

Reproductive Strategies of Primates: The Influence of Body Size and Diet on Litter Size

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ABSTRACT. The frequency of multiple births, life history parameters, body size, and diet characteristics were obtained from the literature for 70 primate species. The general pattern within the primate order is to have single infant litters, yet multiple births regularly occur in a number of species in specific phylogenetic groups. Primates which have large litters tend to be small, have short gestation periods and give birth to small infants, which are weaned quickly, and mature rapidly. Species in which multiple births are common also have short interbirth intervals and in the Callitrichidae have males which exhibit paternal care. In addition, they are commonly insectivorous. Although it is difficult to isolate the effects of diet on litter size, independent of body size, analyses suggest that after the influence of body size is statistically removed, as the proportion of insects in the diet increases, animals have larger litters. We suggest that by adopting a mixed diet of insects and fruit primates may be able to ensure access to a seasonally stable food resource that is not greatly restricted by the presence of toxins. This diet would allow a relatively high metabolism and facilitate large litters.

Key Words: Litter size; Body size; Diet; Reproductive strategies.

INTRODUCTION

Despite considerable conjecture, the factors governing the size of mammalian litters remain unclear. The documentation of strong relationships between body size and litter size (WESTERN, 1979; EISENBERG, 1981; PETERS, 1983; CLUTTON-BROCK & HARVEY, 1983; HARVEY & CLUTTON-BROCK, 1985; HARVEY et al., 1986) has led to the suggestion that litter size may not be set by the direct action of selection, but is instead a consequence of allometric variation in body size. Some authors have considered potential phylogenetic constraints on the size of litters (LEUTENEGGER, 1973, 1976, 1979), while still others have suggested that food habits, working through metabolic rates, influence, if not set, a number of reproductive traits, including litter size (EISENBERG, 1981; MCNAB, 1980, 1986).

The comparison of allometric relationships between mammal groups which have different litter sizes and different food habits faces a number of difficulties. A group of mammals must be found for which there is sufficient documentation of diets and where there is sufficient variation in diet to facilitate comparisons. Difficulties in interpretation can be minimized by selecting closely related species within a small taxonomic group so that divergence in unrelated traits does not create undue confusion (HARVEY & CLUTTON-BROCK, 1985).

Primates are a suitable group for examining relationships between litter size and life history parameters, allometry, and feeding patterns, for their study offers an opportunity to minimize the above mentioned difficulties. As a group, they are well studied, and there are a large number of investigations which report their feeding patterns using similar methodologies. In addition, within this order there are species which are almost exclusively insectivorous, while others eat primarily fruit or leaves.

Traditionally analyses of determinants of litter size have used the modal value for the species. For primates, this ignores potentially significant variation in litter size and creates a somewhat arbitrary dichotomy between species with a mode of one and those with multiple births. Some of the species which are categorized as having a litter size of one, when the mode is considered, fairly frequently give birth to twins, but at a rate which is slightly less than 50% (e.g., *Lemur catta*, *Hapalemur griseus*, Lorisidae). The variation that is being obscured may be associated with variation in other life history traits, or with behavioural traits such as diet, paternal care, or social organization. In this paper, we use a measure of litter size that circumvents these problems to document allometric relationships between litter size and life history traits. In addition, we describe how litter size is influenced by behavioural traits, such as social organization and paternal care. Lastly, particular emphasis is placed on examining empirical relationships between variation in the incidence of multiple births for primates and their diet.

METHODS

An extensive survey of the literature was conducted to obtain information on the incidence of multiple births, life history traits, body size, and feeding patterns for as many primate species as possible. As mentioned earlier, the standard measure of primate litter size has been the mode. Alternative traditional descriptors are the median and the arithmetic mean. Each of these measures is in some way inadequate. In many species, the mode and the median may obscure significant variation. For primates, the arithmetic mean is not a good measure of central tendency because the distribution of litter size is highly skewed towards one. Such a distribution is difficult to use in regression analyses. Researchers working on group size have similar problems and, as a solution, have represented central tendency with a statistic called "typical size" (JARMAN, 1974). This measure represents the group or litter size experienced by the average animal, not the average group or litter size seen by the observer. Typical size is given by

$$g = \frac{\sum_{i=1}^N g_i^2}{\sum_{i=1}^N g_i},$$

where N is the number of litters and g is the size of each litter.

