

Seasonality and long term change in a savannah environment

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The emergence and spread of savannahs in Africa during the past 5 million years is often cited as a major factor in hominid evolution. Tropical savannahs are different from forests in having less rainfall that is strongly seasonal and often very unpredictable even within seasons (Bourliere and Hadley 1983; Solbrig 1996). Human ancestors are thought to have moved into savannahs as a response to cooling and drying climates, and the exigencies of the savannah 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,b; Klein 1999 Chapters 4 and 5; Reed and Fish this volume). This scenario invites a careful examination of responses to seasonality in extant savannah-dwelling primates.

Like most vertebrates, the large majority of primate species exhibit reproductive seasonality that reflects the seasonality of their habitats (see review in Janson and Verdolin, this volume). Indeed, among savannah-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 savannah to temperate montane grasslands to moist evergreen forest (Estes 1991; Jolly 1993; Kingdon 1997).

38 These shared features of *Papio* and *Homo* – a wide geographic distribution, success in
39 but not restriction to savannah environments, and nonseasonal reproduction – make analyses of
40 seasonality in baboon behavior especially valuable in light of the role that seasonality is
41 proposed to have played in selecting for unique human traits (Foley 1987, 1993). In this chapter,
42 we examine seasonal patterns of behavior in the well-studied population of savannah baboons in
43 the Amboseli basin at the foot of Mt. Kilimanjaro. Amboseli is a semi-arid habitat, and one of
44 the drier habitats in which baboons have been studied (see review in Dunbar 1992). We employ
45 16 years of behavioral data on adult females, combined with demographic and meteorological
46 data, to test hypotheses about the impacts of the seasonal environment on baboon behavior. Our
47 results are preceded first by a description of savannah seasonality and an outline of the
48 hypotheses that we will test with these data, and then by background on baboon ecology and on
49 the Amboseli ecosystem.

50 **The challenges of savannah seasonality.**

51 Savannahs are tropical habitats dominated by grasses, with scattered, drought-resistant
52 trees and shrubs (Bourliere and Hadley 1983; Solbrig 1996; Lincoln et al. 1998; the term
53 savannah is sometimes used to include subtropical grasslands as well). Savannahs show great
54 variability in rainfall across the year, but little variation in mean daily temperature, and
55 temperature fluctuations over the course of any given day are larger in magnitude than those in
56 mean temperatures over the course of a year (Bourliere and Hadley 1983; Solbrig 1996).
57 Accordingly, savannahs do not exhibit the extreme seasonal shutdown of plant productivity
58 exhibited by temperate zone grasslands. However, considerable seasonality of plant productivity
59 still occurs in savannahs, driven by rainfall seasonality. Hence, a primary challenge for animals
60 living in highly seasonal savannah environments is finding enough food and water during the dry
61 season. For highly social species (most primates), social behavior will also be affected by
62 seasonal changes in time spent foraging. Indeed, discussions about seasonal behavior in primates
63 have centered on two issues, (1) the manner in which foraging behavior changes with season and
64 (2) the manner in which social behavior changes with season. For each of these issues,
65 contrasting predictions have been made.

66 **Hypotheses about seasonality of foraging behavior.** The onset of the dry season in
67 savannah habitats marks the beginning of a long period during which plant productivity is highly
68 constrained. Grasses and many shrubs limit or cease their production of new leaves, grass seed

69 heads vanish, the above-ground parts of many forbs disappear entirely, and fruits and flowers of
70 shrubs and forbs become limited in abundance. How might primates in seasonal environments
71 respond to dry season food scarcity? Two alternatives have been proposed (see review in Foley
72 1987, Chapter 8).

73 On the one hand, primates might respond to dry season food scarcities by shifting to
74 foods that are abundant but have low profitability (low ratio of nutrient to harvesting time; Foley
75 1987; see also discussions in S. Altmann 1998; Dunbar 1983; Wrangham et al. 1991, 1998).
76 Such a seasonal shift to "fallback foods" typically will result in increased time spent foraging
77 during the dry season relative to the wet season. Indeed, time spent foraging increases during the
78 dry season for a number of primate species (baboons, Post 1981; muriquis, Strier 1991; two
79 *Eulemur* species, Overdorff 1996; tarsiers, Gursky 2000). Studies of chimpanzees have also
80 provided substantial direct evidence for the fallback foods hypothesis. Chimps increase their
81 intake of herbaceous vegetation during times of fruit scarcity, and work on chimps has formed a
82 model for our understanding of the importance of fallback foods (Wrangham et al. 1991;
83 Malenky and Wrangham 1994; Wrangham et al. 1998).

84 Alternatively, during times of scarcity, primates may seek out novel foods that are highly
85 profitable but difficult to acquire. This is sometimes proposed as the major strategy of early
86 hominids, and the novel, highly profitable food in question is meat (Blumenshine 1987; Foley
87 1987, 1993; Potts 1998a,b; Klein 1999 Chapters 4 and 5; Reed and Fish this volume). There is
88 only limited evidence for this "high-return foods" strategy among tropical human foragers. While
89 many human foragers show marked effects of season on their foraging behavior, this is not
90 commonly manifested as an increase in hunting time or in meat consumption during the dry
91 season (see review in Bird and Bird this volume; see also Bunn et al. 1988; Hawkes et al. 1991).
92 Among non-human primates, too, there is limited evidence that hunting increases during the dry
93 season (baboons, Dunbar 1983; chimpanzees, Stanford et al. 1994, Stanford 1998) but in general
94 dry season food scarcity appears to be a poor explanation for primate hunting (Stanford et al.
95 1994, Stanford 1998; Mitani and Watts 2001; Mitani and Watts this volume).

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

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

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

117 The alternative hypothesis assumes that social time is functionally important for
118 maintaining social relationships, which in turn are critical in mitigating the effects of both inter-
119 and intragroup competition (e.g., Seyfarth 1977; Dunbar and Dunbar 1988; Dunbar 1991). Under
120 this hypothesis, Dunbar and Dunbar (1988) and Dunbar (1992) propose that animals will
121 conserve social time during food scarcity because social activities (primarily grooming) service
122 relationships and hence represent "social glue" that maintains cohesion of social groups (Dunbar
123 1992). This hypothesis acknowledges that animals' time budgets must accommodate changes in
124 foraging time, but predicts that animals will reduce resting time rather than social time in order
125 to accommodate the increased foraging demands of the dry season. We term this the "social
126 glue" hypothesis.

127 **Baboon ecology.**

128 Baboons (genus *Papio*) are large, semi-terrestrial monkeys that occupy a wide range of
129 habitats across the continent of Africa (Altmann and Altmann 1970; Jolly 1993; Kingdon 1997).
130 Baboon populations are typically divided into stable social groups, most of which have between

131 20 and 100 members, including multiple adults and juveniles of both sexes (Altmann and
132 Altmann 1970; Estes 1991). Hamadryas baboons in the horn of Africa deviate markedly from
133 this basic social pattern (Kummer 1968; Stambach 1987), and we exclude them from
134 consideration here because of their unique socioecological adaptations. We use the term
135 "savannah baboon" to refer to all members of the genus other than hamadryas baboons.

136 Savannah baboons are eclectic and omnivorous feeders, but this omnivory is combined
137 with great discrimination. They feed very selectively, often choosing a small component of a
138 plant and forgoing the remainder, or focusing on a single species within a genus (Hamilton et al.
139 1978; Post 1982; Norton et al. 1987; Muruthi et al. 1991; Whiten et al. 1991; Byrne et al. 1993;
140 S. Altmann 1998). Plants are the most important source of nutrients; invertebrate and vertebrate
141 animals are eaten but contribute relatively little in calories and protein. In the habitats in which
142 they are best studied (savannahs) baboons rely heavily on grasses, consuming both the
143 underground storage organs (corms) and the leaves (Post 1982; Norton et al. 1987; Muruthi et al.
144 1991; Whiten et al. 1991; Byrne et al. 1993; S. Altmann 1998). Many of the foods consumed by
145 baboons are available and consumed year-round; in Amboseli these include grass corms, tree
146 gum, material gleaned from the dung of ungulates and elephants, and the blade bases of grasses
147 (containing the meristem). However, some preferred foods, including the fruits of most species,
148 flowers, green *Acacia* seeds, grass seedheads, and green grass blades (consumed in quantity only
149 when they are new and low in fiber) are highly seasonal (Hamilton et al. 1978; Post 1982; Byrne
150 et al. 1993; S. Altmann 1998).

