Body Size and Fatness of Free-Living Baboons Reflect Food Availability and Activity Levels

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We used morphometric techniques and isotope-labeled water to investigate the influence of abundant, accessible food and resultant low activity levels on body size and fatness in free-living adolescent and adult baboons as compared to animals in the same population that experienced more typical, wild-feeding conditions. Females that had access to abundant food from a nearby garbage dump averaged 16.7 kg body mass, 50% more than their wild-feeding counterparts in adjacent home ranges. Little of the difference was due to lean mass: the animals with an accessible abundance of food averaged 23.2% body fat in contrast to 1.9% for the wild-feeding animals. Significant differences between feeding conditions were found for all measured skinfolds and for upper arm circumference but not for linear measurements. Differences between feeding conditions were less for males than for females, perhaps reflecting persistent effects of nutritional conditions during the first eight years of life before dispersal from the group of birth. The difference in fatness between feeding conditions was similar to the difference between humans with frank obesity and those that are considered lean, but in both cases the percentages of body fat in the baboons were considerably less than those observed in humans. In levels of fatness, the relatively sedentary animals resembled their counterparts in group-housed captive conditions. © 1993 Wiley-Liss, Inc.

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INTRODUCTION

As flexible and opportunistic omnivores, baboons (*Papio* spp.) readily vary their diet, ranging patterns, and activities, according to regional or even very local differences in food availability within populations. For baboons as for humans, differences in quantity or quality of available food resources often co-occur with

differences in the distribution and accessibility of foods; these, in turn, result in major differences in activity profiles and travel patterns.

Although the effects of food availability and reduced activity have been investigated in animal models of human obesity, and numerous studies have found significant correlations between obesity and reduced physical activity [reviewed in Stern, 1984], these studies usually involved conditions that were beyond the animals' control. We have recently described a situation in which free-living baboons (*Papio cynocephalus*) reduce their physical activity in the presence of increased food availability [Altmann & Muruthi, 1988; Muruthi, 1989]; one group has self-selected a life near the garbage dump of a tourist lodge and two adjacent groups are totally wild-foraging. Together, the three groups, which are the subjects of the present study, provide a rare opportunity for nutritional studies that complement experimental laboratory investigations [see, e.g., Woods et al., 1988; Kemnitz et al., 1989].

The aim of the current study was to determine the effect of the aforementioned differences in food availability and resultant differences in lifestyle on body size and fatness. We consider our findings in light of the available literature for cercopithecine primates and with respect to similarities and differences with humans.

BACKGROUND

Several previous research projects in the study groups provide the background for the research reported here. In particular, aspects of both activity levels and food intake have been measured through studies of individual baboons. Our methods for estimating the intake of energy or other food components in the field have been described in detail elsewhere [Altmann, 1991; Muruthi et al., 1991]. The wild-feeding adult females did not differ significantly from the garbage-feeding females in average daily caloric intake, the averages being 3,828 kJ and 3,456 kJ, respectively [Muruthi et al., 1991].

Daily (24 h) energy expenditure was also evaluated by systematically sampling daytime activities and measuring characteristics of locomotion in individual animals (basal metabolic expenditure was assumed for the night hours). In a study of wild-feeding females, expenditure was estimated from body size, speed of travel (calculated from pace measurements and pace counts in timed samples), and allometric equations in which variability in speed of travel was taken into account [using equations in Taylor et al., 1982] for the active hours, and body size and allometric equations for basal metabolic expenditure during nightime hours [see Altmann & Samuels, 1992, for details]. In another study, Muruthi [1989] estimated energy expenditure for both wild-feeding and garbage-feeding females by recording activities of individuals at point samples taken on the minute during each observation period. Mean daily (24 h) expenditure for each female was calculated from body size and allometric equations as the daily expenditure on travel (daily distance traveled based on pace measurements and pace counts but without considering diurnal variability in speed of travel) plus the sum over all other activities, of the product of activity-specific expenditure and average time per day that each female spent in that activity. The activity-specific expenditures were estimated as in Coelho [1974; see Coelho, 1986, for a review of time budgets and energetic expenditure].

