SHORT COMMUNICATION

Dietary Variability in Primate Populations

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ABSTRACT. Dietary variability among primates is examined based on a review of 46 long-term studies of wild populations. Results suggest that primates do not consistently combine the same kinds of foods in their diets, as many past categorizations would suggest, but rather, that they often switch between diet categories (e.g., fruit, insects, etc.). Dietary variability, as quantified in our review, did not appear to be constrained by phylogeny or to differ between species placed in different diet categories (e.g., frugivores, insectivores, etc.). In addition, dietary variability was not related to body size, habitat productivity, seasonality, population density, or the number of sympatric primate species.

Key Words: Diet; Dietary variability; Foraging; Food.

INTRODUCTION

A growing number of field studies have documented marked temporal variability in the diets of many animal species (CLUTTON-BROCK, 1977; ROTENBERRY, 1980; CHAPMAN, 1988). Certainly, it is recognized that there are functional-morphological constraints that limit the extent of dietary variability, however, even species classically considered as specialists have been shown to have very flexible feeding patterns (LIEM, 1984; CHAPMAN, 1988). Such dietary flexibility has proven difficult to incorporate into many of the existing views of how feeding strategies develop and are maintained and has frequently been ignored (WIENS, 1977; WIENS & ROTENBERRY, 1979; LIEM, 1984; RICHARD, 1985).

In this paper, we document the temporal dietary variability observed in 46 long-term studies of primates. From this description we ask: Do primates consistently combine the same kinds of foods in their diet, or do they switch between diet categories? Secondly, we attempt to provide an initial empirical examination of the patterns underlying this variability. We consider seven factors that may contribute to differences in temporal dietary variability in primates: phylogeny, diet category, habitat productivity, seasonality, body size, population density, and the number of sympatric primate species.

METHODS

We reviewed the literature for studies which reported the diet of wild unprovisioned populations of primates on a monthly basis. For each month of the study, the diets were categoriezd by the percentage of the diet composed of major food types (fruit, leaves, flowers, insects, and gum). Due to inconsistencies between studies in classifying the ripeness or maturity of plant parts, the foraging efforts devoted to all stages of maturity of a single plant

part were combined. Monthly diets were classified as frugivorous, folivorous, etc., if 50%
or more of the diet was comprised of one food category. If all diet categories were less than
50% in a given month, the diet was classified as "mixed." We estimated the number of month-
ly switches in diet as the total number of times diet changed between months from one
category to another (including switches to and from mixed diets) expressed as a percentage
of the total number of potential monthly switches. We estimated the number of gross month-
ly switches in diet as the total number of times the diet switched from one food category to
another (not including switches to and from mixed diets) expressed as a percentage of the
total number of potential switches. The greatest magnitude of dietary change was estimated
for each study population as the greatest absolute difference in the percentage of use of any
food category.

A weighted measure of dietary variability was calculated as the between-month variance
in the use of a particular food item, multiplied by the percentage of the total diet comprised
of that food item. The sum of these values for all components of the diet was used as a meas-
ure of temporal dietary variability. Weighting the variance by the amount a food item was
used decreased the potential bias produced by variance in infrequently used items. For the
empirical examination of dietary variability we considered seven independent variables:
phylogentic group(Family), dietary classification, body size, habitat productivity, seasonality,
population density, and the number of sympatric primate species. We used the taxonomic and
dietary categorization by RICHARD (1985), and not the one outlined for the calculation of
monthly switches, so that it was somewhat independent of our analysis. When possible,
estimates of the remaining variables were obtained from the same primary sources used to
calculate the temporal dietary variability. However, a number of these studies did not
provide all of the values for the four remaining independent variables. Under such circum-
stances, estimates of these values were calculated from secondary sources. Body mass was
calculated from a number of sources by averaging the adult weights provided for males and
females (CLUTTON-BROCK & HARVEY, 1977; HARCOURT et al., 1981; RICHARD, 1985; HARVEY
& CLUTTON-BROCK, 1985; LEFEBVRE, 1985). Estimates of population density were obtained
from either the original studies, subsequent publications by the same authors, or from
CLUTTON-BROCK and HARVEY (1977). Annual rainfall was determined from either the original
studies, subsequent publications by the same authors or by different authors studying in the
same area, or from WERNSTEADT (1970). Annual rainfall has been shown to reflect habitat
productivity (MURPHY & LUGO, 1986; HARTSHORN, 1983). Net primary productivity of dry
forest averages 50–75% of that of wet forest and the total plant biomass in dry forest is
estmated to be approximately 72% less than that of wet forest (MURPHY & LUGO, 1986).
The seasonal nature of the habitats inhabited by each of the study populations was repre-
sented as the Coefficient of Variation (CV) of the monthly rainfall values. The coefficient of
variation is calculated as the standard deviation expressed as a percentage of the mean and
is thus independent of the magnitude of measurements (SOKAL & ROHLF, 1981). This allows
us to compare the extent of seasonal change in rainfall between areas which experience
different annual rainfall.

