6 Seasonality and long-term change in a savanna environment

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Introduction

The emergence and spread of savannas in Africa during the past five million years is often cited as a major factor in hominid evolution. Tropical savannas are different from forests in having less rainfall, which is strongly seasonal and often very unpredictable, even within seasons (Bourliere & Hadley 1983; Solbrig 1996). Human ancestors are thought to have moved into savannas as a response to cooling and drying climates, and the exigencies of the savanna environment – including the marked seasonal changes in plant food availability – are often cited as key selective pressures shaping the hominid lineage (see reviews and references in Foley [1987, 1993], Potts [1998a, 1998b], Klein [1999], and Chapters 4, 5, and 17). This scenario invites a careful examination of responses to seasonality in extant savanna-dwelling primates.

Like most vertebrates, the large majority of primate species exhibit reproductive seasonality that reflects the seasonality of their habitats (see review in Chapter 11). Indeed, among savanna-dwelling primates, there are only two exceptions to the rule of seasonal reproduction: humans and baboons (genus *Papio*). This shared characteristic – the ability to reproduce throughout the year in seasonal environments – may be related to the extraordinary success of these two genera. While only humans (and their commensals) have spread across the globe, baboons have achieved a nearly continental distribution in Africa. Indeed, the genus *Papio*, increasingly treated as a single species with multiple subspecies (Jolly 1993), occupies habitats ranging from desert to semi-arid tropical savanna to temperate montane grasslands to moist evergreen forest (Estes 1991; Jolly 1993; Kingdon 1997).

These shared features of *Papio* and *Homo* – a wide geographic distribution, success in but not restriction to savanna environments, and nonseasonal reproduction – make analyses of seasonality in baboon behavior especially valuable in light of the role that seasonality is proposed to have played in selecting for unique human traits (Foley 1987, 1993). In this chapter, we examine seasonal patterns of behavior in the well-studied population of savanna baboons in the Amboseli basin at the foot of Mt Kilimanjaro. Amboseli is a semi-arid habitat and one of the drier habitats in which baboons have been studied (see review in Dunbar [1992]). We employ 16 years of behavioral data on adult females, combined with demographic and meteorological data, to test hypotheses about the impacts of the seasonal environment on baboon behavior. Our results are preceded first by a description of savanna seasonality and an outline of the hypotheses that we will test with these data and then by background on baboon ecology and on the Amboseli ecosystem.

The challenges of savanna seasonality

Savannas are tropical habitats dominated by grasses, with scattered drought-resistant trees and shrubs (Bourliere & Hadley 1983; Solbrig 1996; Lincoln *et al.* 1998). The term "savanna" sometimes is used to include subtropical grasslands as well. Savannas show great variability in rainfall across the year but little variation in mean daily temperature, and temperature fluctuations over the course of any given day are larger in magnitude than those in mean temperatures over the course of a year (Bourliere & Hadley 1983; Solbrig 1996). Accordingly, savannas do not exhibit the extreme seasonal shutdown of plant productivity exhibited by temperate-zone grasslands. However, considerable seasonality of plant productivity still occurs in savannas, driven by rainfall seasonality. Hence, a primary challenge for animals living in highly seasonal savanna environments is finding enough food and water during the dry season. For highly social species (most primates), social behavior will also be affected by seasonal changes in time spent foraging. Indeed, discussions about seasonal behavior in primates have centered on two issues: (i) the manner in which foraging behavior changes with season and (ii) the manner in which social behavior changes with season. For each of these issues, contrasting predictions have been made.

Hypotheses about seasonality of foraging behavior

The onset of the dry season in savanna habitats marks the beginning of a long period during which plant productivity is highly constrained. Grasses and many shrubs limit or cease their production of new leaves, grass seed heads vanish, the above-ground parts of many forbs disappear entirely, and fruits and flowers of shrubs and forbs become limited in abundance. How might primates in seasonal environments respond to dry-season food scarcity? Two alternatives have been proposed (see review in Foley [1987] and Chapter 8).

On the one hand, primates might respond to dry-season food scarcities by shifting to foods that are abundant but have low profitability (low ratio of nutrient to harvesting time) (Foley 1987) (see also discussions in Altmann [1998], Dunbar [1983], and Wrangham *et al.* [1991, 1998]). Such a seasonal shift to "fallback foods" typically will result in increased time spent foraging during the dry season relative to the wet season. Indeed, time spent foraging increases during the dry season for a number of primate species (baboons [Post 1981]; muriqis [Strier 1991]; two *Eulemur* species [Overdorff 1996]; tarsiers [Gursky 2000]). Studies of chimpanzees have also provided substantial direct evidence for the fallback foods hypothesis. Chimps increase their intake of herbaceous vegetation during times of fruit scarcity, and work on chimps has formed a model for our understanding of the importance of fallback foods (Wrangham *et al.* 1991, 1998; Malenky & Wrangham 1994).

Alternatively, during times of scarcity, primates may seek out novel foods that are highly profitable but difficult to acquire. This is sometimes proposed as the major strategy of early hominids, and the novel, highly profitable food in question is meat (Blumenschine 1987; Foley 1987, 1993; Potts 1998a, 1998b; Klein 1999) (see also Chapters 4, 5, and 17). There is only limited evidence for this "high-return foods" strategy among tropical human foragers. While many human foragers show marked effects of season on their foraging behavior, this is not commonly manifested as an increase in hunting time or in meat consumption during the dry season (see review in Chapter 9; see also Bunn *et al.* [1988] and Hawkes *et al.* [1991]). Among non-human primates, too, there is limited evidence that hunting increases during the dry season (baboons [Dunbar 1983]; chimpanzees [Stanford 1996; Stanford 1998]), but in general dry-season food scarcity appears to be a poor explanation for primate hunting (Stanford 1996; Stanford 1998; Mitani & Watts 2001) (See also Chapter 8).

These fallback foods and high-return foods hypotheses are not mutually exclusive. While some species or populations may pursue a relatively pure strategy of either type, any given population may pursue both strategies to some extent, shifting to fallback foods but supplementing periodically with high-return foods.

An additional question regarding dry-season foraging is whether primates diversify their diets during times of food scarcity. For species that specialize on one or a few classes of foods (e.g. fruits in the case of chimps), periods of scarcity may prompt the animals both to shift to fallback foods and to diversify their diets to include species and plant parts that are bypassed when fruit is abundant (Foley 1987; Wrangham *et al.* 1991, 1998) (See also Chapter 8). In contrast, for generalists such as baboons, food scarcity will result in reduced diet diversity during the dry season (Post 1982; Norton *et al.* 1987).

Hypotheses about seasonality in social behavior

How might social behavior be affected by the dry season? One hypothesis predicts that the nutritional stresses associated with food scarcity will lead to reduced social activity, while increased competition for food will lead to an expanded spatial distribution within groups. As a consequence, various measures of sociality – grooming rate, time spent in other social interactions, and time spent in proximity to other animals – should decrease in the dry season (Foley 1987) (See also Chapter 8). The underlying assumption here is that social activities are non-essential and will be sacrificed to meet the physiological demands of the dry season; resting time must remain fixed (or not fall below a minimum) as foraging time increases; and the seasonal difference will be taken out of social time. We refer to this as the "dispensable social time" hypothesis.

The alternative hypothesis assumes that social time is functionally important for maintaining social relationships, which in turn are critical in mitigating the effects of both inter- and intragroup competition (e.g. Seyfarth [1977]; Dunbar & Dunbar [1988]; Dunbar [1991]). Under this hypothesis, Dunbar and Dunbar (1988) and Dunbar (1992) propose that animals will conserve social time during food scarcity because social activities (primarily grooming) service relationships and hence represent "social glue" that maintains cohesion of social groups (Dunbar 1992). This hypothesis acknowledges that animals' time budgets must accommodate changes in foraging time but predicts that animals will reduce resting time rather than social time in order to accommodate the increased foraging demands of the dry season. We term this the "social glue" hypothesis.

Baboon ecology

Baboons (genus *Papio*) are large semi-terrestrial monkeys that occupy a wide range of habitats across the continent of Africa (Altmann & Altmann 1970; Jolly 1993; Kingdon 1997). Baboon populations typically are divided into stable social groups, most of which have between 20 and 100 members, including multiple adults and juveniles of both sexes (Altmann & Altmann 1970; Estes 1991). Hamadryas baboons in the horn of Africa deviate markedly from this basic social pattern (Kummer 1968; Stammbach 1987), and we exclude them from consideration here because of their unique socioecological adaptations. We use the term "savanna baboon" to refer to all members of the genus other than hamadryas baboons.

Savanna baboons are eclectic and omnivorous feeders, but this omnivory is combined with great discrimination. They feed very selectively, often choosing a small component of a plant and forgoing the remainder, or focusing on a single species within a genus (Hamilton *et al.* 1978; Post

Figure 6.1 Grass corms are the principal food resource for baboons during the dry season at Amboseli.