151 Savannah baboons do not exhibit seasonal patterns of mating or birth; females may
152 conceive and give birth in any month (Figure 1a and b; Melnick and Pearl 1987, Altmann 1980;
153 Bercovitch and Harding 1993; Bentley-Condit and Smith 1997). However, Amboseli births do
154 show a modest peak in August through October, corresponding to conceptions occurring most
155 often from February through May. In fact, 242 of 495 live births (49%) occurred in the five
156 months of the long dry season, June through October, and this is significantly greater than the
157 expected number of 206 (42%) in this season (G test of goodness of fit, $G = 10.64$, $P < 0.005$).
158 An analysis using circular statistics (Janson and Verdolin, this volume) indicates significant but
159 weak clustering of births during the year (corrected vector length $r = 0.12$, $P < 0.001$)

160 Because gestation duration is the least variable life history stage, dates of live births are
161 almost entirely determined by conception dates. Conception dates, in turn, are determined by the

162 timing of the onset of cycling (menarche or post-partum) and the probability of conception. In
163 baboons, these are both highly variable as a result of both stochastic and deterministic processes.
164 For instance, onset of menarche shows modest seasonality, occurring significantly less often than
165 expected during the long dry season (41 of 138 observed menarches occurred in these months,
166 compared with 58 expected; $G = 10.83$, $P < 0.001$; using circular statistics, corrected vector
167 length $r = 0.18$, $P < 0.01$). In contrast, resumption of cycling after a previous pregnancy shows
168 almost no seasonal effect (205 of 499 resumptions occurred in the long dry season, compared
169 with 208 expected, $G = 0.74$, NS; corrected vector length $r = 0.08$, $P < 0.05$). Hence, two
170 somewhat similar processes, both of which contribute to the timing of births, are very different in
171 the extent to which they show seasonality. We refer the reader to Janson and Verdolin (this
172 volume) for a more detailed discussion of this complex topic.

173 **Amboseli ecology.**

174 The Amboseli basin ($2^{\circ}40'$ S latitude, 1100 m altitude) is a semi-arid short-grass
175 savannah ecosystem located in an ancient lake basin at the base of Mt Kilimanjaro in East Africa
176 (Williams 1972; Western and Van Praet 1973; Behrensmeyer and Boaz 1981; Behrensmeyer
177 1993; Hay et al. 1995). Mean annual rainfall is 348 mm, but the range of annual rainfall is quite
178 large, from less than 150 mm to more than 550 mm (Figure 2a and Altmann et al. 2002).

179 In the pattern typically described for the area, rainfall occurs in two seasons centered in
180 November-December (the "short rains") and in March-May (the "long rains"), with a "short dry
181 season" in January and February and a "long dry season" during June through October.
182 However, the only component of this pattern that does not vary from year to year is the long dry
183 season. The short rains or the long rains, or both, may fail, or substantial rain may fall during the
184 short dry season. This variability contrasts sharply with the predictability of the long dry season:
185 between the end of May and the last few days of October, virtually no rain falls (Figure 2b and
186 Altmann et al. 2002). Mean daily maximum and minimum temperatures exhibit small but
187 predictable seasonal changes; diurnal changes are much larger in magnitude than those that occur
188 seasonally (Altmann et al. 2002).

189 In addition to experiencing year-to-year variability in rainfall, Amboseli has undergone
190 dramatic long-term habitat change over the past four decades (Struhsaker 1973, 1976; Western
191 and Van Praet 1973; Hauser et al. 1986; Isbell et al. 1991; Behrensmeyer 1993; Koch et al. 1995;
192 S. Altmann 1998, p. 15-19; Cutler et al. 1999). In the central part of the Amboseli basin, the

193 dominant tree species, *Acacia xanthophloea* (the fever tree), and various plant species associated
194 with it, have experienced dramatic decline, with complete die-off in some places within
195 Amboseli. At the same time, the number and size of fresh water swamps and ponds has increased
196 substantially in some areas of the basin, although no change in mean annual rainfall has occurred
197 (Figure 2a; Altmann et al. 2002). In addition, mean maximum daily temperature has increased
198 more than 5°C since 1976, a change that is an order of magnitude greater than changes
199 associated with global warming (Altmann et al. 2002).

200 These changes have been attributed variously to heavy browsing of both adult trees and
201 seedlings by elephants and other browsers, to natural aging of the woodlands, to a rising water
202 table, or to a combination of all three (Western and Van Praet 1973; Young and Lindsay 1988; S.
203 Altmann 1998; Altmann et al. 2002). However, the local changes in Amboseli are occurring
204 against the backdrop of a much more high-profile change that has aroused international interest;
205 the glaciers on the top of Mt. Kilimanjaro experienced an 80% reduction during the 20th century
206 and are predicted to disappear entirely between 2015 and 2020 (Hastenrath and Greischar 1997;
207 Thompson et al. 2002). Amboseli lies at the base of Kilimanjaro, and runoff from Kilimanjaro
208 provides the major source of ground and surface water in Amboseli (Behrensmeyer 1993; Hay et
209 al. 1995). While heavy browsing by an increasing population of domestic stock and of some
210 other browsers (Esikuri 1998; Moss 2001) has certainly played a role in the habitat change in
211 Amboseli, the larger-scale changes associated with glacier recession on Kilimanjaro are probably
212 contributing as well.

213 **Ecological and research history of the Amboseli baboon population.**

214 In early 1960's, the baboon population was moderately large and the Amboseli basin was
215 dominated by *A. xanthophloea* (fever tree) habitat, which the baboons relied on for both food and
216 sleeping sites (Altmann and Altmann 1970, Altmann et al. 1985 S. Altmann 1998). Between
217 1964 and 1969 the population underwent a precipitous decline, probably as a consequence of the
218 die-off of the fever tree woodland in the central part of the basin (Western and van Praet 1973,
219 Altmann et al. 1985, S. Altmann 1998). Over the next decade the population stabilized but at a
220 much smaller size than in the early 1960's, and during the late 1980's and 1990's the population
221 grew moderately in size (Altmann et al. 1985; Alberts and Altmann 2003). This growth occurred
222 after several social groups abandoned the home range they had occupied in the central basin
223 during the 1970's and 1980's (Bronikowski and Altmann 1996; Alberts and Altmann 2001;

224 Altmann and Alberts 2003). In each case, the groups moved approximately eight km west (Alto's
225 in 1987-8, Hook's in 1991-2), to an area still within the Amboseli basin, but with a relatively
226 high density of *A. xanthophloea* trees and a relatively low density of baboons. This "western
227 basin" is both slightly elevated relative to the central basin, and was rarely used by elephants or
228 other browsers when the baboon study groups first moved there, perhaps because of poaching or
229 other human disturbance in that area. These two factors may have contributed to the relative
230 health of the western fever tree woodlands at that time – the elevation resulting in slower effects
231 of changes in the water table, and the low elephant density resulting in reduced pressure on the
232 fever tree population. However, during the 1990's the fever trees in the western basin gradually
233 began to show signs of decline, perhaps partly because elephants and other browsers began using
234 the area more heavily during that period. The impact of this new die-off on the baboons, and
235 their response to it, remain to be seen.

236 **METHODS**

237 **Study groups, data collection, and subjects.**

238 Data were collected on wild-feeding adult female baboons between January 1984 and
239 December 1999 (we exclude data from members of Lodge Group, who augmented their diet with
240 human refuse; see Altmann and Muruthi 1988, Muruthi et al. 1991). Our two original study
241 groups, Alto's and Hook's Groups, fissioned in 1989-1991 and in 1994-5, respectively (Figure
242 3). In our analyses we treated Alto's Group and its fission products as one subpopulation, and
243 Hook's Group and its fission products as a second subpopulation.

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

249 Data were collected as 10-minute focal samples (Altmann 1974) on all adult females in
250 the study groups. Adult females within each group were sampled in random order during all
251 active daylight hours, 0700 to 1800 (or 0800 to 1600 between 1988 and 1991). The result was
252 approximately 35,000 focal samples of 10 minutes duration on 124 adult females in two
253 subpopulations (six social groups). The subjects were born between 1962 (estimated) and 11 Feb
254 1995. Birth dates were estimated for 23 of the 124 subjects (those born before July 1971 in

255 Alto's and before October 1977 in Hook's); for all other subjects, birth dates were known
256 exactly. Sampling began in January 1984 on females that were already adult at that time;
257 maturing females were added to the sampling schedule when they reached menarche. Focal
258 subjects were between 4.5 and 27 years of age at the time of sampling.

259 **Focal sampling.**

260 Focal samples involved the collection of "point" data every minute during the sample
261 (signaled by a timer), as well as "all occurrences" data on agonistic interactions, mounts and
262 mate guarding, and grooming. At each "point" the observer recorded the focal's activity (Table
263 1), her position (standing or sitting), the position of her infant and whether it was suckling,
264 whether any other animals (other than her dependent infant) were within 5 meters of her, and
265 details about the identities of any such "neighbors". Three to four 10-minute samples per hour
266 were collected in this manner for the duration of the study.

267 At each point for which "feeding" was recorded, the observer also recorded the type of
268 food being eaten (Table 2); species was recorded only for the more common and well-known
269 species. Data on foods consumed were available only for 1991-1999 for Hook's subpopulation
270 and for 1996-1999 for Alto's subpopulation.

271 **Data analysis.**

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

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

284 To measure the proportion of time spent in social activities, we combined "grooming",
285 "being groomed", and "other social interactions". In practice, the large majority of social time

286 was grooming time; other social interactions were typically brief events and together constituted
287 approximately 2.5% of social time (approximately 0.25% of total time).

