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Foraging in a variable environment: weather patterns and the behavioral ecology of baboons

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Abstract We investigated the long-standing premise in behavioral ecology that the environment affects behavior and demography. We did this by evaluating the extent to which year-to-year variability in the behavioral ecology of a nonhuman primate population could be modeled from meteorological patterns. Data on activity profiles and home range use for baboons (*Papio cynocephalus*) in Amboseli, Kenya, were obtained over a 10-year period for three social groups: two completely wild-foraging ones, and a third that supplemented its diet with refuse from a nearby tourist lodge. The relationships across years among activity budgeting, travel distance, group size, and measures of temperature and rainfall patterns differed among the social groups. Although meteorological variation generally correlated with behavioral variation in the completely wild-foraging groups, different weather variables and direction of relationships resulted for each group. In addition, different relationships among variables were found before and after home-range shifts. The food-enhanced group spent half as much time foraging as did the other groups and therefore could be used to evaluate the relative extent to which foraging time was a limiting factor for resting and social time. Under their relaxed ecological conditions, the food-enhanced animals increased resting time much more than social time.

These findings, combined with supplementary information on the population, lead us to suggest that baboons use a suite of interrelated responses to ecological variability that includes not only changes in activity budgets, but also home-range shifts, changes in the length of the active period, and changes in group size through fissions. Moreover, our results imply that group differences as well as interpopulational and interspecific differences in behavioral ecology provide significant sources of variability. Therefore, social groups rather than populations may be the appropriate unit of analysis for understanding the behavioral ecology of baboons and other highly social primates. The different patterns we observed among groups may have fitness consequences for the individuals in those groups and thereby affect population structure over time.

Key words Baboon · Activity budget · Intrapopulation variability · Meteorological variation · Environmental constraints

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Introduction

Temperature and rainfall have pervasive effects on animals not just directly, but also indirectly by affecting productivity of food and availability of drinking water. Students of primate behavioral ecology have therefore long been intrigued by relationships between primate populations and the weather (e.g., Crook 1970; Kummer 1971; Altmann and Altmann 1970; Dunbar 1992). The broad question can be framed as to what extent can the behavioral ecology of socially living primates be modeled “from the sky down”, that is, predicted from meteorological variables? A few authors have sought predictability at biogeographical scales in either time or space (Wrangham et al. 1993; Rowell 1966) or to explain inter-individual variation in terms of resource availability (Barton et al. 1992; Byrne et al.

1993; Isbell and Young 1993). At the other extreme, they have sought to explain fine-grained variability such as in the daily behavioral decisions made by individual animals (Wagner and Altmann 1973; S. Altmann 1974; Slatkin 1975; Post 1981; Stelzner and Hausfater 1986; Stelzner 1988). In contrast, little research attention has been paid to intermediate time scales other than seasonal differences or to intrapopulation levels of analysis other than individual differences.

Until recently, a major empirical limitation for understanding any primate species has been the absence of data for more than a few sites or more than a few years. Fortunately, with respect to the first constraint, baboons (*Papio*) have now been studied at a diverse range of sites and several of these studies have lasted a decade or more. Dunbar (1992) took advantage of the former development to investigate the relationships between weather and baboon behavioral ecology from an interpopulation perspective. He combined several short-term studies of populations located across sub-Saharan Africa to evaluate behavioral responses of baboons to meteorological variation. However, each population was represented by a single group, reflecting the fact that baboon studies in which detailed behavioral data are collected are often studies of only a single group. From his analysis, Dunbar predicted what groups of baboons should do in the face of rainfall and temperature variation. The report concluded that baboons should use time available for resting rather than social time when their foraging needs increased. Furthermore, he predicted the distribution of baboon populations and the optimal size of these populations from the equations relating data on behavioral and meteorological variation.

With respect to the second constraint, the tendency of previous research to focus on fine-grained, moment-to-moment variability or on seasonal differences probably reflects the fact that most studies of primate populations are relatively short, averaging less than two years (Dobson and Lyles 1989). Except for species that tend to live in groups that are small and in close proximity to each other, most studies also usually focus on only a single group in a population. Here, we consider variability that has thus far been little investigated and, consequently, that therefore has been implicitly assumed to be negligible: annual variability in behavior and variability among groups within a population. We present herein an intrapopulation analysis of the relationship between annual variability in weather patterns and year-to-year differences in group size, activity budgets, day journey length, and home range shifts, based on data from a long-term study of three baboon groups of the Amboseli basin in southern Kenya.

Semi-arid habitats such as that in Amboseli are potentially the most suitable for testing the relationship between behavioral and weather variation, particularly annual variability. This is because regions that receive relatively low amounts of rainfall experience

greater year-to-year variability in total rainfall than that of more wet environments (Ricklefs 1973, p. 762). Furthermore, marginal habitats such as Amboseli are best for "elucidating the mechanism of action of many ecological factors" (Bourlière 1979, p. 41). For example, studies performed for two separate years in environments with moderate to high rainfall found little difference between the two years in foraging time (Gilgil in Kenya: Harding 1976; Eley et al. 1989; Awash/Metahara in Ethiopia: Aldrich-Blake et al. 1971; Nagel 1973). Moreover, in Dunbar's interpopulation analyses (Dunbar 1992), the lack of year-to-year variability in several wet locales led the author to use either single-year or average meteorological data as available under the assumption that these would be interchangeable (R. Dunbar personal communication).

The present investigation of annual variability across a number of social groups from a single population has several parallels to the previous interpopulation study (Dunbar 1992). However, because we unearthed a number of data problems (see Discussion) and methodological concerns (see Methods) in that earlier report, we do not focus here primarily on testing that study's model. Rather, our primary goal was to ask whether a few meteorological variables could adequately track temporal (annual) changes in the animals' resources as seen through correlations with activities and group measures, and whether the population of social groups was homogeneous in response to the environment. We secondly evaluate the models of Dunbar (1992) by first correcting some errors and then comparing predictions of those models with our results. Finally, we explore time constraints among various activities, the extent to which foraging time serves as a limiting factor for socializing and resting time, and whether baboons may have minimum tolerable times for these latter two activities.

Methods

Study population

Data were collected on individually known adult female baboons of three groups within the Amboseli population (Alto's, Hook's, and Lodge) that were observed from 1982–1990, 1983–1991, and 1986–1991, respectively (for detailed group accounts see Altmann et al. 1977, 1981, 1985; Altmann and Alberts 1987; Altmann and Muruthi 1988). During the observation years, Alto's Group and Hook's Group foraged on natural foods. Lodge Group foraged both on natural foods and on those at a nearby garbage dump adjacent to a tourist lodge (Muruthi et al. 1991).

Meteorological data (summarized in Table 1)

Rainfall (mm) and rainfall variability

Rainfall was measured daily with a rain gauge at the research camp. The daily values were summed to yield annual rainfall for each year.