1982; Norton *et al.* 1987; Muruthi *et al.* 1991; Whiten *et al.* 1991; Byrne *et al.* 1993; Altmann 1998). Plants are the most important source of nutrients; invertebrate and vertebrate animals are eaten but contribute relatively little in calories and protein. In the habitats in which they are best studied (savannas), baboons rely heavily on grasses, consuming both the underground storage organs (corms; Fig. 6.1) and the leaves (Post 1982; Norton *et al.* 1987; Muruthi *et al.* 1991; Whiten *et al.* 1991; Byrne *et al.* 1993; Altmann 1998). Many of the foods consumed by baboons are available and consumed year round; in Amboseli, these include grass corms (Figs 6.2 and 6.3), tree gum, material gleaned from the dung of ungulates and elephants, and the blade bases of grasses (containing the meristem). However, some preferred foods, including the fruits of most species, flowers, green *Acacia* seeds, grass seedheads, and green grass blades (consumed in quantity only when they are new and low in fiber), are highly seasonal (Hamilton *et al.* 1978; Post 1982; Byrne *et al.* 1993; Altmann 1998).

Savanna baboons do not exhibit seasonal patterns of mating or birth; females may conceive and give birth in any month (Fig 6.4) (Melnick & Pearl 1987; Altmann 1980; Bercovitch & Harding 1993; Bentley-Condit & Smith 1997). However, Amboseli births do show a modest peak in August through October, corresponding to conceptions occurring most often from February through May. In fact, 242 of 495 (49%) live births occurred in the five months of the long dry season, June through October, and this is significantly greater than the expected number of 206 (42%) in this season (G test of goodness of fit: $G = 10.64$, $P < 0.005$). An analysis using circular statistics (see Chapter 11) indicates significant but weak clustering of births during the year (corrected vector length $r = 0.12$, $P < 0.001$).

Figure 6.2 Adult baboon digging grass corms (underground storage organs) to consume during the dry period of food scarcity at Amboseli.

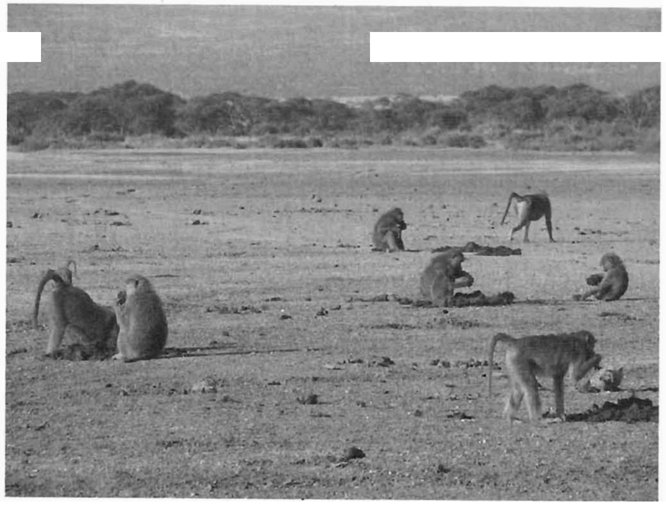

Figure 6.3 Baboons gleaning food from elephant dung during the dry season at Amboseli.

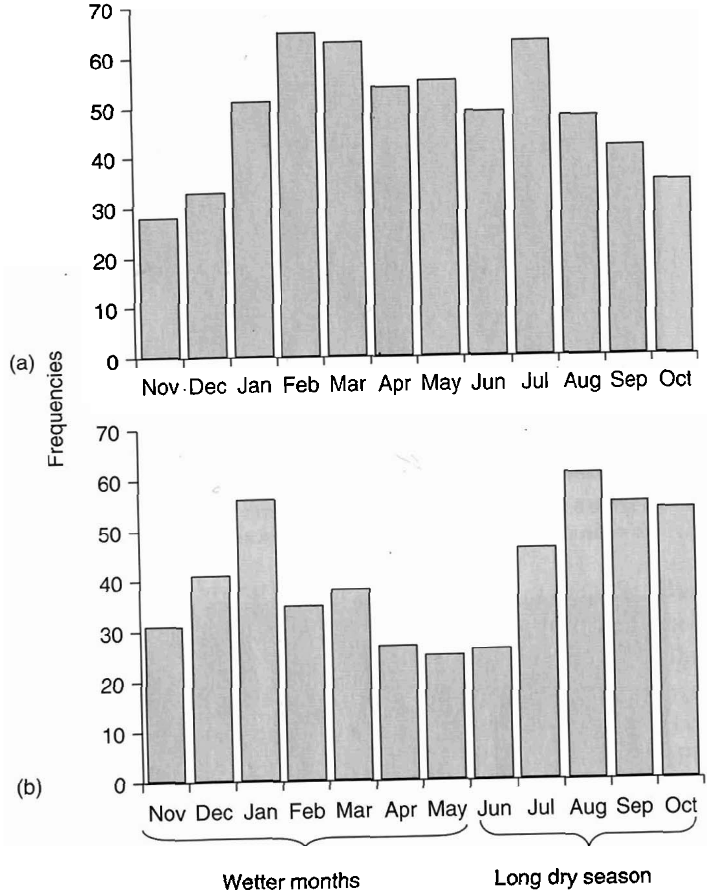

Figure 6.4 Distribution, by month, of (a) conceptions ($n = 586$) and (b) live births ($n = 495$) in Amboseli baboons. The x-axis represents the hydrological year in Amboseli, beginning with the onset of the rains in November (see Fig. 6.2). The difference between the total number of conceptions and the total number of live births represents a combination of miscarriages, stillbirths, and females that died during pregnancy.

Because gestation duration is the least variable life history stage, dates of live births are determined almost entirely by conception dates. Conception dates, in turn, are determined by the timing of the onset of cycling (menarche or postpartum) and the probability of conception. In baboons, these are both highly variable as a result of both stochastic and deterministic processes. For instance, onset of menarche shows modest seasonality, occurring significantly less often than expected during the long dry season (41 of 138 observed menarches occurred in these months, compared with 58 expected; $G = 10.83$, $P < 0.001$; using circular statistics, corrected vector length $r = 0.18$, $P < 0.01$). In contrast, resumption of cycling after a previous pregnancy shows almost no seasonal effect (205 of 499 resumptions occurred in the long dry season, compared with 208 expected, $G = 0.74$, not significant (NS); corrected vector length $r = 0.08$, $P < 0.05$). Hence, two somewhat similar processes, both of which contribute to the timing of births, are very different in the extent to which they show seasonality. We refer the reader to Chapter 11 for a more detailed discussion of this complex topic.

Amboseli ecology

The Amboseli basin (2°40′ S latitude, 1100 m altitude) is a semi-arid short-grass savanna ecosystem located in an ancient lake basin at the base of Mt Kilimanjaro in east Africa (Williams 1972; Western & van Praet 1973; Behrensmeyer & Boaz 1981; Behrensmeyer 1993; Hay *et al.* 1995). Mean annual rainfall is 348 mm, but the range of annual rainfall is quite large, from less than 150 mm to more than 550 mm (Fig. 6.5a) (Altmann *et al.* 2002).

In the pattern typically described for the area, rainfall occurs in two seasons centered in November–December (the "short rains") and in March–May (the "long rains"), with a "short dry season" in January and February and a "long dry season" during June through October. However, the only component of this pattern that does not vary from year to year is the long dry season. The short rains or the long rains, or both, may fail, or substantial rain may fall during the short dry season. This variability contrasts sharply with the predictability of the long dry season: between the end of May and the last few days of October, virtually no rain falls (Fig. 6.5b) Altmann *et al.* 2002). Mean daily maximum and minimum temperatures exhibit small but predictable seasonal changes; diurnal changes are much larger in magnitude than those that occur seasonally (Altmann *et al.* 2002).