288 We also measured the proportion of time spent with no neighbor within 5 meters. We
289 view time spent with no neighbor as an indirect and inverse gauge of the time devoted of
290 socializing. The presence of neighbors facilitates interactions and probably increases interaction
291 rates, so that as time spent with no neighbor increases, socializing will generally decrease. We
292 also view time spent with no neighbor as a gauge of the intensity of competition. Animals should
293 tolerate greater proximity when foraging competition is less intense. Thus, an increase in time
294 spent with no neighbors will generally reflect an increase in overall levels of foraging
295 competition within the group.

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

306 (c) Bivariate analysis of seasonal effects on activities. In our first analysis, we
307 categorized each sample according to season, year, and subpopulation. We then calculated the
308 total proportion of time spent in each activity for each subpopulation each year. This resulted in
309 27 “subpopulation-years” of data for the wetter months and 31 “subpopulation-years” of data for
310 the long dry season (because we were missing complete “wetter months” data for four
311 subpopulation-years). We next took the mean proportion of time spent in each activity for dry
312 versus wetter months across all years, and used t-tests to examine seasonal differences in
313 foraging, resting, socializing, and time spent with no neighbor within 5 meters. Because
314 successive years within a subpopulation may not be independent of each other, this procedure
315 may result in some pseudo-replication. However, we also know that temporal changes in activity
316 patterns have occurred over the years (Bronikowski and Altmann 1996; this study), so that

317 pooling across years will obscure important temporal differences. We dealt with the potential
318 pseudoreplication by employing a P-value for significance of $P = 0.01$ rather than the traditional
319 $P = 0.05$.

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

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

335 (f) Phenology. Baboon foods in Amboseli fall into three categories of seasonality. Some
336 show year-round availability. Others are highly seasonal, available only after the rains. The third
337 category exhibits what we call "damped seasonality". That is, individual species can be highly
338 seasonal in their productivity, but baboons can eat foods in this category in most months of the
339 year (Table 3). This is because the "seasons" vary greatly between species and so collectively do
340 not correspond to the "dry season – wetter months" dichotomy that we have presented. The
341 consequence is that, by careful searching and by exploitation of many different species, baboons
342 can eat foods in this category in most months of the year (Table 3).

343 The phenology of baboons' foods in Amboseli is well described (Post 1982; S. Altmann
344 1998 pp. 12-14, 74-78). We supplemented these published descriptions with a new analysis of
345 presence-absence data collected between 1985 and 1994 on fruits, *Acacia* pods, and the leaves of
346 shrubs and forbs, three of the more seasonal foods in the diet. Phenological information from
347 these various sources is summarized in Table 3.

348

349 **RESULTS**350 **Time spent making a living changed with season and changed over time.**

351 Female baboons spent more time foraging and less time resting in the long dry season
352 than during the wetter months (Table 4; Figures 4 and 5). The clear but unsurprising inference is
353 that quality of life is higher during the wetter months, and that the dry season represents an
354 ecological challenge for the animals.

355 Female activity profiles also changed substantially over time (Table 4; Figure 5). From
356 the mid-1980's to the mid-1990's, baboons in both subpopulations decreased foraging time and
357 increased resting time (Figure 5). This change coincided with the move that each subpopulation
358 made to the western part of the Amboseli basin, where the fever tree woodland was large and
359 healthy. From the middle to the end of the 1990's, however, foraging time increased for both
360 subpopulations in each season, and resting time decreased. This may signal the end of a phase of
361 relatively rapid density-independent growth that occurred immediately after each group moved.
362 Alternatively or in addition, the decrease in quality of life may be a consequence of the gradual
363 decline of the fever tree woodlands that we observed in the western basin as the 1990's
364 progressed.

365 The two subpopulations show remarkable similarity in their activity profiles; no effect of
366 subpopulation on time spent in any activity is evident in the analysis. While activity patterns
367 varied significantly across years, this variability was not predicted by yearly differences in
368 rainfall. Similarly, female group size, which varied from 6.5 to 18 adult females, did not predict
369 time spent time spent foraging or resting (Table 4).

370

371 **Social time was unaffected by season but changed over time.**

372 Both the bivariate analysis and the analysis of variance indicated that season had no
373 effect on time spent in social activities or on time spent with no neighbor (Figures 4 and 6).
374 However, both of these measures of socializing changed over time (Table 4). Specifically, as
375 quality of life increased after the move west, time spent alone decreased and time spent
376 socializing tended to increase in both seasons (Figure 6). Neither subpopulation nor yearly
377 rainfall affected social life. However, when groups were smaller, females showed a trend
378 towards spending more time with no neighbor ($P = 0.026$; Table 4).

379

380 Baboon diets had seasonal components but showed relative stability across seasons.

381 Only four food types showed highly seasonal patterns of consumption in Amboseli: grass
382 corms, grass blades, grass seedheads, and shrub/forb leaves (Figure 7, Table 5; grass seedheads
383 are not significantly seasonal in our model because they show a pattern of consumption that is
384 slightly shifted – by one month – relative to our definition of season). Shrub and forb leaves
385 constitute a very small fraction of feeding time (Table 2, Figure 7), indicating that grasses – their
386 corms, blades, and seedheads -- are the only foods in the Amboseli baboon diet that exhibit
387 important seasonal patterns of consumption (Table 5, Figure 7).

388 By far the largest set of food types in the baboon diet were those that showed damped
389 seasonality. Each species shows a different temporal pattern of availability of, for instance, fruit,
390 but the baboons mitigate this variability by exploiting a succession of species that are productive
391 at different times of the year (Table 3, Table 5). Thus, the baboons achieve stability in their diet
392 by carefully searching for and exploiting a large number of different species and plant parts
393 across the year. They cannot achieve complete stability of food intake in this way; foods with
394 damped seasonality still show considerable heterogeneity across months in their contribution to
395 the diet (Figure 8). However, this is not strictly linked to patterns of rainfall and the dry season
396 because, as described above, different species have different phenologies. The result is that,
397 while the baboons eat different species of *Acacia* seeds in different months, they eat *Acacia*
398 seeds in some quantity in almost every month. This is also true of flowers. Fruits show a
399 complex pattern of availability across species, but fruits of some sort are available and consumed
400 in every month (Table 3, Figure 8).

401 Vertebrate animals accounted for a tiny fraction of the feeding time of female baboons in
402 Amboseli (less than 0.1% of feeding time; Table 2). Post (1982) recorded that 1% of feeding
403 time in Amboseli was devoted to vertebrates and invertebrates combined, suggesting that in his
404 study, as in ours, little feeding time was devoted to vertebrate prey, even for the adult males in
405 his study. Post (1982) notes that animal prey may be nutritionally important even if little time is
406 devoted to it. This point may be relevant for invertebrates, which show measurable consumption
407 in most months of the year. However, vertebrate prey in particular occupied so little feeding time
408 in this study that it cannot be of great general importance for Amboseli females.

409 Almost no variable in our model other than season affected the proportion of time spent
410 on different food types (Table 5). Gum is consumed more heavily in drier years, and the leaves
411 of shrubs and forbs have experienced a decrease in consumption over the course of the study.
412 However, as noted, shrub/forb leaves occupy a very small proportion of feeding time overall,
413 suggesting that this decrease may not be biologically significant for the animals. The two
414 subpopulations showed no significant differentiation in diet.

415 **Baboon diets changed over time.** We did not observe any changes in time spent on
416 different food types over the 1990's (our feeding data were available only for this decade; see
417 Methods). However, we do have evidence to suggest that baboon diets have experienced
418 substantial shifts over the three decades of our long term study. Both Post (1982) and S.
419 Altmann (1998) documented Amboseli baboon diets in the mid-1970's. In that period *A.*
420 *xanthophloea* products occupied substantially more feeding time than they did during the 1990's
421 (Figure 9). This change in the importance of fever tree products is related to the change in the
422 density of these trees in Amboseli. As the trees became less abundant, the baboons
423 accommodated by altering their diets.

424

425 **DISCUSSION**

426 **The "fallback foods" strategy versus the "high-return foods" strategy.** Female
427 baboons in Amboseli certainly employed fallback foods: grass corms, available all year round,
428 were the focus of intensive foraging activity only during the dry season, when key preferred
429 foods (notably green grass blades and fruit) were scarce (Figures 7 and 8; see also Post 1982;
430 Byrne et al. 1993; S. Altmann 1998). As a consequence, foraging time increased dramatically
431 during the dry season. Grass corms require considerable processing time, so that although they
432 are reasonably rich in both protein and energy (Altmann et al. 1987; Byrne et al. 1993; S.
433 Altmann 1998), their profitability is low. High-return foods played little role in the dry season
434 diet of Amboseli females; vertebrate prey occupied only a tiny fraction of feeding time, and
435 invertebrate prey were consumed in low quantities throughout the year, with a marked peak in
436 one of the wetter months (Tables 2 and 5, Figure 8).

437 **Baboon foraging as a "handoff" strategy that mitigates seasonality.** Only a few food
438 types – notably the grasses – showed marked seasonality in their consumption by baboons, while
439 many other important food types, including fruits, tree gum, material gleaned from dung,

440 flowers, and invertebrates were consumed in almost every month of the year. Indeed, even the
441 grasses can be viewed as contributing to the diet in a constant manner across the year – the
442 baboons simply switched from above-ground parts to below-ground parts during the dry season.