Table 1 Annual rainfall and temperature data

Year	(<i>P</i>) Rain (mm)	(<i>I</i>) Shannon Diversity	(<i>Z</i>) Simpson Diversity	(<i>V</i>) Dry months < 50 mm	(<i>T</i> _{min}) Average Minimum	(<i>T</i> _{max}) Average Maximum	(<i>T</i>) Average temperatures (°C) Mean
1982	349	0.667	0.835	9	14.90	31.61	23.26
1983	376	0.615	0.812	10	14.16	33.03	23.59
1984	132	0.525	0.767	10	13.39	32.92	23.16
1985	297	0.681	0.862	10	13.81	31.38	22.60
1986	317	0.671	0.854	10	14.25	31.92	23.08
1987	250	0.733	0.893	10	14.12	33.03	23.57
1988	408	0.717	0.891	7	14.80	33.48	24.14
1989	488	0.756	0.902	7	14.10	32.58	23.34
1990	326	0.704	0.877	10	14.24	32.78	23.51
1991	407	0.605	0.797	10	14.72	33.60	24.16
Mean	335	0.667	0.849	9.3	14.25	32.63	23.44
SD	97.8	0.070	0.040	1.2	0.46	0.76	0.47
Correlation with annual rainfall	1	0.54	0.45	-0.63	0.64	0.14	0.42

In addition, we calculated a measure of rainfall variability because the vegetation available in an area may be influenced not only by total annual rainfall, but also by the patterning of that rainfall within a year, the seasonality (Rosenzweig 1968; Le Houerou and Hoste 1977; Deshmukh 1984). Based on the analysis of Bronikowski and Webb (1996), variability of rainfall across months was represented with an evenness-of-rainfall measure using the Shannon diversity index (See Bronikowski and Webb, 1996 Table 1 for formula). For months with no rainfall, we substituted 1×10^{-6} mm of rain to obtain a natural logarithm. In order to test and evaluate the models of Dunbar (1992) with our data, however, we also calculated the two rainfall variability measures used in those models: the Simpson diversity index and the number of dry months for a given year defined by Dunbar as months with less than 50 mm of rain. This cutoff of 50 mm is close (47 mm for Amboseli) to the criterion suggested by Le Houerou (1989) of months with rainfall less than ($2 \times$ mean annual temperature) which approximates the water requirements of most African crops.

Temperature (°C)

Daily records of minimum and maximum temperature were collected at the research camp and mean daily temperature was computed as the average of these two. Annual average daily minimum, maximum, and mean temperatures were then calculated as the average, for each year, of these daily values. Although mean temperature is commonly used in studies and may sometimes be the only value available in published meteorological tables, minimum and maximum temperatures might very well each be important for thermoregulation and resource availability. Hence we used both average minimum and maximum temperature instead of just average mean daily temperature as independent variables in our analyses. The correlation between each year's average daily minimum and average daily maximum temperature for 1982–1991 was negligible ($r = +0.15$, $n = 10$, $P = 0.68$).

Behavioral data (summarized in Table 2)

Group size

Group size for each of the three groups was taken as the July 1 census in each year for that group.

Annual average daily travel distance

We estimated daily travel distance as the distance traveled from 0800–1700 hours. At each hour within this time (excepting the 1200 hour), the location of the current focal animal was noted on aerial photographs of the Amboseli basin. The photographs were marked with 1 inch quadrats that corresponded to 165 m² as determined with a Magellan GPS NAV 5000 PRO global positioning system. (The United States government adds a random error of up to 100 m in GPS readings. Therefore, we reduced the noise in this calculation by positioning landmarks of known location for a correction factor, by averaging over 20–100 readings for all locations, and by taking additional readings on different days.)

When the quadrat of location changed, we assumed that on average, the group moved a distance equal to the distance from the center of the old quadrat to the center of the new quadrat. In this way, from 0800 to 1700 hours, we estimated the travel distance during each hour (e.g., the 0800 hour travel distance was the distance from the center of the 0800 hour quadrat to the center of the 0900 hour quadrat). (The 1100 travel distance was a 2-hour estimate from 1100 to 1300 hours.) We calculated daily travel distance for each year from 0800 to 1700 hours by first averaging the hour-of-day travel distance across days for that year and then summing these averages across hours.

For years starting in 1987, we did not have data for 1600–1700 hours. We therefore used the information from 1982–1986 to estimate the 1600 hour travel distance for the subsequent years in the following way. The 1600–1700 hour travel distance for 1982–1986 was used to estimate the percent of total daily distance traveled in that hour of the day. We then increased the annual average daily travel that was based on 0800–1600 hour data by this amount for 1987–1991 (12% for Alto's Group and 10% for Hook's Group).

Annual home range

A group's location within the Amboseli basin was assumed to extend to, and include, the outermost quadrats used each year in both the east-west and north-south directions. Although we do not use home range location as an independent variable, we felt that broadscale changes in the location of the groups' home ranges might be an important source of heterogeneity among years and groups.

Time budgets

Time budgets were estimated from instantaneous (point) samples (J. Altmann 1974) on focal adult females. Activity state was

Table 2 Behavioral data for each social group

Year	Group size (<i>N</i>)			Daily Travel Distance (<i>D</i>) (km/9-h day)	
	Alto's	Hook's	Lodge	Alto's	Hook's
1982	53	41		5.4	
1983	56	45		5.2	6.1
1984	63	48		4.7	6.9
1985	64	48		4.4	5.1
1986	64	57	38	5.1	4.7
1987	65	58	43	5.3	5.8
1988	62	64	51	5.0	4.5
1989	67	60	56	3.8	5.3
1990	77	59	54	3.0	4.6
1991	78	54	47		5.9

Year	Percent of daytime (9-h day)											
	Feeding (<i>F</i>)			Moving (<i>M</i>)			Socializing (<i>S</i>)			Resting (<i>R</i>)		
	Alto's	Hook's	Lodge	Alto's	Hook's	Lodge	Alto's	Hook's	Lodge	Alto's	Hook's	Lodge
1982	37			31			6			26		
1983	41	44		28	25		10	10		21	21	
1984	60	58		16	17		6	8		18	17	
1985	59	55		20	22		8	9		13	14	
1986	50	49	23	25	27	19	11	9	13	14	15	45
1987	41	50	22	27	31	17	10	7	12	22	12	49
1988	38	47	24	25	27	18	13	8	15	24	18	43
1989	38	47	22	28	31	18	9	8	14	25	14	46
1990	39	46	25	26	32	24	10	9	14	25	13	37
1991		37	26		31	19		9	12		23	43

noted on each minute for 10 minutes. We assumed that the point samples were independent based both on Slatkin's autocorrelation analysis (Slatkin 1975) and on subsequent studies in which bout durations were found to be less than one minute (Post et al. 1980; Stacey 1986; Alberts et al. 1996; J. Altmann unpublished work). The sampling order for females was determined using a table of random numbers. These 10-min time intervals were evenly distributed across adult females among the active hours from 0800 through 1700 hours (excepting 1200 hour) for an average of 7 days of every month for each group. Activity state was recorded as either feeding, moving, socializing (essentially time spent grooming), or resting (e.g., Altmann 1980; Post 1981; Dunbar and Dunbar 1988). If an animal was both feeding and moving, the activity was coded as feeding, and hence moving time was underestimated. We therefore constructed an additional variable, foraging time, defined as time spent feeding, moving, or doing both simultaneously. Over 79,000, 70,000, and 31,000 point samples were collected for Alto's, Hook's, and Lodge Groups respectively.

