Energetics of Foraging in *Macaca fascicularis* and *Pongo pygmaeus* and a Selective Advantage of Large Body Size in the Orang-utan

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ABSTRACT. Small animals differ from large animals in their relative and absolute metabolic requirements and energetic expenditures. A preliminary study of the behavioral effects of these size dependent variables were investigated in two arboreal, sympatric and frugivorous anthropoid species: *Macaca fascicularis* and *Pongo pygmaeus*. Data on both species were collected in East Kalimantan, Indonesia during a 20-month field study which focused on *M. fascicularis*. There are marked size dependent behavioral differences between the two species which show the constraints of large body size.

Existing hypotheses of the selective advantage of large body size in the orang-utan have either overlooked its advantages by describing it as a remnant of Pleistocene terrestriality and predator defense or attributed its advantage to greater access to resources. Contrasts between the energetics of foraging in the monkey and the ape suggest an alternate hypothesis for selection of large body size relating to the increased capacity of large body size to store fat energy and to subsist on lower quality foods in a relatively marked spatial-temporal unpredictable microhabitat of fruiting and flowering trees. Body size and energetics may play an important role in our models of the evolution of behavior and in the evolution of the great apes.

INTRODUCTION

The relationship between behavior, energy and structure of primates is an exciting and recent focus of attention (CLUTTON-BROCK & HARVEY, 1977a, b; COELHO et al., 1976; COELHO, BRAMBLETT & QUICK, 1979; GAULIN & KONNER, 1977; GAULIN & KURLAND, 1976; GRAND, 1977a, b; HAMILTON & BUSSE, 1978; HYLANDER, 1975; KAY, 1975; MILTON, 1979; RODMAN, 1979). This synthetic focus derives from the knowledge that natural selection operates on the entire phenotype of an individual. The purpose of this article is to suggest that body size is an important variable in this synthesis. The effects of body size are examined in two sympatric species of diurnal arboreal frugivores of the Bornean rain forest: the crab-eating monkey, *Macaca fascicularis*, and the orang-utan, *Pongo pygmaeus*. This paper discusses three areas of importance relating to the evolution of body size: (1) the temporal and spatial availability of energy or food resources; (2) the day to day manner of obtaining and expending energy in these two anthropoids; and (3) the storage of energy in the form of adipose tissue for future use.

BACKGROUND

A 20-month field study of *M. fascicularis* was made at the Hilmi Oesman Memorial Research Station located on the northern border of the Kutai Nature Reserve (0° 32′ N, 117° 25′ E) in the province of East Kalimantan, Indonesia (Fig. 1). The study site contains two generally distinct microhabitats: a nonriverine primary lowland forest and a riverine secon-
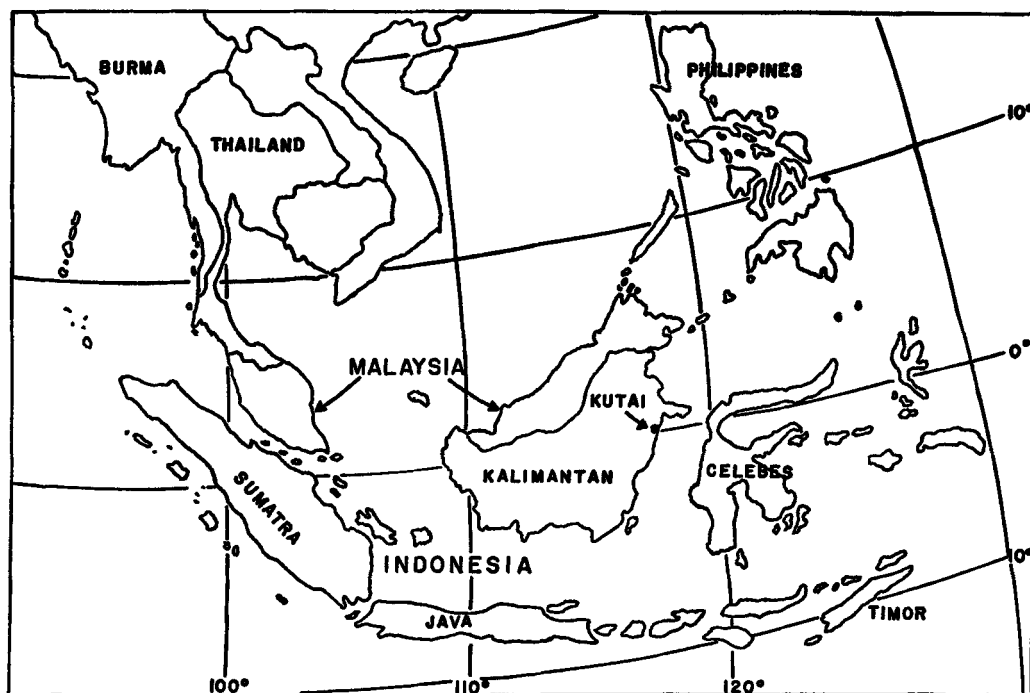
Fig. 1. Map of Southeast Asia showing the location of the Kutai Nature Reserve in Indonesian Borneo or Kalimantan.

dary forest dominated by pioneer tree species. The primary forest contains mixed dipterocarps up to 60 m tall dominated by *Shorea* spp., *Eusideroxylon-zwageri*, *Anthocephalus cadamba* and *Litsea* spp. (DIREKTORAT PERENCANAAN, 1973). The secondary forest, as defined by RICHARDS (1966), contains trees up to 30 m tall dominated by *Macaranga pruinosa, Callicarpa farinosa* and *Pterospermum* sp. More detailed analyses of the structure, composition and physiognomy of the latter forest are presented elsewhere (WHEATLEY, 1979).

