

Goro Hanya · Colin A. Chapman

Linking feeding ecology and population abundance: a review of food resource limitation on primates

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Abstract We review studies that consider how food affects primate population abundance. In order to explain spatial variation in primate abundance, various correlates that parameterize quality and quantity of food in the habitat have been examined. We propose two hypotheses concerning how resource availability and its seasonality determine animal abundance. When the quality of fallback foods (foods eaten during the scarcity of preferred foods) is too low to satisfy nutritional requirement, total annual food quantity should determine population size, but this relationship can be modified by the quality or the quantity of fallback foods. This mechanism has been established for Japanese macaques and sportive lemurs that survive lean seasons by fat storage or extremely low metabolism. Second, when fallback food quality is high enough to satisfy nutritional requirement but quantity is limited, quantity of fallback food should be a limiting factor of animal abundance. This is supported by the correlation between fig density, which is a high-quality fallback food, and gibbon and orangutan abundance. For a direct test of these hypotheses, we need more research that determines both the quality of food that animals require to satisfy their nutritional requirement and the quantity of food production. Leaves are often regarded as superabundant, but this assumption needs careful examination.

Keywords Bottleneck · Population density · Fallback food · Nutrition · Seasonality

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G. Hanya (✉)
Primate Research Institute, Kyoto University, Inuyama,
Aichi 484-8506, Japan
E-mail: hanya@pri.kyoto-u.ac.jp
Tel.: +81-568-630542
Fax: +81-568-630564

C. A. Chapman
Department of Anthropology and McGill School of Environment,
McGill University, Montreal, Canada

Introduction

One of the primary goals in animal ecology is to reveal how environmental factors determine animal abundance. This topic has recently taken on a heightened significance as many animal populations are declining under increasing human pressure, and understanding the factors affecting their populations is necessary for conservation and management. Although various factors, such as climate (Iwamoto and Dunbar 1983; Barton and Zalewski 2007), predation (Peek 1980; Isbell 1990), and stress or disease (Milton 1996; Harvell et al. 1999; Berger et al. 2001; Chapman et al. 2006), can affect animal abundance, the effect of food has typically been considered of paramount importance.

Primates are ideal subjects to study both animal abundance and feeding ecology. Since they are diurnal and standardized census methods are established (National Research Council 1981; Whitesides et al. 1988), comparable data on abundance are available for many species, often from a number of populations. Furthermore, since most primates are diurnal and have large body sizes, detailed behavioral observation is feasible and there have been many studies of their feeding ecology (Clutton-Brock 1977; Hohmann et al. 2006). Primates are generalist consumers and are dependent on a diverse array of resources, such as leaves, fruits/seeds, flowers, gum/sap, barks, and insects (Kay 1984). These food resources vary in their nutritional and distributional properties, thus comparative primate research can clarify various mechanisms concerning how food affects abundance.

For primary consumers, the simplest mechanism of food resource (hereafter resource) limitation suggests that habitats can sustain an increasing number of animals up to the point where the total consumption by the population equals the production of food by the plant community. Coelho et al. (1976) concluded that primates are unlikely to be limited by resource, based on 2 months of behavioral observations of two species of

primates (*Alouatta pigra* and *Ateles geoffroyi*). They estimated the primates' energy requirements based on their activity budget, and calculated the total energy requirement of the populations of the two species to be $13,640 \text{ kcal km}^{-2} \text{ day}^{-1}$. This was lower than the pulp production of only one species of their main food (*Brosimum alicastrum*; $716,000 \text{ kcal km}^{-2} \text{ day}^{-1}$). These calculations were used to suggest that this one fruiting tree species could sustain $1,700 \text{ individuals km}^{-2}$ of primates, which is implausibly high. This conclusion was criticized by Cant (1980) who pointed out that (1) food availability changes both seasonally and supra-annually and one cannot conclude that animals are free from resource limitation with only 2 months of data; and (2) food quality was not considered. He argued that even if resources are super-abundant in most seasons, animals experience "ecological crunches" when resources are in short supply and their populations can be limited by these periods. In the three decades since the publication of these papers a great deal of data on primate feeding ecology and population abundance has accumulated that can be matched to data on forest productivity and food quality, thus now is the time to revisit Cant's (1980) question: "What limits primates?"