Annual time budgets were constructed by first calculating average feeding, moving, socializing, and resting percents for each hour of the day except 1200 hour (e.g., Alto's 1984 0800 hour: 5% feeding, 10% moving, 40% socializing, 45% resting). These hourly values for a group were then averaged for each year to obtain an annual average daily time budget. In this manner, we first accounted for potential trends across the daytime in activity.

Statistical analysis

To determine the meteorological variables that might be good predictors of annual daily travel distance and of time spent in each of feeding, moving, socializing, and resting, we first calculated the Pearson correlation coefficients between each group's annual mean value for each of the behavioral variables and each meteorological variable (Table 3). We then performed multiple regression analysis of each behavioral variable on a linear combination of the meteorological variables (Table 4).

Statistical analyses were done in Statview 4.01 for the Macintosh. A subset of analyses were also run in PC SAS and Systat 5.2 for the Macintosh to verify our results. Finally, we performed an analysis-of-variance on the foraging data treating year, month, and group as the main effects.

Although forward stepwise multiple regression was used to develop the interpopulation models in Dunbar (1992), we did not use this technique in our analyses because the approach has a number of problems, particularly with observational data (Kerlinger and Pedhazur 1973; James and McCulloch 1990). These authors argue that stepwise regression should not be used because it does not consistently choose the same "important" explanatory variables between analyses. Instead, a balance between univariate analysis and multiple regression should be used to determine significant predictor variables, the approach we took, as described above. In addition, different software packages have slightly different algorithms for performing forward stepwise regression and some require *F*-value inclusion criteria, while others require a significance level inclusion criterion, while still others require both. In trying to replicate the equations published in Dunbar (1992), we used three different software programs (see above) to verify our results which differed in a number of ways from the published models (see Results).

Results

Amboseli travel distance, feeding, moving, social, and resting time

Correlation analysis

Alto's Group. Alto's Group traveled farther in years when group size was smaller (Fig. 1), contrary to expect-

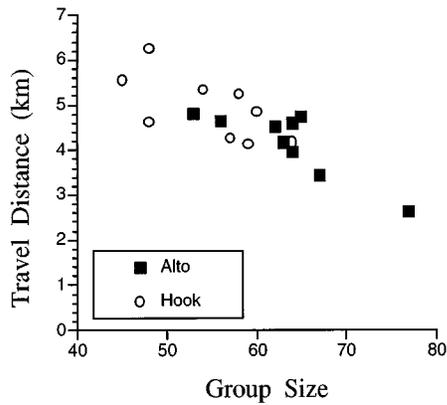


Fig. 1 The relationship between travel distance and group size for Alto's and Hook's Groups. See Table 3 for statistical detail

tations (see baboons: Barton et al. 1992; Dunbar 1992; macaques: van Schaik et al. 1983). The animals of Alto's Group spent more time feeding in years with lower rainfall, years with less even rainfall, and years with lower minimum temperatures (Fig. 2a–c). In years with greater rainfall and those with higher daily minimum temperatures, the group spent more time moving (Fig. 2d and f) but less time in overall foraging. Their social time did not correlate with any variables.

Finally, in years with greater daily minimum temperatures, they spent more time resting.

Feeding, moving, and resting were interdependent (Table 3). In years when Alto's Group spent more time feeding, they always devoted less time to each of these other activities. Perhaps as a consequence, moving and resting times were related such that greater time spent doing one corresponded to greater time spent doing the other.

Hook's Group. Hook's Group, like Alto's Group, also traveled longer distances when group size was smaller (Fig. 1). In addition, they traveled farther in years with less even rainfall. Hook's Group, like Alto's Group, spent more time feeding in years with lower rainfall and in those with lower minimum temperatures (Fig. 2a and c). Hook's Group spent more time moving in years with greater rainfall, years when rainfall was more even, and in those with higher minimum daily temperatures (Fig. 2d–f). Combined feeding and moving time (i.e., foraging time) was also greater in years when rainfall was more even. Social time for Hook's Group, like Alto's Group, was not correlated with any predictor variables. Hook's Group rested more in years with greater maximum daily temperatures. The relationship among the activities of Hook's Group was the same as

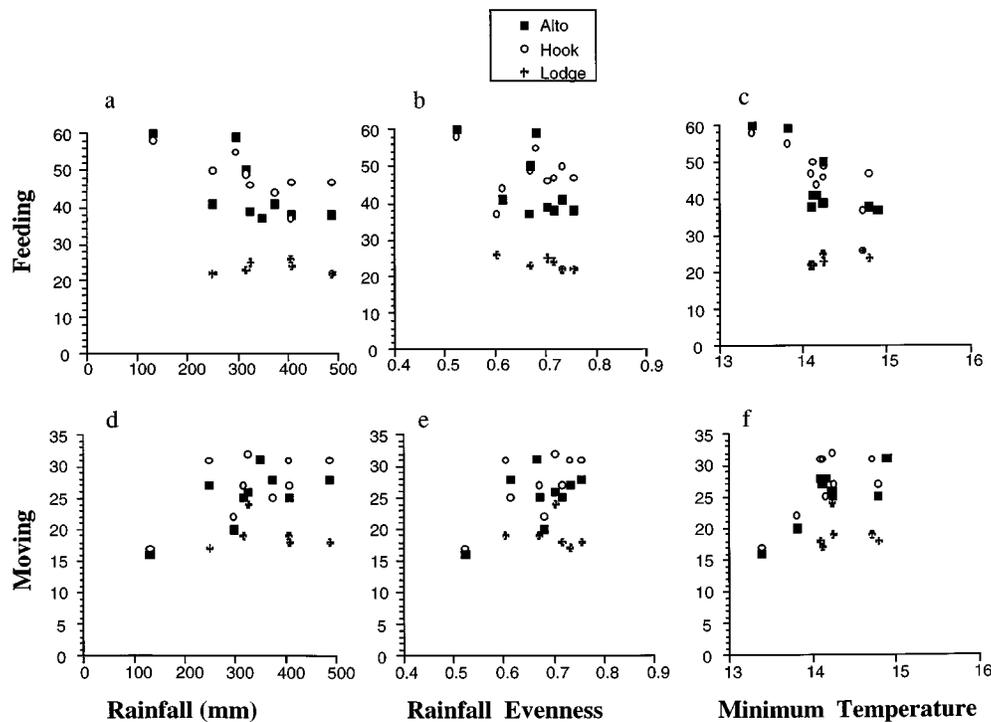


Fig. 2a–f Graphical representations of suggestive correlations between behavioral variables and meteorological variables. When a correlation was suggestive for one social group, the other groups

were included for comparison. For correlation coefficients and significance levels, see Table 3

for Alto's Group in years when Hook's Group spent more time feeding, they spent less time doing each of moving and resting.

