

# The Evolutionary Past and the Research Future: Environmental Variation and Life History Flexibility in a Primate Lineage

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## CHAPTER SUMMARY

The chapters in this volume demonstrate that baboons (genus *Papio*) are a diverse and flexible group that occupies a wide range of habitats. Further, the habitats occupied by baboons are characterized by frequent short-term environmental change (particularly seasonal change) and, for at least some populations, striking long-term change as well. Some of the environmental change is relatively predictable but some is highly unpredictable. What is the relationship between the diversity we observe in baboon life history and behavior and the variability the baboons experience in their physical and social

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environments? We explore answers to this question in the context of a recent hypothesis for hominid evolution proposed by Potts (1996, 1998a,b), the variability selection hypothesis. This hypothesis proposes that the constantly changing environments that typified the East African paleoenvironment resulted in selection for flexible, generalist organisms (such as humans and baboons) that possess the ability to take advantage of the new ecological opportunities that emerged with habitat change. We propose that baboons are a particularly good lineage in which to explore the consequences of variability selection—selection in response to changing environments. We provide examples of baboons' adaptability, particularly in the context of environmental variability and change, and we suggest directions for future research that take advantage of the remarkable opportunity for comparative work in this species, given the relatively large number of baboon field studies. We emphasize that understanding the response of baboons to environmental variability and change is potentially important both because of the light it can shed on the role of changing environments in selecting for flexible species like baboons and humans, and because environmental change will increasingly characterize the global environment in which wild primates—most of them less flexible than baboons—will need to persist.

### 1. BABOON ADAPTABILITY AND LIFE IN CHANGING ENVIRONMENTS

The glaring heat of mid-day in the Amboseli basin, Kenya, is followed by a 20°C temperature drop during the cool night. A few months of lush grasses, hordes of insect larvae, and tree blossoms are quickly replaced by a long dry season of dust, bare earth, and grass stubble. Renewal occurs with the rains but the rains fail, unpredictably, approximately 1 year out of 5, and are highly variable even when they do not fail. These short-term changes, both predictable and unpredictable, occur against a backdrop of larger scale ecological changes that accumulate over decades—once thick woodland becomes open grassland, daily temperatures increase, the water table rises, and the ice caps shrink on Mt. Kilimanjaro, the mountain that dominates Amboseli's landscape (Struhsaker, 1973; Western and van Praet, 1973; Struhsaker, 1976; Hauser et al., 1986; Isbell et al., 1990, 1991; Behrensmeier, 1993; Hastenrath and Greischar, 1997; Altmann, 1998; Altmann et al., 2002; Thompson et al., 2002).

Our work in the Amboseli basin indicates that short- and long-term habitat change has profound consequences for the behavior and life history of the baboons that occupy the basin. Foraging patterns change over seasons and across years as rainfall, temperature, and habitat productivity change. Home ranges shift in response to ecological changes, as tree die-offs in one part of the basin force the baboons to take advantage of new ecological opportunities—with attendant new risks—in other parts of the basin. Vital rates change, sometimes dramatically, as birth rates increase in rich habitats and decrease in poorer ones, and mortality rates rise and fall as well (Bronikowski and Altmann, 1996; Altmann and Alberts, 2003a,b; Alberts et al., 2005). Change in weather and habitat of the sort described for Amboseli—both short term and long term—is typical of the environments in which baboons live. The habitats of every population described in this volume show strong seasonal changes and most probably experience long-term change as well, although this is much more difficult to document and requires long-term ecological data.

Baboons (genus *Papio*) have achieved a nearly continental distribution in Africa and occupy habitats ranging from moist evergreen forests to deserts, from seashore to mountains, and from equatorial to subtropical regions (Estes, 1991; Jolly, 1993; Kingdon, 1997). They are increasingly treated as a single species, *P. hamadryas* (Jolly, 1993; Newman et al., 2004; but see Kingdon, 1997; Groves, 2001), which places them, among primates, second only to humans in geographical and environmental range. Thus, baboon populations experience very different environments and perhaps different degrees of variability and predictability. In addition, any single population of baboons experiences variability over time and space. The environmental variability typical of baboon habitats is accompanied by marked behavioral and life history flexibility. Probably the most striking and best-studied example is foraging behavior. Baboons are very flexible foragers, combining omnivory (plants, invertebrates, small vertebrates) with great selectivity on particular plant species and parts (Hamilton et al., 1978; Post, 1982; Norton et al., 1987; Whiten et al., 1991; Byrne et al., 1993; Altmann, 1998; Alberts et al., 2005). In other words, they are highly selective generalist foragers, and the dietary flexibility that results undoubtedly lies at the heart of baboons' evolutionary success. As this volume illustrates, however, baboons are strikingly diverse in a number of other areas of behavior and life history as well.