In addition to experiencing year-to-year variability in rainfall, Amboseli has undergone dramatic long-term habitat change over the past four decades (Struhsaker 1973, 1976; Western & van Praet 1973; Hauser *et al.* 1986; Isbell *et al.* 1991; Behrensmeyer 1993; Koch *et al.* 1995; Altmann 1998: 15–19; Cutler *et al.* 1999). In the central part of the Amboseli basin, the dominant tree species, *Acacia xanthophloea* (the fever tree), and various plant species associated with it, have experienced dramatic decline, with complete die-off in some places within Amboseli. At the same time, the number and size of freshwater swamps and ponds has increased

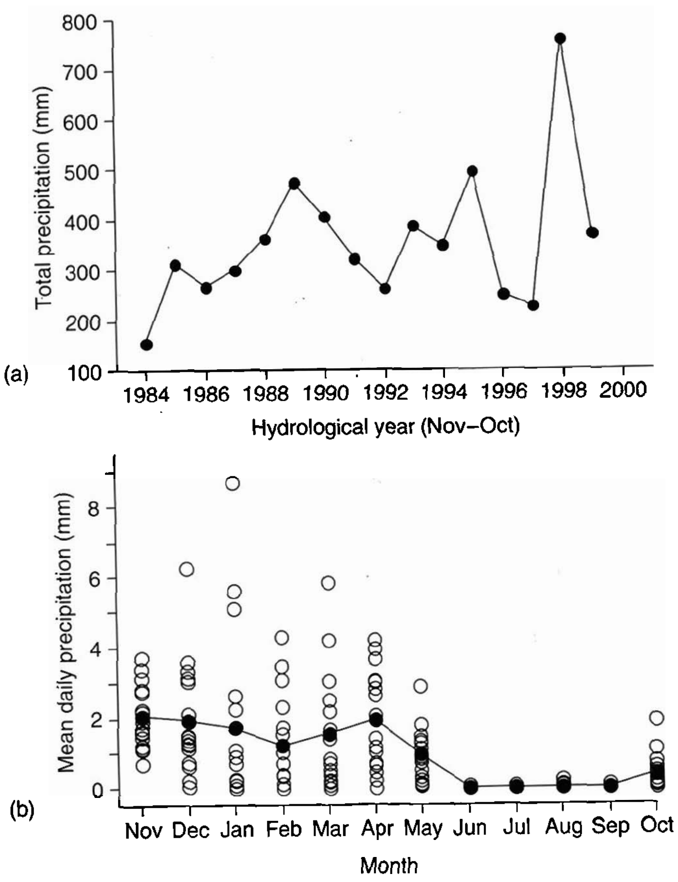

Figure 6.5 Rainfall in Amboseli, 1984–99. (a) Total annual precipitation, by hydrological year. Hydrological year 1984 begins in November 1983. Hydrological year 1998 was a large El Niño event; there has been no trend of increasing or decreasing rainfall over time. (b) Mean daily precipitation by month. Values for individual years are indicated by open circles; mean across years indicated by closed circles. Virtually all rain in October occurred in the last few days of the month. Figure modified from Altmann *et al.* (2002); see that reference for rainfall and climate in Amboseli over a longer time period.

substantially in some areas of the basin, although no change in mean annual rainfall has occurred (Fig. 6.5a) (Altmann *et al.* 2002). In addition, mean maximum daily temperature has increased by more than 5 °C since 1976, a change that is an order of magnitude greater than changes associated with global warming (Altmann *et al.* 2002).

These changes have been attributed variously to heavy browsing of both adult trees and seedlings by elephants and other browsers, to natural aging of the woodlands, to a rising water table, and to a combination of all three (Western & van Praet 1973; Young & Lindsay 1988; Altmann 1998; Altmann *et al.* 2002). However, the local changes in Amboseli are occurring against the backdrop of a much more high-profile change that has aroused international interest: the glaciers on the top of Mt Kilimanjaro experienced an 80% reduction during the twentieth century and are predicted to disappear entirely between 2015 and 2020 (Hastenrath & Greischar 1997; Thompson *et al.* 2002). Amboseli lies at the base of Kilimanjaro, and runoff from Kilimanjaro provides the major source of ground and surface water in Amboseli (Behrensmeyer 1993; Hay *et al.* 1995). While heavy browsing by an increasing population of elephants, domestic stock, and some other browsers (Esikuri 1998; Moss 2001; Western & Maitumo 2004) certainly has played a role in the habitat change in Amboseli, the larger-scale changes associated with glacier recession on Kilimanjaro are probably contributing as well.

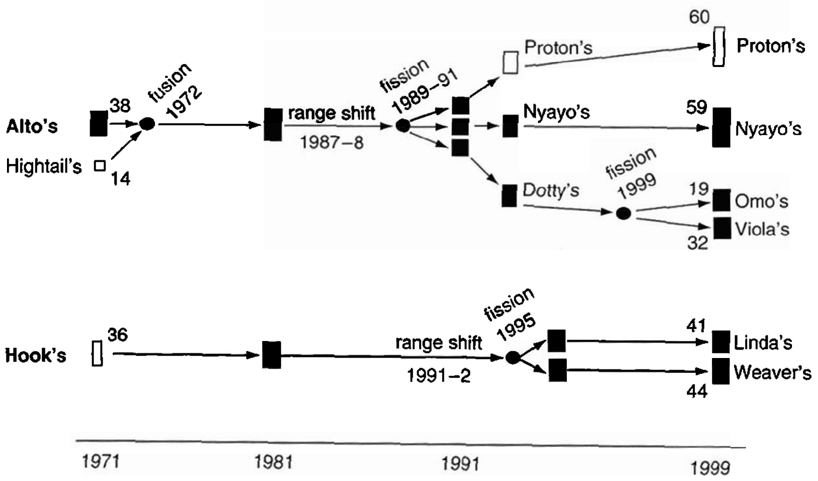

Figure 6.6 Amboseli study groups through time. Solid rectangles represent study groups; open rectangles represent non-study groups that were monitored opportunistically. Both Alto's and Hook's groups underwent permanent fissions, and each also underwent a home range shift prior to fission (see text for details). Group sizes in 1971 and at the end of 1999 are indicated next to the group symbols.

Ecological and research history of the Amboseli baboon population

In the early 1960s, the baboon population was moderately large and the Amboseli basin was dominated by *A. xanthophloea* (fever tree) habitat, which the baboons relied on for both food and sleeping sites (Altmann & Altmann 1970; Altmann *et al.* 1985; Altmann 1998). Between 1964 and 1969, the population underwent a precipitous decline, probably as a consequence of the die-off of the fever tree woodland in the central part of the basin (Western & van Praet 1973; Altmann *et al.* 1985; Altmann 1998). Over the next decade, the population stabilized, but at a much smaller size than in the early 1960s, and during the late 1980s and 1990s the population grew moderately in size (Altmann *et al.* 1985; Alberts & Altmann 2003). This growth occurred after several social groups abandoned the home range that they had occupied in the central basin during the 1970s and 1980s (Bronikowski & Altmann 1996; Alberts & Altmann 2001; Altmann & Alberts 2003). In each case, the groups moved approximately 8 km west (Alto's in 1987–88, Hook's in 1991–92), to an area still within the Amboseli basin but with a relatively high density of *A. xanthophloea* trees and a relatively low density of baboons. This "western basin" is slightly elevated relative to the central basin and was rarely used by elephants or other browsers when the baboon study groups first moved there, perhaps because of poaching or other human disturbance in that area. These two factors may have contributed to the relative health of the western fever tree woodlands at that time – the elevation resulting in slower effects of changes in the water table and the low elephant density resulting in reduced pressure on the fever tree population. However, during the 1990s, the fever trees in the western basin gradually began to show signs of decline, perhaps partly because elephants and other browsers began using the area more heavily during that period. The impact of this new die-off on the baboons, and their response to it, remains to be seen.

Methods

Study groups, data collection, and subjects

Data were collected on wild-feeding adult female baboons between January 1984 and December 1999 (we exclude data from members of Lodge Group, who augmented their diet with human refuse; see Altmann & Muruthi [1988] and Muruthi *et al.* [1991]). Our two original study groups, Alto's and Hook's groups, fissioned in 1989–91 and 1994–95, respectively (Fig. 6.6). In our analyses, we treated Alto's group and its fission products as one subpopulation and Hook's group and its fission products as a second subpopulation.

Data were collected by R. S. Mututua, S. N. Sayialel, J. K. Warutere, and P. M. Muruthi, who have a cumulative 47 person-years of experience observing baboons. Further, Mututua has contributed between 30 and 100% of the point samples in every year of data collection and has been active in training all the other observers, ensuring great consistency over the entire 16-year period.

Data were collected as ten-minute focal samples (Altmann 1974) on all adult females in the study groups. Adult females within each group were sampled in random order during all active daylight hours, 07.00–18.00 (or 08.00–16.00 between 1988 and 1991). The result was approximately 35 000 focal samples of ten minutes' duration on 124 adult females in two subpopulations (six social groups). The subjects were born between 1962 (estimated) and February 11, 1995. Birth dates were estimated for 23 of the 124 subjects (those born before July 1971 in Alto's and before October 1977 in Hook's); for all other subjects, birth dates were known exactly. Sampling began in January 1984 on females that were already adult at that time; maturing females were added to the sampling schedule when they reached menarche. Focal subjects were between 4.5 and 27 years of age at the time of sampling.

Focal sampling

Focal samples involved the collection of "point" data every minute during the sample (signaled by a timer), as well as "all occurrences" data on agonistic interactions, mounts and mate guarding, and grooming. At each "point," the observer recorded the focal's activity (Table 6.1), her position (standing or sitting), the position of her infant and whether it was suckling, whether any other animals (other than her dependent infant)

Table 6.1 *Mutually exclusive and exhaustive activity categories of focal subjects*

Activity	Definition
Feed	Focal handles or processes food item, or puts food item into the mouth
Move	Focal walks, runs, or climbs
Groom	Focal systematically picks through the fur of another individual with the hands and sometimes the mouth (self-grooming is not recorded as groom)
Be groomed	Another individual picks through focal's fur
Other social	Focal engages in a social interaction other than grooming (agonistic interaction, greeting, play, etc.)
Rest	Focal is sedentary, not feeding, and not interacting

were within 5 m of her, and details about the identities of any such "neighbors." Three to four ten-minute samples per hour were collected in this manner for the duration of the study.

