

## Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness

(primate behavior/reproductive success/optimal diets/foraging)

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**ABSTRACT** The foraging of yearling baboons (*Papio cynocephalus*) was studied in Amboseli National Park, Kenya. The nutrient content of the diets of individual females was compared with the composition of energy-maximizing optimal diets. Energy in the diets of all individuals fell appreciably short of their respective optima. Nonetheless, linear combinations of just two variables, protein intakes in excess of requirements and proximity of energy intakes to those specified in the optimal diets, were sufficient to provide good predictions of reproductive lifespans, numbers of infants and juveniles produced, and probability of surviving to adulthood.

A critical stage in the life of any mammal is weaning—that is, the transition from dependence on mother's milk to nutritional independence. For eclectic, omnivorous mammals, with their limited repertoire of inborn specific hungers (1), an infant's success at making this transition depends heavily on the timely acquisition of a considerable repertoire of selective foraging and harvesting skills. In turn, individual differences in ability to negotiate this transition may be reflected in subsequent differences in life history characteristics that affect biological fitness. Relationships between actual diets, energy-maximizing optimal diets, and realized fitness were studied in a cohort of wild baboons in Africa at 30–70 weeks of age, that is, during weaning. If the selected criteria for optimal diets are valid, then those individuals that come closest to their dietary optima should have the highest expected fitness.

### METHODS

**Field Methods.** The foraging behavior of yearling yellow baboons (*Papio cynocephalus*) was studied in Amboseli National Park, Kenya. All subjects were members of the same social group, Alto's Group, which has been the focus of numerous studies over many years (e.g., refs. 2 and 3). The animals have been habituated to the presence of noninterfering human observers. During a 12-month period in 1975–1976, I sampled all infants in the group that were between 30 and 70 weeks of age ("yearlings"); two other yearlings in the same group were sampled the previous year. Only results from the six female subjects are included here: only for females do I have accurate measures of reproductive success.

Each sample day, I sampled the behavior of one yearling until all had been done, then began the next round of sample days. During each sample day, I sampled the foraging behavior of that day's subject for 20 min out of every hour between 0700 and 1800. Time of onset and termination of each feeding bout and the food being eaten were recorded. When observations permitted, I also recorded the number of food items eaten in bouts of known length.

Food samples were collected during the phenophase in which each food was eaten and from within the home range of the study group (4). When taking these samples, we attempted to duplicate the food actually consumed by baboons, matching as closely as possible the consumed part of the plant, degree of ripeness, and so forth. For nutrient analysis, these samples were preserved in 3–5% oxalic acid or by freezing.

As part of our long-term monitoring of Amboseli baboons, investigators record daily the reproductive state of every female in the group they are sampling. Consequently, the reproductive history of each female is known. (Two of the females, Dotty and Eno, were still alive at the cutoff date for these data, December 31, 1988.) From these long-term records, I calculated for each subject several measures or estimators of fitness: length of reproductive period, age at puberty, age at first conception, number of live births, live births per thousand days of reproductive period, number of yearlings produced, yearlings per thousand days of reproductive period, and survival to age 6 years.

**Data Analysis.** I consider food components not only in the conventional sense of chemical compounds (e.g., riboflavin) or classes of compounds (e.g., lipids and proteins), for each of which the amount obtained from a given food is some fraction of the consumed mass of that food, but also in a more general sense that includes properties such as energy content, foraging time, exposure to hazards, and others that are expressed in units other than mass if, in particular cases, they are linear functions of the amounts of foods that are ingested. From samples of feeding bouts, intake rates, and food compositions I estimated, for any given food component  $i$ , the average amount ingested per day by each individual.