## 2. THE EVOLUTIONARY PAST: THE "VARIABILITY SELECTION" HYPOTHESIS FOR THE EVOLUTION OF ADAPTABILITY

What is the relationship between the variability we observe in baboon life history and behavior and the variability they experience in their environments? More specifically, can phenotypic flexibility be understood as a consequence of environmental variability? This is not a question about the socioecological model, which posits that different sets of environmental conditions require particular responses so that the dry habitat of hamadryas baboons selects for small foraging parties and eventually one-male social units. Instead, we are asking whether the flexibility that baboons exhibit within subspecies and populations can be understood as a common adaptive, evolved response to the fact that they occupy—and are successful in—constantly changing and often unpredictable environments. To explore this question we turn to a hypothesis for human evolution developed by Potts (1996, 1998a,b).

The emergence and spread of African savannas over the past 5 million years, such as Amboseli and others described in this volume, is a cornerstone for hypotheses of hominid evolution. According to these hypotheses, early human ancestors moved into savannas in response to increasing climatic cooling and drying. Under such conditions, the exigencies of the savanna environment were central selective pressures that shaped the hominid lineage (see reviews in Foley, 1987, 1993, 1994; Potts, 1998a,b; Klein, 1999). A common thread in a number of these hypotheses is that climatic change occurred at a single, critical point in human evolution.

However, in recent years a novel and more compelling scenario for the evolution of the human lineage has emerged: Potts (1996, 1998a,b) has proposed that it is not the savanna environment per se that represents the key selective force shaping human evolution. Rather, the key selective force shaping human evolution was the persistent pattern of environmental change over millennia, a pattern that has characterized the African environment both during and after the initial emergence of savannas.

Potts (1998a,b) first marshals evidence from marine and ice core oxygen isotope records, ocean dust records, sedimentary analysis, and a number of other sources to describe the East African paleoenvironment, particularly during the past 6 million years, as one of the dramatic environmental changes of increasing magnitude over time. This analysis is supported by a number of independent sources and seems uncontroversial. He then develops the

hypothesis that, in the face of such environmental change, organisms will experience "multiple, substantial disparities in selective environment over time" resulting in selection for "complex mechanisms for dealing with unexpected, episodic change" (Potts, 1998a, p. 112). Specifically, variability selection will select for traits that result in highly flexible, generalist organisms that are able to cope not only with a range of habitat types, but with environmental change as well, particularly relatively unpredictable change. Potts describes several lineages—including papionins and hominids—which he says show evidence of variability selection (Potts, 1998b). He also describes several alternative "environmental hypotheses" for hominid evolution and describes specific tests of these hypotheses in comparison to the variability selection hypothesis (Potts, 1998a,b). Recently Bobe and Behrensmeyer (2004) conducted comparative tests of these hypotheses and found good support for the variability selection hypothesis.

Whether or not the variability selection hypothesis ultimately provides an explanatory framework for understanding human evolution, it underscores the fact that environmental variability and change, whether predictable or unpredictable, short term or long term, provide organisms with both challenges and opportunities. Understanding responses to environmental change will provide crucial insights into both current population processes and the history and future of species.

## 3. BABOON FLEXIBILITY: INSIGHTS INTO THE OUTCOME OF VARIABILITY SELECTION

For several reasons, baboons provide a good model for understanding how variability selection—selection for a flexible, generalist organism driven by environmental change—might shape life history and behavior in humans, nonhuman primates, and other taxa. First, baboons share important evolved characteristics with humans. Baboons have adapted to a very wide range of environments, and in most habitats they show little or no seasonality in reproduction (e.g., Melnick and Pearl, 1987; Bercovitch and Harding, 1993; Bentley-Condit and Smith, 1997; Alberts et al., 2005; Cheney et al., this volume). In these characteristics they are like humans and are unlike the large majority of other primate species. In other words, baboons have both adapted to diverse habitats and, in major aspects of their life histories, have largely broken free of the seasonal constraints in even highly seasonal habitats. This is an



ability shared by very few other primates. In addition, baboons and humans share traits that Potts proposes evolved in response to variability selection, including a high encephalization quotient like other primates (Dunbar, 1998), a flexible locomotor system (baboons readily utilize both arboreal and terrestrial habitats; Estes, 1991; Fleagle, 1999), and a flexible mating and social system (e.g., Altmann and Altmann, 1970; Dunbar and Dunbar, 1977; Barton et al., 1996; Henzi et al., 1999; Henzi and Barrett, 2003, and chapters in this volume).

Second, *Papio* baboons survived Pleistocene environmental change while closely related taxa went extinct. Potts (1998a) cites *Papio* as an example of a taxon that survived periods of extensive Pleistocene environmental change by evolving ecological flexibility, possibly in response to variability selection. By contrast, the closely related taxon *Theropithecus oswaldi*, which presumably exhibited less ecological flexibility, went extinct 600,000–800,000 years ago.