We estimated the relationship between temporal dietary variability and the independent
variables with the simple regression model: Log dietary variability = log $a+b$ log inde-
pendent variable. Logarithmic transformations of both axis were used to fit a linear model.

This study produced a data set of 46 studies which provided data on monthly dietary
variability. This compilation contains a number of potential shortcomings typically as-

sociated with such surveys. First, for a number of the studies dietary composition was ex-
pressed graphically in the original publications, so the actual numerical value used here was
estimated from the graphs provided. Secondly, since studies have not been divided equally
among all species in the primate order, certain groups (e.g., terrestrial foragers) are over-
represented relative to other groups (e.g., arboreal insectivores). Third, the majority of the
studies categorized their study species' diet by employing observational techniques and re-
ported the proportion of the total observation time spent eating different types of foods.
Other studies determined diet based on stomach content data, or estimates of the weight of
foods ingested. All techniques were considered to be equal.

RESULTS AND DISCUSSION

In reviewing these field studies we encountered a number of examples of primate popula-
tions which exhibited large shifts in diet between months (Table 1). For example, MAC-
KINNON (1974, 1977) described the diet of the orangutan (*Pongo pygmaeus*) in Sumatra. In
one month, the orangutans were primarily frugivorous, spending 90 % of their total feeding
time eating fruit, and only 5 % eating leaves, and 5 % eating insects. In another month this
population was primarily folivorous, spending 75 % of their feeding time eating leaves, 15 %
eating bark, and only 10 % eating fruit. The spider monkey (*Ateles geoffroyi*) is typically
considered a fruit specialist (KLEIN & KLEIN, 1977). CHAPMAN (1988) described that in one
month the spider monkey community studied in Santa Rosa National Park, Costa Rica
ate only fruit. However, in another month the same community ate primarily leaves (86.3 %
of their feeding time) and ate little fruit (13.7 %). In yet another month, insects were a major
component of their diet (30.2 % of their feeding time). In the studies examined we found a
number of similar examples of extreme shifts in diet (e.g., HARRISON, 1984; HLADIK, 1977a).
The greatest absolute difference in the use of a food category averaged 54.1 % among the
study populations (range 20–100 %, SD = 20.8). The categorization of the type of diet was
only consistent over the entire study period in 17.4 % of the investigations, while 82.6 % of
the populations exhibited two or more different types of diets in different months. On average,
31.7 % (range 0–100 %, SD = 27.1) of the consecutive months involved switches in diet to
a mixed diet or a different diet category, and 15.3 % of the consecutive months involved
switches between different gross diet categories (e.g., frugivore to folivore, range 0–100 %,
SD = 22.2).

We attempted to identify possible factors which would explain the temporal variation in
primate diets. There was no evidence to indicate that the temporal variability of primate
diets was set by phylogenetic constraints, as dietary variability did not differ between families
($F = 0.961, p = 0.453$). Similarly, we found no evidence to indicate that there was differences
between the dietary variability of species categorized as having different types of diets (e.g.,
frugivore, insectivore, $F = 0.005, p = 0.995$).

An obvious hypothesis that requires examination is that the magnitude of the variability
in diet is a consequence of the primates tracking the seasonal changes in the environment.
In contrast to what might be expected there was no relationship between the seasonality of
the habitat and the degree of dietary variability exhibited by the populations ($r = 0.099$,
$p > 0.05$). It may be that many of the food resources used by the primates do not closely
follow the rainfall regime of the environment (MILTON et al., 1982; CHAPMAN, 1988).

WHEATLEY (1982) suggested that body size might constrain the types of foods that are

Table 1. The dietary variability calculated for 46 studies and the corresponding independent variables used in the regression analyses.

