

12 *How does food availability limit the population density of white-bearded gibbons?*

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Introduction

For decades primatologists have assumed that food availability is the primary determinant of primate population density (Terborgh & van Schaik, 1987; Davies, 1994). Observations of temporal changes in population density related to food availability have supported this assumption. For example, Dittus (1979) documented a 15% decrease in the size of a population of Toque macaque (*Macaca sinica*) during a period of reduced food availability. Similarly, populations of vervet monkeys (*Cercopithecus aethiops*) (Struhsaker, 1973; Lee & Hauser, 1998) and of yellow baboons (*Papio cynocephalus*) (Hausfater, 1975) also diminished in size when their resource base was reduced. Altmann *et al.* (1985) reported a 34-fold decrease in the population of yellow baboons in Amboseli over a 15-year period and attributed this decline to drastic environmental change that reduced the availability of high-quality food. Finally, the population density of mangabeys (*Cercocebus albigena*) at Kibale increased over a 20-year period, most likely because the forest was regenerating after logging and the density of mangabey food trees had substantially increased (Olupot *et al.*, 1994).

Comparisons of the same or closely related species at different locations have also provided some insight into the role of food availability in limiting primate populations. However, such studies typically involve populations separated by substantial distances (e.g., McKey, 1978; Oates *et al.*, 1990; Ganzhorn, 1992; Gupta & Chivers, 1999), thereby defying interpretation because of the many potentially confounding factors such as human disturbance (Struhsaker, 1999), biogeographic history (Gupta & Chivers, 1999), and differences in research methodology (Chapman *et al.*, 1999). More recent studies, notably those of Chapman and colleagues (e.g., Chapman & Chapman, 1999) have examined variation in primate densities on a more refined spatial scale and shown that variation in density between sites is correlated with the abundance of food resources.

These results, and many others, suggest that food availability is an important force in limiting primate biomass. This robust conclusion prompts the question of whether there exist specific classes of foods whose abundance sets the carrying capacity for tropical forest primates. A key distinction may be between preferred and fallback foods. Preferred foods are those that are eaten more often than would be predicted based on their availability at any given time (i.e., overselected, *sensu* Leighton, 1993; Manly *et al.*, 2002). Fallback foods are classified as foods whose use is negatively correlated with the availability of preferred food items across time (Conklin-Brittain *et al.*, 1998). Basic foraging theory (Stephens & Krebs, 1986) suggests that preferred foods are those that can be efficiently harvested (i.e., yield high energy

returns/foraging effort compared with other food items). Empirical study has confirmed that this suggestion is valid, at least for species that have been investigated (e.g., orangutans: Leighton, 1993). Gibbons exhibit a strong preference for fleshy fruits (McConkey *et al.*, 2002; Leighton, unpublished data) whose sugar-rich pulp provides relatively high rates of energy return. Fallback foods are utilized when these energy-rich fleshy fruits are scarce. These low-preference “fallback foods” may be available at other times but are ignored during periods of high, preferred fruit availability (Leighton & Leighton, 1983). As the spatial and temporal availability of preferred and fallback foods may vary independently, their effects on primate populations may be different.

Primate dietary intake is subject to wide seasonal variation because of fluctuations in the phenology of food resources (Terborgh, 1986; Oates, 1987; Janson & Chapman, 1999). During periods of high food availability, surplus energy (i.e., above the amount required for physiological maintenance) becomes available, enabling growth and reproduction (Charnov & Berrigan, 1993). The greater the abundance of these items in a habitat, the greater the maximum energy availability during productive periods. Since an increase in net energy availability during these periods should enable higher reproductive rates, areas with a higher availability of preferred foods should maintain a higher primate density than areas that are relatively depauperate of these resources. During times of low fruit availability, most primates tend to rely more heavily on less preferred food resources to fulfill the caloric demands of physiological maintenance (Leighton & Leighton, 1983; Terborgh, 1986). In most organisms that are limited by resources, classic ecological theory predicts that periods of food shortage will set the population size. This is especially true for species whose populations grow at relatively slow rates (e.g., primates) since they are unable to closely track temporal fluctuations in food availability (Wiens, 1977). For such species, food may be superabundant most of the time, and populations can go for many months (or years) without experiencing any resource limitation (Cant, 1980). However, occasional periods of food scarcity may cause an increase in mortality levels (Foster, 1974; Wiens, 1977), resulting in bottlenecks that ultimately limit population size (Milton, 1982; Davies, 1994).