In this paper, we review studies on primate abundance at the population level and propose hypotheses concerning the mechanism of resource limitation under seasonally fluctuating conditions. Subsequently, we critically evaluate what information is necessary to test these hypotheses and discuss future research directions.

Approaches to study resource limitation at the population level

Approaches to study resource limitation at the population level can be categorized as dynamic or static. Animal populations often fluctuate in size over time and the dynamic approach examines the environmental factors that correlate with changes in population size between one period and the next. One can also manipulate environmental factors experimentally and observe the numerical response to it over time. The static approach compares the natural variation in animal abundance among different ecological settings over space and examines which environmental factors correspond to the differences. Although the dynamic approach can tell the immediate cause of population changes (i.e., one can identify what environmental factor changed just prior to the population change), it does not necessarily reveal why the abundance in one population is higher than the others, or which difference far exceeds the degree of variability of one population.

Primates have been studied largely using the static approach. If animals change their number rapidly, as seen with rodent population cycles or ungulate migrations (Kaji et al. 1988; Wolff 1996), the static approach may not be useful. Although many primates change their

number over time, the scale over a year or the duration of most studies is much smaller than that of many other mammals (Hanya 2009). Experiment on resource limitation in primates is usually difficult because both spatial and time scales are too large for researchers to mimic. For example, provisioning or food removal experiments with rodents and pigeons were conducted at a scale of 1.7–3.5 ha and 1.8 ha, respectively (Adler 1998; Moegenburg and Levey 2003), which is much smaller than a home range of a single group of most diurnal primates ($5 \text{ ha}–24 \text{ km}^2$) (Mitani and Rodman 1979). Large-scale provisioning of free-ranging primates is conducted mainly for tourism or for management of introduced colonies. Although their effect on population changes has been confirmed (Mori 1979a; Sugiyama and Ohsawa 1982; Watanabe et al. 1992), food abundance has been manipulated for management, not for research on resource limitation. These studies took several decades to observe population changes, which is much longer than the response observed in rodent or pigeon studies ($< 1 \text{ year}$) (Adler 1998; Moegenburg and Levey 2003). Therefore, although data on provisioned populations directly tests whether primates are food limited, studies based on the comparison of natural populations are indispensable in exploring natural mechanism of resource limitation.

Previous studies on primate abundance

Density has been estimated for many primate populations, but only a small proportion of these studies have examined the environmental factors affecting variation among populations (static) or within a population over time (dynamic). Of those that do speculate on environmental drivers of density, the majority only make qualitative comparisons among vegetation types or study sites (Freese et al. 1982; Weisenseel et al. 1993; White 1994; Yoshihiro et al. 1999; Mathews and Matthews 2002; McConkey and Chivers 2004). Other studies examined vegetational correlates of primate abundance, such as tree density, basal area, shrub cover, and tree species diversity (Butynski 1990; Chapman and Chapman 1999; Balcomb et al. 2000; Wiczowski 2004; Worman and Chapman 2006; Hamard et al. 2010). While this is useful information regarding habitat preference, their ability to determine determinants of animal abundance is limited. For example, vegetation structure evaluates food quantity only in the most general way. Such studies do not evaluate the seasonal changes in food availability, the importance of fallback foods (foods that are eaten during the scarcity of preferred foods), or the type of resource limiting the animal.

Such studies examining vegetational correlates of primate abundance can be used in meta-analyses; however, since it is usually difficult to collect data on both primate and habitat variables in a comparable fashion, primate abundance is usually correlated with indirect

measure of forest productivity, such as rainfall or forest type. Forest type can explain the difference in primate abundance in a rudimentary fashion (Ganzhorn et al. 1999; Peres 1999; Peres and Dolman 2000), but climate usually cannot (Chapman and Balcomb 1998; Gupta and Chivers 1999; van Schaik et al. 2005). However, using direct measures of food abundance, such as fruit fall, significant results are found (Stevenson 2001).