Species	Reference	Body size (kg)	Rainfall (mm)	No. of sympatric	Population density[1]	Dietary variability[2]
Indri indri	POLLOCK, 1977	12.5	1705	7	12.5	2000
Indri indri	POLLOCK, 1977	12.5	1705	7	12.5	3221
Propithecus verreauxi	RICHARD, 1977, 1978	3.6	1619	7	—	3855
Propithecus verreauxi	RICHARD, 1977, 1978	3.6	1619	7	—	1532
Propithecus verreauxi	RICHARD, 1977, 1978	3.6	630	7	—	6440
Propithecus verreauxi	RICHARD, 1977, 1978	3.6	630	7	103.0	5376
Cebus capucinus	CHAPMAN, 1988	2.6	1600	3	—	7156
Alouatta palliata	CHAPMAN, 1988	7.1	1600	3	—	5223
Alouatta palliata	ESTRADA, 1984	5.7	4500	0	22.1	10764
Alouatta palliata	MILTON, 1980	5.7	2730	2	—	3094
Ateles belzebuth	KLEIN & KLEIN, 1977	6.0	—	—	13.5	166
Ateles geoffroyi	CHAPMAN, 1988	6.0	1600	3	—	5365
Brachyteles arachnoides	MILTON, 1984	5.8	1263	4	28.4	1197
Colobus badius	MARSH, 1981	8.8	550	5	186.5	2853
Colobus badius	CLUTTON-BROCK, 1975	8.8	1400	7	186.5	1340
Presbytis senex	HLADIK, 1977a	8.2	1700	4	154.0	3140
Presbytis senex	HLADIK, 1977a	8.2	1700	4	154.0	3517
Presbytis entellus	OPPENHEIMER, 1978	12.8	—	2	57.0	725
Presbytis entellus	HLADIK, 1977a	12.8	1700	4	57.0	3362
Presbytis obscura	MACKINNON & MACKINNON, 1978, 1980	6.2	1982	6	31.0	4346
Presbytis melalophos	MACKINNON & MACKINNON, 1978, 1980	6.1	1982	6	74.0	3690
Cercocebus albigena	FREELAND, 1978	7.7	1475	7	2.7	1103
Cercopithecus mitis	RUDRAN, 1978	4.5	1475	7	42.0	2711
Cercopithecus mitis	RUDRAN, 1978	4.5	1475	7	42.0	2342
Cercopithecus aethiops	HARRISON, 1984	4.1	954	3	14.3	3646
Cercopithecus aethiops	KAVANAGH, 1978	4.1	1450	—	112.0	4418
Cercopithecus aethiops	KAVANAGH, 1978	4.1	650	—	112.0	7318
Cercopithecus nictitans	GAUTIER-HION, 1980	5.4	1350	15	30.0	4302
Cercopithecus cephus	GAUTIER-HION, 1980	3.5	1350	15	25.0	514
Cercopithecus pogonias	GAUTIER-HION, 1980	3.8	1350	15	23.0	246

(continued)

Table 1. (continued)

Species	Reference	Body size (kg)	Rainfall (mm)	No. of sympatric	Population density[1]	Dietary variability[2]
Macaca fascicularis	MacKinnon & MacKinnon, 1978, 1980	5.0	1982	6	39.0	2385
Macaca fascicularis	Aldrich-Blake, 1980	4.6	1982	6	50.0	6026
Macaca fascicularis	Wheatley, 1982	5.0	—	—	50.0	12098
Macaca fuscata	Koganezawa, 1975	—	3000	0	10.0	2838
Macaca fuscata	Maruhashi, 1980	10.5	—	0	30.0	833
Macaca fuscata	Iwamoto, 1982	10.5	—	0	—	3479
Mandrillus sphinx	Hoshino, 1986	19.0	2129	9	—	912
Papio cynocephalus	Post, 1982	17.1	230	1	4.0	1608
Hylobates syndactylus	MacKinnon & MacKinnon, 1978, 1980	10.7	1982	6	4.5	1095
Hylobates syndactylus	Chivers, 1977	10.7	1982	6	3.8	2059
Hylobates lar	MacKinnon & MacKinnon, 1978, 1980	5.5	1982	6	6.1	947
Pongo pygmaeus	Rijksen, 1978	53.0	3000	5	1.0	2260
Pongo pygmaeus	Rodman, 1977	53.0	2177	8	2.0	4132
Pongo pygmaeus	MacKinnon, 1974, 1977	53.0	1328	6	2.0	6134
Pongo pygmaeus	MacKinnon, 1974, 1977	53.0	4860	6	2.0	772
Pan troglodytes	Hladik, 1977b	45.0	1700	15	2.5	917

1) Individuals/km²; 2) calculations of dietary variability outlined in text.

suitable for a primate to eat. For instance, small primates may not have the option of eating leaves, since leaves tend to be high in fiber and low in energy, and thus can not meet their metabolic needs. In the data set collected here, temporal variability in diet was not related to body size ($r = -0.198$, $p = 0.193$). One might expect that if food abundance was low, animals might be forced to be more flexible in their feeding strategy, switching to alternative foods during months when preferred food types were scarce. In the studies examined here, there was no relationship between rainfall, our measure of habitat productivity, and dietary variability ($r = -0.080$, $p = 0.620$). Similarly, neither the population density of the species ($r = -0.256$, $p = 0.126$), nor the number of potential sympatric primate competitors ($r = -0.280$, $p = 0.089$), influenced temporal dietary variability.

Our review of primate diets on a monthly temporal scale suggests that primates do not always consistently include the same kinds of foods in their diets. Instead, primate populations frequently switch between diet categories. This raises a number of questions; such as what conditions favour dietary flexibility, what are the preferred diets of the populations, and what are the consequences of dietary flexibility in terms of morphological specializations and learned feeding strategies?

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