443 This suggests that the baboon foraging strategy might be thought of as a "handoff"
444 strategy rather than a "fallback" strategy. Baboons achieve relative dietary stability partly by
445 carefully tracking a large number of species and plant parts over the year and selectively
446 exploiting foods as they become available. Even acknowledging that the succession of foods
447 exploited – for instance the fruits and flowers of different species – are not equivalent in their
448 nutrient content (Altmann et al. 1987; Byrne et al. 1993; S. Altmann 1998), the result will be a
449 constantly changing diet that probably allows the animals to maintain a relatively steady nutrient
450 intake throughout the year. Detailed descriptions of the diets of other baboon populations support
451 this notion (chacma baboons in Okavango, Botswana and Kuiseb, Namibia; Hamilton et al.
452 1978; yellow baboons in Mikumi, Tanzania, Norton et al. 1987; chacma baboons in the
453 Drakensberg Mountains, South Africa, Byrne et al. 1993; see also Whiten et al. 1991). This
454 handoff strategy occurs even in populations with no fallback reliance on grass corms: in two of
455 these populations, grass corms play a very small role in the baboon diet (Hamilton et al. 1987;
456 Norton et al. 1987).

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

470 Thus, baboons and vervets have rather different modes of adaptation to the savannah
471 environment in spite of extensive overlap in habitat and diet (Struhsaker 1967; Wrangham and
472 Waterman 1981; S. Altmann et al. 1987; S. Altmann 1998, Table 9.6). Vervets forage on fewer
473 food types, restrict their foraging to a well-defended and relatively small territory, and employ a
474 fallback strategy during the dry season. Baboons forage widely in large, undefended home
475 ranges and employ a handoff strategy to utilize a broad and constantly changing set of foods.
476 These differences may contribute importantly to the fact that vervets experience strong seasonal
477 constraints on their reproduction while baboons cycle and conceive throughout the year.

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

487 Reliance on fallback foods has multiple costs. One is an increase in foraging time for
488 fallback foods that are time-consuming to process. Another was noted by S. Altmann (1998, pp.
489 26-30): every food presents a "packaging problem" to the consumer, in that nutrients and toxins
490 are packaged together and quantities of each vary from species to species and season to season.
491 Dietary diversity decreases during the dry season, at least for baboons (Post 1982; Norton et al.
492 1987), so the packaging problem is compounded by the fact that at this time of year the animals
493 have fewer alternative foods. *Acacia tortilis* seeds constitute important potential fallback foods
494 for both vervets (Wrangham and Waterman 1981) and baboons (Figure 8, Table 3). However,
495 these seeds contain phenolics (including hydrolysable tannins) and trypsin inhibitor, both of
496 which are toxic (Wrangham and Waterman 1981; S. Altmann et al. 1987; S. Altmann 1998).
497 Thus, this easy-to-harvest and nutrient-rich food source is consumed in much lower quantities
498 than one might expect, by both baboons and vervet monkeys, even though it reaches peak
499 abundance during times of when other foods are scarce (Wrangham and Waterman 1981; S.

500 Altmann 1998). A third and critical cost of a fallback strategy, exemplified by the Amboseli
501 vervets, is local extinction in the face of habitat change if the major fallback food declines.

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

510 **The "dispensable social time" hypothesis versus the "social glue" hypothesis.** Does
511 social time represent "social glue", so that baboons conserve social time and sacrifice resting
512 time when resources are scarce? This certainly appears to be true with respect to seasonal
513 changes. Amboseli baboons conserved their social time and reduced their resting time
514 significantly to accommodate the increased foraging demands of the season. However, on the
515 larger scale of habitat change over time, the baboons sacrificed social time, and reduced their
516 time with neighbors, in lower-quality habitats that demanded more foraging time (see also
517 Bronikowski and Altmann 1996).

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

531 was 12.9% (range 1.4% to 23.2%), much greater than mean seasonal differences. In other words,
532 yearly changes in time spent foraging tended to be larger than changes within any one year.

533 A key prediction of the social glue hypothesis is that when groups are not able to
534 maintain adequate time spent socializing, group cohesion will be lost (Dunbar 1992) and groups
535 will presumably experience permanent fission. The prediction is not supported by our data. In
536 fact, our social groups did fission, but not during periods when social time was limited. Instead,
537 in each case they did so after they shifted to new habitats and experienced *decreases* in foraging
538 time and *increases* in socializing time (Figures 3, 5, 6). Indeed, in Hook's group the fission
539 occurred during 1995, the end of a three-year period when socializing time was at its peak and
540 approached levels reported for Lodge Group (Bronikowski and Altmann 1996), a food-
541 augmented group with minimal nutritional or time constraints (compare Bronikowski and
542 Altmann 1996, Table 2 with this study, Figure 6). Further, in the years before they shifted their
543 home ranges, the study groups consistently fell below Dunbar's estimated minimum social time
544 necessary for group cohesion (Dunbar 1992, Equation 8), and they did so without experiencing
545 fission. Even given the difficulties of accurately estimating a minimum social time requirement,
546 this suggests that social time *per se* is not a major predictor of group cohesion.

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

555 **Seasonal change versus habitat change as a selective force in primate evolution.**

556 Traditional hypotheses for human evolution attribute the emergence of unique human traits to
557 movement into the savannah habitat, and to the particular challenges of that habitat, including
558 marked seasonality (Foley 1987 Chapter 8, 1993; Potts 1998a,b; Klein 1999 Chapters 4 and 5;
559 Reed and Fish this volume). In contrast, a recently articulated "variability hypothesis" suggests
560 that unique human traits were selected for under a regime of constant habitat change (Potts 1996;
561 Potts 1998a,b; Potts 2002). The behavioral flexibility exhibited by humans is proposed to be a

562 direct consequence of a long term selection regime for traits that promoted survival in a
563 fluctuating environment. Under this scenario, genes that promoted contingent behavioral
564 responses that allowed adaptation to a range of habitats experienced strong positive selection
565 because human ancestors experienced relatively dramatic habitat change over the course of the
566 late Pliocene and early Pleistocene.

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

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

582 As noted earlier, baboons and humans share a number of key traits – a wide geographic
583 distribution, success in but not restriction to savannah environments, and nonseasonal
584 reproduction. We have also shown that baboons can be successful in the face of fairly dramatic
585 environmental change, another key human trait under the variability hypothesis for human
586 evolution (Potts 1996 and sequelae). Finally, they share three traits that Potts (1998) proposes
587 evolved in response to variability selection: (1) they are moderately highly encephalized, with a
588 high neocortex-to-cortex ratio (Dunbar 1998); (2) they exhibit a flexible locomotor system and
589 readily utilize both arboreal and terrestrial habitats (Estes, 1991; Fleagle 1999); and (3) they
590 exhibit a highly flexible social system (Altmann & Altmann 1970; Barton et al. 1996; Dunbar &
591 Dunbar 1977; Henzi, 1999).

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

607

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621

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882 Table 1. Mutually exclusive and exhaustive activity categories of focal subjects.

883

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.

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Table 2. Types of food eaten by female baboons in Amboseli (see also Figure 7). The 5% of feeding time not accounted for by these foods is accounted for by a variety of opportunistically consumed foods (see Post 1982; S. 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 (\pm s.e.)
Grass corms	1	Small perennial underground storage organs of grasses. The major representative is <i>Sporobolus rangei</i> (formerly <i>kentrophyllus</i>).	0.31 \pm 0.03
Fruits	2	Fruits of shrubs and forbs. The major representative is <i>Trianthema ceratosepala</i> but other species contribute importantly as well. See table 3.	0.22 \pm 0.03
Grass blades	3	Green leaves of grasses. Baboons eat a wide variety of species.	0.079 \pm 0.013
Tree gum	4	The vast majority of gum consumed is from the fever tree, <i>Acacia xanthophloea</i> ; occasionally gum of <i>Acacia tortilis</i> is consumed as well.	0.065 \pm 0.007
Material gleaned from dung	5	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 \pm 0.010
Flowers	6	Blossoms and buds from forbs, shrubs and trees. Three species represent the large majority of flowers eaten: <i>Acacia tortilis</i> , <i>Acacia xanthophloea</i> , and <i>Ramphicarpa montana</i> (an annual, highly-rain dependent forb).	0.053 \pm 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. <i>Sporobolus consimilis</i> (elephant grass) is the main grass consumed in this way.	0.040 \pm 0.004
Acacia seeds	8	Green and sometimes brown (dried) seeds removed from pods of <i>Acacia tortilis</i> or <i>Acacia xanthophloea</i> . Greens seeds of <i>tortilis</i> trees are primarily available July through September, while green <i>xanthophloea</i> seeds are available Dec-Jan.	0.036 \pm 0.007
Grass seedheads	9	The baboons eat seedheads from a wide range of grass species.	0.035 \pm 0.010
Leaves of shrubs and forbs	10	Major contributors include <i>Lyceum "europeaum"</i> and <i>Salvadora persica</i> but other species contribute as well.	0.032 \pm 0.004
Invertebrates	11	Grasshoppers, beetle larvae and lepidopteran larvae are the major contributors.	0.024 \pm 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

