiment. Afr J Ecol 42:111–121

Western D, Sindiyo DM (1972) The status of the Amboseli rhino population. East Afr Wildl J 10:43–57

Western D, van Praet C (1973) Cyclical changes in the habitat and climate of an East African ecosystem. Nature 241:104–106

Widdig A, Nürnberg P, Krawczak M, Streich WJ, Bercovitch FB (2001) Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. Proc Natl Acad Sci USA 98:13769–13773

Wroblewski EE (2010) Paternity and father-offspring relationships in wild chimpanzees, *Pan troglodytes schweinfurthii*. PhD thesis, University of Minnesota, Minneapolis

Ziegler TE, Santos CV, Pissinatti A, Strier KB (1997) Steroid excretion during the ovarian cycle in captive and wild muriquis, *Brachyteles arachnoide*s. Am J Primatol 42:311–321