During the course of this field study it appeared that orang-utans are ecologically segregated from macaques on the basis of differences in the horizontal utilization of microhabitats. Macaques, for example, spend at least 62% of the day in a hectare containing a stream. The ranging data for macaques show several significant linear negative correlations between the troop's distance from a stream and its utilization of a hectare. For example, as the distance from a stream increases, the following variables decrease on a per hectare basis: average time spent in a hectare, average frequency of visiting a hectare and the average frequency of feeding in a hectare. More detailed information is given in WHEATLEY (1980). Systematic surveys by other researchers also report that the preferred habitat of these macaques is secondary forest, especially riverine secondary habitats (CROCKETT & WILSON, 1980; GALDIKAS, 1978; KURLAND, 1973; RIJKSEN, 1978; RODMAN, 1978; SOUTHWICK & CADIGAN, 1972).

Orang-utans sometimes fed in streamside areas but they were infrequently sighted in these areas probably because their body weight restricted access to the small and generally fragile trees. More systematic data of orang-utans ranging from other researchers also show differential microhabitat usage (GALDIKAS, 1978; MACKINNON, 1974; RIJKSEN, 1978; RODMAN, 1978). For example, at the Mentoko (0° 34' N, 117° 25' E) RODMAN (1978, 1979) reported that *M.*

fascicularis were more frequently contacted and had a greater density in the riverine zone than in deep forest in contrast to orang-utans. Both species utilized the vertical strata of the forest similarly; both averaged 16 m at first contact. The Mentoko is only a half-day's walk from the research station.

The large body size of adult orang-utans denies them access to efficient utilization of food resources in secondary forest, consequently restricting their resources to those in the primary rain forest. This microhabitat restriction suggests that the frugivorous orang-utan must feed on a sporadically available and scarce fruit supply which many primary lowland tropical rain forest trees are noted for, in contrast to trees of the secondary rain forest (JANZEN, 1974; WHITMORE, 1975; WOOD, 1956).

This paper examines various energetic predictions and constraints of large body size by a preliminary comparison of orang-utans to crab-eating macaques. For example, how does body size affect diet, feeding bouts, activity profiles and day range? The constraints of large body size may explain why previous hypotheses have overlooked an energetic selective advantage to large body size. This paper makes a preliminary test of an energetic hypothesis.

METHODS

A test was made of the hypothesis that the two microhabitats did not differ in their phenological patterns. The data were collected by surveying the same 1,200 m of trails every two weeks for 16 months. The presence or absence of the following phenological states were recorded for each 0.5 m wide by 100 m long trail segment: fresh fruits and flowers, fresh flowers, fresh fruits and no fresh fruits or flowers. These surveys occurred in two different areas: a streamside secondary forest area and a nonstreamside primary forest or ridge-top area. A streamside area is defined as within 150 m of a stream at approximately 25 m elevation. A nonstream area is defined as greater than 200 m from a stream. This surveyed trail went along a ridge approximately 50 to 100 m in elevation.

The data were arranged in a contingency table and the Shannon information statistic was used to calculate indices of predictability, constancy and contingency according to procedures outlined by COLWELL (1974). Predictability has two summed components: constancy and contingency. Constancy is maximal when there is complete certainty with regard to phenological state once the point in time is specified. Contingency is maximal when the number of non-zero entries in each survey day and in each phenological state approaches one. Contingency is minimal when the survey days of the data matrix are homogeneous. Predictability is zero when both constancy and contingency are zero. Predictability in this study is not a measure of seasonality since data were only collected over a 16-month period.

Species comparisons were made on the following behaviors: diet, mean feeding bout length, mean number of feeding bouts per day, activity profiles, mean day range length, mean velocity and percent time arboreal. Food types were classified as to different kinds of fruit, in addition to the general classification of insects, flowers, grasses, leaves, clay and fungi. The relative proportion of dietary items was calculated as a count of the frequency of a food type eaten by an individual on a per hectare basis. If another individual in the macaque troop ate a different food item in the same hectare, then this was scored, but if it ate the same food item in the same hectare, an additional feeding observation was not scored. Feeding data are available for 18 months in *M. fascicularis* and for 16 months in *P. pygmaeus*. Activity profiles were classified as feeding, travelling or resting. Feeding activity consisted of harvest and process

time, thus including gathering and masticating. Feeding was considered terminated when the animal either ceased swallowing food items or left the tree. Travel was movement between food sources, usually between trees. Resting was neither feeding nor travelling and sometimes included behaviors such as grooming.