Lodge Group. The partially food-enhanced Lodge Group traveled about 4 km daily: 1 km from its sleeping trees to the tourist lodge and 1 km to return to the trees plus a small amount of local travel around the lodge area (Muruthi 1988). Travel distance was not mapped for Lodge Group and therefore no analyses of travel distance were performed for this group.

The correlations among Lodge Group's behavior and the meteorological variables revealed only one potentially strong relationship: Lodge Group, like Alto's Group, spent more time feeding in years when rainfall was less even (Fig. 2b). Lodge Group's feeding time, unlike feeding time in the natural feeding groups, had no significant relationships with moving or resting time. In years when Lodge Group spent more time moving, they spent significantly less time resting. In years when they foraged more, they both socialized and rested less.

Multiple regression analyses

Table 4 contains results of the multiple regression analyses of behavioral on meteorological variables. Note that the coefficients in a multiple regression equation are partial regression coefficients. Consequently, the signs of these coefficients cannot be interpreted as

indicating the direction of the univariate effect. The coefficient of X_i in a multiple regression equation represents the regression of Y on X_i when all other X_j are held constant at their means (Sokal and Rohlf 1981). The simple effect of X_i on Y is obtained from the univariate regression of Y on X_i and has the same sign as the correlation coefficient in Table 3.

By analyzing the variation in behavior with a linear combination of the weather variables as opposed to each separately as in the above correlation analysis, complex relationships of the weather variables acting in concert may be revealed. Only three equations of a behavior regressed on a combination of the four weather variables were statistically significant (Table 4) despite the numerous suggestive correlations above. These were Alto's Group's foraging time, Hook's Group's foraging time, and Hook's Group's resting time. In no case did the regression of Lodge Group's feeding, moving, socializing, or resting time on the meteorological variables explain any variation (Table 4), i.e., Lodge Group activities were unconstrained by meteorological variability.

Both the correlation and regression analyses indicate that groups cannot be said to respond similarly to meteorological variation. Our results point to patterns of temperature and rainfall variability across years that were only partially reflected in the behavior of the Amboseli baboons. In fact, there are more dissimilarities than similarities among the three social groups both with respect to which meteorological variables are important and the directionality of the correlations.

Table 4 Multiple regression of behavioral variables on weather variables (significant partial regression coefficients appear bold). Because the daily activities were proportional data, we adjusted the data with the arcsin – square root transformation before use in the analyses. For simplicity of interpretation, however, we present the untransformed results because we found that they have equivalent

coefficients of determination to the transformed regressions. Travel distance (D) and activity budgets (F, M, S, R) on the meteorological variables: rainfall (P), Shannon rainfall diversity (I), minimum temperature (T_{min}), and maximum temperature (T_{max}). The R^2 values have been adjusted for intercorrelation among the weather variables

	Intercept	Predictor variables				Adjusted R^2	F ($df = 4, 4$)	P
		(P)	(I)	(T_{min})	(T_{max})			
Alto's Group								
Distance (D)	– 5.39	– 0.002	– 3.54	+ 0.97	– 0.04	0.00	0.41	$P = 0.79$
Feeding (F)	+ 369	– 0.02	– 24.11	– 11.0	– 4.46	0.65	4.72	$P = 0.08$
Moving (M)	– 58.0	+ 0.01	+ 7.61	+ 5.40	– 0.09	0.37	2.19	$P = 0.23$
Foraging (FM)	+ 305	– 0.01	– 17.4	– 5.05	– 4.55	0.73	6.49	$P = 0.05$
Socializing (S)	– 60.9	+ 0.002	+ 13.0	+ 0.62	+ 1.59	0.09	1.21	$P = 0.43$
Resting (R)	168	+ 0.006	+ 12.8	+ 5.03	+ 3.30	0.20	1.50	$P = 0.35$
Hook's Group								
Distance (D)	+ 8.37	+ 0.001	– 4.29	– 1.48	+ 0.61	0.64	4.51	$P = 0.09$
Feeding (F)	+ 188	– 0.03	+ 24.5	– 7.20	– 1.36	0.64	4.55	$P = 0.08$
Moving (M)	– 103	+ 0.004	+ 39.0	+ 3.22	+ 1.74	0.41	2.41	$P = 0.21$
Foraging (FM)	+ 96.5	– 0.025	+ 63.0	– 3.86	– 0.007	0.92	23.1	$P = 0.005$
Socializing (S)	+ 30.62	+ 0.005	– 11.4	+ 0.80	– 0.84	0.32	1.96	$P = 0.26$
Resting (R)	– 24.5	+ 0.02	– 48.5	+ 2.20	+ 1.06	0.97	65.9	$P = 0.0007$
Lodge Group								
Feeding (F)	+ 4.83	+ 0.001	– 19.5	+ 0.71	+ 0.66	0.00	0.66	$P = 0.71$
Moving (M)	+ 60.3	– 0.001	– 13.4	– 1.32	– 0.37	0.00	0.02	$P = 0.99$
Foraging (FM)	+ 39.0	– 0.001	– 25.6	+ 1.41	+ 0.06	0.00	0.07	$P = 0.98$
Socializing (S)	– 25.0	+ 0.003	+ 21.3	+ 4.28	– 1.19	0.00	0.64	$P = 0.64$
Resting (R)	+ 88.2	0.00	– 3.48	– 6.47	+ 1.55	0.00	0.03	$P = 0.99$

Table 5 Analysis-of-variance of percent of time spent foraging for 1986–1990

Effect	<i>df</i>	Type IV MS	<i>F</i>	<i>P</i>
Year	4	0.138	1.19	0.32
Month	11	0.804	2.51	0.01
Group	2	11.791	202.0	0.00
Year × Month	42	1.328	1.09	0.37
Year × Group	8	0.585	2.51	0.02
Month × Group	22	0.688	1.07	0.39
Error	71	0.029		

Analysis-of-variance

In order to explore further the differences among social groups, we performed an analysis-of-variance (ANOVA) to determine whether foraging behavior varied significantly among years, months, and groups (Table 5). In our ANOVA on foraging behavior from 1986 to 1990 (years for which we had data on all three groups), significant results were obtained for the fixed effects of group and month, and the year × group interaction (i.e., years affected the social groups differently). The respective strengths of association were 55% for group, 2% for month, and 2% for year × group. The striking feature of this analysis was that the overall variation in foraging behavior explained by social group was an order of magnitude larger than that explained by month or year × group. We performed post-hoc comparisons of group mean foraging times using Tukey's Honestly Significant Different (HSD) test (Kirk 1982). All groups were different from each other in foraging times (all tests at $\alpha = 0.05$ significance level).

We also performed post hoc comparisons of mean monthly percent foraging, again using Tukey's HSD test. These tests revealed a significant difference between July and August on the one hand and December through March on the other. July and August were cool dry months and baboons spent more time feed-

ing and moving than in December–March, which included rainy months as well as the hottest months (mean percent of daytime foraging: July = 68%, August = 71%, December = 60%, January = 57%, February = 61%, March = 60%). Consistent with published reports of baboons and other primates (baboons: Dunbar and Dunbar 1974; Barton et al. 1992, vervets: Isbell and Young 1993), these results suggest that all three groups foraged more in dry months.