Third, baboons in at least one well-studied habitat (Amboseli) have experienced environmental change of a type and magnitude typical of the changes that characterized East Africa paleoenvironments, and have persisted in the face of this environmental change. The Amboseli baboon population experienced a dramatic decline in the 1960s at the onset of woodland die-off (Altmann et al., 1985). However, the population recovered even as the woodland die-off continued, and population size has continued to increase somewhat over the past several decades (Altmann et al., 1985; Alberts and Altmann, 2003; Altmann and Alberts, 2003a), although not without fluctuations. The baboons' success is in striking contrast to the failure of Amboseli's vervet monkeys to adapt. Vervet monkeys, like baboons, are widespread savanna-dwelling monkeys, and the two species show considerable overlap in habitat and diet (Struhsaker, 1967; Wrangham and Waterman, 1981; Altmann et al., 1987; Altmann, 1998). However, Amboseli's vervet population has undergone dramatic decline, including local extinction in some locales, as a consequence of environmental change (Struhsaker, 1967, 1973, 1976; Hauser et al., 1986; Isbell et al., 1990).

If baboons represent a model for understanding the behavioral flexibility of early hominids and other species successful in the face of environmental change, what traits might such species have exhibited? A critically important trait, of course, would be dietary and foraging flexibility, the focus of the most diverse range of detailed studies within and between populations (Hamilton et al., 1978; Post, 1982; Norton et al., 1987; Whiten et al., 1991; Byrne

et al., 1993; Altmann, 1998; Alberts et al., 2005). The Amboseli baboons have responded quite effectively to habitat change in this regard, and in contrast to chimpanzees and a number of other species (e.g., Wrangham et al., 1991; Malenky and Wrangham, 1994; Wrangham et al., 1998), the baboons have done this without relying heavily on a few "fallback foods" during difficult times (although fallback foods certainly play a role in their diet; Alberts et al., 2005). Instead, they engage in what we call "handoff foraging," in which temporal variability in food abundance is mitigated by careful tracking and exploitation of shifting food resources as they become available across different seasons and years (Alberts et al., 2005). Concomitant with this skill is an ability to find alternatives when important foods become scarce as the habitat changes.

The chapters in this book point to several other ways in which baboons effectively and adaptively respond to habitat change. One clearly important example is growth and development. Growth rates in young baboons vary substantially and are influenced not only by food availability (e.g., Eley et al., 1989; Strum, 1991) but also by maternal rank and parity (Johnson, 2003; Altmann and Alberts, 2005; Johnson, this volume). A significant result of variation in growth is variation in age at first reproduction; baboons are able to take advantage of temporary increases in food availability to accelerate age at first reproduction in a manner that has substantial implications for their fitness (Altmann et al., 1988; Altmann and Alberts, 2003a, 2005). This might be considered a shift on the "fast versus slow" life history continuum, but differs from interspecific shifts on that continuum in that baboons (and humans) generally do not face trade-offs in other life history parameters by accelerating first reproduction. In particular, contexts that allow earlier age at first reproduction typically also enhance a whole suite of life history components in concert—infant survival will typically increase, interbirth interval will often decrease, and adult body size and reproductive span may increase as well (e.g., Lyles and Dobson, 1988; Sade, 1990; Sterck, 1999).

Leigh and Bernstein's data (this volume) on brain growth also suggest that baboons are particularly well adapted to take advantage of these opportunities, because neonates have relatively large brains (compared to other primates) that may even fall within the adult size range. That is, brain growth in baboons occurs at an earlier ontogenetic stage than other similar-sized primates and is complete earlier. The result is, presumably, a youngster poised for rapid somatic growth and relatively free (compared to similar-sized primates)

of brain growth requirements. This ability to accelerate age at first reproduction when conditions are good is surely a hallmark of a successful species. It depends crucially on the ability baboons have to break free of the seasonal constraints of their habitat and reproduce throughout the year, which in turn depends on flexible foraging.

The early completion of brain growth may not only leave a younger animal better poised to take advantage of subsequent challenges and opportunities, but it may also enhance the importance and lifetime consequences of fetal 'imprinting' (Barker, 2001; Hales and Barker, 2001) and of the so-called maternal effects that occur while the brain growth is ongoing. In fact, maternal investment patterns, too, show illuminating variation. Interbirth intervals vary greatly within as well as between populations (e.g., Altmann et al., 1978; Strum and Western, 1982; Hill et al., 2000; Altmann and Alberts, 2003a; Barrett et al., this volume; Cheney et al., this volume), and the ability of baboons to modify the duration of maternal investment is perhaps one of the most flexible traits of their life history. It reflects both the general lack of birth seasonality in baboons (even populations with measurable birth seasonality generally show births throughout the year) and the ability of females and their maturing infants to respond rapidly to changes in environmental conditions (e.g., Dunbar et al., 2002). While it has long been recognized that interbirth intervals depend strongly on food availability (e.g., Strum and Western, 1982), other determinants are also in play—in particular how readily infants achieve independence in different environments, which depends on more than simply habitat productivity. The presence of particularly appropriate "weaning foods," the travel distance, and energetic expenditure required for foraging, and predation risk will all contribute to the ability of mothers to terminate intense investment in one offspring and initiate investment in the next without entailing an intolerable increase in mortality cost for the weanling (Altmann and Samuels, 1992; Barrett et al., this volume). In addition, variability in social and demographic environment as well as physical environment may be important, males may provide offspring care (e.g., Palombit et al., 1997; Buchan et al., 2003), and the mother's social and demographic environment may contribute to offspring survival (Palombit et al., 1997; Silk et al., 2003; Wasser et al., 2004; Cheney et al., this volume). Thus, maternal investment, facilitating social environments, and offspring development are seen to covary in significant ways.