The data on activity profiles were collected on a focal adult male who was contacted continuously from 0600 to 1800 hrs. There are three days of continual observation on a prime adult male orang-utan, but the three-day contact of the male macaque are not continuous. The latter observations were very difficult and three weeks of effort at the end of the study were required before reasonably accurate data could be obtained.

The daily ranging data for macaques were obtained by averaging the number of hectares entered each day over a sample of 35 days spread out over a 14-month period. Data for the estimate of the percent of time arboreal in the macaques were collected over a sample of 40 days. Day range data on orang-utans were obtained from three days of continual observation. The velocity estimates were obtained by a stop watch when the animals continually and arboreally locomoted for at least 100 horizontal meters. The estimates for macaques were taken during the three-day continual contact periods and those of orang-utans were taken from all recorded observations. The relevant statistical tests on the species comparisons are indicated in the results. A local woodsman assisted in the collection of some of the orang-utan data.

RESULTS

The two microhabitats differed in the production of flowers and fruit. Table 1 shows that the trees of streamside areas were more predictable in their flowering and fruiting patterns than were trees in nonstreamside areas. Fruits and flowers were found in 142/174 (82%) of the surveys of streamside trails in contrast to 59/174 (34%) of the surveys of ridge trails. The predictability score for the phenological patterns of the streamside areas is .67 where constancy contributes 81% of the predictability. The predictability score for the phenological patterns of the ridge areas is .31 where constancy contributes 12% of the predictability. The calculated G-statistic on predictability, constancy and contingency in both areas shows that only the streamside contingency score is not significantly greater than zero. The G-statistics for the ridge survey are $G = 17.2$, $d.f. = 3$, $p<.001$ for constancy; $G = 149.4$, $d.f. = 87$, $p<.001$ for predictability; $G = 132.2$, $d.f. = 84$, $p<.001$ for contingency. For the streamside survey, $G = 262.3$, $d.f. = 3$, $p<.001$ for constancy; $G = 325$, $d.f. = 87$, $p<.001$ for predictability; $G = 62.7$, $d.f. = 84$, not significant. The G-statistic is distributed as χ^2 [see COLWELL (1974) for the details of calculations].

The data comparing diet and foraging behavior for both species are presented in Table 2. The most frequently observed food type for both species was fruit, although the macaque had a greater proportion of fruit in its diet than did the orang-utan. Another difference between the two species was the greater proportion of leaves and bark in the diet of the orang-utan compared to that of the macaque. In the present study no instances of bark-eating were observed in macaques nor was grass-eating ever observed in orang-utans. Macaques appeared to select more fruits on the basis of ripeness than did orang-utans. For example, macaques chose ripe red fruits of *Callicarpa farinosa* whereas orang-utans ignored color differences and ate unripe, green fruits as well.

There were two other differences in feeding behavior between the two species. Feeding bout

Table 1. A comparison of the phenological patterns surveyed in streamside areas (top four rows) and in ridge areas (bottom four rows).*

Streamside

	F	F	M	A	M	J	J	A	S	S	N	D	D	J	F	M	M	A	A	M	M	J	Total
ff	6	5	4	5	6	5	5	6	5	4	3	4	5	5	5	4	4	6	6	5	4	4	142
fl	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	8
nf	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3
fr	0	1	1	0	1	0	0	0	2	1	1	1	1	2	1	1	2	0	0	2	2	2	21
Total																							174

Ridge

	F	F	M	A	M	J	J	A	S	S	N	D	D	J	F	M	M	A	A	M	M	J	Total
ff	4	6	2	3	3	3	1	2	1	1	3	1	0	0	2	1	1	3	3	3	1	1	59
fl	0	0	0	2	0	1	1	0	0	3	0	2	2	2	0	4	4	1	3	2	1	1	31
nf	1	0	2	0	2	0	1	2	2	1	2	3	1	2	2	1	0	0	0	1	1	1	29
fr	1	0	2	1	1	4	4	3	3	1	1	1	4	4	2	0	1	2	0	0	3	3	55
Total																							174

* The columns represent the months of survey and the rows represent phenological state (ff: flowering and fruiting; fl: flowering only; nf: no flowering or fruiting; fr: fruiting only). The numbers in the matrix represent the presence of the relevant phenological state summed for each 100-m trail surveyed. For example, the first streamside survey began in the first week of February 1975 and each of the six 100-m trails contained fallen fruits and flowers for a sum of 6.

Table 2. A Comparison of traits related to foraging behavior in *Pongo pygmaeus* and *Macaca fascicularis* (data filled in where available).