Intrapopulation test of Dunbar (1992) predictions

As shown in the results below, we first reanalyzed the baboon data that Dunbar (1992) used to generate the interpopulation models for travel distance, feeding, moving, social, and resting time. In doing so, we identified and corrected errors in those published equations. Second, we used the resulting corrected equations to produce expected activity times for the three groups of baboons at Amboseli and compared these expected values to the observed data. To be consistent with Dunbar (1992), we used stepwise multiple regression (but see Methods) after first performing the natural logarithm transformation on all variables as done in that publication.

Table 6 Reanalysis of data in Dunbar (1992) (Travel distance (*D*), feeding (*F*), moving (*M*), resting (*R*), socializing (*S*), rainfall (*P*), Simpson diversity (*Z*), number of months with rainfall < 50 mm (*V*), group size (*N*), average daily temperature (*T*))

		R^2	$F(df)$	<i>P</i>
Day journey (km):				
Re-analysis	$\ln(D) = 2.68 + 0.68\ln(N) - 0.61\ln(P)$	0.72	21.59 (2,14)	$P < 0.001$
Dunbar's	$\ln(D) = 1.34 + 0.78\ln(N) - 0.47\ln(P)$	0.69	18.87 (2,18)	$P < 0.001$
Feeding time (%):				
Re-analysis	$\ln(F) = 6.39 + 5.12\ln(Z) - 0.68\ln(T)$	0.37	4.82 (2,11)	$P < 0.05$
Dunbar's	$\ln(F) = 7.41 + 4.44\ln(Z) - 0.88\ln(T) - 0.45\ln(V) + 0.16\ln(D)$	0.58	3.15 (4,9)	$P < 0.06$
Moving time (%):				
Re-analysis	$\ln(M) = 2.15 + 0.15\ln(N) + 0.28\ln(V)$	0.64	12.34 (2,11)	$P < 0.005$
Dunbar's	$\ln(M) = 2.21 + 0.16\ln(N) + 0.22\ln(V)$	0.66	10.68 (2,11)	$P < 0.01$
Resting time (%):				
Re-analysis	$\ln(R) = 7.57 - 1.26\ln(F)$	0.63	23.48 (1,12)	$P < 0.001$
Dunbar's	$\ln(R) = 10.55 - 1.33\ln(F) - 0.32\ln(N) - 0.28\ln(P)$	0.78	11.98 (3,10)	$P < 0.01$
Social time (%):				
Re-analysis	$\ln(S) = 1.15 + 0.47\ln(P) - 0.54\ln(F)$	0.50	5.50 (2,11)	$P < 0.01$
Dunbar's	$\ln(S) = -1.60 + 0.49\ln(P) - 4.96\ln(Z)$	0.53	6.31 (2,11)	$P < 0.02$

Reanalysis of Dunbar (1992)

We analyzed the data presented in Table 2 of Dunbar (1992) (but see Discussion for problems with that data set itself) and found some differences from the published results (Table 6). For daily travel distance (D) and moving time (M), the reanalysis agreed except for rounding differences. In contrast to the published models, however, the reanalysis of feeding time (F) excluded dry months (V) and travel distance (D). And for the reanalysis of resting time (R), we found that group size (N) and rainfall (P) were excluded. This statistical result could theoretically be due to different inclusion criteria (unknown for Dunbar 1992); however, we used lenient criteria (F value to enter = 2.00, F value to remove = 1.996) which would result in inclusion of at least as many predictor variables, not fewer.

The largest difference in results had to do with social time (S) (see Table 6). In the reanalysis, feeding time entered the model for social time; in the published model, it did not. In the reanalysis, as feeding time increased, social time decreased (simple regression coefficient of $\ln(S)$ on $\ln(F) = -0.73$, $P = 0.04$). This new result suggests that increased foraging demands are responded to by a reduction in social time. Only when we removed feeding time as a potential predictor variable did we obtain a result similar to the published equation [$\ln(S) = -1.61 + 0.48\ln(P) - 5.43\ln(Z)$].

Does the corrected Dunbar model fit the behavioral ecology of the Amboseli groups?

We used the equations from our reanalysis of Dunbar's interpopulation data to generate expected values of travel distance, feeding, moving, social, and resting time for the Amboseli groups for each year. We then com-

Table 7 Goodness-of-fit (χ^2 test): corrected Dunbar equations and Amboseli data ((distance in km (D), percent of time spent feeding (F), percent of time spent moving (M), percent of time spent socializing (S), percent of time spent resting (R))

	Mean expected	Mean observed	$\chi^2(df)$	P
Alto's (D)	7.1	4.2	12.2 (7)	$P < 0.10$
Alto's (F)	30.5	44.8	139.2 (7)	$P < 0.001$
Alto's (M)	30.0	25.1	13.3 (7)	$P < 0.10$
Alto's (S)	6.4	9.3	17.4 (7)	$P < 0.025$
Alto's (R)	14.8	21.5	16.2 (7)	$P < 0.025$
Hook's (D)	6.2	4.9	3.6 (7)	$P < 0.90$
Hook's (F)	30.5	48.1	143.9 (7)	$P < 0.001$
Hook's (M)	29.1	27.0	8.4 (7)	$P < 0.50$
Hook's (S)	6.2	8.6	13.1 (7)	$P < 0.10$
Hook's (R)	14.2	16.4	7.3 (7)	$P < 0.50$
Lodge (D)	5.8	4.0	13.8 (4)	$P < 0.01$
Lodge (F)	30.5	23.7	29.1 (4)	$P < 0.001$
Lodge (M)	28.6	19.2	18.3 (4)	$P < 0.025$
Lodge (S)	9.0	13.3	11.2 (4)	$P < 0.025$
Lodge (R)	38.5	43.8	4.9 (4)	$P < 0.50$

pared these expected values to the observed values over the study years with a χ^2 test (Table 7).

The three Amboseli groups traveled shorter daily distances than predicted by the model for travel distance in Dunbar (1992), although significantly so only for Lodge Group. The two completely natural feeding groups spent more time feeding than expected (see also Post 1981 and Altmann 1980) while the food-enhanced group spent less time feeding than expected ($P < 0.001$ in all three cases). Lodge Group spent less time moving than predicted. All three Amboseli groups spent more time socializing than expected from Dunbar (1992), but not significantly for Hook's Group. Finally, the three groups spent more time resting than predicted, but significantly so only for Alto's Group. Overall, the completely wild-foraging groups in Amboseli spent more time feeding, socializing, and resting than predicted by the model. Although travel time was as predicted, travel distance tended to be less than predicted, suggesting slower movement, perhaps resulting from travel that is highly interdigitated with feeding and search for food items (Hamilton et al. 1978, S. Altmann 1974). The food-enhanced group spent less time feeding and moving, more time socializing, and traveled less than predicted.