A final way in which baboons exhibit important variability is in their reproductive behavior. A great deal of this variability occurs among subspecies.

Olive and yellow males—particularly middle-ranking males—engage in frequent coalitionary behavior that increases their mating access to reproductive females, whereas male chacmas apparently never do so (e.g., Packer, 1977; Noë, 1986, 1993; Bercovitch, 1988; Bulger, 1993; Henzi et al., 1999; Henzi and Barrett, 2003). The consequence is that high-ranking chacma males obtain nearly exclusive access to reproductive females during their tenure at high rank, while olive and yellow males are more limited in their ability to monopolize access to females (e.g., Packer, 1979; Bulger, 1993; Weingrill et al., 2000; Alberts et al., 2003). Concomitantly, olive and yellow baboons are the most polygynous and polyandrous of the subspecies on short time scales—females frequently change partners within sexual cycles, even within days, and males may move between partners from one day to the next. Female chacmas tend to be monandrous on short time scales, and hamadryas females are monandrous on both short and long time scales (see also discussion by Swedell and Saunders, this volume). And, as a consequence, olive and yellow males are relatively rarely infanticidal whereas male chacmas are commonly so (Janson and van Schaik, 2000; Palombit et al., 2000; Henzi and Barrett 2003; Cheney et al., this volume; data on infanticide in hamadryas are still difficult to characterize, see review in Swedell and Saunders, this volume). To some extent this fascinating variability among subspecies must be associated with the highly flexible nature of other baboon life history and behavioral traits. In that regard, it represents an important set of traits to consider when describing baboon flexibility. However, from another perspective it may reflect limits on baboon flexibility; within-population flexibility in patterns of polygyny, polyandry, and coalitionary behavior is relatively poorly described at the moment. Nonetheless, it is clear that the full range of reproductive behavior seen across subspecies is not exhibited within any subspecies. This suggests that different reproductive patterns have become fixed in different subspecies, and consequently that flexibility—otherwise a cornerstone of baboon biology—has been lost. We consider this and other limits to baboon flexibility in the next section.

#### 4. LIMITS TO BABOON FLEXIBILITY

In spite of the adaptability that baboons exhibit in a number of dimensions, they are relatively invariant in others, and the limits to baboon flexibility may be as illuminating as the flexibility itself. Like most primate species, baboons



have a litter size of one. Moreover, unlike many mammalian species, even if high food availability were to lead to higher twinning rates, twins or triplets would rarely if ever survive in natural environments. This is because of a number of invariant traits, including late development of locomotor independence, milk composition that requires very frequent suckling and almost continuous contact with the mother, long travel distances, and the very lack of seasonal breeding that leads to a low probability of communal suckling or creching. These traits constrain not only litter size but also offspring growth rates; growth rates that are too high would hinder a mother's ability to carry an infant and perhaps extract too high a cost on both mother and offspring (e.g., Altmann and Alberts, 1987, 2005; Altmann and Samuels, 1992).

The chapters in this book also reveal other constraints upon baboons' flexibility. One striking limit lies in the fact that female—and hence male—fertility is limited by the rate at which infants can develop, as illustrated nicely in the chapter by Barrett and colleagues (this volume). This limitation sets baboons at the lower end of the cooperative breeding continuum, distant from humans as well as from callitrichids and possibly siamangs, in which mothers can reproduce even while their current offspring is still highly dependent. Recently, Hrdy (1999, 2005) has developed the hypothesis that broad-sense cooperative breeding, allomaternal care or social facilitation in rearing of young, has been critical in the evolution of both human and non-human primate life histories. Cooperative care of offspring means that young can have long periods of maturation and yet mothers can reproduce repeatedly while their young are still relatively vulnerable. Further, infants in primate species that have higher levels of alloparental care experience more rapid growth (see review in Ross, 1998). The ways in which baboons are and are not able to share the burden of offspring care suggests an interesting comparison; evaluating baboons alongside species that allonurse (e.g., white-faced capuchins; Perry, 1998) or in which helpers other than the mother carry dependent young (e.g., callitrichids; Goldizen, 1987) might shed light on critical differences, as well as similarities, between species that do share offspring care, such as callitrichids and humans, and those that do not.

A related constraint, an ontogenetic and perhaps heritable one as well, is reflected in the surprising pervasiveness of maternal effects on offspring development. In spite of the fact that baboons are poised, ontogenetically, to take advantage of opportunities for rapid growth, their growth patterns are strikingly influenced by maternal effects. Baboon mothers influence the

growth of their offspring through their own dominance rank and their own developmental status, age, and/or parity (Altmann and Alberts, 2005; Johnson, this volume), and these maternal effects persist well past weaning in both Okavango and in Amboseli, when immatures are completely independent of their mothers' direct care. This effect is less surprising for daughters than it is for sons, because the dominance rank of daughters is dependent upon the dominance rank of mothers, providing an avenue for the continued influence of dominance rank, if not parity, on daughters. However, this maternal effect in itself—the dependence of daughters' ranks upon their mothers' ranks—represents an interesting constraint upon female baboons, albeit one with clear benefits for at least some members of the social group (the high-ranking females), and one that is highly phylogenetically conserved (Melnick and Pearl, 1987).