	Pongo pygmaeus					*Macaca fascicularis*			
	RODMAN (1973, 1977)	GALDIKAS (1978)	MACKINNON (1974, 1977)	RIJKSEN (1978)	WHEATLEY	WHEATLEY	RODMAN (1973)	MACKINNON (1978)	CLUTTON-BROCK (1977)
Diet(%):									
Fruit	54	44.5	62	58	59.2	87	96	64.9	52
Leaves	29	23.1	23.5	25	18.4	3.7		25.8	16
Bark	14	11.3	10.5	3	18.4				
Insects	1.0	4.8	<3.0	14	2.7	3.9	4	4.6	23
Flowers & buds	2.0	1.9	1.0		1.3	3.3		4.7	5
Other		14.4	<3.0			2.1			
Average feeding bout lengths (min):									
All items	51 = ♂; 36 = ♀	10–19	54		50.7	10.5			
Fruit only		27.6			58.3	13.8			
Average number of feeding bouts/day	7	20.3 (8.5 fruit only)	3.8–5.1	7(?)	1.75	18.3			
Average day range (m)	305		400–600	650	453	1869		1400	700
Activity profile:									
Feed	46	60	33		26	13	28		35
Travel	11	19	15		29	45	30		34
Rest	43	21	52		45	42	42		20
Average velocity (m/hr)					184	430			
Arboreality (%)	90.5				99	97	100	92.5	
Feeding time		2.0–2.4			.93	.27		2.0	
Travel time	4.1	3.3							

lengths on all food items averaged 10.5 min for macaques ($N = 122$) compared to 50.7 min for orang-utans ($N = 29$). The mean feeding bout length for *M. fascicularis* was significantly less than that for *P. pygmaeus* [t test, $t = 6.7$, $d.f. = 30$, $p<.001$ with a correction for the number of degrees of freedom following the procedures of HAYS (1973)]. This same difference between the two species was maintained when both species ate fruits only, 13.8 min for macaques ($N = 92$) and 58.3 min for orang-utans ($N = 18$). This difference is again significant (t test, $t = 2.7$, $d.f. = 17$ with correction, $p<.01$). When both macaques and orang-utans fed on the same fruit species, the difference in average feeding bout length was 18.47 min for macaques ($N = 19$) and 64.17 min for orang-utans ($N = 6$). The difference is significant [$m = 19$, $z = 2.86$, $p = .0021$, normal distribution approximation to the Mann-Whitney-Wilcoxen statistic, GIBBONS (1976)]. There were two counteracting biases which influenced the estimation of feeding bout lengths in macaques: (1) Feeding bout lengths were underestimated for macaques in some cases because the bouts reflected harvest time and not necessarily process time. For example, when the small, berry-like fruits of *Callicarpa farinosa* were eaten, the animals often filled their check pouches and retires to a larger tree to process the fruit. Food bouts in orang-utans included both harvest and process time. (2) Feeding bout lengths were overestimated in macaques because they were very active during feeding bouts in contrast to sedentary orang-utans. I estimated that about one-third of the macaques' feeding time was spent walking along the tops of branches. In orang-utans, there was a further significant difference in feeding bout lengths on the basis of body size [$m = 16$, $z = 5.3$, $p<.001$, normal distribution approximation to the Mann-Whitney-Wilcoxen statistic with correction for ties, GIBBONS, (1976)]. Large adult males averaged 59.9 min per feeding bout ($N = 16$) in contrast to adult females and small males ($N = 13$) who averaged 39.5 min. The two species also differed significantly in the average number of major feeding bouts per day ($m = 3$, $p = .029$, Mann-Whitney-Wilcoxen test). Macaques averaged 18.3 feeding bouts per day ($N = 3$ days) while orang-utans averaged 1.75 feeding bouts per day ($N = 4$ days). One of the sample days for orang-utans was of an unhabituated adult female who only ate in one bout that day. The other sample days were from continuous observations of a prime adult male who appeared habituated to the observer.

   M. fascicularis spent 13 % of the day feeding, 45% of the day travelling and 42% of the day resting whereas *P. pygmaeus* spent 26% of the day feeding, 29% of the day travelling and 45% of the day resting. A feeding time to travelling time ratio in adult males of both species is significantly different ($m = 3$, $p = .05$, Mann-Whitney-Wilcoxen test). The ratios for *M. fascicularis* are .2, .2 and .4 whereas the ratios for *P. pygmaeus* are .5, .6 and 1.7.

   The comparative data on foraging and ranging for both species are also presented in Table 2. The average daily travel distance of *M. fascicularis* was 1,869 m. This distance was in contrast to and significantly greater than orang-utans who averaged 453 m per day ($N = 4$ days, three continuous observation days on an adult male and one day on an adult female, $m = 4$, $z = 2.9$, $p<.002$, normal distribution approximation to the Mann-Whitney-Wilcoxen statistic).

   The home range of the troop of macaques was about 1.25 km². This figure was obtained by counting all the different hectares that the troop entered during the entire study period. The orang-utans had larger home ranges although just how much larger was unknown. In six months five different large adult males ranged through the study area and I feel confident that they left. An estimated 25 different orang-utans were seen during this time in the study area.