The advantage associated with the use of typical size can best be illustrated by an example analogous to the one given by JARMAN (1974; see his Appendix 2). Imagine two sets of three litters: set A has litters of size 1, 1, and 8, while B has litters of size 4, 3, and 3. The modes of the two sets are respectively 1 and 3, while the arithmetic means are equal at 3.33. The medians are 8 and 3. In set A the modal litter size represents only two animals out of ten, while the means represent the average litter observed, not the litter size the average animals finds itself in. The medians are a more adequate representation of central tendency, but they also obscure a large part of the variation in the data. In contrast, the typical litter sizes of the two sets are 6.6 and 3.4, respectively, values which yield much better estimates of both variation and central tendency.

Typical litter size was thus calculated in all cases where litter size varied within a species. Species that had been adequately studied for which no reports of multiple births were ob-

tained were assigned a typical litter size of 1. Those species for which reports of multiple births were found, but a frequency was not given, were not assigned a typical litter size. Many studies reported information on birth frequencies in primates; where more than one frequency of multiple births was found, a weighted average was calculated at the species level.

Data on adult female body weight, the period of gestation, age at weaning, interbirth interval, neonate weight, and age at sexual maturity (averaged for males and females) were extracted from NAPIER and NAPIER (1967), DeVORE (1965), BUSS (1971), HAFEZ (1971), CHIARELLI (1972), ARDITO (1976), CLARK (1977), HERSHKOVITZ (1977), KLEIMAN (1977), DOYLE and MARTIN (1979), EISENBERG (1977, 1981), MILLAR (1981), HARVEY and CLUTTON-BROCK (1985), and LEFEBVRE (1985).

Paternal care was considered as any behaviour performed by an adult male which relieves the mother of an energetic burden associated with infant care. We thus defined paternal care in terms of carrying, baby sitting, etc. Behaviours such as grooming, playing, predator warning, and territorial defense were not considered as direct paternal care. The primary sources for this data were VOGT (1984) and TAUB and REDICAN (1984). A species was categorized as either exhibiting paternal care or not.

Four categories of social organization were considered; solitary, monogamous, single male, and multimale-multifemale. Data were collected primarily from HARCOURT et al. (1981), KLEIMAN (1977), RICHARD (1985), and NAPIER and NAPIER (1967). When a species was considered to have more than one type of social organization, if one type obviously dominated the other, only the more dominant type was considered in the analysis. However, if a clear dominance was not evident the following protocol was used. If a species was called solitary and monogamous, it was considered monogamous, if a species was labelled as both monogamous and single-male, it was considered single-male, and finally if a species was called single-male and multimale-multifemale, it was considered multimale-multifemale.

All primates were classified by diet as insectivorous, frugivorous, or folivorous. Data on food habits were primarily collected from JOLLY (1972), CLUTTON-BROCK and HARVEY (1977a, b), and RICHARD (1985). Although different field studies employ various methods to estimate this parameter, diet provides a useful means to separate animals in terms of energy intake. The percentage of the diet that each category comprised was obtained from CLUTTON-BROCK and HARVEY (1977a, b) and RICHARD (1985). If studies provided different estimates for a species, the values were averaged.

The literature survey produced a data set of 70 species. This compilation contained a number of potential shortcomings typically associated with such surveys. Since academic interest is not divided equally amongst all species in the primate order, particular species have been studied more than others, and thus may have exerted undue influence on the relationships presented. Also, the accuracy with which litter size was estimated varied among species. In order that this potential bias can be assessed, the number of births from which litter size was calculated are presented in Table 1.