The variability of baboon reproductive behaviors suggests another interesting constraint upon baboon flexibility, at least relative to humans. As noted in "Baboon Flexibility", female baboons exhibit a range of reproductive strategies, from a tendency to mate with a single male over several reproductive events (which results, among other things, in "paternity concentration"), to multiple mating (and consequent "paternity confusion," e.g., Swedell and Saunders, this volume). Male baboons, too, exhibit a range of reproductive strategies that fall along a continuum from permanent associations with females in hamadryas, which exclude other males and persist regardless of the female's reproductive state, to temporary mate-guarding episodes concentrated during the follicular phase of the female's cycle (e.g., Bergman, this volume).

Thus far, baboons are like humans, in that humans exhibit the same range of reproductive behaviors. However, unlike humans, which appear to possess similar mating dispositions the world over in spite of great variation in the number of partners each sex has (e.g., Buss 1990; Schmitt 2003; Gottschall et al., 2004), the clear subspecific differentiation in baboon mating behavior appears to have a genetic basis. Bergman (this volume) and Beehner and Bergman (this volume) describe the behavior of hamadryas-olive hybrids, all living in the same environment (indeed the same social group) as representing a set of clear points along a continuum. Some hybrid individuals consistently exhibited olive-like behavior—same-sex bonding in the case of females and minimal tendencies to herd or lead nonestrous females in the case of males—while others consistently exhibited hamadryas-like behavior—cross-sex



bonding in the case of females and strong tendencies to herd and lead non-estrous females in the case of males—and still others were intermediate in their behavior. This strongly suggests a lack of plasticity (in the classic sense of different phenotypes developing from the same genotype in response to different environments) in mating behavior in these subspecies. Interestingly, the behavior of hybrids was highly correlated with their morphological phenotypes, at least for females; females that appeared more hamadryas-like in their coloring and body shape were more hamadryas-like in their behavior and vice versa (Beehner and Bergman, this volume).

As we have noted, there appears to be clear subspecific differentiation in male-male coalitionary behavior as well; chacma males do not show coalitionary behavior while olive and yellow males—particularly middle-ranking males—do so frequently (Packer, 1977; Noë, 1986, 1993; Bercovitch, 1988; Bulger, 1993; Henzi et al., 1999; Henzi and Barrett, 2003). Unlike the case of mating behavior in hamadryas-olive hybrids, no “natural experiment” involving yellow-chacma hybrids allows us to rule out the possibility that coalitionary behavior is plastic. However, chacma baboons have been studied in many different habitats by many different researchers (although not in the area of overlap between chacmas and yellows, a useful gap to fill), and male coalitionary behavior has not been described (see reviews in Bulger, 1993; Henzi and Barrett, 2003). The consequences of no male coalitionary behavior in chacmas are profound, for both males and females. Chacma males live in a “winner takes all” world in which the highest-ranking male in the group obtains nearly all of the mating opportunities (Bulger, 1993; Palombit et al., 1997; Weingrill et al., 2000; Henzi and Barrett, 2003). In contrast, in olive and yellow groups, high-ranking males are sometimes able to enforce a strict queuing system based upon rank, and to obtain nearly all the mating opportunities, but their ability to do this is contingent upon both their own fighting ability and on the number, and the behavior (particularly coalitionary behavior), of other males (Packer, 1979; Bercovitch, 1988; Alberts et al., 2003). The consequences of these differences for female reproductive options and for infanticidal behavior are enormous, as noted in “Baboon Flexibility” (Palombit et al., 1997, 2000; Henzi et al., 1999; Weingrill et al., 2000; Henzi and Barrett 2003; Cheney et al., this volume; Swedell and Saunders, this volume).

The apparent fixation of different reproductive patterns in different subspecies—the apparent lack of flexibility within subspecies—suggests important

areas of future study. It provides a good opportunity for understanding how different ecological conditions might select for different reproductive behaviors. It also allows us to pose the question: What differentiates a lineage such as humans, in which individuals apparently retain the potential to express a wide range of reproductive patterns in different ecological contexts, from a lineage such as baboons, in which individuals apparently lack this potential even though the entire range is expressed within the taxon? Does protracted gene flow in humans, in contrast with periods of allopatry for baboon subspecies, explain the difference? Or are there additional traits that must be maintained over evolutionary time in order for that kind of flexibility to be exhibited by individuals?