Plausible arguments can be made in support of either preferred foods or fallback foods serving as the limiting factor on primate populations, yet to date no studies have specifically addressed the relative importance of these two classes of foods. Even studies claiming to have demonstrated the effects of preferred food availability have found correlations between important foods (those comprising a substantial percentage of the diet) and biomass, rather than between preferred foods and biomass (e.g., Caldecott, 1980;

Mather, 1992). Though interesting and suggestive, these analyses are inconclusive because they neither explicitly differentiate between preference and importance nor consider the effects of temporal variation in food availability. In addition, since other possible food variables, (e.g., patch size or the availability of fallback foods) were not measured, these results may be confounded by other factors. Thus, the issue of whether different classes of foods have different effects on primate populations remains untested.

Patterns of food availability in Bornean forests

Compared with most other rainforests, Malesian tropical forests exhibit patterns of food availability that are both more temporally variable and less predictable (Leighton & Leighton, 1983; van Schaik, 1986; Whitmore, 1990; Wich & van Schaik, 2000). This heightened variability is largely due to the phenomenon of mast fruiting, which involves the gregarious fruiting of many individual plants, presumably as an adaptation to avoid seed predation (Janzen, 1974; Ashton *et al.*, 1988; Curran & Leighton, 2000). During masts in Malesian forests virtually all taxa in the dominant family Dipterocarpaceae, along with many other common taxa, fruit in synchrony after several years of reproductive inactivity (Medway, 1972; Appanah, 1981; Ashton *et al.*, 1988). This pattern results in extreme temporal fluctuations in food availability for vertebrates (Leighton & Leighton, 1983; van Schaik & van Noordwijk, 1985; Knott, 1998).

In order to generate testable predictions derived from our hypotheses, we assigned each month in the study period to one of four classes based on food availability: masts, high fruit periods, low fruit periods, and crunches. Below we provide a brief description of each category. Figure 12.1 provides schematic diagrams of food availability and dietary composition during each category. As indicated above, mast periods are times during which a large set of the woody plants in the forest (predominantly trees, although there are masting liana species) produce fruit. In addition to this high density of large fruit patches, it is probable that masting taxa produce fruits that are of higher quality (i.e., higher rates of net energy return) than most fruits produced outside the mast, presumably because plants that fruit during masts are subject to heavy intra- and interspecific competition for vertebrate dispersers. Although this concept has yet to be explicitly examined, it is a logical deduction considering the competitive milieu of plants, and both our unpublished data and published results (Leighton, 1993; van Schaik & Knott, 2001) support this claim. This suggests that during masts both the amount

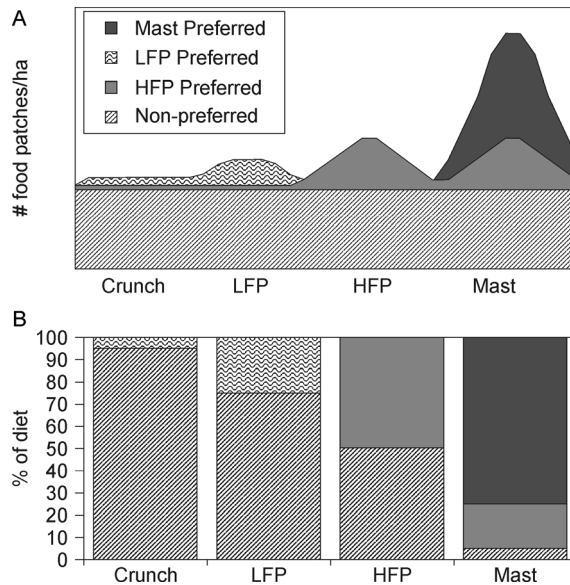


Figure 12.1. Schematic diagrams of (A) food availability (number of food patches/ha) and (B) diet composition during crunches, periods of low (LFP), high (HFP) food availability, and masts. X-axes represent categories of food availability, with total food availability increasing from left to right.

and quality of food resources may be maximal, resulting in diets that are comprised mostly of preferred foods.