ANALYSES

To examine inter-relationships between continuous life history variables and relationships between body size and life history variables we used least-squares regression analyses. Logarithmic transformations of both axes were used to fit a linear model. Regression analyses

Table 1. A compilation of typical litter size, a number of life history parameters, and body size for primate species. (For footnotes, see the end of the table.)

Species ¹⁾	Typical litter size	No. of litter	Body mass (kg)	Gestation period (day)	Age at weaning (day)	Age at sexual maturity (day)	Weight of individual neonate (g)	Inter-birth interval (day)	Paternal care ²⁾	Social organization ³⁾	Diet category ⁴⁾	References
Cheirogalinae												
<i>Cheirogaleus major</i>	2.500	—	0.4	69	46	—	18.0	—	n	s	f	DOYLE & MARTIN, 1979
<i>Cheirogaleus trichotis</i>	2.500	—	—	—	—	—	—	—	n	s	f	DOYLE & MARTIN, 1979
<i>Microcebus murinus</i>	2.500	—	0.07	60	140	257	12.0	312	n	—	i	DOYLE & MARTIN, 1979
Daubentonidae												
<i>Daubentonia ni.</i>	1.000	—	—	—	—	—	—	912	n	s	i	DOYLE & MARTIN, 1979
Indridae												
<i>Propithecus verreauxi</i>	1.000	—	3.5	151	182	912	107.0	360	n	—	i	DOYLE & MARTIN, 1979
<i>Propithecus diademata</i>	1.000	—	7.5	—	182	—	—	—	n	—	i	NAPIER & NAPIER, 1967
<i>Avalhi laniger</i>	1.000	—	0.7	—	—	—	—	365	n	m	i	DOYLE & MARTIN, 1979
<i>Indri indri</i>	1.000	—	7.0	160	151	—	300.0	912	n	m	i	DOYLE & MARTIN, 1979
Lemuridae												
<i>Lemur macaco</i>	1.047	83	2.1	128	135	550	100.0	—	n	p	f	HILL, 1973
<i>Lemur fulvus</i>	1.056	170	2.1	129	135	550	88.2	511	n	p	i	HILL, 1973
<i>Lemur mongoz</i>	1.152	110	1.8	129	166	550	100.0	—	n	p	f	HILL, 1973
<i>Lemur catta</i>	1.304	547	2.2	135	135	646	88.2	511	n	p	f	HILL, 1973
<i>Lemur variegatus</i>	2.465	96	3.0	—	135	—	107.5	365	n	m	—	HILL, 1973; SHIDELER & LINDBURG, 1982
<i>Hapalemur griseus</i>	1.400	—	2.6	—	46	—	48.0	—	n	m	i	HILL, 1973
<i>Lepilemur mustelinus</i>	1.000	—	0.9	135	120	550	34.5	—	n	s	i	NAPIER & NAPIER, 1967
Lorisidae												
<i>Loris tardigradus</i>	1.546	152	0.3	162	182	—	12.7	—	n	s	i	DOYLE & MARTIN, 1979
<i>Nycticebus coucang</i>	1.364	9	1.0	193	71	—	49.3	—	n	sm	i	WILDT & DUKELOW, 1974
<i>Perodictus potto</i>	Report	2	1.3	186	209	646	46.5	349	n	sm	i	COWGILL & ZEMAN, 1980; DALBY & MARUSKA, 1975
Galago crassicaudatus												
<i>Galago senegalensis</i>	1.244	180	0.9	132	120	365	47.4	360	n	sm	i	DOYLE & MARTIN, 1979
<i>Galago senegalensis</i>	1.809	37	0.2	126	71	229	11.5	200	n	sm	i	DOYLE & MARTIN, 1979
Tarsiidae												
<i>Tarsius syrichta</i>	1.000	—	0.1	—	—	—	26.2	—	n	m	i	DOYLE & MARTIN, 1979
<i>Tarsius bancanus</i>	1.000	—	—	—	—	—	—	—	n	m	i	DOYLE & MARTIN, 1979
<i>Tarsius spectrum</i>	1.000	—	0.2	—	—	—	30.0	152	n	m	i	DOYLE & MARTIN, 1979