At each point for which "feeding" was recorded, the observer also recorded the type of food being eaten (Table 6.2); species was recorded only for the more common and well-known species. Data on foods consumed were available only for 1991–99 for Hook's subpopulation and for 1996–99 for Alto's subpopulation.

Data analysis

Time budgets

We estimated the proportion of time spent in each activity from the proportion of sample points for which that activity was recorded. Analysis of time budgets has limitations; time spent feeding, for instance, is not always a good proxy for calories consumed (e.g. see discussions in Alberts *et al.* [1996: 1270] and Altmann [1998: 106]). However, time budgets will broadly reflect the choices that animals make about the relative importance of various activities.

For the purposes of analysis, we combined the categories "moving" and "feeding" into a single category, "foraging." Baboons make a living by moving through their home range, selecting food items as they move. Thus, our activity category "moving" occurs, for the most part, as the baboons move to and between nutrient or water sources, while "feeding" occurs as the baboons harvest and ingest these nutrients. We view time spent feeding and moving combined as reflecting the amount of time that the baboons invest in obtaining food.

To measure the proportion of time spent in social activities, we combined "grooming," "being groomed," and "other social interactions." In practice, the large majority of social time was grooming time; other social interactions were typically brief events and together constituted approximately 2.5% of social time (approximately 0.25% of total time).

We also measured the proportion of time spent with no neighbor within 5 m. We view time spent with no neighbor as an indirect and inverse gauge of the time devoted to socializing. The presence of neighbors facilitates interactions and probably increases interaction rates, so that as time spent with no neighbor increases, socializing will generally decrease. We also view time spent with no neighbor as a gauge of the intensity of competition. Animals should tolerate greater proximity when foraging competition is less intense. Thus, an increase in time spent with no neighbors will

Table 6.2 *Types of food eaten by female baboons in Amboseli (see also Fig. 6.7). The 5% of feeding time not accounted for by these foods is accounted for by a variety of opportunistically consumed foods (Post 1982; Altmann 1998) and by unidentified foods. Water and vertebrate foods are included here for interest but occupy a tiny fraction of feeding time. Food types are ranked according to the relative proportion of feeding time devoted to them*

Type	Rank order	Description	Mean proportion of feeding time devoted to it (± s.e.)
Grass corms	1	Small perennial underground storage organs of grasses; the major representative is *Sporobolus rangei* (formerly *kentrophyllus*)	0.31 ± 0.03
Fruits	2	Fruits of shrubs and forbs; the major representative is *Trianthema ceratosepala*, but other species contribute importantly as well (see Table 6.3)	0.22 ± 0.03
Grass blades	3	Green leaves of grasses; baboons eat a wide variety of species	0.079 ± 0.013
Tree gum	4	The vast majority of gum consumed is from the fever tree, *Acacia xanthophloea*; occasionally gum of *Acacia tortilis* is consumed as well	0.065 ± 0.007
Seeds and material gleaned from dung	5	Seeds on ground and items gleaned from the dung of ungulates and elephants; baboons search primarily for seeds, but adult and larval invertebrates are sometimes abundant in the dung as well	0.057 ± 0.010
Flowers	6	Blossoms and buds from forbs, shrubs, and trees; three species represent the large majority of flowers eaten: *Acacia tortilis*, *Acacia xanthophloea*, and *Ramphicarpa montana* (an annual, highly rain-dependent forb)	0.053 ± 0.011
Grass blade bases	7	The meristematic tissue at the base of grass blades; to consume this, baboons will pull a blade of grass out of its sheath, bite off the lower portion of the blade, and discard the remainder; *Sporobolus consimilis* (elephant grass) is the main grass consumed in this way	0.040 ± 0.004

Table 6.2 (*cont.*)

Acacia seeds	8	Green and sometimes brown (dried) seeds removed from pods of *Acacia tortilis* or *Acacia xanthophloea*; green seeds of *tortilis* trees are available primarily in July through September, while green *xanthophloea* seeds are available in December–January.	0.036 ± 0.007
Grass seedheads	9	The baboons eat seedheads from a wide range of grass species	0.035 ± 0.010
Leaves of shrubs and forbs	10	Major contributors include *Lyceum* "*europeaum*" and *Salvadora persica*, but other species contribute as well	0.032 ± 0.004
Invertebrates	11	Grasshoppers, beetle larvae, and lepidopteran larvae are the major contributors	0.024 ± 0.007
Vertebrates	NA	Small vertebrates, including reptiles, birds, and mammals	Less than 0.001
Water	NA	During the dry season, permanent water holes and wells dug by the local Maasai people are the sources of water; during the wetter months, the baboons take advantage of seasonal rain pools	Less than 0.005

s.e., standard error.

generally reflect an increase in overall levels of foraging competition within the group.

Seasons

As noted above, the only reliable aspect of the yearly rainfall patterns in the study habitat was the long dry season, June through October. The remaining seven months of the year were highly variable from year to year. Rather than define seasons differently for each year according to the rainfall pattern in that year, we simply grouped the five months of the reliable long dry season, June through October, into a single period and the seven more variable months of November through May into a second period (the "wetter months"). Grouping November through May into a single season will undoubtedly obscure some behavioral variation that is dependent on rainfall; in particular, because those months were often dry, it will tend to reduce our ability to detect seasonal differences. Hence, this is a relatively conservative approach to examining patterns of seasonality.

Bivariate analysis of seasonal effects on activities

In our first analysis, we categorized each sample according to season, year, and subpopulation. We then calculated the total proportion of time spent in each activity for each subpopulation each year. This resulted in 27 "subpopulation-years" of data for the wetter months and 31 "subpopulation-years" of data for the long dry season (because we were missing complete "wetter months" data for four subpopulation-years). We next took the mean proportion of time spent in each activity for dry versus wetter months across all years, and used *t*-tests to examine seasonal differences in foraging, resting, socializing, and time spent with no neighbor within 5 m. Because successive years within a subpopulation may not be independent of each other, this procedure may result in some pseudo-replication. However, we also know that temporal changes in activity patterns have occurred over the years (Bronikowski & Altmann 1996), so that pooling across years will obscure important temporal differences. We dealt with the potential pseudo-replication by employing a P value for significance of $P = 0.01$ rather than the traditional $P = 0.05$.

Analysis of variance in time budgets

We also used a general linear model (using JMP™ software) to analyze variance in time spent in each activity. The predictor variables in our model were season (long dry versus wetter months), subpopulation, mean number of adult females in each group (as a measure of group size), total annual rainfall (total in millimeters fallen during the hydrological year), and year of study. We included subpopulation as a predictor variable because of the possibility that differences in home range between the two subpopulations contributed to differences in time budgets. We included mean social group size because a number of models predict that this should affect time budgets (e.g. Altmann [1980]; Dunbar [1992]). We included year of study because we knew from previous work that activity patterns change over the years, due to habitat changes, yearly variation in rainfall, and shifts in home range by the study groups (Bronikowski & Altmann 1996).

Analysis of variance in food eaten

We categorized baboon foods into the food component or plant part that the animals ate. We then analyzed variance in the proportion of feeding time devoted to each food type as a function of season, year of study, yearly rainfall, and subpopulation.

Phenology

Baboon foods in Amboseli fall into three categories of seasonality. Some show year-round availability. Others are highly seasonal, available only after the rains. The third category exhibits what we call "damped seasonality." That is, individual species can be highly seasonal in their productivity, but baboons can eat foods in this category in most months of the year (Table 6.3). This is because the "seasons" vary greatly between species and so collectively do not correspond to the "dry season–wetter months" dichotomy that we have presented. The consequence is that, by careful searching and by exploitation of many different species, baboons can eat foods in this category in most months of the year (Table 6.3).

The phenology of baboons' foods in Amboseli is well described (Post 1982: 12–14; Altmann 1998: 74–78). We supplemented these published descriptions with a new analysis of presence–absence data collected between 1985 and 1994 on fruits, *Acacia* pods, and the leaves of shrubs and forbs, three of the more seasonal foods in the diet. Phenological information from these various sources is summarized in Table 6.3.