Macaques also travelled at a significantly greater mean velocity [t test, $t = 5.5$, $p<.001$, $d.f. = 37$ with correction according to HAYS (1973)]. The average velocity in *M. fascicularis* was 430 m/hr ($N = 38$) whereas that of *P. pygmaeus* was 184 m/hr ($N = 19$).

Both species are predominantly arboreal. Macaques spent more than 97% of the time in the trees ($N = 400$ hr). Most of the terrestrial observation time was spent on the banks of the Sengata River, especially when it was low. The animals were seen on the ground in the forest on 29 occasions, especially in areas where the trees were small in relatively less canopy overlap. Orang-utans spent more than 99% of the observation time in the trees ($N = 61$ hr).

ENERGETIC REQUIREMENTS AND FAT STORAGE

The body weights for wild Bornean orang-utans and crab-eating macaques for both sexes average about 55 kg and 5 kg, respectively (ECKHARDT, 1975; FOODEN, 1971, 1976). The figures for orang-utans appear somewhat low considering estimates given by other fieldworkers (GALDIKAS, 1978; MACKINNON, 1974, 1977; RIJKSEN, 1978; RODMAN, 1979) and considering weights on captive animals.

One method of comparing the gains and costs of foraging is to estimate a total daily energy requirement for both species. This energetic comparison will be useful in suggesting the greater selective value that exists for the larger body size of orang-utans.

There are several methods of calculating total daily energy requirements. The equations used by COELHO et al. (1976) and COELHO, BRAMBLETT and QUICK (1979) require estimated or measured speeds over vertical and horizontal distances, which unfortunately are not available in *M. fascicularis* and *P. pygmaeus*. For example, *M. fascicularis* travel at a rapid trot, yet their horizontal arboreal velocity is only 430 m/hr, much less than an average travel speed of 5.5 km/hr for *M. sinica* measured by GRAND (1976). Consequently there is a significant nonlinear component to travel which needs to be accounted for. The method used here follows MOEN (1973) whose equations for total daily energy requirement are calculated as a multiple of basal metabolism. These equations were estimated from data for domestic animals studied in the laboratory or in pastures. Since the equations derive energy expenditure per hour, the actual activity budget estimates for both species can be included (Table 3). The total daily energy requirement is the sum of basal metabolic energy expenditure and of activity expenditure. Production expenditure or the energy necessary for the growth body tissue, of the fetus, production of milk and the additional cost to maintain homeothermy were not included in these calculations. The equations used are: (1) basal metabolism $= 70(W_{kg}^{0.75})$; (2) resting $= [70(W_{kg}^{0.75}) (1.1)]/24$; (3) running $= [70(W_{kg}^{0.75}) (8)]/24$; (4) walking 1 km on level $= (.59) (W_{kg}) (D_{km})$; (5) vertical ascent of 0.1 km $= (6.45) (W_{kg}) (H_{km})$; and (6) foraging $= (0.54) (W_{kg})$, where $W_{kg} =$ weight in kg; $D =$ distance in km; $H =$ vertical height ascended expressed as percentage of km on level. With the exception of the basal metabolism equation which is a daily rate, all of the above equations are hourly rates. The

Table 3. Activity budgets for an adult male orang-utan and an adult male crab-eating macaque averaged over a 3-day period.

Activity (hr/day)	*P. pygmaeus*	*M. fascicularis*
Feeding	2.53	1.44
Travelling	2.78	4.72
Resting	4.25	5.17
Total	9.56	11.33

equation for resting is actually that for standing as given in MOEN (1973). This latter equation is used rather than basal because field measurements of resting in *M. fascicularis* and *P. pygmaeus* include social behavior and movement within a tree. These two activities will slightly raise energetic requirements.

The results of the orang-utan's daily energy requirements are: 1,414 kcal for basal metabolism; 569 kcal for arboreal locomotion on 50% gradient; 75 kcal for feeding and 275 kcal for resting. The total is approximately 2,333 kcal/day for a 55-kg animal. The requirement for arboreal locomotion is calculated as the sum of level walking and vertical ascent and descent times 2.78 hr engaged in travel. I have arbitrarily assumed that half of the day range is spent in vertical ascent and half in vertical descent. Because the cost of the latter activity is approximately equivalent to the cost of walking on the level (MOEN, 1973), the distance walked is .68 km yielding a cost of 22 kcal. The cost for vertical ascent of .2265 km is 80 kcal. The sum of these locomotor costs is arbitrarily doubled to account for nonlinear arboreal travel. The equation for walking is used rather than running because orang-utan locomotion is very slow, awkward and deliberate. In fact, Indonesians use the word *bertahan* which means to endure or suffer when referring to travelling orang-utans. This awkward locomotion may give the orang-utan a somewhat greater cost of transport (FEDAK & SEEHERMAN, 1979).