(continued)

Table 1. (continued)

Species	Typical litter size ¹⁾	No. of litter	Body mass (kg)	Gestation period (day)	Age at weaning (day)	Age at sexual maturity (day)	Weight of individual neonate (g)	Inter-birth interval (day)	Paternal care ²⁾	Social organization ³⁾	Diet category ¹⁾	References
Callitrichidae												
<i>Saguinus nigricollis</i>	1.906	—	—	—	—	—	43.5	—	n	m	i	HERSHKOVITZ, 1977
<i>Saguinus oedipus</i>	1.897	—	0.4	141	66	692	43.2	280	y	m	i	HERSHKOVITZ, 1977
<i>Saguinus fuscicollis</i>	1.970	—	—	—	—	—	40.0	242	y	m	i	HERSHKOVITZ, 1977
<i>Saguinus Geoffroyi</i>	1.987	—	—	—	—	—	50.0	243	n	m	i	WISLOCKI, 1939; HAMPTON et al., 1977
<i>Callithrix jacchus</i>	2.341	—	0.3	145	55	513	28.0	157	y	m	i	WISLOCKI, 1939
<i>Callithrix argentata</i>	1.909	—	0.3	—	120	437	—	—	y	m	—	HAMPTON et al., 1977
<i>Cebuella pygmaea</i>	2.062	—	0.1	145	76	550	16.0	154	y	m	i	HERSHKOVITZ, 1977
<i>Leontopithecus rosalia</i>	2.064	—	0.5	135	74	676	53.6	304	y	m	i	HERSHKOVITZ, 1977
Cebidae												
<i>Alouatta</i> sp.	1.160	23	5.9	180	646	1380	480.0	675	n	p	i	SCHULTZ, 1948
<i>Alouatta palliata</i>	Report	1	5.9	180	646	1380	480.0	675	n	p	i	SCHULTZ, 1948; CHAPMAN & CHAPMAN, 1987
<i>Alouatta seniculus</i>	Report	2	—	180	—	—	—	—	n	p	i	SCHULTZ, 1921
<i>Saimiri sciureus</i>	1.000	—	0.6	170	182	1122	195.0	414	n	p	i	NAPIER & NAPIER, 1967
<i>Ateles fusciceps</i>	1.000	—	5.8	—	—	1660	—	760	n	p	f	NAPIER & NAPIER, 1967
<i>Ateles Geoffroyi</i>	1.000	—	5.8	—	—	1660	426.0	870	n	p	f	NAPIER & NAPIER, 1967
<i>Cebus apella</i>	Report	—	2.1	160	—	—	—	—	n	p	f	STOTT, 1946
<i>Pithecia pithecia</i>	1.000	—	1.4	—	—	1445	—	—	—	—	—	NAPIER & NAPIER, 1967
<i>Aotus trivirgatus</i>	Report	20	1.0	—	—	—	98.0	220	y	m	i	MERRITT, 1980
<i>Callicebus torquatus</i>	1.000	—	—	—	—	—	—	365	y	m	i	MERRITT, 1980
Cercopithecidae												
<i>Cercocebus torquatus</i>	1.035	56	—	—	—	—	—	—	—	p	f	WILDT & DUKELOW, 1974
<i>Cercopithecus</i> sp.	1.045	40	2.3	197	366	—	—	—	n	p	i	STOTT, 1946
<i>Cercopithecus sabaeus</i>	1.000	—	3.6	—	—	—	314.0	365	—	p	f	FITZSIMONS, 1919
<i>Cercopithecus mitis</i>	1.000	—	—	—	—	—	402.0	413	—	p	f	SCHULTZ, 1956
<i>Macaca sylvanus</i>	Report	1	—	—	—	—	—	945	y	p	f	BURTON & PELHAM, 1979
<i>Macaca arctoides</i>	1.013	937	—	—	—	1148	—	—	n	p	f	SCHRIER & POVAR, 1984
<i>Macaca fuscata</i>	Report	—	12.5	166	214	1445	503.0	—	y	p	f	NAKAMICHI, 1985
<i>Macaca mulatta</i>	1.007	2989	7.5	166	316	1175	481.0	360	n	p	f	HAFAZ, 1971; KOFORD et al., 1966; VAN WAGENEN, 1972