Table 3. Phenology of baboon foods in Amboseli. See also Post (1982) and S. Altmann (1998; pages 12-14 and 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 <i>Salvadora persica</i> (fruits from July or August until Nov or Dec) and <i>Commicarpus</i> spp (fruits only after rains). Other species available for many months, such as <i>Azima tetracantha</i> (fruits from May or Jun through Jan or Feb). Two are available year-round at least in small quantities: <i>Withania somnifera</i> and <i>Trianthema ceratosepala</i> . 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 Feb – May.
Tree gum	4	Year round	Young trees are especially good sources, but trees exude gum all year round.
Material gleaned from dung	5	Year round	Ungulate and elephant density in the baboons' home range varies seasonally but dung is always abundant on the ground.
Flowers	6	Damped seasonality	Three species are important: <i>A. tortilis</i> and <i>A. xanthophloea</i> , and <i>Ramphicarpa montana</i> . Each is highly seasonal but their peaks are distributed over the year: <i>tortilis</i> in Jan – Apr, <i>xanthophloea</i> in Sep – Nov, and <i>R. montana</i> after any rainy period.
Grass blade bases	7	Year round	Blade bases of <i>Sporobolus consimilis</i> , 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 <i>A. xanthophloea</i> in Dec – Mar, by <i>A. tortilis</i> in Jul – Sep; 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 <i>Lyceum "europaeum"</i> , 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 4. Analyses of Variance in time spent foraging, resting, socializing and alone.

FORAGING

Whole model: Adj. $R^2 = 0.35$, $P < 0.0001$

Effect	F	P
Season	16.8	0.0001
Year	11.54	0.0013
Group size	0.14	0.71
Rainfall	1.49	0.23
Subpopulation	0.0004	0.98

ALONE (no neighbor)

Whole model: Adj. $R^2 = 0.088$, $P = 0.084$

Effect	F	P
Season	0.04	0.84
Year	9.36	0.0035
Group size	5.29	0.026
Rainfall	1.02	0.32
Subpopulation	0.8	0.38

RESTING

Whole model: Adj. $R^2 = 0.33$, $P < 0.0001$

Effect	F	P
Season	17.97	<0.0001
Year	9.04	0.0041
Group size	0.11	0.74
Rainfall	1.21	0.28
Subpopulation	0.49	0.49

SOCIALIZING

Whole model: Adj. $R^2 = 0.16$, $P = 0.015$

Effect	F	P
Season	3.08	0.085
Year	6.28	0.015
Group size	0.04	0.84
Rainfall	0.7	0.41
Subpopulation	2.36	0.13

Figure captions

Figure 1. Distribution, by month, of (A) conceptions (N = 586) and (B) live births (N = 495) in Amboseli baboons. X-axis represents the hydrological year in Amboseli, beginning with the onset of the rains in November (see Figure 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.

Figure 2. Rainfall in Amboseli, 1984 - 1999. (A) Total annual precipitation, by hydrological year. Hydrological year 1984 begins in Nov 1983, etc. 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.

Figure 3. 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.

Figure 4. Seasonal differences in (A) time spent foraging and resting, and (B), time spent socializing and with no neighbor. Each point represents the mean value (\pm 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.

Fig 5. Amboseli baboons spend more time foraging (circles) and less time resting (triangles) in the dry season (A) than they do 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 4). From 1984 to the mid-1990's 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-1990's. These temporal effects are evident in both dry and wetter months (curves are fitted second-order polynomials; see Table 4 for ANOVAs).

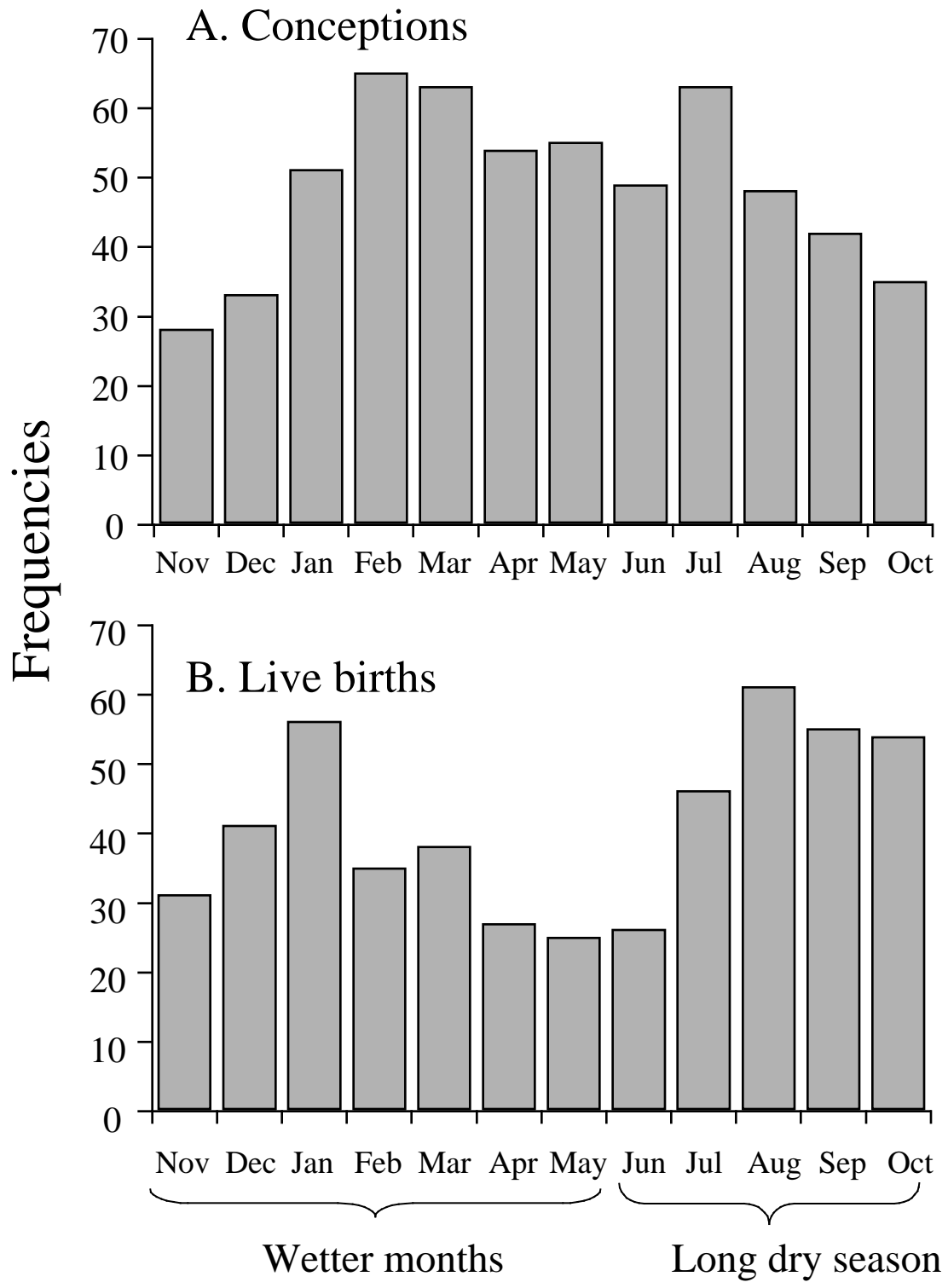
Fig 6. There is no significant effect of season on time spent alone (squares) or time spent socializing (diamonds), but a marked effect of year is evident (A: dry season, B: wetter months). Proportion of time with no neighbors within 5 m reached a low point in the mid-1990's, when foraging time was at its lowest and resting time at its highest (see Figure 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 4).