High fruit periods (HFP) are non-mast periods during which a substantial number of food taxa fruit together. These peaks occur on a roughly annual basis, although their arrival seems less predictable in forests on Indonesian islands than in most African or Neotropical rainforests, presumably due to less predictable patterns of rainfall at the Indonesian sites (Whitmore, 1990; Janson & Chapman, 1999). We found that most gibbon fruit taxa that fruit during HFP also fruit during mast periods and are thus likely to be subjected to intense competition for dispersal agents. Therefore, although food availability during HFP is not as high as during masts, the selection of fruits with high net rates of energy return for frugivores results in the availability of a substantial number of preferred foods during HFP. Consequently, diets during HFP comprise a substantial proportion of high-quality, preferred items.

Low fruit periods (LFP) are periods during which both the availability and relative quality of foods are low. As plants require some period of reproductive inactivity following fruiting so as to recoup sufficient nutrient

status in order to fruit again, and since the majority of food trees fruit during masts or HFP, LFP are a direct consequence of masts and HFP. Plant taxa whose reproductive strategy is to fruit during periods of low overall food availability experience relatively little competition for dispersers, and therefore can afford to produce fruits that provide meager energetic returns. Therefore, the quality of fruits produced during LFP is expected to be substantially lower than those produced during times of higher food availability, and the diets of consumers comprise a lower percentage of preferred foods. This claim is also supported by available data (Leighton, 1993, and unpublished data). Vertebrate consumers must make up the balance of their diets during LFP with foods that provide low rates of net energy return and are of low preference rank.

Crunch periods refer to rare times of extreme food shortage. Crunch periods differ from LFP in degree; food availability is drastically reduced and there are virtually no plants fruiting that provide preferred, high-quality foods. During these periods reproduction is probably impossible for most frugivorous primates and the lack of food may temporarily cause elevated mortality and potentially limit population size.

Phenological patterns of plant taxa

The overall temporal pattern of food availability in Bornean forests is the result of the summation of the phenological patterns of numerous individuals from hundreds of different plant taxa. In order to characterize the phenological patterns of gibbon food taxa, we defined four general classes of phenology. These categories classify plant taxa according to their availability relative to overall patterns of food availability in the forest and were defined to highlight the temporal variation that is presumably most relevant to gibbons. These categories are: (1) *masting taxa*, defined as taxa that fruit predominantly during mast periods; (2) *HFP fruiters*, defined as taxa that fruit mainly during the regular forest-wide peaks in food availability and may or may not also fruit during mast periods; (3) *LFP fruiters*, defined as taxa that fruit mainly during times of low overall food availability and may or may not fruit at other times; and (4) *crunch fruiters*, defined as taxa that are available predominantly during periods of extreme food shortage. Figure 12.2 provides examples of each of the four categories from the phenology data used for this analysis.