Discussion

Test of the Dunbar (1992) interpopulational model with Amboseli data

Why was the interpopulational model, intended to be predictive of intrapopulational variability (Dunbar 1992), a poor predictor of such variability in Amboseli even after correction of the original analyses? The answer to this question may lie in problems with the statistical method of stepwise regression (see Methods) or with data used (see below).

Travel distance data used in Dunbar (1992)

We could not always ascertain from the citations within Dunbar (1992) how many hours were monitored for travel distance in these studies. Dunbar (personal communication) assumed that the studies were all approximately dawn to dusk. If so, the overestimation in travel distance may have been due to our measuring travel distance for a shorter day. We note, however, that our data give essentially the same travel distance values as those in Post (1981) who sampled from 0700–1800 hours and Altmann (1980) who sampled from 0800–1800 hours, both in the mid-1970's.

Meteorological data used in Dunbar (1992)

The meteorological data for Dunbar's model were varied in origin, and many values in Table 2 of Dunbar (1992) either cannot be found in the cited references or contradict the values given in these references. Through communication with Dunbar (June, 1994), we understand that when the data were available, the monthly rainfall and temperature data that were collected concurrently with the behavioral data were used to compute annual rainfall, diversity of rainfall, and number of dry months. However, the requisite weather data were not always reported in which case values for other years and relatively nearby locales were substituted for monthly values of temperature, rainfall diversity and dry months. Finally, in a third class of studies, rainfall data were obtained from a world compilation that had averages sometimes 20 years prior to the study year. As a result, rainfall diversity, dry months, and temperature did not usually correspond to the year or location at which behavioral data were collected. Furthermore, the length of this time or space lag was inconsistent.

Dunbar (personal communication) justified using averages over past years rather than weather data from the study year by analyzing a subset of studies for which he had both. He found that there were no differences between using the actual study year data versus using averages over past years. However, this conclusion derived from analyses for habitats that had high annual rainfall (Dunbar 1992, p. 36 for studies used). In practice, this means that making the assumption that Dunbar did for low rainfall environments such as Amboseli or Gilgil would result in variables that were more mismatched than would be the case for wetter environments. In a modeling endeavor, the net result of using meteorological data collected at different times or at different locations could be large errors.

Derived measures of rainfall variability

Problems arise with the two rainfall variability measures, Z and V , used in Dunbar (1992). The Simpson index (Z), is not the best diversity measure to capture evenness of rainfall (Bronikowski and Webb, 1996). It is by definition, highly dependent on the number of wet months. The problem with the other measure used as an independent variable, the number of dry months (V), where dry is defined by a high cutoff (50 mm) is this variable's relationship to another independent variable, annual rainfall. These two variables are *a priori* statistically dependent and the potential variance in V is correlated with annual rainfall. For example, for years with very little rain, only large values of V are possible (e.g., 8 is the minimum value for V defined by 50 mm for an annual rainfall of 200 mm). In contrast, for years with much rain, V can take on the full range

of values from 0 to 12 (e.g., a year with 600 mm rainfall can have 0 months with less than 50 mm).

The problems we have focused on deal with methods and with the basic initial regression equations, the only ones against which we tested the Amboseli data. The remainder of the 1992 paper proceeds to use these initial equations in an increasingly imbedded analysis to eventually predict, for example, meteorological conditions under which baboons should not be found and parameter values where they should be found. These subsequent analyses are flawed by the errors and questionable weather data in the original data base and by problems with the choice of variables and analyses. They are also flawed by the use of false significance levels and measures of variance in the subsequent analyses that don't take into account that estimates were used that themselves have associated variances. As a result, although the line of model development is an interesting one, the flawed analyses and logic mean that any test of the model's predictions cannot provide a test of the conclusions presented in Dunbar (1992).

Amboseli social groups: intrapopulation variability

The main goal of our study was to determine whether predictable patterns of behavioral response to weather variation exist among social groups within a population. The relationships between meteorological and behavioral variables across the three social groups studied in this population differed in a number of interesting ways. Not surprisingly, the greatest consistency was found for the two wild-foraging groups, Hook's and Alto's. They fed less and moved more in years with greater annual rainfall and in those with higher daily minimum temperatures. A linear combination of weather variables produced multivariate models that explained 73% of the annual variability in foraging time for Alto's Group and 92% for Hook's Group (see Table 4). In years that these two groups spent more time foraging, they spent less time in both moving and resting, whereas socializing remained fairly invariant.

Despite these similarities, the two wild-feeding groups differed in some of their relationships between behavior and meteorological values. Year-to-year variability in weather explained 64% of the variation in travel distance for Hook's Group but none for Alto's Group (see Table 4). Alto's Group foraged less in years with more even rainfall, whereas Hook's Group foraged more in such years. Furthermore, foraging time was significantly different between these groups from 1986 to 1990 (see Table 5) and the observed differences cannot be attributed solely to differences in group size. Not only were the groups fairly comparable in size, but group size as a predictor did not correlate in a consistent manner either for travel distance or activity budgets (see Table 3).

The food-enhanced Lodge Group was virtually unaffected by meteorological variability. This suggests that the effect of weather on annual variability in baboon activity is primarily an indirect one that arises from the effect of weather on food production rather than a direct effect of temperature and rainfall on activities. Even Lodge Group, however, experienced some year-to-year variability in foraging time. During years that they foraged more, they spent less time resting, a finding that was also true of the completely wild-foraging groups. In addition, Lodge Group females, like those in the wild-foraging groups, fed more during the cool dry months of July and August than during December through March (hot months that also included appreciable rainfall). Despite these few responses, Lodge Group appears to be a group unconstrained by annual variability in weather patterns. Their short daily travel distances and low time spent foraging suggests that they provide a baseline model of activity distribution for baboons when ecological constraints are relaxed by having both high food availability (unlike most wild situations) and large amounts of space (unlike most captive conditions).

Minimal, maximal, and ideal time spent in various activities

What insight into ideal and minimum tolerable time for various activities is provided by Lodge Group's unconstrained activities? On average, Lodge Group females spent only 43% of their time foraging, approximately two-thirds of that spent by the fully wild-foraging groups. Most of this reduction in foraging time was attributable to reduced feeding time which was only half that of the other groups. Relative to Hook's and Alto's Groups, Lodge Group animals had 30% more time available for resting and socializing. The Lodge Group females averaged 13.3% socializing and 43.8% resting. Although they spent significantly more time than Alto's and Hook's females in each of these activities (Alto's: 9.3% socializing and 21.5% resting, Hook's: 8.6% socializing and 16.4% resting), the vast majority of the time freed from foraging activity accrued to resting, not to socializing (Fig. 3). These animals chose to spend only 13% of their time socializing even when they had considerably more time free.