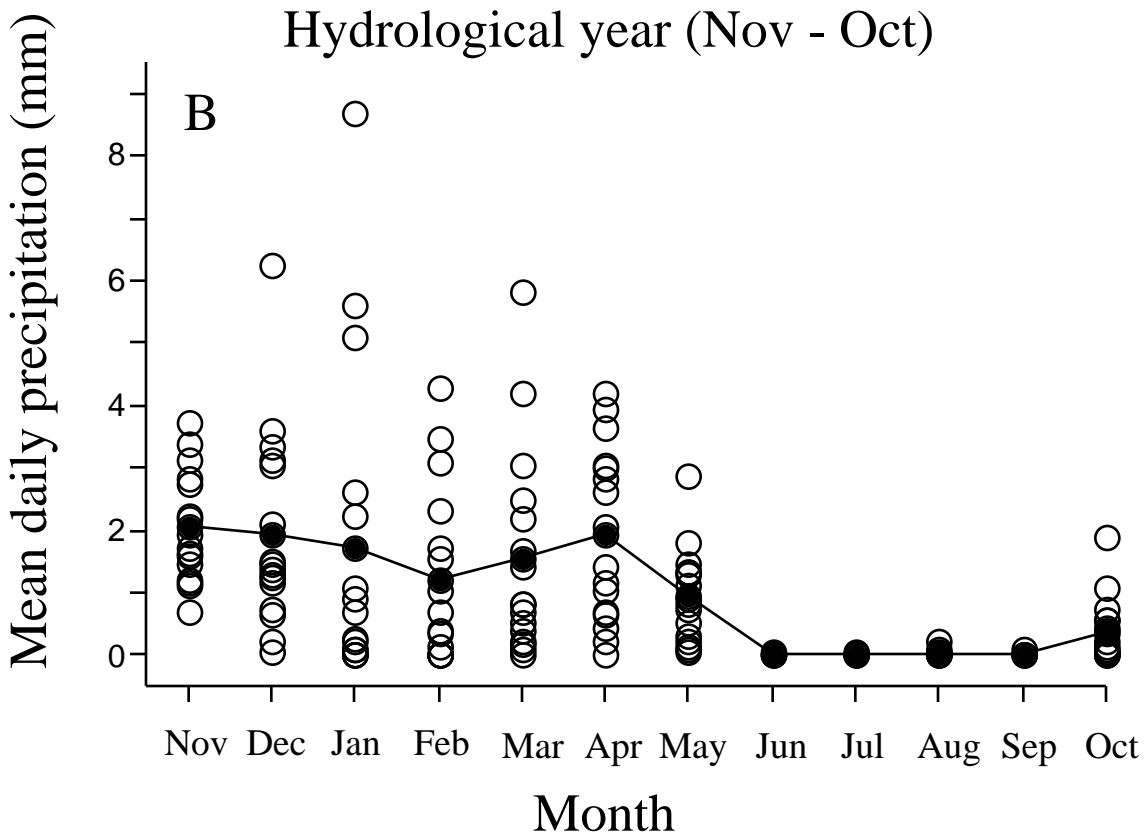
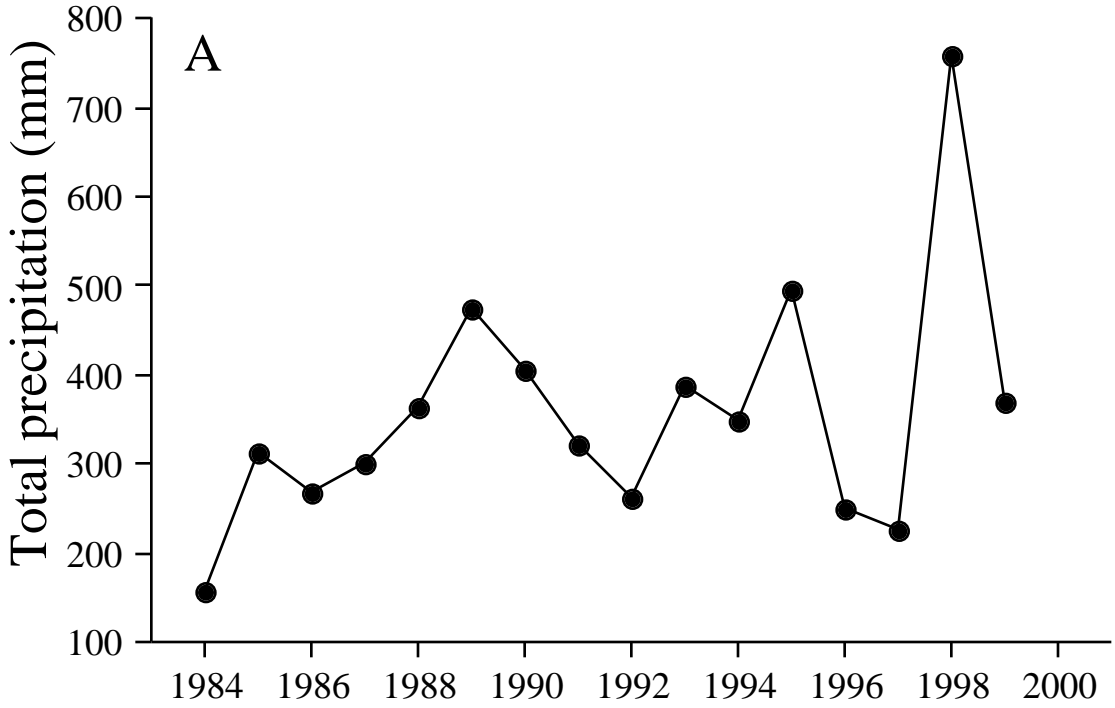
Figure 7. Food types that show seasonal patterns of consumption. Mean proportion of feeding time (\pm s.e.) devoted to each food type is plotted against month of the year,

beginning with November (the first wet month after the long dry season in Amboseli). Shaded boxes enclose the long dry season (Jun through Oct). See also Tables 2, 3, 5.

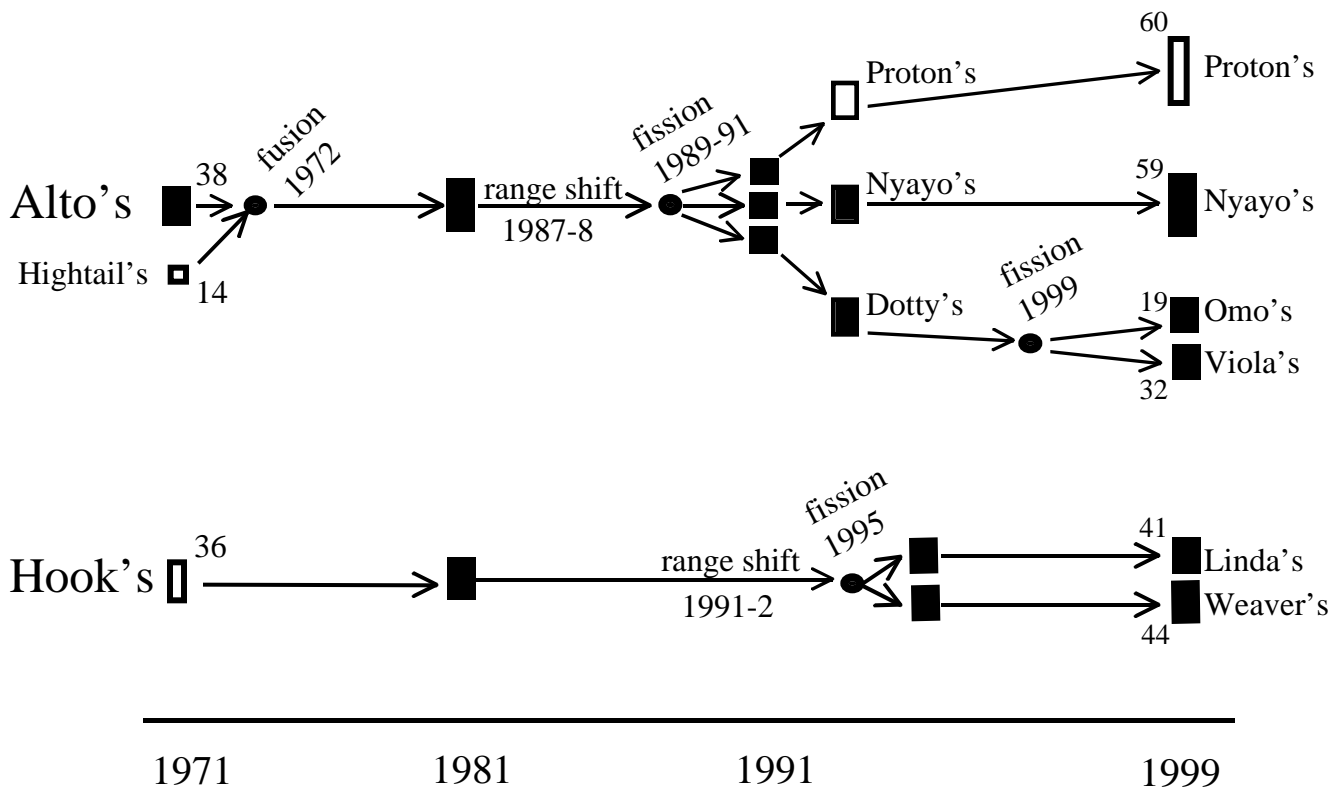
Figure 8. Patterns of consumption for food types that show damped seasonality in consumption patterns. In all cases, heterogeneity across months is evident, but consumption of the fruits, seeds or flowers of at least some species occurs in both the long dry season and the wetter months. Conventions as in Figure 7; see also Tables 2, 3, 5.

Figure 9. Proportion of feeding time spent on the 10 major food types of Amboseli baboons. A. Data reported by Post (1982) for the year 1974-5, with rank order of the food written above the bars for the top five foods (totaling 90% of feeding time). B. Data from this study, pooling the two subpopulations, Hook's (1991-1999) and Alto's (1996-1999). Subpopulations are pooled in the graph because subpopulation explained no variance in feeding on various foods (Table 5). Numbers above the bars in B 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 1990's both foods had dropped in importance, reflecting the fact that *Acacia* trees were less abundant in the 1990's than in the 1970's. Note also that in the 1990's, the top five foods constituted only 73% of feeding time.