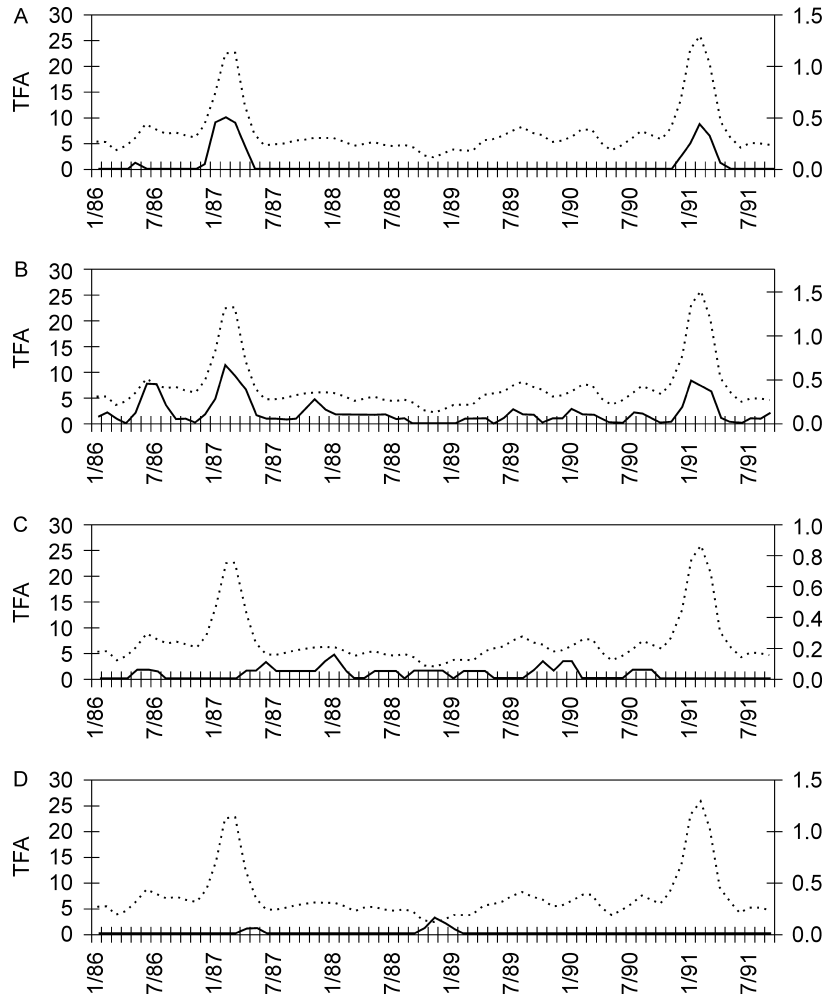


Figure 12.2. Phenology of sample taxon in each of the four classes used to categorize gibbon foods in Bornean rainforests between January 1986 and September 1991 at Gunung Palung. The dotted line indicates Total Food Availability (TFA; patches/ha), and the black line indicates the number of patches/ha of a sample masting taxon (A: *Neoscortechinia kingii*), HFP taxon (B: *Rourea minor*), LFP taxon (C: *Porterandia sessiliflora*), and crunch taxon (D: *Gnetum sp. 1*). See text for additional details.

Specific hypotheses to be tested

The primary goal of this chapter is to examine how food availability limits gibbon population density across seven habitat types at our site in Gunung Palung National Park (GPNP), West Kalimantan, Indonesia. In particular, we assess whether preferred or fallback foods set the habitat-specific carrying capacity (i.e., maximum population size that can be sustained indefinitely) for gibbons. Gibbon densities at GPNP have remained stable in each habitat over the last 20 years and no hunting has occurred within the study site, suggesting that these populations are at carrying capacity (Mitani, 1990; Marshall, 2004). Therefore correlations between the availability of certain types of food and gibbon density would support the hypothesis that a certain type of food limits gibbon populations. We therefore tested the following hypotheses.

H1: Gibbon density is limited by the total availability of food

If food resources are the principal limitations on gibbon population density, then it is plausible to hypothesize that variation in population density between habitats is related to the total availability of foods. Although this hypothesis seems oversimplified and does not incorporate temporal variation in food availability or food quality, it is essentially the logic upon which many previous attempts to explain variation in population density are based (e.g., Mather, 1992; Chapman & Chapman, 1999). In these studies, the densities of food plants or their basal area serve as the measure of food availability. *H1* predicts that variation in the density of gibbons across the seven habitats at GPNP is positively correlated with measures of the overall abundance of food in each habitat.