Results

Time spent making a living changed with season and changed over time

Female baboons spent more time foraging and less time resting in the long dry season than during the wetter months (Table 6.4; Fig. 6.7 and 6.8). The

Table 6.3 *Phenology of baboon foods in Amboseli (see also Post [1982: 12–14] and Altmann [1998: 74–88]). Foods are listed in rank order (according to proportion of feeding time devoted to them)*

Type	Rank order	Basic phenology	Phenological description
Grass corms	1	Year round	Year-round availability for the predominant species, although corms may vary somewhat in nutrient content across seasons
Fruits	2	Damped seasonality	Some species highly seasonal, such as *Salvadora persica* (fruits from July or August until November or December) and *Commicarpus* spp. (fruits only after rains); other species available for many months, such as *Azima tetracantha* (fruits from May or June through January or February); two are available year round, at least in small quantities: *Withania somnifera* and *Trianthema ceratosepala*; this latter contributes the largest amount of fruit to the diet as baboons forage for it intensively during the dry season
Grass blades	3	Seasonal	New growth occurs immediately after rains begin; peak in February–May
Tree gum	4	Year round	Young trees are especially good sources, but trees exude gum all year round
Seeds and material gleaned from dung	5	Year round	Ungulate and elephant density in the baboons' home range varies seasonally, but dung and seeds are always abundant on the ground
Flowers	6	Damped seasonality	Three species are important: *A. tortilis* and *A. xanthophloea*, and *Ramphicarpa montana*; each is highly seasonal, but their peaks are distributed over the year: *tortilis* in January–April, *xanthophloea* in September–November, and *R. montana* after any rainy period
Grass blade bases	7	Year round	Blade bases of *Sporobolus consimilis*, a large perennial grass that is the largest contributor to this food type, are available year round
Acacia seeds	8	Damped seasonality	New pods/seeds are produced by *A. xanthophloea* in December–March, by *A. tortilis* in July–September; dry brown pods with dried seeds available all or most of the year
Grass seedheads	9	Seasonal	Development occurs approximately one month after rains begin
Leaves of shrubs and forbs	10	Seasonal	The preferred leaf is of *Lyceum "europaeum,"* which is deciduous during dry periods. Many species of shrubs and forbs are evergreen, but the baboons prefer new leaves, which are rain-dependent in most species
Invertebrates	11	Damped seasonality	Peak availability of larvae is seasonal but varies across species

Table 6.4 *Analyses of variance in time spent foraging, resting, socializing, and alone*

Foraging			**Resting**	
Whole model: adjusted $R^2 = 0.35$, $P < 0.0001$			Whole model: adjusted $R^2 = 0.33$, $P < 0.0001$	
Effect	***F***	***P***	***F***	***P***
Season	**16.8**	**0.0001**	**17.97**	**< 0.0001**
Year	**11.54**	**0.0013**	**9.04**	**0.0041**
Group size	0.14	0.71	0.11	0.74
Rainfall	1.49	0.23	1.21	0.28
Subpopulation	0.0004	0.98	0.49	0.49
Alone (no neighbor)			**Socializing**	
Whole model: adjusted $R^2 = 0.088$, P = 0.084			Whole model: adjusted $R^2 = 0.16$, P = 0.015	
Effect	**F**	**P**	**F**	**P**
Season	0.04	0.84	3.08	0.085
Year	**9.36**	**0.0035**	**6.28**	**0.015**
Group size	**5.29**	**0.026**	0.04	0.84
Rainfall	1.02	0.32	0.7	0.41
Subpopulation	0.8	0.38	2.36	0.13

Bold type indicates terms with significant effects ($P < 0.01$) or strong trends.

clear but unsurprising inference is that quality of life is higher during the wetter months and that the dry season represents an ecological challenge for the animals.

Female activity profiles also changed substantially over time (Table 6.4; Fig. 6.8). From the mid 1980s to the mid 1990s, baboons in both subpopulations decreased foraging time and increased resting time (Fig. 6.8). This change coincided with the move that each subpopulation made to the western part of the Amboseli basin, where the fever tree woodland was large and healthy. From the middle to the end of the 1990s, however, foraging time increased for both subpopulations in each season, and resting time decreased. This may signal the end of a phase of relatively rapid density-independent growth that occurred immediately after each group moved. Alternatively, or in addition, the decrease in quality of life may be a consequence of the gradual decline of the fever tree woodlands that we observed in the western basin as the 1990s progressed.

The two subpopulations show remarkable similarity in their activity profiles; no effect of subpopulation on time spent in any activity is evident in the analysis. While activity patterns varied significantly across years, this variability was not predicted by yearly differences in rainfall. Similarly, female group size, which varied from 6.5 to 18 adult females, did not predict time spent foraging or resting (Table 6.4).

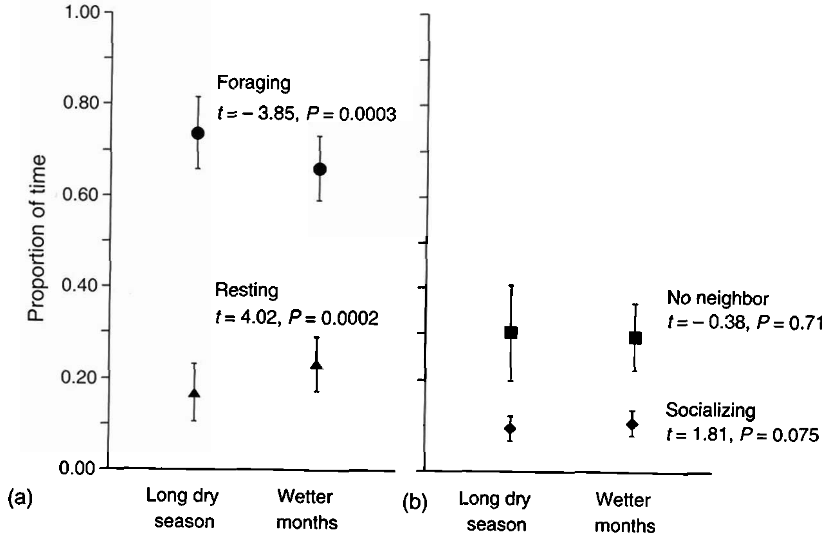

Figure 6.7 Seasonal differences in (a) time spent foraging and resting and (b) time spent socializing and with no neighbor. Each point represents the mean value (± standard deviation) of 31 group-years for long dry season and 27 group-years for wetter months (see text). Foraging time is calculated as the sum of moving and resting time. *t*-Tests are two-tailed.

Social time was unaffected by season but changed over time

Both the bivariate analysis and the analysis of variance indicated that season had no effect on time spent in social activities or on time spent with no neighbor (Figs. 6.7 and 6.9). However, both of these measures of socializing changed over time (Table 6.4). Specifically, as quality of life increased after the move west, time spent alone decreased and time spent socializing tended to increase in both seasons (Figure 6.9). Neither subpopulation nor yearly rainfall affected social life. However, when groups were smaller, females showed a trend towards spending more time with no neighbor ($P = 0.026$) (Table 6.4).

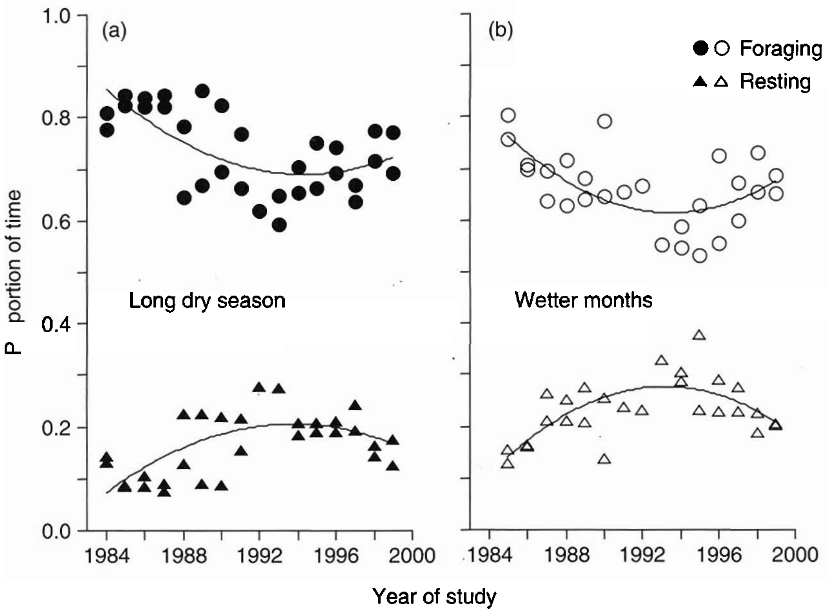

Figure 6.8 Amboseli baboons spend more time foraging (circles) and less time resting (triangles) in the dry season (a) than in the wetter months (b). Each point represents the yearly value for one subpopulation, and subpopulations are pooled in the graph because subpopulation explained no variance in activity budgets (Table 6.4). From 1984 to the mid 1990s, a gradual improvement in living conditions is evidenced by the decrease in foraging time and increase in resting time, but this reverses after the mid 1990s. These temporal effects are evident in both dry and wetter months (curves are fitted second-order polynomials; see Table 6.4 for analysis of variances).

Baboon diets had seasonal components but showed relative stability across seasons

Only four food types showed highly seasonal patterns of consumption in Amboseli: grass corms, grass blades, grass seedheads, and shrub/forb leaves (Fig. 6.10; Table 6.5) (grass seedheads are not significantly seasonal in our model because they show a pattern of consumption that is slightly shifted – by one month – relative to our definition of season). Shrub and forb leaves constitute a very small fraction of feeding time (Table 6.2; Fig. 6.10), indicating that grasses – their corms, blades, and seedheads – are the only foods in the Amboseli baboon diet that exhibit important seasonal patterns of consumption (Table 6.5; Fig. 6.10).