Studies on folivorous primates are exceptional because a single habitat parameter is known to correlate with their biomass. Milton (1979) proposed that the protein-to-fiber ratio of leaves was an important criterion for leaf selection by primates, whereby leaves with higher protein and low fiber ratios were selected. This preference has been demonstrated for a large number of primates (Chapman and Chapman 2002; Ganzhorn 2002; Hanya and Bernard 2012). Fiber is often considered an antifeedant because it requires fermentation by symbiotic microbes and the cellulose and hemicellulose components of the fiber is typically only partially digestible by folivores (McNab 2002). Furthermore, nitrogen is the limiting nutrient in many terrestrial ecosystems and since it is found primarily in protein, herbivores should compensate for this limitation by choosing high protein foods (White 1993). These important ideas proposed by Milton have been applied at the population level by others (McKey et al. 1981; Waterman et al. 1988; Oates et al. 1990; Davies 1994; Chapman et al. 2002). For example, Waterman et al. (1988) proposed that the weighted contributions of the protein-to-fiber ratios of the mature leaves of the most abundant trees in a particular area could predict the biomass of folivorous colobines. This index of dietary quality has been applied successfully to predict the biomass of folivorous monkeys at local (Chapman et al. 2002; Ganzhorn 2002) and regional (Waterman et al. 1988; Oates et al. 1990; Ganzhorn 1995; Chapman et al. 2004; Fashing et al. 2007) scales. Davies (1994) suggested that the year-round availability of digestible mature leaves with high protein-to-fiber ratios, which are used by colobus species when other, more preferred foods are unavailable, serves to limit the size of colobine populations (i.e., high protein-to-fiber mature leaves are important fallback foods). However, some colobines rarely eat mature leaves since young leaves are always available, yet their biomass can still be predicted by this index (Chapman et al. 2004). Thus, the protein-to fiber ratio of mature leaves in an area may be correlated with the protein-to-fiber ratio of foods in general. This is supported by the fact that, in a sample of leaves from Kibale National Park, Uganda, it was documented that the protein-to-fiber ratio of mature and young leaves were strongly correlated ($r = 0.837$, $P < 0.001$; Chapman et al. 2004). Thus, measuring the protein-to-fiber ratio of mature leaves may be useful because it correlates with the general availability of high-protein, low-fiber foods, and thus is a useful index of habitat quality for colobus monkeys. The mechanism on how this parameter affects primate abundance remains

unclear as this ratio may correlate with other leaf constituents that really drive the relationship (Chapman et al. 2002). For example, Wallis et al. (2012) suggests that the available nitrogen concentration of leaves, which covers both fiber and tannin content, is a real influencing factor on folivore leaf choice. More research is needed to determine why the protein-to-fiber index predicts folivore biomass.

Studies of frugivorous primates similarly indicate the importance of food resources, but suggest that, in addition to food quantity, seasonality is also critical in regulating primate populations. For example, Hanya et al. (2004) examined the effects of both total annual fruit production and the degree of seasonality in fruiting (number of months when no fruit is available) on the density of a Japanese macaque (*Macaca fuscata*) population in Yakushima. They indicated that total annual fruit production affected density more than seasonality. Japanese macaques survive the lean season (winter) not only by consuming the food available during that period (mature leaves) but also by using the fat accumulated by eating fruits and seeds during the period of high fruit availability (Hanya 2004). Therefore, in an altitudinal zone where fruit production is low, macaques need to range over a large area to accumulate sufficient fat stores and, as a result, density is low. Hanya et al. (2006) tested this idea through a meta-analysis across the species range and documented that density was consistently higher in evergreen as compared to deciduous habitats (Takasaki 1981a, b; Hanya et al. 2006). In winter, Japanese macaques rely on mature leaves in evergreen forest and on buds and barks in deciduous forest (Iwamoto 1982; Nakagawa 1989a; Hill 1997; Tsuji et al. 2008); thus, food deficiency in winter is more severe in deciduous than in evergreen forests (Nakagawa et al. 1996). Therefore, even if the total annual fruit production is constant, macaques in deciduous forest need to range over a larger area before winter to accumulate sufficient fat stores to survive the winter. In fact, home range size tends to be the largest in summer or autumn, not in winter (Hanya et al. 2006). The combined influence of the seasonality and total annual food abundance on primates is supported by the meta-analysis of 16 frugivorous primate communities in the Old and New Worlds (Hanya et al. 2011). In this study, the best-fit model predicting primate abundance included both total annual fruit fall (+) and its seasonality (–, assessed by coefficient of variation of monthly fruit fall). This result suggests that, when food availability varies seasonally, primates have access to less food or lower-quality food during the food-scarce season than when food is equally available throughout the year.