H2: Gibbon density is limited by the average availability of food

A second hypothesis is that average food availability in a habitat may serve as the key limitation on gibbon population density. This hypothesis implies that short-term fluctuations in food availability have little effect on gibbon populations, and that it is mean food availability over time that sets the carrying capacity of a habitat. *H2* predicts that variation in the density of gibbons across the seven habitats at GPNP is positively correlated with measures of the mean food availability/month in each habitat.

H3: Gibbon density is limited by the availability of preferred foods

H3 predicts that the density of gibbons is positively correlated with the availability of preferred taxa. We test three versions of this hypothesis: that gibbon density is correlated with the availability of preferred mast taxa, preferred HFP taxa, or the overall density of preferred foods.

H4: Gibbon density is limited by the availability of fallback food resources

H4 predicts that gibbon density is positively correlated with the availability of fallback food resources. We tested this hypothesis in two ways. First we examined the correlation between gibbon density and the availability of foods during LFP and crunch periods. Our second test involved the identification of specific food resources as fallback foods. We identified fallback foods using the definition provided above and examined correlations between the habitat-specific density of specific fallback food items and gibbon density.

Materials and methods

Study site

We conducted research at the Cabang Panti Research Station (CPRS) and surrounding areas in GPNP (1°13'S, 110°7'E). GPNP comprises a small coastal mountain range surrounded by seasonally flooded swamp, peat, and mangrove forests (Cannon & Leighton, 2004). We gathered data in seven distinct habitat types within the CPRS trail system: peat swamp, freshwater swamp, alluvial bench, lowland sandstone, lowland granite, upland granite, and montane forests. General descriptions and detailed data on the plant composition of each habitat are provided in Webb (1998), Cannon & Leighton (2004), and Marshall (2004). These habitats are contiguous, thus minimizing differences in rainfall, latitude, seasonality, gamma diversity, and predation pressure that could confound results (Cannon & Leighton, 2004). Since GPNP is located near the Bornean coast, its elevational gradient is compressed (the Massenerhebung effect, see Whitmore, 1984), allowing for ease of data collection in several different upland habitats.

Study subjects

Our study species was the Bornean white-bearded gibbon (*Hylobates albibarbis*). The taxonomic status of the gibbons living between the Kapuas and Barito Rivers in southwest Borneo has been the source of considerable debate (Groves, 1984, 2001; Marshall & Sugardjito, 1986). Here we use the species designation *H. albibarbis*, but remain open to the possibility that this taxon could be more appropriately designated as a subspecies of either *H. muelleri* or *H. agilis*. Gibbons typically specialize in ripe, non-fig fruit and augment

their diet with figs, flowers, and young leaves during periods of low preferred fruit availability (Leighton, 1987).

Field methodology and data analysis

Habitat-specific gibbon density

We measured gibbon density by establishing a pair of replicate census routes in each of the seven habitats found at CPRS ($n = 14$ total census routes). Census routes averaged 3.42 km in length (range 2.90–3.80 km) and followed existing trails through the forest. AJM and his assistants walked a total of 409 censuses (1374 km) between September 2000 and June 2002. All walks were conducted at the same speed and data collection followed a standard protocol. An average of 58 censuses (range 38 to 87) were walked in each habitat. We followed standard methodologies for the analysis of line transect data using Distance 4.0 Release 2 (Thomas *et al.*, 2002), calculating detection functions separately in each habitat and controlling for size bias in sampling (Buckland *et al.*, 2001).

Diet composition

We used all the independent feeding observations gathered on censuses between April 1985–December 1991 and August 2000–August 2002 and opportunistically compiled a list of food taxa utilized by gibbons. Following the logic described below, we used the genus as the taxonomic level of analysis. Our resulting food list contained 91 genera.