By far the largest set of food types in the baboon diet comprised those that showed damped seasonality. Each species shows a different temporal pattern of availability of, for instance, fruit, but the baboons mitigate this variability by exploiting a succession of species that are productive at different times of the year (Tables 6.3 and 6.5). Thus, the baboons achieve stability in their diet by carefully searching for and exploiting a large number of different species and plant parts across the year. They cannot achieve complete stability of food intake in this way; foods with damped seasonality still show considerable heterogeneity across months in their contribution to the diet (Fig. 6.11). However, this is not linked strictly to patterns of rainfall and the dry season because, as described above, different species have different phenologies. The result is that although the baboons eat different species of *Acacia* seeds in different months, they eat *Acacia* seeds in some quantity in almost every month. This is also true of flowers. Fruits show a complex pattern of availability across species, but fruits of some sort are available and consumed in every month (Table 6.3; Fig. 6.11).

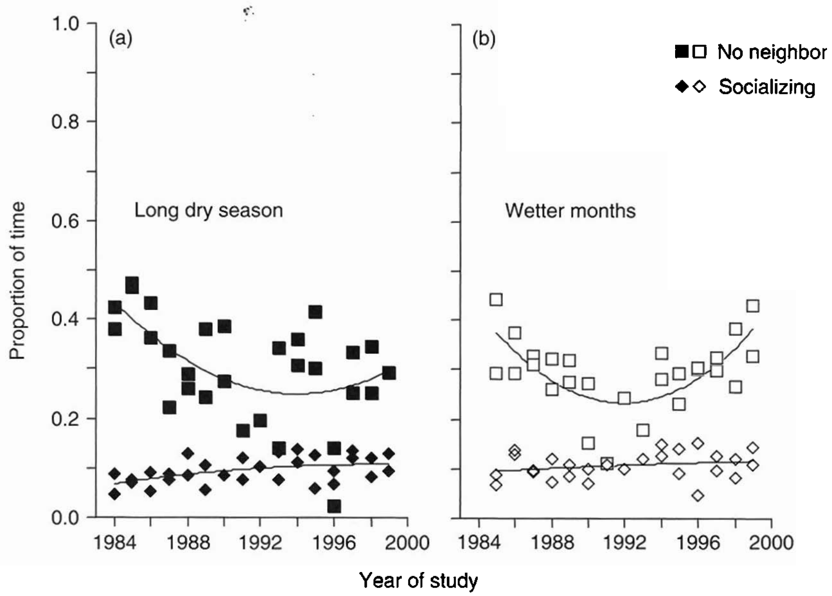

Figure 6.9 There is no significant effect of season on time spent alone (squares) or time spent socializing (diamonds), but a marked effect of year is evident. Proportion of time with no neighbors within 5 m reached a low point in the mid 1990s, when foraging time was at its lowest and resting time at its highest (see Fig. 6.5). Each point represents the yearly value for one subpopulation; subpopulations are pooled in the graph because subpopulation explained no variance in activity budgets (Table 6.4).

Table 6.5 *Analyses of variance in proportion of feeding time devoted to each food type. Food types are shown in* ***bold face*** *if the model explained variance in their consumption; similarly, effects are shown in* ***bold face*** *if they explained a significant amount of the variance in feeding on that food type. Foods are ranked according to proportion of feeding time devoted to them. See Table 6.3 for detailed phenology*

Rank order	Food type	Phenology	Whole model		Effect of season		Effect of year		Effect of rainfall		Effect of subpopulation	
			Adjusted R^2	P	F	P	F	P	F	P	F	P
1	**Grass corms**	Year round	**0.78**	**< 0.0001**	**64.95**	**< 0.0001**	1.4	0.25	**7.61**	**0.0125**	2.06	0.17
2	Fruits	Damped seasonality	0.24	0.0567								
3	**Grass blades**	Seasonal	**0.53**	**0.0008**	**29.76**	**< 0.0001**	0.01	0.94	0.22	0.64	0.05	0.82
4	**Gum**	Year round	**0.43**	**0.005**	0.42	0.52	1.72	0.21	**20.09**	**0.0003**	0.05	0.82
5	Material gleaned from dung	Year round	0	0.95								
6	Flowers	Damped seasonality	0	0.5								
7	Grass blade bases	Year round	0.21	0.0736								
8	*Acacia* seeds	Damped seasonality	0	0.72								
9	**Grass seedheads**	Seasonal	**0.37**	**0.0105**	2.45	0.13	6.68	0.0182	1.44	0.24	0.24	0.63
10	**Shrub/forb leaves**	Seasonal	**0.72**	**< 0.0001**	**26.21**	**< 0.0001**	**9.07**	**0.0072**	1.32	0.26	**5.4**	**0.031**
11	Invertebrates	Damped seasonality	0.13	0.16								

Bold type indicates terms with significant effects or strong trends.

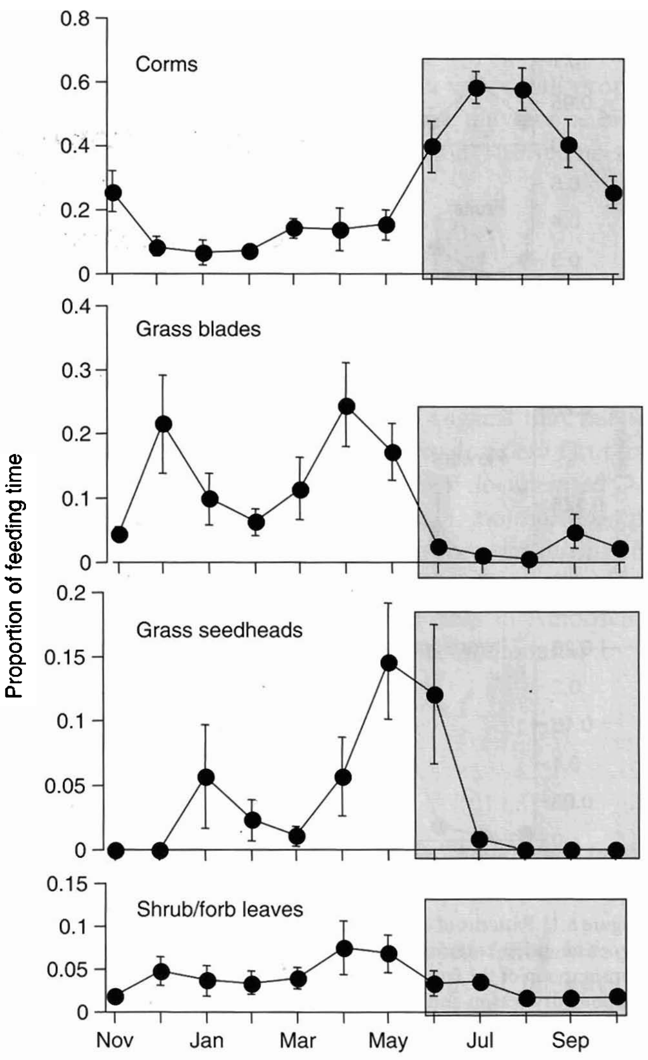

Figure 6.10 Food types that show seasonal patterns of consumption. Mean proportion of feeding time (± standard error [s.e.]) devoted to each food type is plotted against month of the year, beginning with November (the first wet month after the long dry season in Amboseli). Shaded boxes enclose the long dry season (June through October). See also Tables 6.2, 6.3, and 6.5.

Vertebrate animals accounted for a tiny fraction of the feeding time of female baboons in Amboseli (less than 0.1% of feeding time) (Table 6.2). Post (1982) recorded that 1% of feeding time in Amboseli was devoted to vertebrates and invertebrates combined, suggesting that in his study, as in

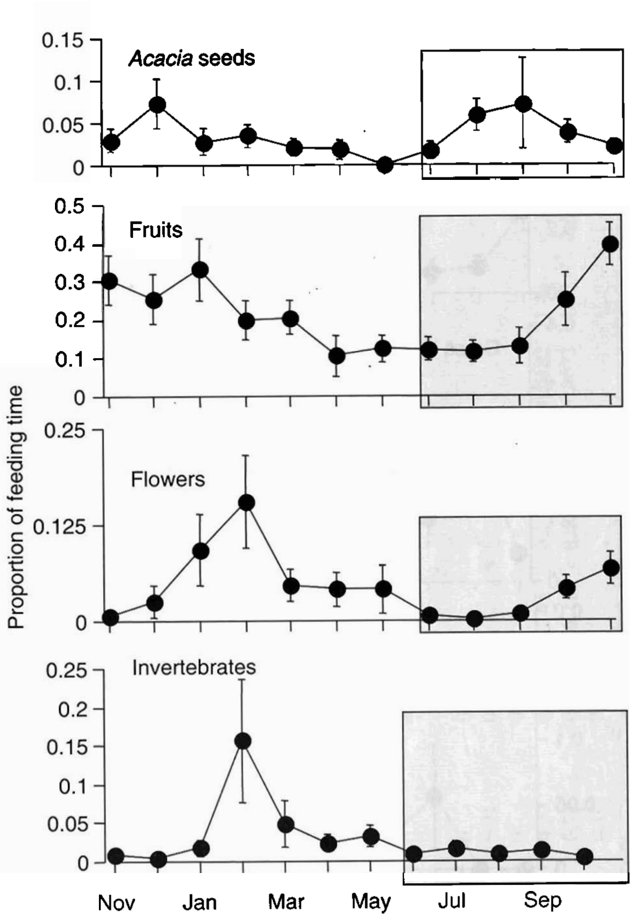

Figure 6.11 Patterns of consumption for food types that show damped seasonality in consumption patterns. In all cases, heterogeneity across months is evident, but consumption of the fruits, seeds, or flowers of at least some species occurs in both the long dry season and the wetter months. Conventions as in Fig. 6.7. See also Tables 6.2, 6.3, and 6.5.

ours, little feeding time was devoted to vertebrate prey, even for the adult males. Post (1982) notes that animal prey may be nutritionally important even if little time is devoted to it. This point may be relevant for invertebrates, which show measurable consumption in most months of the year. However, vertebrate prey in particular occupied so little feeding time for females in this study that it cannot be of great general importance.