The estimated intake of any food component  $i$  was obtained from the sum (over all foods) of the products (one for each food,  $j$ ) of estimated means of the following factors: food-specific bout length (minutes of feeding on food  $j$  per bout of feeding on  $j$ ), food-specific bout rate (bouts on food  $j$  per potential feeding minute), potential feeding time per day (taken to be the 660 min from 0700 to 1800), food-specific unit intake rate (intake units of food  $j$  eaten per minute of feeding on food  $j$ ), food-specific unit mass (grams of food  $j$  per unit), and food-specific composition (grams of component  $i$  per gram of food  $j$ ). In estimating nutrient intakes in this way, I assumed covariances among the above factors to be negligible (5). Individual values were calculated for feeding bout rates and bout lengths; these are the sources of the individual differences reported here. For the other variables, pooled values were used. Means of censored feeding bouts—that is, those bouts whose beginning or ending was not timed, either because it occurred outside the sample period or because the animal went out of sight—were estimated by the product-limit method (6).

**Optimal Diet Model.** On the assumption that energy is the primary fitness-limiting component of the baboons' diets, I took optimal diets to be those that maximize daily energy

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intake while simultaneously remaining above the minima for nutrients and below the maxima for various constraints, such as toxin tolerances, time limitations, and so forth (7, 8). Let  $p_{ij}$  be the amount per unit mass (e.g., proportion, J/g, min/g, etc.) of the  $i^{\text{th}}$  component in the  $j^{\text{th}}$  available food, and let  $M_i$  and  $T_i$  be respectively the minimum daily requirement and the maximum daily tolerance for the  $i^{\text{th}}$  component. A diet is an ordered  $n$ -tuple  $F = \{F_1, \dots, F_n\}$  of nonnegative numbers, where  $F_j$  represents the average amount of food  $j$  that is eaten per day and  $n$  is the number of available foods. Thus, in any diet  $F$ , the amount of, say, the first component will be  $p_{11}F_1 + \dots + p_{1n}F_n$ . If  $m$  components are to be considered and the animal has  $n$  foods from which to choose, its adequate diets (i.e., those within its upper and lower bounds) are the set of all points satisfying  $m$  constraints of the form  $M_i \leq \sum_{j=1}^n p_{ij}F_j \leq T_i$  ( $i = 1, \dots, m$ ).

If  $e_j$  designates the energy coefficient (J/g) of the  $j^{\text{th}}$  food, the amount of energy in any diet  $F$  will be  $E(F) = e_1F_1 + \dots + e_nF_n$ . The problem of finding an energy-maximizing optimal diet is that of finding values  $F_1^*, \dots, F_n^*$  of  $F_1, \dots, F_n$  that maximize  $E$  subject to requirement and tolerance constraints. (The constraints that I used are described below.) The constraint equations determine a closed, bounded, and convex subset of Euclidean  $n$ -space, representing all nutritionally adequate diets. The optimum is a corner point of this convex set or an edge or facet defined by several such points (7). Computations were carried out by means of LINDO, a computer program for linear optimization (9).

Altogether, the yearlings ate 277 foods. However, they devoted 95% of their feeding time to just 54 foods. With water and unidentified foods eliminated, the remaining 52 "core foods" accounted for 93.4% of the yearlings' feeding time; for practical reasons, I restricted the analysis to these core foods. I assumed that on average the remainder of their feeding time was equally productive, and I compensated accordingly.

Optimal diets were calculated subject to several constraints. In any specified diet, let us designate the total quantities (g/day) of various macronutrients as follows:  $A$  = minerals ("ash"),  $P$  = proteins,  $B$  = fiber,  $C$  = other carbohydrates,  $E$  = energy (MJ/day),  $L$  = lipids ("fat"),  $W$  = water. Also, let  $\Phi = \sum_i F_i$  = diet mass (g/day) and  $M$  = body mass (kg). The baboons' optimal diets were subject to the following macronutrient constraints:  $A \geq 0.0173\Phi$  (mineral minimum);  $A \leq 0.131\Phi$  (mineral maximum);  $L \geq 0.8M^{3/4}$  (lipid minimum);  $P \geq 1.14 + 1.51M^{3/4}$  (protein minimum);  $B \geq 0.0035(\Phi - W)$  (fiber minimum);  $E \geq 0.4193M^{3/4}$  (energy minimum);  $\Phi \leq 1002.4$  g/day (consumption capacity). Although baboons apparently are obligatory drinkers in arid regions such as Amboseli, diet constraints based on water required for renal clearance and water turnover rate were not included, because the baboons got water not only from their food but also from rainpools, waterholes, and swamps, and the quantities of water from these sources could not be estimated. Body masses of the subjects at the time of my study are unknown, but on the basis of subsequent weighings of baboons in this group (10), mean body masses (kg) of the subjects at various ages were estimated from the regression  $M = 0.775 + 0.0135x$ , where  $x$  is age in weeks. On this basis, adjustments for those constraints that are size-dependent were made for each 10-week age block: 30–40 weeks, . . . , 60–70 weeks, calculated in each case at the midpoint of the interval.