Altmann (1980) proposed that when faced with increased foraging demands, individual animals in a group could more readily reduce social time rather than resting time, whereas Dunbar and Dunbar (1988) argued the opposite based on the primary importance to social primates of maintaining social bonds. The literature (e.g. Lee et al. 1986; Saunders 1988; reviewed in Altmann 1988) is consistent with an intermediate conclusion, and the finding of Saunders (1988) that animals responded to greater nutritional constraints by

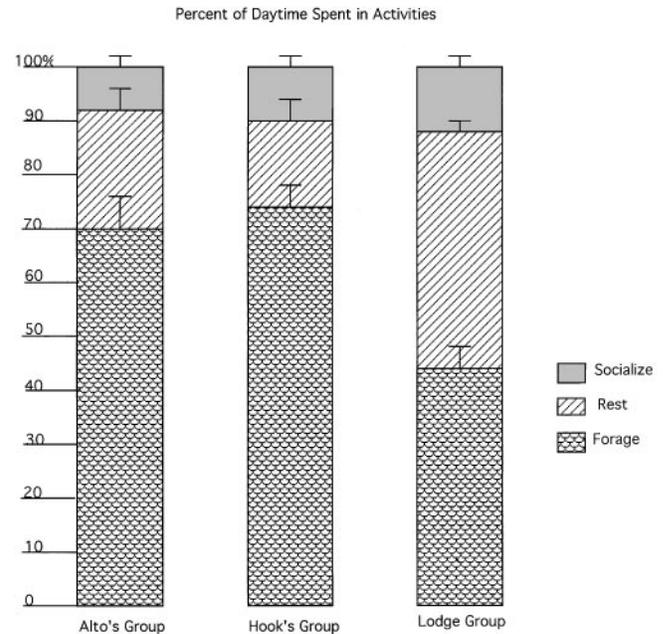


Fig. 3 From 1982 to 1990, Alto's Group foraged $69.8 \pm 5.6\%$, rested $21.5 \pm 5.1\%$ and socialized $9.3 \pm 2.2\%$ of the daytime. From 1983 to 1991, Hook's Group foraged $75.2 \pm 4.3\%$, rested $16.4 \pm 3.7\%$ and socialized $8.6 \pm 0.9\%$ of the daytime. From 1986 to 1991, Lodge Group foraged $43.0 \pm 3.6\%$, rested $43.8 \pm 5.1\%$ and socialized $13.3 \pm 1.2\%$ of the daytime (mean \pm SD where mean is an across-years average)

focusing their reduced grooming time on a smaller number of key social partners is particularly interesting in this respect. Moreover, the present analyses suggest that the answer depends partly on the temporal or demographic level of analysis. Our reanalysis of the interpopulational data in Dunbar (1992) suggested that social time was the flexible activity. In contrast, both the analysis of annual variability in time use and the comparisons among groups in Amboseli suggest that resting time rather than social time serves as the animals' primary flexible time in the range of conditions experienced within this population. The extent to which resting or socializing is treated as flexible time may depend in subtle and complex ways on the demographic and time scale examined, the base level of each activity, and the specific context that might constrain one or the other.

Could tradeoffs between foraging and resting or socializing be identified for the natural feeding groups? We examined trends over the study period in foraging, resting, and socializing. During 1987, Alto's Group shifted its home range 5 km to the west and 5 km south, perhaps as a result of changes in habitat quality. In 1991, Hook's Group shifted its home range 6 km to the west. Both natural feeding groups had suggestive trends of decreased resting time prior to shifting their home ranges and increased resting time afterward (Alto's Group: $r = -0.94$ and $+0.91$, $P = 0.02$ and 0.08 for 1982–1986 and 1987–1990, respectively;

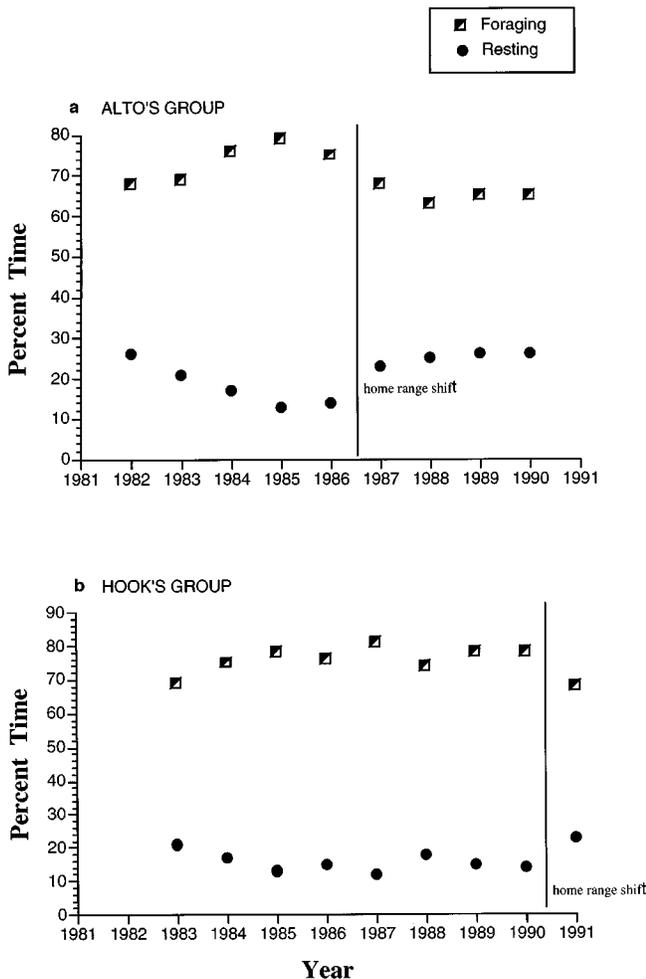


Fig. 4 Resting and foraging time for Alto's and Hook's Groups before and after shifts in their home ranges. See text for statistical details

Hook's Group: $r = -0.47$, $P = 0.24$ for 1983–1990) (Fig. 4a, b). Furthermore, both groups had a low value of 14% of the day spent resting in the year prior to changing their home range and a value of 23% in the year during which the move took place. Thus, as a first approximation, we propose that 15% resting time for an individual may be the minimum tolerable in this particular habitat.

For the three groups, time spent socializing did not vary from year to year with respect to meteorological variability, foraging time, or group size. The females of Lodge Group nonetheless spent significantly more time socializing than did those in the other groups. Lodge Group females spent 13.3% of the time socializing compared with 9.3% for Alto's and 8.6% for Hook's. Furthermore, the difference is somewhat greater per available social partner; 0.28% per available partner for Lodge females, 0.15% for Alto's, and 0.16% for Hook's. Dunbar (1992) has suggested that the time spent socializing reported for wild-feeding savanna baboons is

abnormally/stressfully low. Whether this assessment is correct by some criteria or not, we might, as a first estimate, consider 0.15% time per partner or 9% for a group of about 55 baboons as a minimum time needed to maintain bonds within a group, and almost double that may be ideal for the same-sized group.