(continued)

Table 1. (continued)

Species	Typical litter size ¹⁾	No. of litter	Body mass (kg)	Gestation period (day)	Age at weaning (day)	Age at sexual maturity (day)	Weight of individual neonate (g)	Interval between births (day)	Paternal care ²⁾	Social organization ³⁾	Diet category ⁴⁾	References
<i>Macaca iris</i>	1.007	270	4.1	166	365	1300	—	—	n	p	f	SCHULTZ, 1956;
<i>Macaca radiata</i>	1.010	199	5.2	162	302	1288	404.0	—	n	p	f	KOFORD et al., 1966
<i>Macaca speciosa</i>	1.024	82	—	—	—	—	—	—	n	p	f	KOFORD et al., 1966
<i>Theropithecus gelada</i>	1.000	—	13.6	—	—	1620	464.0	525	n	p	f	KOFORD et al., 1966
<i>Papio</i> sp.	1.008	1567	14.4	182	450	1660	1068.0	420	n	p	—	SCHULTZ, 1948
<i>Presbytis melalophos</i>	Report	10	6.3	—	—	1380	—	—	—	—	f	HENDRICKS et al., 1968
<i>Presbytis entellus</i>	1.000	—	10.5	182	372	1820	—	—	n	si	l	BENNETT, 1982
<i>Presbytis senex</i>	1.000	—	7.8	—	214	1380	—	—	—	—	l	NAPIER & NAPIER, 1967
<i>Presbytis cristatus</i>	1.000	—	8.1	—	—	1380	—	—	—	si	l	NAPIER & NAPIER, 1967
<i>Colobus polykomos</i>	1.000	—	—	—	—	1380	—	—	—	si	l	NAPIER & NAPIER, 1967
<i>Colobus guereza</i>	1.000	—	9.2	—	390	1650	597.0	380	n	sip	l	NAPIER & NAPIER, 1967
<i>Hylobatidae</i>												
<i>Hylobates lar</i>	1.000	—	5.5	224	724	2188	410.5	969	n	m	f	NAPIER & NAPIER, 1967
<i>Hylobates agilis</i>	1.000	—	5.5	—	724	—	—	—	n	m	f	NAPIER & NAPIER, 1967
<i>Hylobates hooleck</i>	1.000	—	5.5	—	724	2188	—	—	n	m	f	NAPIER & NAPIER, 1967
<i>Hylobates concolor</i>	1.000	—	5.5	—	724	2570	—	—	n	m	f	NAPIER & NAPIER, 1967
<i>Hylobates klossi</i>	1.000	—	5.5	—	724	3311	—	—	n	m	f	NAPIER & NAPIER, 1967
<i>Hylobates moloch</i>	1.000	—	5.5	—	724	—	—	—	n	m	f	NAPIER & NAPIER, 1967
<i>Pongidae</i>												
<i>Gorilla gorilla</i>	Report	—	93.1	257	550	2951	2110.0	1460	n	si	l	KIRCHSHOFER et al., 1968; ROSEN, 1972
<i>Pongo pygmaeus</i>	1.064	481	35.5	257	912	2754	1728.0	1025	n	si	f	GUILLOUD, 1969; PEACOCK & RODGERS, 1959
<i>Pan troglodytes</i>	1.106	162	37.0	234	1413	4365	1756.0	1825	n	p	f	BOND & BLOCK, 1982
<i>Hominidae</i>												
<i>Homo sapiens</i>	1.024	—	55.0	269	912	5888	3300.0	1440	y	—	—	STRANDSKOV, 1945