For females, activity levels, in contrast to caloric intake, differed considerably between the two conditions of food availability. Estimated energetic expenditure for the wild-feeding females was 3,494 kJ per 24-h day [Altmann & Samuels, 1992], which agrees closely with our results from isotope-labeled water (in prep). The activity-based estimates, which were modified only for daily travel distance

and not diurnal variability in speed, indicate that the garbage-feeding females expended approximate 16% less energy than their wild-feeding counterparts [Muruthi, 1989]. Until comparable data are available for males, we make the assumption that they, too, differ in energetic expenditure based on conditions of food availability.

SUBJECTS AND METHODS

The 34 females (≥40 months of age) and 29 males (≥96 months of age) who were subjects of the present study were members of the three study groups that have been part of a longitudinal observational research project in Amboseli National Park, Kenya, and the surrounding basin since 1971, 1980, and 1984, respectively. The histories of almost all females and of those males that were born in the study groups are known since birth [see, e.g., Altmann et al., 1981, 1988]. The unusually high degree of habituation of the animals that was achieved during these prior studies was essential to the capturing techniques of the present project, described below.

Darting

During the dry seasons of 1989 and 1990, the hands-off observational work was primarily replaced for several months by the present project, involving morphometric measurements, parasite evaluations, and collection of blood samples. Subjects were anaesthetized with Telazol℠ (tiletamine hydrochloride and zolazepam) that was injected from a syringe propelled from a blowpipe at less than 10 m. Animals were darted only when they were out of the sight of other baboons and when their backs were turned, so as to preclude anticipatory stress or loss of habituation. To control for diurnal variability in physiological variables, darting was only done between 0730 and 1030. As a result of these various constraints, at most four animals could be captured each day, and almost always fewer were. Females were not darted if they were past the first trimester of pregnancy or in lactational amenorrhea with dependent young infants. Because two wild-feeding groups were available and only one garbage-feeding group, and because females in the garbage-feeding group spend most of their time pregnant or lactating, sample sizes of wild-feeding females are much greater than those of garbage-feeding females.

Morphometry

Physical characteristics were examined by several morphometric and physiological techniques, as follows. As soon as was practicable after darting, a number of measurements were taken (using the left side whenever there was a choice), including body mass, crown-to-rump length, humerus length, and radius length. In addition, females were measured for upper-arm circumference, triceps skinfold, subscapular skinfold, and abdominal skinfold. The limb and crown-rump measurements were summed to produce a measure referred to below as "body length." A body-mass index (BMI) was calculated as mass/(body length)^2; our summed linear measurement replaces 'height' in the Quetelet index used in human studies (see review in Garrow 1983). In the literature for nonhuman primates, various authors have used various different functions of crown-rump length as the linear measurement in a body-mass index; no single measurement or function thereof has been used consistently. We have checked our results using several of these alternatives, such as replacing our 'body length' with crown-rump length in the Quetelet index, and the conclusions remain unchanged.

Skinfolds, upper-arm circumference, and crown-to-rump length were taken as

in Coelho [1985] with the exception that the abdominal skinfold (which was measured below the umbilicus by Coelho) was measured lateral to the umbilicus (3 cm in our case), as in humans [see Grant & DeHoog, 1985]. All morphometric measurements were taken three times and then averaged. Limb measurements were taken according to Schultz [1929].

Measurement of Body Composition

For 18 adolescent and adult females and 4 subadult and adult males, we were also able to evaluate fatness from total body water, measured by stable isotope dilution. A first blood sample was obtained as soon as we could safely bleed subjects [see Sapolsky, 1982; Sapolsky & Altmann, 1991, for details]. Blood was withdrawn by venipuncture, and water that was labeled either with a mixture of ^{18}O and deuterium or with deuterium alone was administered intravenously. The doses were 0.1 g/kg of deuterium oxide or 0.15 g/kg of $H_2^{18}O$ and were determined by weighing ($\pm 0.6\%$) the syringe before and after administration. The use of the ^{18}O label was discontinued after 1989 because of a shortage of isotope. A second blood sample was obtained at 1–3 h after the dose ($\bar{x} = 160.5$ min., SD = 33.5; range = 69, 187). Previous investigations in nonanaesthetized humans indicate that the intravenously administered stable isotope should be nearly equilibrated within 1 h of administration and fully equilibrated within 2 h [Schloerb et al., 1950]. The same equilibration time is reported for pig-tailed macaques, *Macaca nemestrina* [Kodama, 1970] and 30 minutes for rhesus monkeys, *Macaca mulatta* [Walker et al., 1984]. Blood samples were centrifuged on site and the plasma was frozen with dry ice until returned to the United States.