The ratio of locomotion time (primarily movement time between feeding sites) to hands-on feeding time averaged 0.514:1 in this group of baboons (last row of table II in ref. 11). Feeding time therefore was limited to 436 min/day, which, with the entailed time for locomotion, would exhaust the 11 hr/day available for foraging. In addition, for each of the 52 core foods, I imposed a "seasonality constraint" that reflects

the proportion of the year that each food was available and the relative amount of sampling undertaken when it was available.

Finally, cation requirements (12) and tolerances (13) used in my optimality models are as follows, in g/day:  $0.0022\Phi \leq \text{Na} \leq 0.035\Phi$ ;  $0.0024\Phi \leq \text{K} \leq 0.03\Phi$ ;  $0.006\Phi \leq \text{Ca} \leq 0.02\Phi$ ;  $0.003\Phi \leq \text{P} \leq 0.015\Phi$ ;  $0.001\Phi \leq \text{Mg} \leq 0.005\Phi$ ;  $0.0001\Phi \leq \text{Fe} \leq 0.003\Phi$ ;  $(2 \times 10^{-5})\Phi \leq \text{Zn} \leq 0.001\Phi$ ;  $(5 \times 10^{-7})\Phi \leq \text{Cr} \leq 0.001\Phi$ ;  $(2 \times 10^{-5})\Phi \leq \text{Mn} \leq 0.001\Phi$ ;  $(2 \times 10^{-6})\Phi \leq \text{Cu} \leq 0.0008\Phi$ ;  $\text{Al} \leq 0.001\Phi$ ;  $\text{Ba} \leq (2 \times 10^{-3})\Phi$ ;  $\text{Sr} \leq 0.003\Phi$ ;  $\text{B} \leq (15 \times 10^{-5})\Phi$ . As before,  $\Phi$  represents the total mass of the diet (g/day). To date, cation analysis, by emission spectroscopy, has been carried out for only three core foods, so for cations, only the upper bounds were used: for each cation, the total from these three foods could not exceed the corresponding maximum.

For each infant in each 10-week age block during which the infant was sampled, I calculated an optimal diet that maximizes mean daily energy intake, subject to the above constraints, in the following way. An age-specific and semi-month-specific optimal diet was calculated for each semi-month during which the infant was that age. Then I calculated a weighted mean intake (hypothetical) across the appropriate semimonths for each food in those optimal diets, where the weighting coefficients were the relative amounts of sample time on the infant at that age during each semimonth. The first 15 days of each month were taken to be one semimonth; the remaining days, another. Semimonthly intervals were used because of the rapidity of phenological changes in Amboseli; only foods actually available in a given semimonth were allowed in the optimal diets for that semimonth.

The composition of each of these energy-maximizing optimal diets was calculated as described above and compared with the baboons' actual diets as follows. In each 10-week age block, I calculated the deviations in percent of energy and protein content of a given yearling's actual diet from those of its optimal diet for that age. Then, over all ages at which the yearling was sampled, I calculated the unweighted means of these deviations and of several other characteristics of the baboons' energy and protein intakes. These means were used as predictor variables in regression models of realized fitness. Fitness measures reported here are defined in Table 1; predictor variables, in Table 2.