Habitat-specific density of food trees and lianas

AJM randomly placed 10 plots in each habitat to assess the density of key tree and liana taxa in each of the seven forest types. All fig roots and liana stems within 10 m on either side of the transect midline and whose diameters at breast height (DBH, 137 cm above the ground) were greater than 4.5 cm were included, resulting in 5 ha of plots ($0.5 \text{ ha/plot} \times 10 \text{ plots/habitat}$) for these forms in each habitat. The same plot size was used for trees with DBH greater than 34.5 cm. Five meters on either side of the transect midline, all trees with boles greater than 14.5 cm were included, resulting in 2.5 ha plots/habitat for smaller trees ($0.25 \text{ ha/plot} \times 10 \text{ plots/habitat}$). We used these data to calculate the mean density and total basal area of each food taxon in each habitat.

Identification of trees and liana

In the field, AJM and his three field assistants identified family, genus, and (when possible) species of each stem in the density plots. We used genera as

the taxonomic unit for food items in all analyses for several reasons. First, after a substantial training period and validation through double-blind tests involving the identification of trees identified at our site by recognized experts (e.g., P. Ashton, P. Stevens, M. van Balgooy) we were able to reliably identify genus of individuals in the field without collecting leaf and bark samples. This made our plot work highly efficient and allowed us to sample a far larger area than would have been possible if we had collected the voucher specimens that would have been required to identify stems at the species level. Second, since some of the largest and most diverse plant families and genera have not been taxonomically revised recently, and systematic sampling in highly diverse Bornean forests such as those found in GPNP has been limited, many taxa at CPRS have not yet been assigned formal species names. Third, our data show that most fruits within the genera eaten by gibbons at our site are similar in the aspects of phenology and chemistry relevant to these analyses (Leighton, 1993, and unpublished data). Therefore, the lumping of two or more species under a single taxonomic designation probably did not obscure important differences relevant to gibbons. We retained more fine-grained taxonomic classification for genera in which lumping all species into one genus would have introduced bias (e.g., genera containing species that exhibited different growth forms or whose fruits were of different dispersal syndromes and/or of substantially different nutritional value). *Ficus* stems were identified to subgenus, following taxonomy in Laman & Weiblen (1998). Nomenclature followed that of the *Tree Flora of Malaya* series (Whitmore, 1972, 1973; Ng, 1978, 1989).

Temporal availability of food

We used data from 126 phenological plots that were monitored monthly between January 1986 and September 1991 ($n = 69$ months) to assess temporal variation in food availability. Phenology plots were 0.10 ha in size and were placed using a stratified random design across all seven habitat types (Cannon & Leighton, 2004). In these plots all trees larger than 14.5 cm dbh, all lianas larger than 3.5 cm dbh, and all hemiepiphytic figs whose roots reached the ground were measured and tagged. The phenological phase of each tagged stem in these phenology plots was recorded each month as one of six mutually exclusive categories: reproductively inactive, or containing flower buds (i.e., developing flowers were visible, but no flowers were at anthesis); mature flowers (i.e., at least one flower on the tree was at anthesis); immature fruit (i.e., fruits in which the seed was undeveloped); mature fruit (i.e., full-sized fruits that were unripe but had seeds that were fully developed and hardened); or ripe fruit (i.e., at least one fruit on the tree was ripe, usually signaled by a change in color or softness).

These data were used to calculate total food availability/ha and total number of fruiting taxa in each habitat in each month. Since the vast majority of gibbon feeding observations (93%) were of ripe fruit eating, we counted only food taxa stems with ripe fruit crops in a particular month as available food.

Classification of periods of food availability

In order to determine whether fruiting peaks were synchronized between habitats, we calculated the correlation between food availability in each habitat and the food availability in all other habitats during the same month. We conducted food availability analysis separately for any habitat whose phenological patterns were negatively correlated or weakly positively correlated ($r < 0.4$), with those of other habitats. We used objective, operational definitions based on the number of fruiting stems/ha and the diversity of fruiting species to identify each month as a mast, HFP, LFP, or crunch based on examination of the patterns of fruit availability over the 69 months sampled (see Marshall, 2004 for details).