The isotope dilution spaces were determined as previously described [DeLany et al., 1989]. Briefly, the blood serum was forced through a 100,000 dalton exclusion filter, then either equilibrated with CO_2 or distilled and reduced over zinc for mass spectrometric determination of the isotopic abundance. Dilution space was calculated from the isotopic enrichment of the 3 h sample relative to the predose sample. Total body water was taken as 4% less than the deuterium space or 1% less than the ^{18}O space. Previous studies have demonstrated the equivalence of these two labels after correcting for nonaqueous exchange by 4 and 1% respectively [Schoeller 1988]. In the ten baboons that received both labels simultaneously, the ratio of the deuterium to ^{18}O dilution spaces averaged 1.04 with a standard deviation of 0.03. Based on the SD, and because body fat is calculated by difference from total body mass, the resultant estimates of the percentage of body fat from ^{18}O only are estimated to be $\pm 4\%$ of body mass [Schoeller, 1992].

Fat-free mass was calculated from total body water, assuming a hydration ratio of 0.732 [Harrison et al., 1936]. Recently, it has been suggested that the hydration of fat-free mass may increase with increasing fatness of baboons [Lewis et al., 1986]. We have, however, decided to use the older, constant hydration factor because the slope suggested by this work is so great as to raise doubts about the accuracy of the measurement of hydration. Specifically, a hydration of fat-free mass of 0.88 for obese baboons means that solids comprise only 12% of fat-free mass, a value too low to allow for reasonable amounts of mineral and protein. In any case, with respect to our investigation of differences in body composition between feeding conditions, the differences described below would be even greater if fatness and hydration were positively related.

Statistical Analyses

We tested the hypothesis that measures of body size and of fatness did not differ between feeding conditions, explored the correlation structure among fatness

measures within feeding conditions and in the female sample as a whole, and used stepwise linear regression to predict isotope-determined fatness from morphometric measurements. For females we first present analyses of morphometric data for all animals at least 40 months of age regardless of feeding condition; thereafter, we delete the six wild-feeding animals that had not reached the average age of menarche for their respective feeding condition (as indicated in the relevant sections of the Results), because use of a constant age cutoff based on adolescence in captivity or among the garbage-feeding animals results in inclusion of juveniles among wild-feeding animals. The second series of analyses, therefore, is based on constant life-stage, the first on constant age; each has its relevance for different purposes. Computationally, we used the procedures in SAS/STAT [SAS Institute, 1988]. Group differences were analyzed using SAS's t-test procedure and, where needed, Cochran's correction for unequal variances [SAS Institute, 1988].

RESULTS
Females

The garbage-feeding females weighed half again as much as the wild-feeding ones (Table I). Average body length, however, did not differ between conditions ($P = 0.25$), except when the six juvenile, wild-feeding females were included ($P = 0.03$). Despite 50% greater body mass in the Lodge Group than in the wild-feeding groups, total body water was greater by only 23% in the Lodge Group. In contrast to this relatively modest increase in lean mass, percent fat was dramatically different between feeding conditions ($P < 0.001$) with fat mass accounting for 76% of the greater body mass in the Lodge Group. Skinfolds, which were surprisingly small in the wild-feeding females, were very much greater in the Lodge Group but were still fairly small based on scaling from humans (see Discussion): the maximum observed skinfold was an abdominal fold of 13.9 mm in a 24 kg Lodge Group female.