**Fitness Models.** To find a small set of efficacious predictor variables, I regressed each quantitative fitness measure in turn (measures 1–7, Table 3) on 15 potential predictors that represent several aspects of the baboons' intake of protein and energy and of their social relationships. Stepwise multiple linear regressions were used. That analysis demonstrated that all quantitative fitness measures except rate of infant production are highly predictable (adjusted  $R^2 > 0.99$ ;  $P \leq 0.05$ ), each from some combination of just two or three variables, primarily aspects of energy and protein intake. In the resulting regression models, two diet variables—protein surplus (relative excess of protein above requirement levels) and energy shortfall (relative deviation of energy intake from the potential energy yield of their respective optimal diets)—appear far more often than others as predictors. How well can fitness be predicted from just these two diet variables? To answer that, the seven quantitative fitness measures were regressed against them, both individually and in linear combination.

Model I regressions were used throughout (14); although both the fitness variables and their predictors are random variables subject to error, multivariate versions of model II regression apparently are not yet available. All regression coefficients have been adjusted for the number of variables.

To determine whether early diet affects survivorship, I carried out a discriminant analysis. I used data both from the six female weanlings reported on here and from five male

Table 1. Individual values for fitness measures

Name	Reproductive period,* days	Age at puberty,† days	Age at 1st conception,‡ days	Live births§	Live births per 1000 days¶	Yearlings§	Yearlings per 1000 days**
Alice	2550	1862	2353	2	0.784	2	0.784
Dotty	4035	1637	2073	5	1.239	4	0.991
Eno	3158	1844	2284	4	1.267	3	0.950
Pooh††	0	—	—	0	—	0	—
Summer	2677	1628	2117	4	1.494	2	0.747
Striper	1532	1657	2191	2	1.305	0	0

\*Days from puberty to death or December 31, 1988, whichever is earlier.

†Age at first persistent sexual skin swelling that was followed by menstruation (16).

‡Age at onset of deturgescence of sexual skin in first conception cycle.

§Through December 31, 1988.

¶(1000) (number of live births)/(length of reproductive period).

||Number of offspring surviving 12 months.

\*\* (1000) (number of offspring surviving 12 months)/(length of reproductive period).

††Died before sexual maturity.

members of their group and cohort that were sampled concurrently and at the same ages. The yearlings' diets at age 30–70 weeks were used to predict whether or not each would survive to 6 years of age (the eighth fitness measure in Table 3). That cut-off age covers essentially the prepubertal period of parental dependency. It is also an age up to which we know survivorship for almost all of our subjects, both male and female: emigration of males from their natal groups after that age means that we do not always know their age at death. Because of the demonstrated efficacy of energy shortfall and protein surplus at predicting other aspects of fitness, these two diet variables were selected as predictors in the discriminant analysis, as before using for each individual the mean value for all 10-week age blocks in which it was sampled. On the assumption that nutrient intakes are multivariate normal, a parametric discriminant analysis was carried out via SAS System software.

Further details on methods, habitat and subjects, results of the stepwise multiple linear regression, and justifications for the requirement and tolerance values that I used will be provided in a forthcoming publication.

## RESULTS

The energy intake of each individual in each 10-week age block was well below that of their respective optimal diets (note negative coefficients in Table 2). Nonetheless, mean energy shortfall of each female provides excellent predictions of the length of her reproductive life-span, the number of infants that she produced in her lifetime, and the number of her offspring that survived the first year of life (Table 3). The last two measures probably are the best available estimators of realized fitness, and the last measure has the merit of spanning one full generation, yearling to yearling. On the other hand, these energy shortfalls, by themselves, do not

Table 2. Individual values for predictor variables

Name	Sample ages, weeks	Energy shortfall *	Protein surplus †
Alice	30–70	−0.576	0.655
Dotty	50–60	−0.440	0.743
Eno	30–60	−0.452	0.771
Pooh	40–70	−0.733	0.499
Summer	30–60	−0.484	0.750
Striper	50–60	−0.619	0.671

\*Unweighted mean, across 10-week age blocks, of relative deviations, (actual − optimal)/optimal, of mean daily intakes of energy from energy in energy-maximizing optimal diets at each age.

†Unweighted mean, across 10-week age blocks, of relative deviations, (actual − minimal)/minimal, of mean daily intakes of protein from requirements at each age.

provide significant predictions of age at puberty or first conception, or of the rates at which infants and yearlings were produced (offspring per 1000 days of reproductive life-span). Differences in the first group of fitness variables (those predicted) depend primarily on differences in survival; those in the second (not predicted), on differences in fecundity.