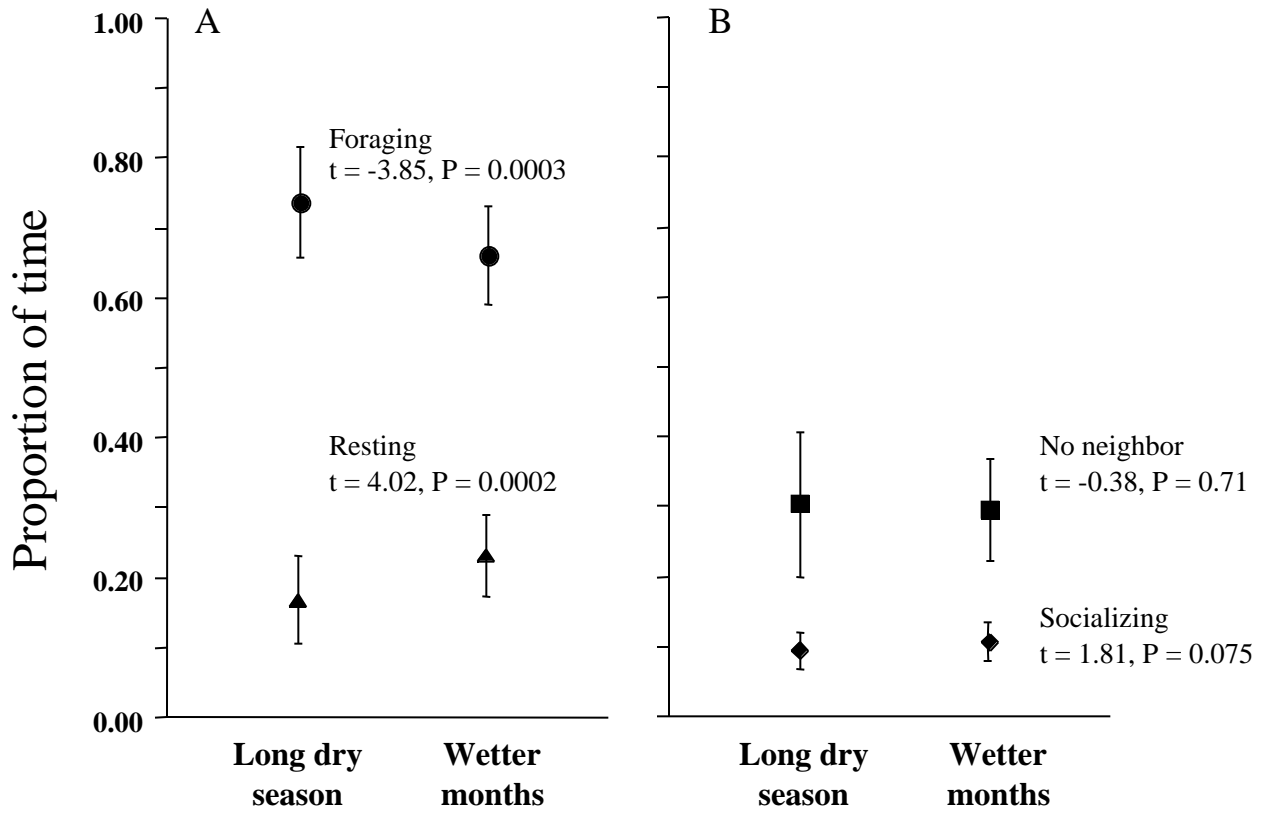


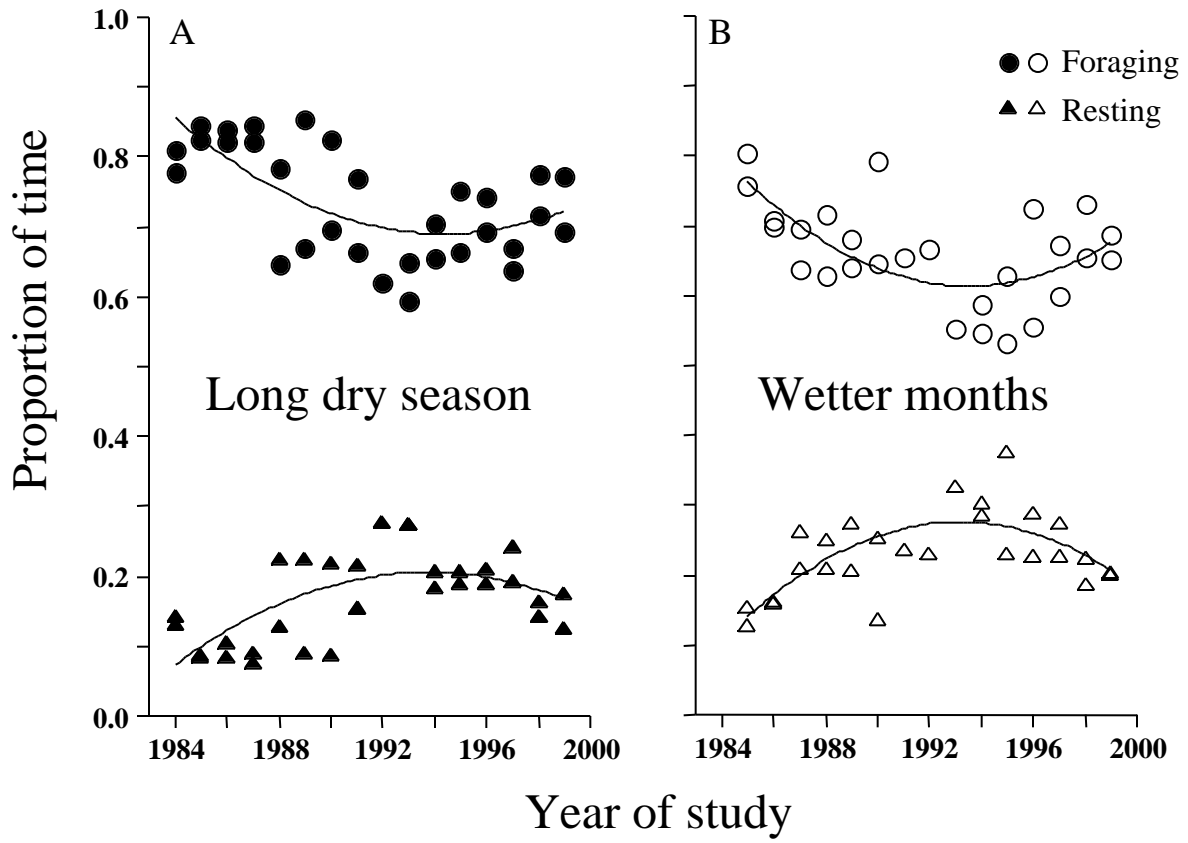


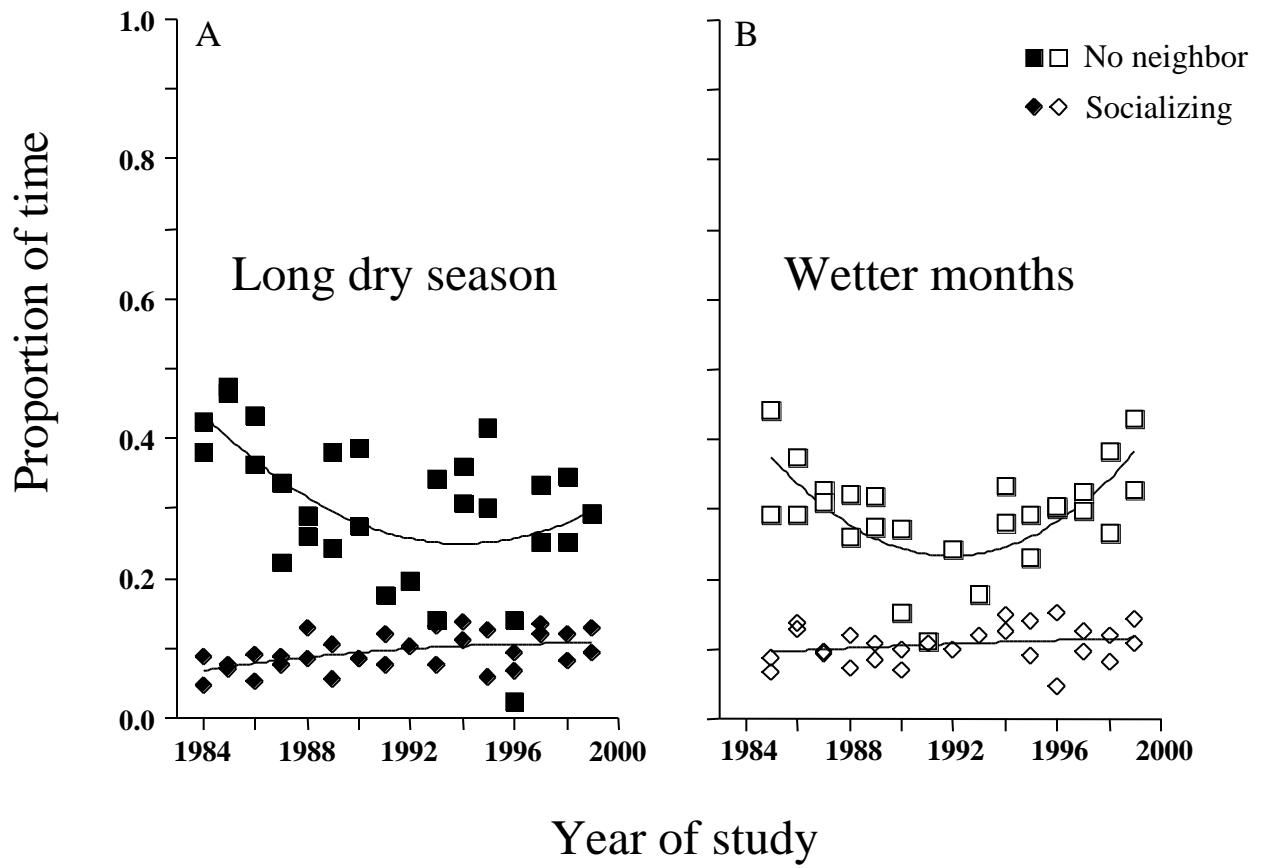
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