Coping with seasonality: two hypotheses on resource limitation

Primates respond primarily to seasonal variation of food availability by shifting their diet (van Schaik et al. 1993).

Recent studies on primate feeding ecology have categorized foods into preferred and fallback foods (Lambert 2007; Marshall and Wrangham 2007; Marshall et al. 2009). Preferred food is one that is of high quality and is eaten more than the relative abundance in the habitat. Availability of preferred foods is usually limited and its seasonal consumption correlates with that of availability. Fallback food is one which is of lower quality than preferred foods but available throughout the year and eaten when preferred foods are less available. Among the above-mentioned Japanese macaque foods, for example, fruit and seed are preferred foods, and mature leaf, bud, and bark are fallback foods (Hanya 2004; Tsuji et al. 2008). Fallback foods can vary in quality from those that are sufficiently nutritious to support the population to those that cannot (Lambert 2007).

Which is more important in limiting primate populations, preferred or fallback foods? This question is central to the problem of how seasonality affects primate abundance. Food may be sufficiently abundant most of the year, but when it decreases dramatically in one season, it may act as an “ecological crunch” or “bottleneck” and primate density may be limited by food availability only during this lean season (Cant 1980). From this view, fallback foods could serve as limiting factors of primate abundance. Studies on Japanese macaques indicate that both fallback food quality and total annual abundance of preferred food affect macaque density (Hanya et al. 2004, 2006). However, three conditions influence the nature of how fallback food influence populations: (1) animals cannot satisfy nutritional requirements only by fallback foods; (2) animals are capable of “saving” foods, such as fat accumulation or scatter-hoarding; and (3) fallback food is superabundant. With regard to the first condition, some primates rely on fallback foods that are of higher quality, such as fig fruits, than those of Japanese macaques (Lambert 2007). Unlike Japanese macaques, animals may be able to satisfy nutritional requirements with

these foods, but availability is expected to be limited (Lambert 2007). In fact, fig tree density correlates with orangutan (*Pongo abelii*) and gibbon (*Hylobates* spp.) density in some locations (Wich et al. 2004; Marshall and Leighton 2006). Gibbon density was not correlated with the overall food tree density, suggesting abundance of fallback food is more important than the total annual food availability (Marshall and Leighton 2006). Concerning the second condition, fat accumulation has been reported in temperate macaques, orangutans, many lemurs, and humans (Wada 1975; Zhao 1994; Knott 1998; Atsalis 1999; Muroyama et al. 2006), but it has not been examined carefully for most species. As for the third condition, leaves are often considered a superabundant fallback food; however, the quality of leaves is quite variable and primates are very selective with respect to leaf quality (Milton 1979; Ganzhorn 1992; Chapman and Chapman 2002; Hanya and Bernard 2012). To determine if leaves can be a superabundant fallback food, we need to know if the leaf quality that is required for the animal’s digestive ability to extract sufficient nutrients is suitable, and that leaf production of this required quality is sufficiently high to maintain the primate population. This information is generally unavailable, but there is a growing body of evidence that even folivorous primates experience food competition (Snaith and Chapman 2007; Tombak et al. 2012).