In the full pooled sample of females at least 40 months of age from both feeding conditions, all the fatness variables—BMI, skinfolds (triceps, abdominal, subscapular), upper arm circumference, and percentage body fat as measured with labeled water—were highly correlated with each of the others (all r's 0.70–0.98, all P's less than 0.001). The highest pairwise correlations were between BMI and upper arm circumference, and between percent body fat and subscapular skinfold (both r>0.90, n = 33 and 17, respectively). In a linear regression analysis predicting percent body fat, subscapular skinfold was the single best predictor of fatness (adjusted $r^2 = 0.82$, slope = 6.84% fat per mm skinfold, intercept = −11.76% fat) and was the only statistically significant one in a stepwise regression.

Within the garbage-feeding subset, the highest pairwise correlations among body measures were between BMI and upper arm circumference and between percent body fat and subscapular skinfold (Table II, lower left). Although the remaining correlations between body measures were also similar to those in the pooled sample, most were weaker within the set of garbage-feeding animals than in the full sample.

Sample sizes for the wild-feeding adolescents and adults were much larger than those for their garbage-feeding counterparts; nonetheless, few patterns among variables emerged among the wild-feeding females. The only strong or significant relationships among fatness measures were those among upper arm circumference, mass, and BMI, and between abdominal and triceps skinfolds (Table II, upper right). Note, however, that differences among the wild-feeding females in the skinfolds, and perhaps also in the isotope-based measures of fatness, may have been below the resolution of the measurements.

TABLE I. Morphometric Values and Body Composition for Females (Mean, SD, n in Each Case)[†]

		Garbage-feeding, $\geq$40mo	Wild-feeding, $\geq$40mo	Wild-feeding, $\geq$56mo
Body mass	Mean	16.7	11.0	11.9
(kg)	SD	±3.48	±1.94**	±1.41**
	n	10	24	18
Body length	Mean	0.994	0.950	0.976
(m)	SD	±0.05	±0.06*	±0.04
	n	10	24	18
Body mass	Mean	17.5	12.1	12.4
index (BMI)	SD	±2.51	±0.94**	±0.82**
(kg/m²)	n	10	24	18
Upper arm	Mean	21.2	16.6	16.9
circumference	SD	±2.74	±1.28**	±1.26**
(cm)	n	9	24	18
Total body	Mean	10.6	(Same	8.7
water (kg)	SD	±1.49	animals)	±0.92**
	n	5		13
Fat percent	Mean	23.2	(Same	1.9
(isotope)	SD	±5.73	animals)	±4.81**
	n	5		13
Triceps	Mean	1.7	1.1	1.1
skinfolds	SD	±0.36	±0.10**	±0.10**
(mm)	n	9	24	18
Subscapular	Mean	4.2	2.3	2.2
skinfolds	SD	±1.18	±0.39**	±0.38**
(mm)	n	9	24	18
Abdominal	Mean	5.9	1.6	1.7
skinfolds	SD	±4.53	±0.31**	±0.31**
(mm)	n	9	24	18

[†]Significance levels of 0.05, 0.01, and 0.001 for comparisons between garbage-feeding and wild-feeding animals are indicated by *, **, and ***, respectively.

Among the wild-feeding adolescent and adult females but not the garbage-feeding ones, age was significantly related to both body mass ($r = 0.61$, $P = 0.007$) and body length ($r = 0.52$, $P = 0.03$): growth continues past menarche longer and more consistently among the wild-feeding animals than among the garbage-feeding females.

Males

For the 29 males that were at least 96 months of age (onset of young adulthood and approximate age of first emigration), no significant relationship was found between age and any of body mass, BMI, or length, either in the pooled data set or for either feeding condition separately ($P > 0.25$ in each case). Body mass and BMI, but not body length, were significantly greater for garbage-feeding than for wild-feeding males (Table III). The heaviest adult males were the youngest ones, and therefore natal, in the garbage-feeding condition, who consequently accounted for most of the difference between feeding conditions. Percentage of body fat was

TABLE II. Correlational Patterns Among Fatness Indicators Within Each Feeding Condition[†]