1) Report: Multiple births reported in this species but the sample size was not provided in the original study;

2) y: yes; n: no; 3) s: solitary; m: monogamous; p: polygamous; si: single male; 4) f: frugivore; l: folivore.

assume that there is negligible error in the measurements of the independent variables (SOKAL & ROHLF, 1981). However, the importance of this source of error decreases when the independent variables cover a broad range of values (PETERS, 1983), as is the case with the majority of our variables with the exception of litter size.

Analysis of variance was used to identify differences in litter size between species with different social organizations, with or without paternal care, and with different diets. However, certain types of diets have been shown to be limited to certain sizes of primates; e.g., small bodied species cannot obtain the energy required to maintain their metabolism by eating energy poor, often toxic, leaves (KAY, 1984). Thus, multiple regression analyses were used to examine the effect of diet on litter size, with typical litter size as the dependent variable and body size and the percentage of the diet which one of the three diet categories (leaves, fruit, insects) comprised, as the independent variables. In these analyses the partial correlation coefficients were examined. The percentage of the diet was arcsin transformed (SOKAL & ROHLF, 1981).

RESULTS

BASIC PATTERNS

Many of the life history parameters examined showed considerable variation across the primate order (Table 1). The mode for typical litter size was one, however it ranged from 1.0 to 2.5, and a considerable number of species were found to regularly have multiple births. The occurrence of multiple births was not evenly distributed through the order ($F = 28.8$, $p < 0.001$ analyzed at the Family level). Typical litter size was largest in the prosimians (Strepsirhini, mean = 1.40) and in the New World Callitrichidae (mean = 2.02). For the remainder of the Haplorhini, excluding the Callitrichidae, the average typical litter size was 1.02. Similarly, the other life history variables exhibited considerable variation across the order (Table 2).

The litter size for species exhibiting paternal care (mean = 1.783) was significantly higher than that of species with no paternal care (mean = 1.239; $t = 3.28$, $p = 0.002$). The potential energetic burden on the female of raising young is probably proportional to the number of offspring. Thus, it may be advantageous for the male to provide care for the young to increase their probability of survival (TERBORGH & WILSON GOLDIZEN, 1985). Species with monogamous or solitary social organizations had a higher litter size than species with a multimale-

Table 2. The mean and range of typical litter size, life history parameters, and body size for a sample of primate species. Also an indication of whether these variables differed between the categorical variables considered.

	Mean	Range	Paternal care	Mating system	Taxon	Diet
Typical litter size	1.287	1-2.5	*	*	*	*
Gestation (day)	165	60-269	—	*	*	—
Weaning age (day)	346	25-1413	—	*	*	*
Interbirth interval (day)	555	152-1825	—	*	*	*
Neonate weight (g)	397	6.6-3300	—	*	*	*
Age at maturity (day)	1469	257-5888	—	*	*	*
Body weight (kg)	7.6	0.2-95.1	—	*	*	*

*The variable differed between the categories; —: the difference was non-significant.

Table 3. Product moment correlations of a series of life history variables and body size for a sample of primate species.