##### 5. THE RESEARCH FUTURE: PRIORITIES FOR BABOON RESEARCH IN THE COMING DECADES

The behavioral and life history flexibility of baboons makes them critical potential contributors to a number of key research problems. They certainly represent an important model for understanding the attributes of a successful species. However, because they occur in a wide range of habitats, and because some of their traits vary systematically across these habitats, they represent an important model for understanding how life history and behavioral traits are likely to evolve or vary in response to environmental variability and change. Crucially, this also means that they represent a model—probably a best-case scenario—for how primates may cope with global climate change.

The diversity and duration of field research on baboons, at sites from Ethiopia through South Africa, is unparalleled among mammals. This provides an opportunity for comparative work that is just beginning to be realized (e.g., Bulger, 1993; Bronikowski et al., 2002). The manifestations of baboon flexibility and adaptability described in this chapter and others in this volume, and the limits to baboon flexibility that we have identified, present a number of compelling opportunities for advancing our understanding of baboon ecology and evolution. In our view, these compelling opportunities for comparative work fall into five major categories: (1) understanding the impact of short- and long-term, predictable and unpredictable environmental change on baboon behavior, particularly foraging behavior and social behavior; (2) identifying the manner in which life history components (fertility and survival) vary and covary under different environmental conditions; (3)



describing the suite of covarying traits associated with subspecific differences in male and female reproductive behavior; (4) identifying the genetic, ontogenetic, and physiological bases of subspecific differences; and (5) facilitating comparative research across sites.

### 5.1. Understanding the impact of environmental change—short- and long-term, predictable and unpredictable—on baboon behavior

Although not discussed in depth in this volume, evidence suggests that an ability to respond to changing environments is of primary importance to the success of baboons. The wide geographical and environmental range that they occupy suggests that they are quite adaptable in this regard. Further, as we noted above, baboons have survived and adapted to a changing environment in Amboseli, while vervet monkeys, with whom they share many resources and behavioral strategies, have experienced local extinction (Struhsaker, 1973, 1976; Hauser et al., 1986; Isbell et al., 1990, 1991). Baboons have a number of behavioral traits that are likely to contribute to flexibility in changing environments.

The most urgent demands of a changing environment involve nutritional intake. The ability to track and adapt to changing food sources, and to actually alter their own environment by finding and moving to more suitable habitats (Altmann and Alberts, 2003a; Alberts et al., 2005), are characteristics of baboons that warrant more study. In addition, social bonds appear very important to baboons. For instance, females that are socially well-integrated experience enhanced infant survival relative to poorly integrated females (Silk et al., 2003) and females attend carefully, and appear to have a sophisticated understanding of, their own social relationships and those of others (Bergman et al., 2003). These and other data suggest that a well-buffered social organization in which individual relationships are carefully serviced may be a cornerstone of successful adaptation to environmental change.

Habitat change will influence many ancillary behaviors as well. For instance, it will affect the demographic environment by intensifying, or alleviating, the effects of density as conditions deteriorate, or improve, respectively. The demographic environment has profound consequences for both males and females because both sexes experience density dependence in some aspects of their behavior and life history (e.g., Bulger and Hamilton, 1987; Packer et al., 2000; Alberts et al., 2003; Wasser et al., 2004). As with the

effects of habitat change on food availability, the effects of habitat change on the demographic environment may be mitigated to some extent by the ability of both sexes—males through dispersal and females through permanent social group fission—to modify their own group membership. For males, this is a frequently recurring but relatively high-risk opportunity; for females the opportunity is quite rare, probably only occurring about once in each female's lifetime, but is relatively low risk and garners many potential benefits—most notably a temporary return to density-independent survival and fertility.

It is important to evaluate all of these responses both in terms of long- versus short-term habitat change, and in terms of predictable versus unpredictable habitat change, as the two dimensions offer very different types of challenges and opportunities and are likely to result in different types of adaptations. Baboons in many parts of Africa will increasingly experience changing environments, and the manner in which they respond behaviorally to this change must become an important area of study as primates the world over face both shrinking and fragmented habitats, and local as well as global climate change.

### 5.2. Identifying how life history components vary—and co-vary—under different environmental conditions

The consequences of environmental variability for baboons are profound. Variation in the extent of birth seasonality among baboon populations can be directly attributed to variation in the patterns and extent of seasonality in habitats (e.g., compare Bercovitch and Harding, 1993; Bentley-Condit and Smith, 1997; Alberts et al., 2005; Barrett et al., this volume; Cheney et al., this volume). Variation in growth patterns and in mortality patterns, adults and immatures, are partly attributable to variable habitats (e.g., Altmann and Alberts, 2003a, 2005; Johnson 2003). Variation in infant development and survival, where lifetime fitness has its highest sensitivity, is certainly partly attributable to environmental variation (e.g., compare Bentley-Condit and Smith, 1997; Packer et al., 2000; Altmann and Alberts, 2003a; Wasser et al., 2004; Barrett et al., this volume; Cheney et al., this volume; Beehner et al. in press). These life history traits also covary, and life history correlations probably change as habitats change, in ways that are not as yet described. Variation in social organization—in mating patterns, in the extent and nature of social bonds between individuals—is often attributed to



differences between habitats, but may also be attributable to variability within habitats. That is, the extent to which habitats are predictable in their productivity patterns may contribute to selection for large versus small group sizes, and for fission–fusion versus stable groupings. This may contribute not only to the variety of baboon social organizations across habitats but also to the sometimes highly flexible organizations within habitats (Galat-Luong et al., this volume).