Based on this, we propose two hypotheses concerning mechanisms of resource limitation (Table 1). First, when fallback food quality is too low to satisfy nutritional requirement but it is superabundant, total annual food quantity of preferred foods should affect animal abundance. This relationship can be modified by the quality (condition C in Table 1) of fallback foods. Fat-accumulating Japanese macaques are one example (Hanya et al. 2004) for the hypothesis, but an example of folivorous sportive lemur (*Lepilemur ruficaudatus*) may suggest that another mechanism is feasible for this hypothesis to work. This species eat nutrient-rich young

Table 1 Hypotheses on the mechanism of food resource limitation on primates with respect to the quality and abundance of fallback foods

Condition	Quality of fallback food is enough to satisfy nutrition requirement	Abundance of fallback food	Mechanism of resource limitation	Possible examples
A	Yes	Superabundant	(Not limited by food resource)	Mentawai leaf monkeys (Watanabe 1981) living at extremely high density
B	Yes	Limited	Limited by the quantity of fallback food	Gibbons and orangutans depending on fig fruits as fallback foods (Wich et al. 2004; Marshall and Leighton 2006)
C	No	Superabundant	Limited by the quantity of preferred food	Japanese macaques (Hanya et al. 2004), sportive lemurs (Ganzhorn 2002)
D	No	Limited	Limited by the quantity of either preferred or fallback food	–

leaves and reproduce in the wet season and fall back to mature leaves in the dry season when young leaves are not available. They survive the lean season by keeping an extremely low metabolic rate and low levels of activity (Schmid and Ganzhorn 1996). Their abundance correlates with the product of quantity (number of food trees) and quality (protein to fiber ratio) of young leaves during the food-abundant wet season (Ganzhorn 2002). This index would likely correlate with the quantity of young leaves that is above a certain level of nutritional quality, thus the findings of this species support our hypothesis.

Second, when fallback food quality is high enough to satisfy nutritional requirements, but their quantity is limited, quantity of fallback food should determine animal abundance (condition B in Table 1). Gibbons and orangutans, which are limited by fig density, support this hypothesis (Wich et al. 2004; Marshall and Leighton 2006). Whether food saving adaptations modifies the relationships depends on the animal's saving ability, their activity and metabolic levels, and on the required home range size to secure fallback and preferred foods.

In addition to the above two conditions, two more conditions are conceivable. When fallback food quality is too low to satisfy nutritional requirement, and its quantity is limited (condition D), we cannot make predictions because in principle both preferred and fallback food quantity can affect animal abundance. We expect that animal abundance would be determined by the food that is more limited (i.e., the one that requires larger home range to secure the species requirements). When fallback food quality is high enough to satisfy nutritional requirement and quantity is superabundant, animals are, in principle, not limited by food (conditions A). It is not clear whether this last condition occurs naturally, but colobines living at extremely high density, exceeding 200 individuals km⁻² (Watanabe 1981), may be included in this category. In fact, Yeager and Kirkpatrick (1998) consider the abundance of Asian colobines to be limited by non-food factors, such as social stress. However, the assumed quantity and quality of fallback foods available to colobines has recently been questioned (Snaith and Chapman 2007).

Studies on resource limitation at the behavioral level

It is important to know whether animals can satisfy their nutritional requirements by the consumption of fallback foods. The simplest means of examining this is to quantify if the animals' intake is lower than their requirements. For Japanese macaques, their energy intake becomes only 60–90 % of the requirement in winter, when they fall back to mature leaves, buds, and barks (Iwamoto 1982; Nakagawa 1989a; Tsuji et al. 2008). They become energy deficient in two ways (Nakagawa et al. 1996). First, the energy content of mature leaves that are their fallback foods is sometimes

so low that animals cannot extract sufficient nutrients even if they eat up to their gut capacity (Mori 1979b). Second, some foods, such as buds, are so small that animals cannot eat enough even if they spend most of their day feeding (Nakagawa et al. 1996). In fact, Japanese macaques in deciduous forest spend almost 70 % of their day feeding in the winter (Nakagawa 1989b).

Deficiency in macronutrients can also be shown by urinalysis that quantify ketone and c-peptide concentrations as indices of energy balance (Harris et al. 2009; Harrison et al. 2010; MacIntosh et al. 2012) and urea and $\delta^{15}\text{N}$ for protein balance (Vogel et al. 2012a). Using these techniques, Bornean orangutans (*Pongo pygmaeus*) are shown to suffer from severe energy and protein deficiencies during periods of fruit scarcity (Knott 1998; Vogel et al. 2012b).