	Body mass	BMI	Upper arm	Fat %	Triceps (Skinfolds)	Subscapular	Abdominal	
					Wild-feeding females (upper-right triangle)			
Mass	_____	0.87***	0.67**	0.31	−0.05	0.34	−0.13	Mass
	—	18	18	13	18	18	18	
BMI	0.79**	_____	0.72***	0.07	0.14	0.20	0.07	BMI
	10	—	18	13	18	18	18	
Upper arm	0.89***	0.88**	_____	0.38	0.26	0.33	0.19	Upper arm
	9	8	—	13	18	18	18	
Fat %	0.48	0.78	0.71	_____	0.27	0.29	0.21	Fat %
	5	5	4	—	13	13	13	
Triceps	0.43	0.70*	0.43	0.77	_____	0.24	0.64**	Triceps
	9	8	9	4	—	18	18	
Subscapular	0.72*	0.71*	0.60	0.96*	0.66	_____	0.17	Subscapular
	9	8	9	4	9	—	18	
Abdominal	0.81**	0.74*	0.75*	0.66	0.75*	0.79*	_____	Abdominal
	9	8	9	4	9	9	—	
				Garbage-feeding females (lower-left triangle)				

[†]Correlations for wild-feeding females at least the average age of menarche (56 months) appear in the upper-right-hand triangle, those for garbage-feeding females at least the average age of menarche in that condition (40 months) appear in the lower-left-hand triangle. Cell values represent Pearson correlation coefficients and sample sizes. Significance levels of 0.05, 0.01, 0.001 are indicated by *, **, and ***, respectively.

TABLE III. Morphometric Values (Mean, SD, n in Each Case) for Males ≥96 Months Old[†]

	Garbage-feeding	Wild-feeding
Body mass (kg)	30.4 ±4.40 9	25.8 ±2.90** 20
Body length (m)	1.23 ±0.06 9	1.20 ±0.04 20
Body mass index (BMI) (kg/m^2)	19.9 ±1.8 9	17.8 ±1.6** 20

[†]Significance levels of 0.05, 0.01, 0.001 are indicated by *, **, and ***, respectively.

estimated by means of labeled water for one seven-year-old (82 months of age) garbage-feeding male, for whom the estimate was 16.4%, and for three adult wild-feeding males, for whom the values were 0.8%, 8.7%, and 9.3%.

DISCUSSION
Levels of Fatness in Cercopithecines and Humans

All previous nonmorphometric estimations of fatness for adult female cerco-pithecines come from studies of captive macaques. For animals not considered obese, mean fatness was 12.7% for pigtailed macaques housed in small group cages [Walike et al., 1977], 17.1% for singly-housed rhesus [Kemnitz et al., 1989], 7.8% and 18.3% for corral-housed nulliparous (= adolescent) and multiparous rhesus, respectively [Walker et al., 1984]. Animals classed as obese in the first two studies had mean fatness levels of 40.5% and 40.8%, respectively. Mean fatness levels for males considered normal in the Kemnitz were 10.3%; those considered obese (body mass approximately 2.5 SD above the mean for the others) had 46.8% body fat. No Amboseli animals had fatness levels comparable to the captive animals that were considered obese. Percent body fat of the garbage-feeding animals were in the range, though slightly higher than that for the several groups of captive macaques that were considered non-obese.

For baboons, morphometric data on fully provisioned or semi-provisioned animals come from garbage-feeding or crop-raiding animals in East Africa and from captive animals, group-housed in corrals or relatively large cages of varying sizes [Coelho, 1985; Eley et al., 1989; Phillips-Conroy et al., in prep; Altmann & Samuels, unpublished data from *Papio papio* at Brookfield Zoo] in addition to the data from this study. Although differences surely exist across the conditions (e.g., nutrient intake and expenditure) and animals (e.g., distribution of females by age and reproductive condition), and these differences cannot be fully identified from the literature, the findings are in close agreement. Across all these food-enriched conditions, average female body size varied only from approximately 15–17 kg and subscapular skinfolds from about 4–5 mm. Moreover, these same studies (excluding the captive ones [Coelho; Altmann and Samuels]) also provide data on body mass and skinfolds in wild-feeding females, for which average body mass is approximately 11–13 kg and subscapular skinfolds 2–3.5 mm across studies.