Baboon studies also offer the opportunity to solve a long-standing puzzle: Why do the effects of dominance rank on female reproductive success vary across study populations (and also primate species)? Different baboon studies (and studies on other primates as well) show different effects of rank on age at first reproduction, fertility, offspring survival, offspring sex ratio and growth, to name some key traits (reviewed in Silk, 1987; Bercovitch and Harding, 1993; Packer et al., 2000; Altmann and Alberts, 2003a; Johnson, 2003; Wasser et al., 2004; Cheney et al., this volume; Johnson et al., this volume). One possible explanation for this is that the effects of rank on female reproductive success are density dependent as they are for male baboons (see e.g., Wasser et al., 2004). Alternatively or in addition, the effects of rank may vary depending upon the nature and quantity of food resources—possibly, rank “matters more” in some foraging contexts than in others. Similarly, the importance of kin may change as density or habitat changes. Baboon studies—especially long-term studies where such effects may vary over time in the same population—offer particularly good opportunities to examine these questions.

### 5.3. Describing the suite of covarying traits associated with subspecific differences in male and female reproductive behavior

The fascinating and well-documented variation across baboon subspecies in reproductive behavior has received increasing attention in recent years. The time is ripe for comparative work aimed at clearly describing the suite of traits that characterize each subspecies. One possibility is that the hamadryas suite of traits initially arose in response to habitats that selected for small foraging groups, with resulting high infanticide risks when foraging parties encountered each other or exchanged males (Dunbar, 1988; Anderson, 1990; Kummer, 1990, 1995; Henzi and Barrett, 2003; Swedell and Saunders, this volume); the behavioral precursor to male hamadryas behavior would have

consisted of extended mate guarding (Bergman, this volume). In this view, the chacma pattern, with multimale groups, no male coalitions, a tendency of the highest-ranking male to monopolize mating, and high risk of infanticide after takeovers, represents the next point on the continuum; the lack of male coalitions results from an evolutionary history of small group sizes in which suitable coalition partners were rare (Henzi et al., 1999; Henzi and Barrett, 2003). Yellow and olive baboons fall further along the continuum and represent a response to habitats that allow and/or possibly select for larger foraging group sizes, resulting in opportunities for males to form coalitions and, therefore, a breakdown of the relatively strict rank-based queuing system observed in chacmas.

Some key and relatively easy to test predictions arise from this proposed scenario. We would expect male chacmas to have smaller testes than yellow or olive baboons, but larger than hamadryas (see Jolly and Phillips-Conroy, this volume). We might also expect male chacmas to have shorter maximum adult lifespans than yellow or olive males, because their reproductive lifespan is shorter and hence their reproductive value drops more rapidly after their prime years. The work of Bergman (this volume) predicts that high-ranking male chacmas should show interest in cycling females earlier in the follicular phases than their high-ranking olive or yellow counterparts, and by extension we would predict that high-ranking olive and yellow males would show greater selectivity among females in the follicular phases of their cycles, preferring more fertile females (multiparous females, and those in conceiving versus nonconceptive cycles) over less fertile ones (adolescent and other nonconceptive females).

With respect to female behavior, we might predict that the extent to which female preferences—either through overt choice or cryptic choice—influence mating behavior and mating outcomes will vary systematically as a function of the intensity of male–male competition over particular cycles. For instance, in chacmas, where high-ranking males generally monopolize mating opportunities and females are therefore relatively monandrous in the short term, overt female choice may be relatively minimal, but selection for cryptic female choice would certainly occur. In contrast, in contexts where even low-ranking males may achieve paternity, females may have more opportunity to play a role in determining the success of preferred males in maintaining mate-guarding episodes. A related set of traits, which may either differentiate or unify baboon subspecies, concerns paternal behavior. It has long been known that male and



female baboons sometimes form preferences for opposite-sex partners that persist beyond the follicular phase of the female's sexual cycle, and that these preferences, on the part of males, may be related to paternity (e.g., Altmann, 1980; Smuts, 1985; Palombit et al., 1997, 2000). What has recently emerged is that males play a more pronounced paternal role than had previously been suspected—they provide direct paternal care and differentiate their own offspring from those of other males (Palombit et al., 1997, 2000; Buchan et al., 2003). Many aspects of this paternal behavior remain unexplored. For instance, males may contribute to the survival of their offspring not only by protecting them against infanticide, but also by providing paternal care in noncrisis situations, carrying and grooming them, providing a buffer one for uninterrupted foraging, and reducing common harassment. Males may facilitate the development of paternal sib relationships (Widdig et al., 2001; Smith et al., 2003) by providing a common relationship—a connection—through which paternal sibs become familiar with each other. And males may provide assistance during agonistic encounters that facilitates rank attainment—for both sons and daughters—in the same way that assistance from mothers facilitates rank attainment for daughters. Indeed, fathers may be even more effective allies than mothers in this regard because of their large size. They can assist sons, which mothers generally cannot when their sons' opponents surpass them in size, and they can assist daughters against higher-ranking females, which mothers are more limited in their ability to do. None of these possible male social functions has been tested, but all represent key aspects of baboon social and behavioral flexibility that need to be understood.