Calculations of the macaques' daily energy requirements are: 234 kcal for basal metabolism; 561 kcal for arboreal locomotion on an assumed 50% gradient; 4 kcal for feeding and 55.5 kcal for resting. The total is about 855 kcal/day for a 5-kg animal. The method of calculations were similar to that used for orang-utans except that the equation for running was used for macaque locomotion. In contrast to orang-utans, macaques are very active animals and Indonesians use the word *jalan* which is the word for travel. If the macaque engages in arboreal running for half of his total travel time and this value is doubled to account for nonlinear arboreal travel, then his cost of running is about 368 kcal. The remaining locomotor costs for walking, 1.3 km, and vertical ascent, 0.93 km, are summed and doubled for nonlinear arboreal travel and multiplied by 2.84 hr, yielding a total of 193 kcal. I have added .48 hr to the travel time because approximately one-third of the animals' feeding time is spent walking along the branches of a tree.

The calculations for daily energy requirements in both species are only rough approximations to be used for comparative purposes. The feeding requirements, for example, are probably underestimated. The macaque's estimate is large compared to an estimate of 100 kcal/kg for an adult rhesus monkey given in one study (NATIONAL ACADEMY OF SCIENCES, 1972), but the estimate reported here appears justified considering the travel costs. The requirements for the macaque using the equations of COELHO, BRAMBLETT and QUICK (1979) are 72.5 kcal for resting, 34 kcal for feeding, 560 kcal for travelling and 117 kcal for basal for a total of 784 kcal. The calculations for travel assumed a speed of 5.5 km/hr.

Accurate estimates for energy storage capacity (fat only) are not available for either species, but I arbitrarily estimate that the orang-utan has about twice the fat storage capacity in percentage of total body weight (16%) than the macaque (8%). These estimates are based on GRAND (1977a, b, pers. comm.) who estimated that one obese adult male orang-utan was 20% fat. The cheek callosities and jugal dewlap weighed 3.2% of his total body weight. WALIKE et al. (1977) measured about 10% adipose tissue/body weight in captive *M. nemestrina*. Scaling down these percentages for wild animals and for a smaller species of macaque might reasonably yield the relative fat capacities above.

The absolute amount of adipose tissue in *M. fascicularis* may then weigh about 400 g

whereas in *P. pygmaeus* it may weigh 8,800 g. The amount of energy stored in these estimated amounts of adipose tissue is about 87% (NEWSHOLME & START, 1973) which yields 348 g and 7,656 g, respectively. The physiological fuel value per gram of fat is about 9 kcal (HARRIS, 1966) so that the stored energy of fat in *M. fascicularis* is about 3,132 kcal and in *P. pygmaeus* about 68,904 kcal.

These calculations show that the energy reserve of *M. fascicularis* has a much narrower margin of safety than that of *P. pygmaeus*. For example, if necessary, macaques would use about one-quarter of their stored fat energy per day whereas orang-utans would use about 3% of their stored fat energy per day (see Table 3). A more dramatic comparison shows that macaques might fast or risk starvation after only about four days whereas orang-utans might fast for about 30 days. The activity budget for orang-utans presented in Table 3 is somewhat different from that reported by other researchers such as GALDIKAS (1978), MACKINNON (1974) and RODMAN (1977). If the figures of these researchers are used, however, to calculate a daily energetic requirement, there is little difference with the figures reported here. For example, the longer average day length reported by RODMAN on habituated animals yields longer absolute feeding and resting durations, but the fewer number of travel hours (1.2) combine for only a 192-kcal smaller difference per day for a 55-kg animal than the figures reported here. RODMAN (1979) calculated a total daily energetic cost for an orang-utan of larger body size using slightly different methods, but obtained an approximately similar figure as reported here.

DISCUSSION

Natural selection affects individual reproductive fitness by operating on the entire phenotype of an individual, such as its behavior, morphology and physiology. One crucial consideration of an individual's fitness is its utilization of energy. To survive and reproduce, an animal needs to balance the amount of energy acquired through eating against the amount of energy expended. Throughout its lifetime the temporal and spatial availability of food resources may be an important evolutionary constraint on a foraging animal. Energy gain may be stored in the form of adipose tissue to be utilized for greater competitive ability in dealing with the vagaries of the social and physical environment and for favorable periods of reproduction. The efficient utilization of resources through trade-offs in current reproductive effort and residual reproductive value (CALOW, 1979; PIANKA, 1976) may finally influence lifetime reproductive success in shaping a species' life history.