The garbage-feeding females of Lodge Group appeared plump or obese and their average of 23% body fat constitutes an increment in fatness of 21% relative to the wild-feeding animals. This difference is comparable to the incremental difference between lean and obese humans. Nonetheless the absolute percentage of body fat in these plump animals is only in the range of the average value observed in young adult women [Forbes, 1988]. This apparent contradiction between observed obesity and percentage of body fat is, of course, partially a function of the dramatically low level of body fat in the wild-feeding baboons, but it may also reflect a difference in body-fat distribution [Pond & Mattacks, 1987]. Specifically, the baboons in all three groups had very small subcutaneous fat deposits as evidenced by the small skinfolds. Not only were skinfolds taken on the limbs in both conditions extremely small (0.9–2.5 mm) and thus below the range typically reported for humans [for example, see Jackson & Polock, 1982], but subscapular skinfolds were also small. Even in the semi-provisioned group, these were all at the extreme low end of the human range. As summarized above, similar skinfold results have been found in the other studies of food-enriched baboons. Body size scaling accounts for only a much smaller difference between baboons and humans in skinfolds than that reported here, e.g., an average subscapular skinfold of over 8 mm for baboons would be comparable to 13 mm for humans taking into account their difference in body mass. The extremely small subcutaneous fat deposits inferred from the skinfold measurements probably account for the majority of the 15–20% offset in body fat between humans and cercopithecine primates. Kemnitz

et al. [1989] found similar relationships between skinfolds and percent body fat for rhesus monkeys as those we report for baboons.

Review of human and nonhuman primate literature revealed the extent to which norms of fatness and of activity are not consistent or grounded in standardized biological criteria, and the extent to which existing categorizations are subject to cultural norms and researcher experience. A baboon that is plump in the eyes of a field researcher probably is not so to a laboratory worker, nor has obesity had the same definition or meaning for humans in different times and places. The wild-feeding baboons in the present study have rates of physical maturation, mortality, and reproduction that lead to stable and stationary population demography, rates that are similar to those of other wild-living non-expanding baboon populations [Altmann et al., 1988, and references therein].

Even the garbage-feeding Amboseli baboons, which have self-selected a "leisure-class" lifestyle in the presence of abundant food, still traverse 2–4 km per day, and their counterparts in captivity probably are baboons and macaques that are corral-housed rather than ones in smaller cages. Whereas these activity levels appear sedentary compared to wild-feeding animals, and may provide the best activity model for a human sedentary lifestyle, they are still in sharp contrast to the lifestyle of singly housed monkeys in the size range of baboons. Singly housed animals in many laboratories conduct their activities within a space less than a cubic meter, a complete living area comparable for humans to a room with an approximate floor area of only a square meter and a ceiling height of two meters. The consequences for activity, energetics, and physiology are not well documented but are currently under investigation by Coelho and his colleagues (pers. comm.).

Interspecific and Intraspecific Variability in Size and Fatness

In Amboseli, the discarded food-stuffs at the nearby garbage dump provided the Lodge Group baboons with food that was not only abundant and of relatively high digestibility, but that also required little travel to the feeding site and virtually no travel or strenuous food extraction during feeding, all in sharp contrast to the situation for wild-foraging animals in the same habitat [Altmann & Muruthi, 1988; Muruthi, 1989; Muruthi et al., in prep]. The Lodge Group animals exhausted neither the available time nor the available food, yet they apparently regulated food intake to levels similar to those obtained during natural foraging [Muruthi et al., 1991] and did so despite their lower level of energy expenditure.

The differences in energetic balance between feeding conditions were associated in the present study with large differences in body mass and fatness. Among females, the absolute difference in mean fat mass, 3.65 kg, was three times greater than the absolute difference in fat-free mass, 1.16 kg. Viewed alternatively, the 3.65 kg of additional fat mass represents more than a tenfold increase over the 0.23 kg fat mass of the wild-feeding females, whereas the 1.16 kg of additional fat-free mass represents only a 10% increase over the 11.67 kg of wild-feeding females' fat-free mass. The differences in total fat mass that dramatically reflected the differing resource conditions experienced by the baboons in our study were apparent in skinfold measurements, primarily abdominal and subscapular. The subscapular measurement provided the best predictor of percentage body fat, as measured by isotope dilution, in the pooled data set and within the semi-provisioned sample.