	Litter size	Body weight	Gestation period	Weaning age	Interbirth interval	Neonate weight	Age at maturity
Litter size	—	-0.63*	-0.45*	-0.71*	-0.65*	-0.66*	-0.55*
Body weight		—	0.52*	0.81*	0.85*	0.96*	0.88*
Gestation period			—	0.59*	0.74*	0.46*	0.31
Weaning age				—	0.91*	0.88*	0.83*
Interbirth interval					—	0.83*	0.81*
Neonate weight						—	0.95*
Age at maturity							—

*The relationship has a $p < 0.05$. Not all sample sizes are the same because of missing values for some variables.

multifemale social organization ($F = 2.98$, $p = 0.0205$; Scheffe < 0.10). The species that were solitary were all prosimians. The larger litter sizes found in these animals may represent the maintenance of an ancestral trait (LEUTENEGGER, 1979). Although these strategies represent the trend across the order, monogamous primates do not all have large litters (e.g., *Aotus*, *Callicebus*, *Indri*, *Tarsius*, *Hylobates*). However, the monogamous callitrichids do have large litters. Similarly, primates with male paternal care do not have large litters, only callitrichids do. Apparently, for callitrichids it is a package deal, large litters are associated with small body size, monogamy (or polyandry), and male paternal care. Other primates may have one or more of these components in association with increased litter size, but they are not so closely associated as in the Callitrichidae.

The food habits of the primates also had an impact on litter size. The litter size of insectivores was significantly larger than that of either folivores or frugivores ($F = 6.99$, $p = 0.002$; Scheffe < 0.05).

ALLOMETRIC RELATIONSHIPS

A number of previous studies have demonstrated strong relationships between body size and life history parameters (WESTERN, 1979; EISENBERG, 1981; HARVEY & CLUTTON-BROCK, 1985). Body weight in primates covers a broad range, from *Tarsius syrichta* weighing 0.14 kg to the gorilla, *Gorilla gorilla*, which weighs 95.1 kg. The correlation matrix for the logarithmic transformed life history variables and body weight are presented in Table 3. Two major patterns are evident in this table. First, the life history parameters are correlated with each other and with body size, with the exception that the length of the gestation period is not related to age at maturity. Secondly, species who have large litters, tend to be small primates which have short gestation periods, produce small infants, which are weaned quickly, and then mature at a young age. Following the birth of a litter, females from small sized species are capable of quickly becoming pregnant and producing a second litter.

INFLUENCE OF DIET ON LITTER SIZE

We have just shown that litter size differs between species categorized as having different diets (Table 2), and that litter size is related to body size (Table 3). However, diet also varies systematically with body size ($F = 6.99$, $p = 0.002$, tested between diet categories, fruit, leaves, and insects). As a result it is difficult to separate the effects of body weight and diet on litter size. However, to examine this question we performed multiple regression analyses

with typical litter size as the dependent variable and body size and the proportion of the diet which one of the food types comprised as independent variables. Subsequently, we examined the partial correlation coefficients. This analysis can be interpreted as the correlation between litter size and the proportion of the diet composed of a certain food type, when the linear effects of body size have been removed. When the percentage of leaves ($r = -0.246$, $p = 0.358$) or fruit ($r = 0.039$, $p = 0.882$) changed in primate diets, there was no change in litter size when the effect of body size was removed. However, when there was a change in the dependency on insects, there was a tendency for litter size to also change, when body size was held constant ($r = 0.701$, $p = 0.079$).