Crab-eating macaques and orang-utans differ considerably in their manner of obtaining and expending energy. These differences are predictable on the basis of body weight. The energetic requirements of resting metabolism, for example, are proportional to the body weight of a mammal to the .75 power. Consequently, small animals differ from large ones in their relative and absolute maintenance requirements (KLEIBER, 1961; SCHMIDT-NIELSEN, 1972). Resting daily metabolism per gram in a 55-kg orang-utan is about half that of a 5-kg macaque, and the former species' daily energetic requirement per gram is about 25% of the macaque. Since large body size enables an animal to digest less per gram for maintenance, we can predict that their diets will be high in relatively abundant but nutrient-poor fiber, such as leaves, stems and bark (BELL, 1971; GAULIN & KONNER, 1977). A smaller animal should have an energy-rich diet of nonstructural carbohydrates, such as fruit. Table 2 shows that although both species eat fruit most frequently, the primary dietary difference is that the over-

all diet of orang-utans includes less nutritious food than that of macaques, that is, more leaves and bark. Macaques also appear more selective in choosing ripe fruits and feeding in more bouts per day than orang-utans. The absolute maintenance requirement of an animal per day, however, is greater in a large animal than in a small animal. Consequently, orang-utans spend twice the amount of time feeding per day than do the macaques and the average bout length is also much longer in orang-utans (Table 2). Macaques have more time to be selective as suggested in the smaller feeding to travelling time ratio (Table 2), and they can maintain themselves on a food supply which might be too sparse for a larger animal, such as the small quantities of ripe fruit in an average fruiting pioneer tree species.

Energetic expenditure is also a function of body size. Again, as in the acquisition of energy, small-bodied animals differ from large-bodied animals in their relative and absolute expenditures. The cost of horizontal locomotion, for example, is proportional to the body weight to the .6 power. Small animals have a relatively higher energy cost for level running than larger animals but smaller absolute costs (TAYLOR, CALDWELL & ROWNTREE, 1972). Running uphill has a relatively smaller increase in energy expenditure over horizontal running for small animals than for large animals. Consequently, large arboreal animals may compensate for their energetic disadvantage in a relative and absolute sense compared to small animals by minimizing their travel costs. The data in Table 2 also support this prediction. The foraging patterns of both species illustrate the constraints of the large-bodied orang-utan compared to the macaque. The orang-utan spends less time in travel throughout the day and ranges for much shorter distances per day at slower speeds than the macaque. Again, the ratio of time feeding to time travelling indicates the marked contrast between the life styles of these two species.

There are other aspects of body size which affect resource utilization, such as gaining access to resources, but the effects of differential utilization are difficult to evaluate. For example, the orang-utan may be denied access to resources where the trees and branches are too small or too weak to support a heavy animal in contrast to the lighter macaque. To some extent access to food at terminal branches by heavier animals may be compensated for by their greater strength so that branches may be broken or bent towards the foraging animal. In areas where tree diameters are large with nonoverlapping canopies, the great strength and reach of a larger animal would permit access to resources. Greater strength alone can also gain access to tough seeds and stripping of tree bark.

The data in this paper are limited, but it is likely that these study results are generally species differences because comparable figures from other researchers are in general agreement (Table 2). Strict comparison of the figures in this table between study sites is cautioned. For example, differences in diet and average feeding bout frequency and length, as well as other figures between the Kutai and Tanjung Puting probably reflect habitat differences with the former site having taller and larger emergents with a greater quantity of fruit (GALDIKAS, 1978).

SELECTION FOR LARGE BODY SIZE

The increase in body size in some evolutionary lineages is a commonly observed trend (COPE, 1896; DOBZHANSKY et al., 1977; SIMPSON, 1953), but few hypotheses exist which explain the adaptive mechanisms involved. One common hypothesis is that of protection from predation (RENSCH, 1960), and it has been suggested that in the absence of predators there may be little benefit for large size (WASSERSUG et al., 1979). Of those advantages of large body size

which have been considered (STANLEY, 1973), no attention has been given to an energetic hypothesis.

Most researchers on orang-utans have maintained that nonhuman predation on *P. pygmaeus* is insignificant even in Sumatra where tigers occur (MACKINNON, 1971, 1974; RIJKSEN, 1978; RODMAN, 1979). MACKINNON (1971, 1974) and RIJKSEN (1978) have speculated that human predation may have selected for an arboreal orang-utan which in the past may have been more terrestrial. Consequently, one hypothesis of the orang-utan's large body size is that it is a vestigal remnant of Pleistocene terrestriality and predator defense (MACKINNON, 1971; SMITH & PILBEAM, 1980). This is a difficult hypothesis to test. The evidence for this hypothesis is indirect and relies only on the large size of fossil teeth (HOOIJER, 1948, 1949). Even if fossil orang-utans were larger in the past, this does not demonstrate that they were terrestrial, nor does it demonstrate that predation on the ground is worse than predation in the trees. Fossil postcrania are needed, especially because the long, curved phalanges and many other skeletal and muscular features are indicative of a long arboreal history (SCHULTZ, 1968; SUSMAN, 1974; TUTTLE & BASMAJIAN, 1974).