For males, not only was the difference between the feeding conditions in total body mass less than that for females, but the few measurements of labeled water suggest that males also have a smaller discrepancy between differences in fat and fat-free mass. No significant differences between feeding conditions were found in

body length for either males or females. In sum, body-mass dimorphism, but not body-length dimorphism was different between feeding conditions.

Lower body-mass dimorphism in the high-availability feeding condition than in the wild-foraging one [also clear in Eley et al., 1989; Table IV] seems inconsistent with the sex difference found for growth among immature cercopithecines; young males show a greater responsiveness than do females to food enrichment both in controlled laboratory experiments [e.g., Rutenberg & Coelho, 1988] and in comparative studies of macaques [van Schaik et al., ms] and baboons [Strum, 1991; Altmann, ms]. The present results also seem to contradict the hypothesis and findings that sexual dimorphism is greater where food is more abundant [Popp, 1983; Dunbar, 1990]. In contrast to the situations considered by Popp and Dunbar, however, in which comparisons were made across populations, the data provided in the present study and that of Eley et al. [1989], deal with heterogeneity of feeding conditions among groups within single populations. For a population of animals living in a heterogeneous habitat, and in which males but not females leave their natal group as young adults—which is the case for baboons as well as for most other cercopithecine primates—movement of some adult males from poor to rich areas and others in the opposite direction will decrease adult size dimorphism in the rich areas and increase it in the poor ones unless response to the new nutritional conditions is complete and relatively rapid. Although temporary periods of food enhancement or restriction in very young baboons are followed by catch-up or -down growth subsequently [Rutenberg & Coelho, 1988], the two data sets from wild baboon populations suggest that major food differences that persist throughout most or all of the eight years of life before adult dispersal have some permanent effects.

Differences in body mass between and within species might reflect genetic differences resulting from processes such as natural or sexual selection or genetic drift. Alternatively, or in interaction with genetic differences, such differences may reflect responses to ontogentic or proximal environmental differences such as in food supply or energetic expenditure. The documentation from both Gilgil and Amboseli of considerable within-population variability in body size suggests a predominance of facultative responses within the life histories of individuals rather than genetic differences in response to selection. Facultative responses may also account for much of the differences in body mass and mass-dimorphism within populations that contain more than one of the baboon species or subspecies, as suggested by Phillips-Conroy & Jolly [1981]. For example, in a large sample of wild baboons in Ethiopia (anubis, hamadryas, and their hybrids), the coefficients of variation in body mass across sex and species ranged from 10.0% to 13.1% [Phillips-Conroy & Jolly, 1981: Table 1, after correcting the value for female hybrids (Phillips-Conroy, pers. comm.)], and among corral-housed, provisioned anubis baboons it was 15% for females and 14% for males [Coelho, 1985], whereas the coefficients of variation in our study, with all subjects of each sex pooled, were 24.5% for females and 14.5% for males. The greater variability among Amboseli females probably reflects their responses to a greater range of conditions.

CONCLUSIONS

1. Among adult baboons, body mass and fatness, but not body length was significantly less for wild-feeding animals than for those of the same free-living population that had abundant, accessible food resources.

2. Adult females differed more in body mass between feeding conditions than did adult males, probably because males and not females disperse at adulthood

and, therefore, may experience feeding conditions as adults that differ considerably from those during the eight years of maturation.

3. Subscapular skinfold size was the morphometric measure that provided the best predictor of body fat as measured by isotope dilution methods.

4. For comparable levels of body fat, baboons and macaques have skinfold values that are lower than those expected based on allometric scaling down from values for humans.

5. Wild-feeding female baboons that travelled 8–10 km/day had only 2% body fat. Those that fed from a very accessible garbage dump and traveled less than 4 km/day averaged 23% body fat, similar to values for group-housed captive macaques. Body size and skinfold measurements for the baboons with accessible food were comparable to corral-housed captive baboons.

6. Energetic expenditure has received little attention in the primate nutritional literature. Information on cage sizes and activity levels for captive animals will facilitate comparisons among studies. Likewise, standard biologically relevant criteria for obesity in the literature would facilitate use of the term and the ability to compare across studies.

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