Almost no variable in our model, other than season, affected the proportion of time spent on different food types (Table 6.5). Gum is consumed more heavily in drier years, and the leaves of shrubs and forbs have experienced a decrease in consumption over the course of the study. However, as noted, shrub/forb leaves occupy a very small proportion of feeding time overall, suggesting that this decrease may not be biologically significant for the animals. The two subpopulations showed no significant differentiation in diet.

Baboon diets changed over time

We did not observe any changes in time spent on different food types over the 1990s (our feeding data were available only for this decade; see Methods). However, we do have evidence to suggest that baboon diets have experienced substantial shifts over the three decades of our long-term study. Both Post (1982) and Altmann (1998) documented Amboseli baboon diets in the mid 1970s. In that period, *A. xanthophloea* products occupied substantially more feeding time than they did during the 1990s (Figure 6.12). This change in the importance of fever tree products is related to the change in the density of these trees in Amboseli. As the trees became less abundant, the baboons accommodated by altering their diets.

Discussion

The "fallback foods" strategy versus the "high-return foods" strategy

Female baboons in Amboseli certainly employed fallback foods: grass corms, available all year round, were the focus of intensive foraging activity only during the dry season, when key preferred foods (notably green grass blades and fruit) were scarce (Figs. 6.10 and 6.11) (see also Post [1982], Byrne *et al.* [1993], and Altmann [1998]). As a consequence, foraging time increased dramatically during the dry season. Grass corms require considerable processing time, so although they are reasonably rich in both protein and energy (Altmann *et al.* 1987; Byrne *et al.* 1993; Altmann 1998), their profitability is low. High-return foods played little role in the dry season diet of Amboseli females; vertebrate prey occupied only a tiny fraction of feeding time, and invertebrate prey were consumed in low quantities throughout the year, with a marked peak in one of the wetter months (Tables 6.2 and 6.5; Fig. 6.11).

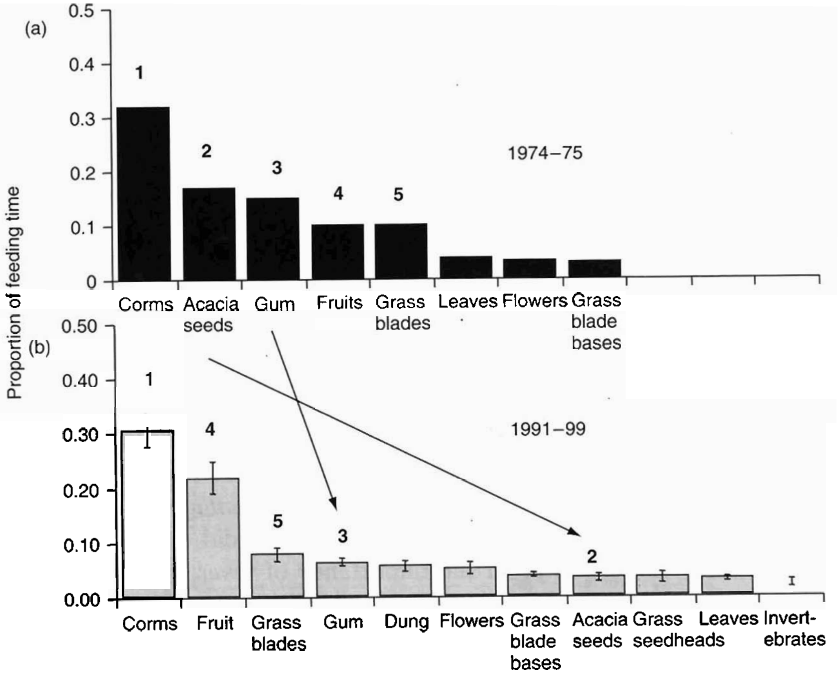

Figure 6.12 Proportion of feeding time spent on the ten major food types of Amboseli baboons. (a) Data reported by Post (1982) for the year 1974–75, with rank order of the food given above the bars for the top five foods (totaling 90% of feeding time). (b) Data from this study, pooling the two subpopulations, Hook's (1991–99) and Alto's (1996–99). Subpopulations are pooled in the graph because subpopulation explained no variance in feeding on various foods (Table 6.5). Numbers given above the bars indicate the rank order for the food type in Post's study. Note that in Post's study, *Acacia* gum and seeds were rank-ordered 2 and 3, respectively. By the 1990s both foods had dropped in importance, reflecting the fact that *Acacia* trees were less abundant in the 1990s than in the 1970s. Note also that in the 1990s, the top five foods constituted only 73% of feeding time.

Baboon foraging as a "handoff" strategy that mitigates seasonality

Only a few food types – notably the grasses – showed marked seasonality in their consumption by baboons, while many other important food types, including fruits, tree gum, material gleaned from dung, flowers, and invertebrates, were consumed in almost every month of the year. Indeed, even the grasses can be viewed as contributing to the diet in a constant manner across the year – the baboons simply switched from above-ground parts to below-ground parts during the dry season.

This suggests that the baboon foraging strategy might be thought of as a "handoff" strategy rather than a "fallback" strategy. Baboons achieve relative dietary stability partly by tracking carefully a large number of species and plant parts over the year and selectively exploiting foods as they become available. Even acknowledging that the succession of foods exploited – for instance, the fruits and flowers of different species – are not equivalent in their nutrient content (Altmann *et al.* 1987; Byrne *et al.* 1993; Altmann 1998), the result will be a constantly changing diet that probably allows the animals to maintain a relatively steady nutrient intake throughout the year. Detailed descriptions of the diets of other baboon populations support this notion (chacma baboons in Okavango, Botswana, and Kuiseb, Namibia [Hamilton *et al.* 1978]; yellow baboons in Mikumi, Tanzania [Norton *et al.* 1987]; chacma baboons in the Drakensberg Mountains, South Africa [Byrne *et al.* 1993]; see also Whiten *et al.* [1991]). This handoff strategy occurs even in populations with no fallback reliance on grass corms; in two of these populations, grass corms play a very small role in the baboon diet (Hamilton *et al.* 1978; Norton *et al.* 1987).

Baboons contrasted with vervet monkeys

The fact that baboons have almost entirely escaped reproductive seasonality suggests that the handoff strategy represents a very successful mode of adaptation to the savanna environment. In this regard, baboons represent an interesting and important contrast to vervet monkeys (*Cercopithecus aethiops*), the other widespread savanna monkey with which baboons often share habitat. Unlike baboons, vervet monkeys show relatively strong seasonality in birth and mating, with the birth peak in Amboseli occurring from October through January (Cheney *et al.* 1988). Further, Amboseli vervets are much more specialized feeders than baboons, focusing more intensively on *Acacia* products and relying on them as fallback foods particularly heavily in the dry season (Struhsaker 1967; Wrangham & Waterman 1981). Not surprisingly, the die-off of *A. xanthophloea* woodlands in the central basin of Amboseli resulted in the decline and eventually the local extinction of the vervet population in that area, although the vervet population persisted in parts of Amboseli in which fever trees persisted (Struhsaker 1973, 1976; Hauser *et al.* 1986; Isbell *et al.* 1990, 1991).

Thus, baboons and vervets have rather different modes of adaptation to the savanna environment in spite of extensive overlap in habitat and diet

(Struhsaker 1967; Wrangham & Waterman 1981; Altmann *et al.* 1987; Altmann 1998: Table 9.6). Vervets forage on fewer food types, restrict their foraging to a well-defended and relatively small territory, and employ a fallback strategy during the dry season. Baboons forage widely in large, undefended home ranges and employ a handoff strategy to utilize a broad and constantly changing set of foods. These differences may contribute importantly to the fact that vervets experience strong seasonal constraints on their reproduction while baboons cycle and conceive throughout the year.