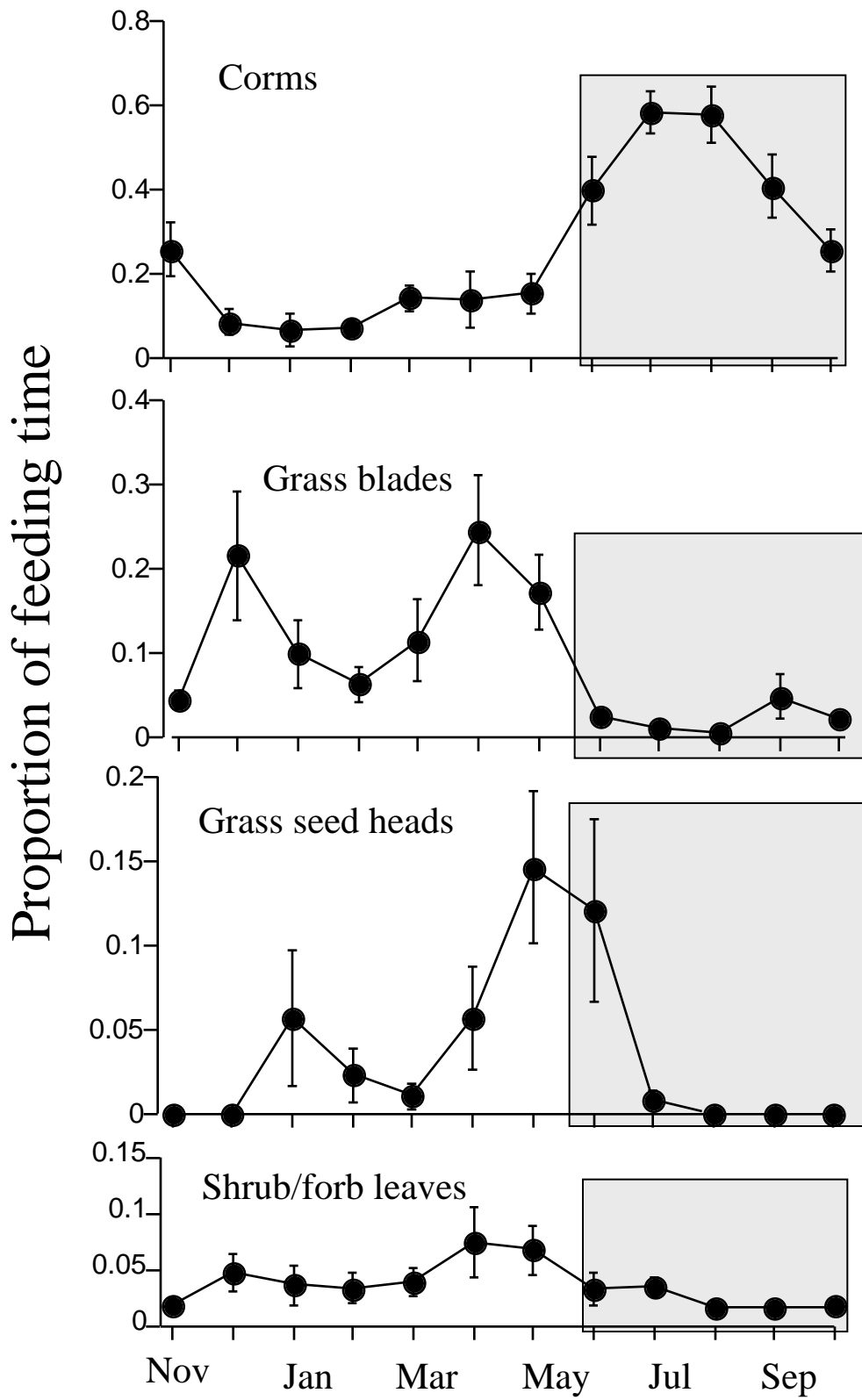


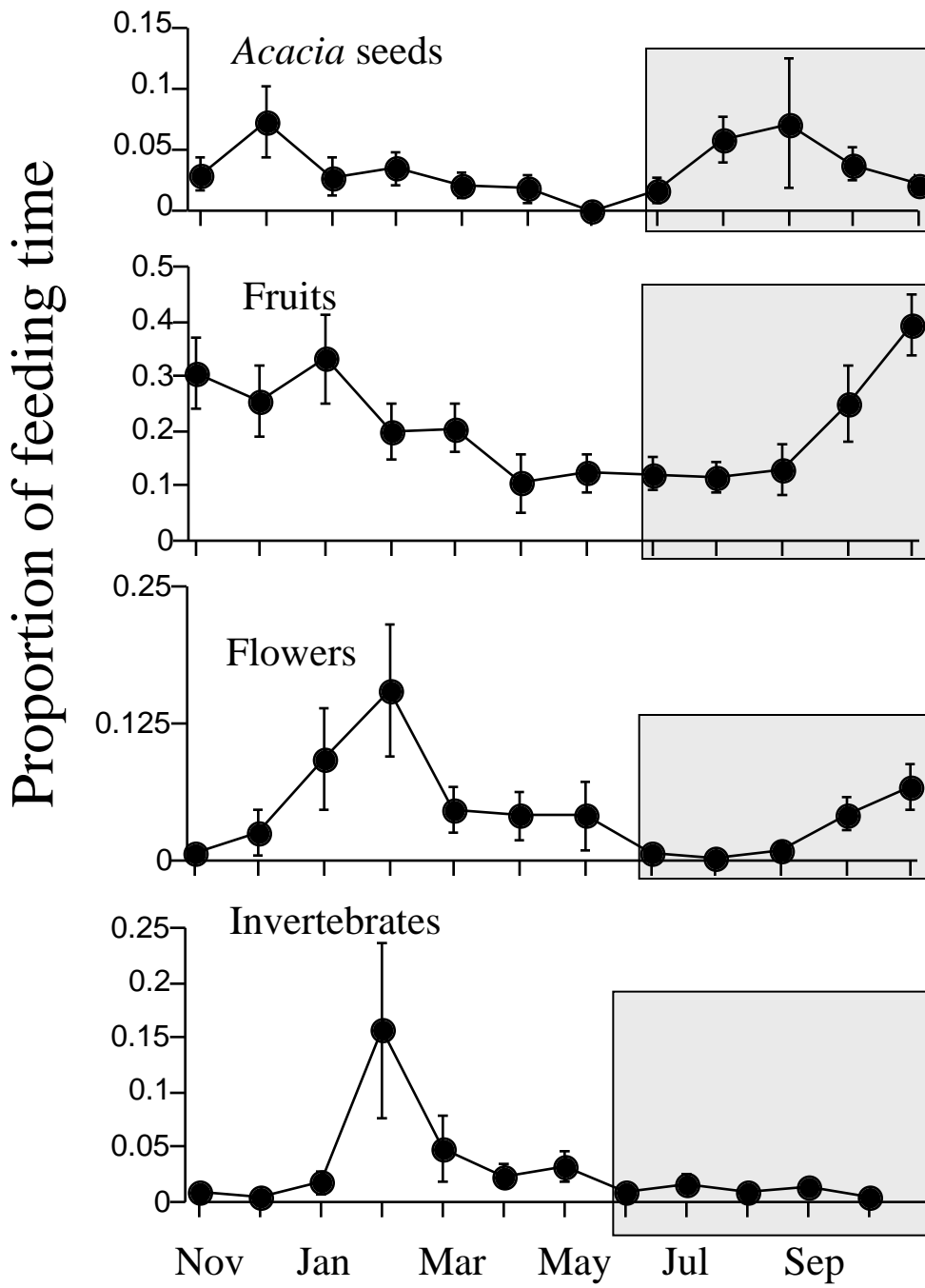
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Proportion of feeding time