#### 5.4. Identifying the genetic, ontogenetic, and physiological bases of subspecific and intrapopulation differences

As more data emerge from more sites, the hypothesis that baboon populations have undergone behavioral differentiation in allopatry—that subspecies are genetically differentiated with respect to behavior—is receiving greater support. Some differences are relatively well described, while others are still being explored. For instance, while the chacma-olive-yellow differences in male reproductive behavior have received a good deal of recent attention, some data suggest that behavioral and genetic differentiation may have occurred within the chacma lineage as well, with the more southern populations representing a morphological extreme relative to the more northern

populations, and behavioral differentiation perhaps occurring on an even finer geographic scale (Anderson, 1990; Newman et al., 2004; Babb et al., 2005).

the suites of traits that describe each subspecies become better defined, the opportunity for identifying the genetic bases of these differences becomes real. Candidate gene approaches will increasingly be an option, with new high-throughput genotyping technologies. Studies of quantitative trait loci (QTLs) may be realistic even sooner, if hybrid populations (captive or wild) can yield pedigrees of even moderate depth, with good phenotypic behavioral data and high-quality genetic samples to accompany them. QTL analysis in combination with candidate gene approaches will be the most powerful technique in the immediate future, as exemplified by work on other organisms (e.g., Geiger-Thornsberry and Mackay, 2004; Pasyukova et al., 2004; Wheeler et al., 2005).

Behavioral and life history differences arise at various demographic levels and under various environmental conditions. Another major research agenda should be to identify the processes—not only genetic, but also ontogenetic, and in terms of both organizing and activating physiological mechanisms—by which such differences arise. Several new technologies, such as the increasing study of steroid hormones through noninvasive sampling, make this feasible. Hypotheses can be developed and tested that relate behavioral experience, ontogenetic trajectories, and differences in steroid concentrations to behavioral differences, not only among juveniles and adults within the same population, but also among populations. This research agenda will require individual-based longitudinal life history studies.

As new technologies become available, both the puzzle of subspecific differentiation and the ontogeny of differences among individuals within populations will certainly be tackled. In this context, biologists with good phenotypic data on wild populations will hold an increasingly valuable resource.

#### 5.5 Facilitating comparative research across sites

Finally, to accomplish the agenda that we outline as well as other priorities that emerge, a high priority will need to be given to methods of data collection, analysis, and presentation that facilitate comparison and more rigorous theory testing. For example, while it has emerged relatively clearly



that chacma, yellow, and olive males differ in their tendencies to form male-male coalitions, the related question of whether females in the subspecies differ in coalition formation remains unanswered (Henzi and Barrett, 2003; Silk et al., 2004). This is simply because researchers at different sites have tended to use different measures of coalition frequency and formation, making it difficult to compare across sites (Silk et al., 2004). Additionally, efforts that are collaborative across study sites—using the same methodology to produce the similar data sets that can be directly compared (e.g., Bronikowski et al., 2002; Barrett et al., this volume)—are likely to have rich payoffs that will make the greater time investment and leaps of trust well worth the effort.

Indeed, this is true not only across baboon studies, but also across primate studies more generally. For instance, rhesus macaques, like baboons, appear highly adaptable and have a very large geographic range. This makes them a prime candidate for comparisons with baboons. Studies on the two species have generally differed markedly in that behavioral studies of macaques have involved primarily captive or provisioned populations, while studies on baboons have involved primarily wild populations, and this must be taken into consideration in comparative studies, as it constrains the kinds of comparisons that can be made. Nonetheless, there is interesting potential for identifying patterns of flexibility common across the two species.

## 6. CONCLUSIONS

Baboons show great flexibility within populations and also interesting differentiation among subspecies. This provides a remarkable opportunity for comparative work in this species, especially given the relatively large number of baboon field studies, several of them now with long-term data. We have identified key areas for future research—which we view as priorities—that represent just a subset of the opportunities that baboons provide. As the habitats of wild primates become increasingly fragmented, and as both global and local climate change proceed, the urgency of producing good comparative work within a single, well-studied species increases. The potential fruits include an understanding of behavioral and life history diversity as generated in response to environmental variability and change, and a comprehensive understanding of the limits to adaptability that primate species can be expected to exhibit.

## ACKNOWLEDGMENTS

This work was supported by NSF-IOB 0322613, NSF BCS-0323553, NSF IOB-0322781, NSF BCS-0323596, R03 MH65294, and the Chicago Zoological Society. Our long-term research in Amboseli is facilitated by cooperation from the Office of the President, Republic of Kenya, the Kenya Wildlife Services, its Amboseli staff and Wardens, the Institute of Primate Research, the National Museums of Kenya, and the members of the Amboseli-Longido pastoralist communities.

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