Costs of fallback foods

During periods of food scarcity, most primate species probably lie somewhere along a continuum between a pure fallback strategy (i.e. relying extremely heavily on just one or a few food types) and a pure handoff strategy (i.e. moving from one food type to the next with no extra reliance on any particular type). Amboseli baboons clearly had elements of both strategies; along with their handoff approach, they also fell back on grass corms during the dry season. The baboon–vervet contrast suggests that a species' position on that continuum may have important consequences. In Amboseli, the purer fallback strategy (greater dietary specialization) of vervets was associated with greater vulnerability to local extinction as well as with a more seasonal physiology.

Reliance on fallback foods has multiple costs. One is an increase in foraging time for fallback foods that are time-consuming to process. Another was noted by Altmann (1998: 26–30): every food presents a "packaging problem" to the consumer, in that nutrients and toxins are packaged together and quantities of each vary from species to species and from season to season. Dietary diversity decreases during the dry season, at least for baboons (Post 1982; Norton *et al.* 1987), so the packaging problem is compounded by the fact that at this time of year, the animals have fewer alternative foods. *A. tortilis* seeds constitute important potential fallback foods for both vervets (Wrangham & Waterman 1981) and baboons (Fig. 6.11; Table 6.3). However, these seeds contain phenolics (including hydrolysable tannins) and trypsin inhibitor, both of which are toxic (Wrangham & Waterman 1981; Altmann *et al.* 1987; Altmann 1998). Thus, this easy-to-harvest and nutrient-rich food source is consumed in much lower quantities than one might expect, by both baboons and vervet monkeys, even though it reaches peak abundance during times when other foods are scarce (Wrangham & Waterman 1981; Altmann 1998). A third and critical cost of a fallback strategy, exemplified by the Amboseli vervets, is local extinction in the face of habitat change if the major fallback food declines.

The baboons' handoff strategy exhibits three characteristics that are probably critical to their relative success, particularly in the face of habitat change. First is their ability to range widely and even shift home ranges as the environment changes; vervets defend small territories and probably are unable to do this. Second is the fact that they are less reliant on any one food type than vervets are; they pursue a more full-blown handoff strategy. Third is their ability to utilize grasses to a greater extent than vervets. The first two characteristics will contribute to success in any habitat, while the third may be critical in determining how successfully a species adapts when woodland mosaic transitions to more open savanna.

The "dispensable social time" hypothesis versus the "social glue" hypothesis

Does social time represent "social glue," so that baboons conserve social time and sacrifice resting time when resources are scarce? This certainly appears to be true with respect to seasonal changes. Amboseli baboons conserved their social time, and reduced their resting time to accommodate the increased foraging demands of the season. However, on the larger scale of habitat change over time, the baboons sacrificed social time, and reduced their time with neighbors, in lower-quality habitats that demanded more foraging time (see also Bronikowski & Altmann [1996]).

Why might the baboons respond differently to seasonal changes in food availability than they do to habitat changes? They successfully absorbed seasonal demands on their foraging time budget without sacrificing social time, so why did they sacrifice social time when habitat quality deteriorated? One possible explanation is that seasonal changes were of smaller magnitude than the habitat changes that have occurred in Amboseli and that seasonal changes therefore taxed baboon energy reserves less than longer-term changes. This notion is supported by a comparison of foraging time differences within years (wet versus dry season foraging) with foraging time differences across years. On average, baboons spent 7.7% (range −4.5% to 22.2%) more time foraging in each dry season than they did in the corresponding "wetter months" (remember that these months are quite variable in rainfall, and that rains sometimes fail entirely). To contrast this with differences across years, we took the maximum yearly value for time spent foraging (81.3% for Alto's in 1985) and compared all other years with it (i.e. we subtracted the value for each year from this maximum). We found that the mean difference from the maximum time spent foraging was 12.9% (range 1.4% to 23.2%), much greater than mean seasonal differences. In other words, yearly changes in time spent foraging tended to be larger than changes within any one year.

A key prediction of the social glue hypothesis is that when groups are not able to maintain adequate time spent socializing, group cohesion will be lost (Dunbar 1992) and groups will presumably experience permanent fission. This prediction is not supported by our data. In fact, our social groups did fission, but not during periods when social time was limited. Instead, in each case they did so after they shifted to new habitats and experienced *decreases* in foraging time and *increases* in socializing time (Figs. 6.6, 6.8, 6.9). Indeed, in Hook's group, the fission occurred during 1995, the end of a three-year period when socializing time was at its peak and approached levels reported for Lodge group (Bronikowski & Altmann 1996), a food-augmented group with minimal nutritional or time constraints (cf. Bronikowski & Altmann [1996: Table 2] with this study, Figure 6.9). Further, in the years before they shifted their home ranges, the study groups consistently fell below Dunbar's estimated minimum social time necessary for group cohesion (Dunbar 1992: Equation 8), and they did so without experiencing fission. Even given the difficulties of estimating accurately a minimum social time requirement, this suggests that social time per se is not a major predictor of group cohesion.

However, Dunbar's prediction that animals will conserve social time in the face of food scarcity remains salient for interpreting seasonal changes in behavior. The difference we observed between seasonal and longer-term responses to habitat change may simply reflect the fact that baboons are fairly good at coping with seasonal changes but less successful at coping with more extreme changes in habitat quality. That is, baboons may indeed *attempt* to conserve social time as food availability fluctuates, but they are able to do this only within a fairly narrow range of habitat change – namely, the change experienced over the course of a year as the rains come and go.

Seasonal change versus habitat change as a selective force in primate evolution

Traditional hypotheses for human evolution attribute the emergence of unique human traits to movement into the savanna habitat, and to the particular challenges of that habitat, including marked seasonality (Foley 1987: Chapter 8, 1993; Potts 1998a, 1998b; Klein 1999: Chapters 4 and 5) (see also Chapter 17). In contrast, a recently articulated "variability hypothesis" suggests that unique human traits were selected for under a regime of constant habitat change (Potts 1996, 1998a, 1998b, 2002). The behavioral flexibility exhibited by humans is proposed to be a direct consequence of a long-term selection regime for traits that promoted survival in a fluctuating environment. Under this scenario, genes that promoted contingent behavioral responses that allowed adaptation to a range of habitats experienced strong positive selection because human ancestors experienced relatively dramatic habitat change over the course of the late Pliocene and early Pleistocene epochs.

In other words, Potts (1996) argues that it was long-term habitat change rather than the features of a particular habitat that ultimately selected for unique human traits. Under this hypothesis, seasonality would represent a relatively minor challenge to early hominids, while long-term habitat change would impose strong selection. Our data suggest that for Amboseli baboons, too, seasonal changes were relatively minor in their impact on behavior, while long-term habitat changes posed a greater challenge for the animals.

The success of the Amboseli baboon population in coping with challenging habitat change is notable. Their coping strategies have included decreasing the time devoted to socializing during hard times, modifying their diet as the habitat changed, and adaptively shifting their home range in the face of habitat deterioration (Bronikowski & Altmann 1996; Altmann & Alberts 2003). These strategies have been so successful that in recent decades, the baboon population in Amboseli has increased (Alberts & Altmann 2003), and several social groups have fissioned after growing in size (Altmann & Alberts 2003). The success of the baboons is in striking contrast to the local extinction experienced by vervets in areas of Amboseli that lost fever tree woodlands (Struhsaker 1973, 1976; Hauser *et al.* 1986; Isbell *et al.* 1991).

As noted earlier, baboons and humans share a number of key traits – a wide geographic distribution, success in but not restriction to savanna environments, and non-seasonal reproduction. We have also shown that baboons can be successful in the face of fairly dramatic environmental change, another key human trait under the variability hypothesis for human evolution (Potts 1996). Finally, they share three traits that Potts (1998a) proposes evolved in response to variability selection: (i) they are moderately highly encephalized, with a high neocortex-to-cortex ratio (Dunbar 1998); (ii) they exhibit a flexible locomotor system and readily utilize both arboreal and terrestrial habitats (Estes 1991; Fleagle 1999);

and (iii) they exhibit a highly flexible social system (Altmann & Altmann 1970; Barton *et al.* 1996; Dunbar & Dunbar 1977; Henzi & Barrett 2003).

Perhaps, then, baboons represent a model for understanding the behavioral plasticity of early hominids. If so, what traits might early hominids have exhibited? One would be handoff foraging, in which temporal variability in food abundance was mitigated by careful tracking and exploitation of food resources as they became available. Concomitant with this skill would be an ability to find alternatives when important foods became scarce as the habitat changed. A third trait would involve a well-buffered social structure in which individual relationships were serviced carefully. This might mean substantial investment in relationships, but the baboon model suggests that if forced to limit time investment during food scarcity, then alternative, equivalent modes of interacting might be pursued in order to maintain relationships with less cost. Finally, the baboon model suggests that a fourth very important trait would be the flexibility to actually alter one's own environment by finding and moving to more suitable habitats. As yet, the components of the variability hypothesis for hominid evolution have not been explored in a non-human primate system. Our analysis suggests that such an exploration could shed considerable light on the manner and consequences of the response of primates to environmental change.

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