Addition of protein shortfall to the regressions, both as the single predictor variable and in linear combinations with energy shortfall, resulted in a total of seven significant models for the same three measures of fitness: reproductive life-span, number of infants produced, and number of yearlings produced (Table 3). In each case, the best of the three models accounted for at least 84% of the variance in fitness among individuals. All three fitness measures primarily reflect differences in survival.

Further evidence for the effects of early diet on survival was provided by the discriminant analysis. On the basis of the baboons' energy shortfall and protein surplus, the discriminant function perfectly predicted which individuals would survive to age 6 years. Equality of class means was rejected at a 0.005 level by all four tests generated by the SAS program. These results must be regarded with caution, however, because if 11 data are selected from a multivariate normal population, a discriminant function would perfectly split off any 2 given individuals 15–16% of the time, according to a simulation run by Peter McCullach (Department of Statistics, University of Chicago). A logistic regression, which avoids many of the strong assumptions of discriminant analysis (such as that the data are multivariate normal), also gave a perfect prediction of which individuals would survive to age 6 years and which would not. The constant and coefficients for the discriminant function and for the logistic regression equation are given in Table 3.

## DISCUSSION

In this study, fitness was related not to feeding behavior *per se* but to its dietary consequences—to performance. The task of measuring selection on traits, whether morphological, physiological, or behavioral, is simplified by breaking the task into two parts: measurement of the effects of trait variation on performance and measurement of the effects of performance on fitness (15). This study is a contribution to the latter task. Differences in the traits by which these primates achieve their individual diets and the heritability of those traits are largely unstudied.

Although one expects some consistency in life histories, the degree of predictability of lifetime fitness in Table 3, on the basis of childhood diet, is remarkably high. These results clearly call for confirmation in other studies, on other pop-

Table 3. Female fitness predicted from energy shortfall and protein surplus

Fitness measure	$R_a^2$	$P$	y intercept	Energy shortfall	Protein surplus
1. Reproductive life-span	0.887	**	8,764	11,707	—
	0.859	NS	—	—	—
		*	12,905	14,744	-3633
2. Age at puberty	(No significant model found)				
3. Age at first conception	(No significant model found)				
4. Number of infants	0.958	**	11.520	15.80	—
	0.848	**	-8.863	—	17.20
	0.944	**	11.77	15.98	-0.2174
5. Infants per 1000 days	(No significant model found)				
6. Number of yearlings	0.755	*	8.751	12.58	—
		NS	—		
	0.939	**	33.22	30.53	-21.47
7. Yearlings per 1000 days	(No significant model found)				
8. Survival to age 6 years					
Discriminant function		**	90	-62.16	-9.798
Logistic regression			-24.29	41.69	91.27

For each quantitative fitness measure (nos. 1–7), coefficients of three linear regression models are listed based (in order) on the mean relative deviation of each female's energy intake from that of her energy-maximizing optimal diet ("energy shortfall"), the mean deviation of her protein intakes from her protein requirements ("protein surplus"), and their linear combination. Variables are scaled as in Tables 1 and 2. NS, not significant ( $P > 0.05$ ); \*\*,  $P \leq 0.01$ ; \*,  $0.05 \geq P > 0.01$ ;  $R_a^2$ , adjusted  $R^2$ .

ulations, and on larger samples, but they suggest that by 70 weeks of age, before the completion of weaning, a female baboon's lifetime fitness is largely established. Yet, at that age they still nurse, still sleep in their mothers' arms, are still about 3 years away from puberty, and about 4 years from when they will conceive their own first offspring.

Do some animals have higher fitness because they eat better, or do they eat better because they are more fit? In many cases, I suspect that both are true. In turn, dietary selection and fitness each are related to many other characteristics of animals. The causal links among traits cannot be measured in a study such as this: correlation is not causation. Regardless of whether fitness is affected by diet, either directly through effects of reproductive success or indirectly through effects on other traits, the results at hand suggest that in these wild primates, fitness itself is highly predictable from diet at a remarkably early age.

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