DISCUSSION

We have demonstrated that, in general, primates which have large litters, are small, have short gestation periods, and give birth to small neonates, which they wean rapidly and mature quickly. Similar observations have been made for primates and other mammals (HARVEY & CLUTTON-BROCK, 1985; LEUTENEGGER, 1979; EISENBERG, 1981; TUOMI, 1980). The most direct energetic link between these findings and diet concerns the metabolic rates of these primates. Animals expend energy in activities such as maintenance and reproduction. Many authors have stressed that metabolic rates are set by body size and diet and may strongly influence a number of life history parameters (MCNAB, 1969, 1980, 1983, 1986; HENNEMAN, 1983; TUOMI, 1980). Thus, animals attempt to have the highest possible metabolism as can be maintained by the quality and quantity of the foods they eat. In this fashion food habits determine the amount of energy that can be allocated to reproduction. MCNAB (1969) documented that the metabolic rates of bat species which were frugivorous, nectivorous, or carnivorous were higher than those of insectivorous species. Similar relationships between diet and basal metabolic rates have subsequently been demonstrated for members of other mammals (EISENBERG, 1981; MCNAB, 1980, 1986; RASMUSSEN & IZARD, 1988). Low metabolic rates are thought to be associated with a diet of nutritionally poor or toxic foods, or foods exhibiting great seasonal fluctuations in abundance (MCNAB, 1983). Insectivores are faced with a resource that can be both highly toxic and very seasonal. For instance, some tropical insect communities live in habitats which experience long severe dry seasons, where little if any rain falls for six to seven months of the year. In such situations there are marked changes in abundance of insects between seasons (JANZEN & SCHOENER, 1968; JANZEN, 1973, 1987). Many insects have elaborate chemical defences to deter predation. Some insect species store toxins that may compose up to 20% of their body weight (SCHMIDT, 1979). Folivores are also faced with a resource that can be very toxic. Leaves frequently contain toxic chemicals which may serve to deter insect or vertebrate damage (JANZEN, 1978). However, the effect of many of these toxins on specific vertebrates is often unclear. For example, black colobus consume large quantities of *Rauvolfia vomitoria* leaves which contain alkaloids toxic to man (MCKEY et al., 1981). In contrast, many tree species produce attractive fruits which are designed to encourage their consumption by certain vertebrates, once they are ripe, and thereby ensure the dispersal of the seeds contained in the fruit (JANZEN, 1978). Depending on the type of forest, the availability of fruit may be relatively constant or may exhibit marked seasonal fluctuations (CHAPMAN & CHAPMAN, in prep). Such seasonality can have strong influences on the timing of reproductive events (RASMUSSEN, 1985) or the structuring of primate populations (MILTON, 1982).

Unfortunately, the data on basal metabolic rate in primates are extremely limited (MULLER

et al., 1983; HILDWEIN & GOFFART, 1975). McNAB (1978) suggested that arboreal mammals which feed on leaves should have low basal metabolic rates. To our knowledge, this prediction has only been examined twice with primate species. MULLER et al. (1983) found that captive colobus (*Colobus guereza*), which are considered to be folivores, had basal metabolic rates that were 85% of the value predicted from body mass. In contrast, MILTON et al. (1979) measured the metabolic rates of howler monkeys (*Alouatta palliata*), the most folivorous New World monkey, and rejected McNAB's prediction. These authors found that the metabolic rate of howlers was 5% higher than that predicted from body size. These conflicting findings may result from the fact that both *Colobus guereza* and *Alouatta palliata* have mixed leaf-fruit diets, and the prediction of how basal metabolic rate is affected by mixed diets is not clear. For instance, a high metabolic rate could result from a mixed diet if leaves are eaten as nutritional supplements and energetic requirements are met by eating fruit. On the other hand, a low metabolic rate may result if leaves are eaten seasonally when fruit is unavailable and metabolism is set by the worst conditions (McNAB, 1986).

Our results suggest that when the effect of body size is statistically removed, litter size increases as the proportion of insects in the diet increases. This was not initially expected since insects are often toxic and their abundance fluctuates seasonally. We suggest that this unexpected result stems from the fact that the majority of the species classified as insectivores really have mixed insect-fruit diets. By exploiting fruit resources these animals may find adequate food resources when insects are not abundant. Also, they may be able to avoid problems associated with the toxins found in insects by switching to eating fruit when toxins derived from eating insects in a day build up to a potentially hazardous level. Also, in many environments the peak abundance of insects coincides closely with the onset of the rains and is fairly predictable. Thus, it may be possible for animals to time the periods of peak energetic demands on producing females, so that they correspond with the time when food resources are most abundant. RASMUSSEN (1985) has shown that a similar scenario does occur with frugivorous lemurs. The timing of births in 11 species of lemurs coincides with the end of the dry season.

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