The only proposed advantage of large body size in the orang-utan is that this imparts greater strength allowing access to resources, that is, opening hard fruits, stripping lianas and bark (MACKINNON, 1971, 1974; GALDIKAS, 1979; RODMAN, 1977). While greater strength may be an advantage of large body size, does it outweigh the disadvantages? For example, many animals should prefer to exploit nutrient-rich foods but smaller animals appear to have an advantage on such scarce items (BELL, 1971; GAULIN & KONNER, 1977). Dietary fiber is potentially a high energy source, but there is little morphological evidence in the orang-utan that supports the considerable mechanical and chemical processing which is necessary to utilize the energy. The gut morphology of the orang-utan is not as specialized as most colobines and the wide incisors of the orang-utan are typical of frugivores (HYLANDER, 1975; KAY, 1975; MILTON, 1978). It is possible, however, that enlarged incisors may be equally useful in obtaining bark (pers. obs.). In molar morphology, the orang-utan's large crushing surface may be a folivorous adaptation for grinding (KAY, 1975). One advantage that large species have is that fiber may be retained in large quantities and allowed to ferment (GRAND, 1978).

This paper proposes an alternative hypothesis for selection of large body size relating to the increased capacity of large body size to store energy and to subsist on lower quality foods in a relatively marked spatial-temporal unpredictable microhabitat of fruiting and flowering trees. Such an environment should impose strong selection for resistance to food shortages. GALDIKAS (1978, 1979), for example, has indicated that orang-utans of South Kalimantan were faced with a shortage of fruit in 1973 and ate bark as their primary food source for several months. GEIST (1977) has emphasized that large body size itself is an indication of environmental instability in food production. The relatively unpredictable nature of fruiting trees has also selected for a very unusual type of social organization in this large ape: it is solitary (GALDIKAS, 1978, 1979; KLOSS, 1908; MACKINNON, 1974; RIJKSEN, 1978; RODMAN, 1979).

The evolution of adipose tissue is one mechanism for storing energy to be used for maintenance, reproduction and other activities, such as migration, territorial and harem defense. Fat is light in weight compared to stored glycogen or protein because it can be stored in a relatively water-free state (CAHILL, 1970; WILLIAMS, 1976). This more concentrated form of energy is especially useful in an arboreal animal with vertical travel requirements. One

evolutionary role of fat storage is to ensure an adequate source of energy in the face of tem-
porary food shortages (CAHILL, 1970; GAULIN & KONNER, 1977; LYTLE, 1977; MASORO, 1977;
POND, 1978; WILLIAMS, 1976; YOUNG, 1976). The muscles can derive energy from adipose
tissue during prolonged hard work and during restricted food intake when carbohydrate
stores are exhausted. There is also evidence of metabolic changes in the gastro-intestinal
tract leading to increased accumulation of fat relative to lean body mass under a dietary re-
gime of feast and famine (LYTLE, 1977).

The important role of fat storage in the orang-utan has only received very cursory mention
(MacKINNON, 1971, 1974; MONTAGU, 1966; RIJKSEN, 1978; RODMAN, 1981) although the
ability of the orang-utan to store large amounts of fat leading to obesity is well-known in
captivity (MacKINNON, 1971). Whether this ability is under genetic control as it apparently is
in some other animals is, however, not known (BRAY & YORK, 1979; LYTLE, 1977). The large
fat reserves of large animals appear important in other species such as in deer (DROŻDŻ &
OSIECKI, 1973; MOEN, 1973). During winter food shortages, for example, the loss of body
weight in a male deer may be as high as 35% where the 1.5 kg of fat reserves enables survival
for one month. A small deer would rapidly deplete its fat reserves and starve to death during
severe winters.

Body size appears to play a large role in a number of theoretical areas. First, a bioenergetic
approach to selected aspects of the behavioral ecology of a species shows more promise than
past socioecological approaches. This paper has suggested that body size is an important
variable of predictive value when other variables relating to ecological categories are held
constant. Recent reviews are beginning to test some of these predictions in a wide variety of
primates (CLUTTON-BROCK & HARVEY, 1977a, b). A comparison of the larger-bodied siamang
to the gibbon, for example, shows many of the same patterns described in this paper. The
siamang has a larger feeding time to travel time ratio, eats more fruit, travels shorter distances
per day, feeds for longer periods of time per day and feeds at less sites per day (MacKINNON,
1977). Secondly, man (Hominidae) and the great apes (Pongidae) have large-sized bodies in
comparison to all other extant primates. The selective advantage of large body size in these
taxa may be more than just a remnant of a past life, and a bioenergetic approach may be a
useful hypothesis in the origin of the great apes. For example, the orang-utan appears to more
efficiently maximize its energy gain in contrast to the more selective crab-eating macaque.
The orang-utan's large body size and its more efficient energy budget may partly explain why
researchers have stated that the orang-utan rather than any other arboreal species eats the
largest proportion of fruits in the primary rain forest (MacKINNON, 1971, 1974; RIJKSEN,
1978). WEINER (1964) has proposed a productive or extractive ratio in order to evaluate the
efficiency of food productive economies. This ratio is the amount of work involved in meeting
daily energy requirements, and WEINER predicted that the ratio for nonhuman primates would
be around 70% since food-collecting appeared to be continual. The ratio for the crab-eating
macaque is 66% according to the calculations in the results of this paper, but the ratio for the
orang-utan is 28% which is within the range of human subsistence economies.

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