If the baboons indeed have minimum requirements for resting and for socializing times, the sum of those values would leave a maximum amount of time available for foraging. If we estimate that those minimal times for resting and socializing for groups of about 55 animals are 15% and 9% respectively, (totaling 24%), 76% would be the maximum tolerable foraging time. Examining patterns over time in Hook's and Alto's Groups is interesting with these values in mind. For both groups, foraging time tended to increase in the years prior to the home range shifts (Alto's Group: $r = +0.80$, $P = 0.10$; Hook's Group: $r = +0.57$, $P = 0.13$) (Fig. 4). These patterns suggest that the animals in both groups may have experienced conditions that exceeded their ability to respond by adjusting their activity budgets without unacceptable decreases in resting or socializing. In each case, the animals responded by shifting their home range instead of eroding time spent socializing or resting beyond these limits. Similar data for other populations and species would allow evaluation of the activity limits suggested by the Amboseli analyses.

Alternative behavioral responses and additional ecological constraints

Home range shifts are just one of a number of possible behavioral responses to environmental variability that animals might use in addition to changes in activity budgets. Another potential response is that of shortening or extending the animals' active day (a parameter not measured in either Dunbar (1992) or the present study in which fixed daily start and stop times were used for observation). Nonetheless, our impression is that such plasticity in the active period has been an important mode of adaptation for the baboons of Amboseli.

By modeling behavior as a function of meteorological variables, we and others have focused on factors thought to affect food availability. The quantity, quality, and distribution of these resources have long been considered to limit primate demography and behavior (Rowell 1966; S. Altmann 1974; Post 1981; Barton et al. 1992; Byrne et al. 1993). For most primate populations, however, life is not so simple. If food is abundant enough to support high rates of birth and survival, groups will grow, perhaps leading to density-dependent costs: higher rates of disease, greater traveling requirements, the inability to coordinate a large group. Even in the absence of such density dependent factors, however, life in high-rainfall areas, and thereby food-rich

areas, may entail costs. To the extent that these high-rainfall areas have greater vegetational cover, predator populations may be larger or better able to hide, and higher rainfall areas will probably also support greater populations of ecto- and endoparasites (Freeland 1976; Saunders and Hausfater 1985; Saunders 1988). An area rich in shrubs and trees may also be one in which maintenance of group integrity is more difficult because of interference in visual and auditory communication. Groups of animals may differ in their ability to deal with one or another of these costs and for whatever reason, may choose one tradeoff over another. Even in the absence of negative correlations among ecologically advantageous factors, areas that are similar from the standpoint of food availability may differ greatly in predator pressure or other factors that affect demographic parameters and behavior (see Abrams 1993 for a theoretical treatment). This variability may result in some populations or groups responding differently to any given set of meteorological conditions.

Although ecological factors such as predation and disease may be important and may covary with the ecological measures considered here and in Dunbar (1992), quantitative data on these variables were not available either for the previous interpopulational or current intrapopulational analyses. Nonetheless, the recent history of the Amboseli groups provides some examples. In Amboseli, predator populations have fluctuated greatly during the past three decades and in some cases differ from one part of the basin to another. For example, during the period covered by the present analyses, lion populations declined and those of hyenas increased. The Lodge Group was essentially immune to daytime predation in the area of human settlement but their sleeping groves were home to several of the few remaining lions and leopards in the area. Since the period covered by this study, Lodge Group changed their sleeping area to groves within the human-inhabited area. This reduced their vulnerability to predation, but caused them to spend less time in their sleeping trees because these groves are only available during hours of darkness. The changes discussed here would not be reflected in the current models. In addition, when Alto's Group shifted its range, the group increased in size, soon fissioned into three groups, and continued to shift its range into an area of increased woodland that also had more waterholes. More recently, Hook's group has similarly fissioned into two smaller groups. Predators seem to be more abundant in the new areas, however, and mortality rates have increased (J. Altmann, unpublished work). Whether the groups come back together and thereby obtain better predator protection, whether they shift back to their previous range, or whether they persist in the new situation, remains to be seen. In any case, these factors are all extraneous to meteorological models of group behavior. Also extraneous are non-meteorological factors that affect food availability. These include soil types,

water table, and food competitors, all of which have shown dramatic changes in the Amboseli ecosystem during the past three decades where rising water tables and levels of salinity, elephant damage to tree foods, and changing populations of wild and domestic grazers (Western and van Praet 1973) have all impacted the food resources utilized by baboons.

Fitness considerations and behavioral responses on different temporal and spatial scales

In this study, we have examined the relationship between yearly behavioral and meteorological variation in social groups. Changing the scale of investigation from yearly to monthly or daily correlations could result in different trends and directionalities from those observed here. Similarly, changing the spatial scale of the question from social groups to populations or individuals might also result in different trends than those observed in this study. For example, the responsiveness of plants to rainfall is expected to be different between daily rain and annual rain (Le Houerou and Hoste 1977). The same is most certainly true for demographic parameters. Interbirth intervals average 2 years in baboons and would not be affected by a dry day, but have been shown to be affected by dry years (Altmann et al. 1988). For foraging behavior in particular, ours and other studies have shown that baboons forage more in dry months (Dunbar and Dunbar 1974; Barton et al. 1992), but other studies found that baboons forage less in dry years (Harding 1976; Eley et al. 1989; Alto's Group in this study). Constraints and opportunities may very well differ among the spatial scales of population, group or individual (e.g., life-history variation in primates: Harvey and Clutton-Brock 1985; Harvey et al. 1987; daily decisions in baboons: Wagner and Altmann 1973). Studies of the benefits to an individual of foraging alone in terms of resource acquisition versus the benefit of foraging in a group in terms of predation protection provide evidence (Ranta et al. 1993; van Schaik and van Noordwijk 1986). The options and constraints that pertain for individuals, groups, or populations, and from moment to moment, daily, or on longer time frames, are not necessarily the same and may result in different relationships between ecological factors and behavioral response under these different conditions.

Although Dunbar (1992) sought a model that would explain behavioral variation in baboons, both across and within populations, our intrapopulation analysis showed that behavior varies not only among years, but also across social groups. The different regression models we obtained even for the two natural foraging groups supports the idea that groups, for some purposes, should be regarded as mini-populations that may respond differently to environmental variation, probably due to different resources in their home ranges.

Other primate studies report social group differences in behavior and lend support to this statement (vervet monkeys: Isbell and Young 1993, baboons: Barton et al. 1992; Brain 1990). Ultimately, these differences in the behavior of social groups could lead to group differences in demographic rates and thus could have fitness consequences.

Significant alterations in the foraging behavior of individuals within social groups that correlate with weather patterns may represent adaptability made possible by ontogenetic plasticity, that is, by an individual's ability to alter its foraging phenotype. Some studies have suggested that baboons decrease their travel distance and forage less as vegetative biomass increases (Barton et al. 1992; Rowell 1966). Whether this ability is adaptive would depend on the fitness consequences of such variability. For example, Altmann (1991) found that the diets of baboon yearlings predicted their lifetime reproductive success. Behavioral variation may affect fitness by affecting the age-specific birth and survival rates of individuals. Several studies suggest that food availability can affect the length of the interbirth interval in baboons (Strum and Western 1982; Bercovitch 1987; Altmann et al. 1988; Smuts and Nicolson 1989; Bercovitch and Strum 1993) and this could be a link between behavioral variation and an individual's lifetime reproductive success.

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