Animals showing no sign of negative energy or protein balance may still suffer from resource limitation. Animals may prioritize the intake of one nutrient over others, which can lead to consuming some nutrients more than needed. Geometrical framework of nutrition intake is a model allowing one to examine difference in priority among nutrients. To date we are aware of only two examples of application of this method in primate feeding ecology, and the results show interesting differences among species. Frugivorous spider monkeys (*Ateles chamek*) prioritize protein intake over energy (i.e., although the carbohydrate and lipid intake varies between 0.7 and 20 MJ day⁻¹, their protein intake remained constant (0.19 MJ \pm 0.01 SE) (Felton et al. 2009). In contrast, mountain gorillas (*Gorilla gorilla*) prioritize non-protein energy over protein intake (Rothman et al. 2011). Spider monkeys lack adaptations to extract protein from leaves, thus they need to ingest a great deal of fruit to keep a constant protein intake. While, because of their large size and digestive system, gorillas can gain sufficient protein from leaves and herbaceous material, so they must secure carbohydrates and lipids in the fruit-poor environment.

In addition to macronutrients, animals may also be limited by micronutrients, such as minerals or vitamins (Janson and Chapman 1999). Currently very little is known about micronutrient limitation in primates, but several lines of evidence indicates its importance. First, sodium (Na) makes up 90 % of total blood cations and is necessary for animal muscle contraction, nerve impulse transmission, acid–base balance, and metabolism (Robbins 1993), but plants do not require it. Thus, animals eating only plants typically need a sodium source other than their main food. Second, some primates select food with high mineral content (Magliocca and Gautier-Hion 2002; Rode et al. 2003). Third, some primates obtain sodium from unusual feeding locations, such as swamp plants, salt licks, or eucalyptus plantations, and the availability of these locations is often limited (Oates 1978; Harris and Chapman 2007; Matsubayashi et al. 2011). Fourth, mineral availability is known to affect spatial distribution of herbivorous African ungulates (McNaughton 1988) and a colobine monkey (*Colobus gureza*) (Harris and

Chapman 2007). To our knowledge, there is only one study that examines the effect of minerals on primate abundance (Rode et al. 2006). Among the four sites within the Kibale National Park, the density of redtail monkeys (*Cercopithecus ascanius*) was associated with the copper intake level (mg day^{-1}); however, copper availability was not quantified, thus it is difficult to judge what limits this population.

Linking feeding ecology and primate abundance: future perspectives

To determine if populations are resource limited, we need to identify the limiting nutrients, evaluate the balance between the requirement and actual intake of the nutrients by the animal, and assess the production (in case of macronutrients) or availability (in case of minerals) of that nutrients in the ecosystem. With these data, one can calculate the area that an animal requires to secure enough resources, which in turn determines population density. One must also consider seasonality, and the importance of seasonality can be addressed by examining the hypotheses we proposed here.

Given the time it typically takes for primate populations to respond to a change in the nature of their food resources, there are only a few study sites where the data will be likely to be available to study determinants of primate populations in the way that we have just suggested. However, a convenient alternative means of examining this issue is to analyze seasonal variation in home range size. Population density is the inverse of per capita home range size and is modified by the degree of overlap of home range between neighboring groups (Whitesides et al. 1988). Thus, an index of population density can be obtained during the season when the animal range most extensively, which is likely the season that limits animal abundance. Hanya et al. (2006) suggests that the limiting season for Japanese macaques is summer and autumn because home range size becomes largest at that time. Based on our hypotheses concerning the effect of seasonality on animal abundance, animals that are limited by fallback foods are predicted to have the largest home range in the food-scarce period. In contrast, animals that rely on fat accumulated by eating preferred foods are predicted to range most extensively during the food-rich period.

In conclusion, we propose two mechanisms explaining how resource availability and its seasonality determine animal abundance. When fallback food quality is too low to satisfy nutritional requirements, total annual food quantity affects animal abundance, and this relationship is modified by the quality of fallback foods. When fallback food quality is high enough to satisfy nutritional requirement but quantity is limited, quantity of fallback food is a limiting factor. Examinations of seasonal variations of home range size will be useful to determine the limiting season. For a direct test of the

hypotheses, we need to know the threshold value of quality of food that satisfies the animal's nutritional requirements, and the quantity of production in the habitat that supplies nutrients to animals.

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