Temporal availability of each food taxon

We utilized observations collected in the 126 phenology plots that were monitored for 69 months to assess the temporal availability of each food taxon over time. We developed decision rules that assigned each taxon to one of the four categories of food availability based on their phenology relative to our operationally defined seasons (e.g., masting species were defined as those for which $>75\%$ of all fruiting events were in mast month, LFP fruiters were those for which $>50\%$ of fruiting occurred in LFP; see Marshall, 2004 for details).

Preference ranking of each food taxon

For each habitat we compiled a list of all taxa fed upon by gibbons in each of the four food availability categories (i.e., mast, HFP, LFP, crunch) and arranged them in order of decreasing habitat-specific preference. Preference values were calculated by dividing the use of each item (number of independent feeding observations) by its availability (number of patch months/ha). We plotted the cumulative importance (% in the diet during that season) as each new food taxon was added to the list (in order of decreasing preference). For mast periods, all food taxa required to comprise 75% of the diet were categorized as “preferred”; the final 25% were characterized as non-preferred. During HFP the taxa required to explain 50% of the diet were categorized as preferred taxa and the taxa required to explain the remaining 50% of the diet were classified as non-preferred foods. For LFP and crunch periods, the top 25% of foods were classified as preferred and the remainder were

characterized as non-preferred. These cut-off rules reflect the fact that during mast periods the majority of available foods are of high objective preference (high net rates of energy return) whereas during LFP most foods are of low preference. In order to assign each food taxon to one of two classes, this methodology incorporated habitat- and season-specific information on preference and importance.

Statistical analyses

We used ranged major axis regression (RMA) for all analyses because our independent variable (food availability) was subject to measurement error (Legendre & Legendre, 1998). We performed all RMA analyses using the program Model II (Legendre, 2001) and conducted non-parametric Monte Carlo randomization tests of 10 000 iterations to test for significance of slope and correlation estimates (Sokal & Rohlf, 1981; Manly, 1997). All regression analyses were performed on appropriately transformed variables to reduce non-normality and heteroskedasticity.

Results

Habitat-specific gibbon density

Gibbon densities at CPRS varied by more than an order of magnitude, with point density estimates ranging from 0.44 individuals/km² in montane forest to 10.27 individuals/km² in lowland sandstone habitats (Table 12.1).

Table 12.1. *Gibbon population density in seven habitat types*

Habitat	# censuses	Total Distance (km)	# Gibbon obs.	Density (gibbons/km ²)	SE
Peat swamp	87	290.3	50	7.28	1.25
Freshwater Swamp	87	140.4	27	5.90	1.34
Alluvial bench	108	148.9	24	7.10	1.70
Lowland Sandstone	101	129.3	34	10.27	2.12
Lowland granite	61	176.6	37	6.23	1.33
Upland granite	142	229.7	30	4.17	1.17
Montane	166	258.6	4	0.44	0.25

Data include the total number of censuses, distances sampled, number of independent gibbon observations made on censuses, and the point estimate (gibbons/km²) and standard error (SE) of gibbon density in each habitat.

Periods of food availability in each habitat

Examination of interhabitat correlations suggested that fruiting patterns in freshwater swamp, alluvial bench, lowland sandstone, lowland granite, and upland granite habitats were well synchronized ($r > 0.7$, $p < 0.0001$) and that for purposes of classification these habitats could be lumped as mast, HFP, LFP, or crunch months. Montane and peat swamp forests were less well synchronized with the overall phenological patterns of the forest ($r < 0.4$, $p > 0.001$), and were therefore analyzed separately. Figure 12.3 shows temporal variation of food availability in each habitat and the classification of each month.

Hypothesis tests

As a test of *H1* (gibbon density is limited by total food availability), we calculated two measures of the total food availability in each habitat – the total stems of food taxa/ha, and the total basal area (TBA) of food taxa/ha. As TBA/ha incorporated the size of trees, it had the benefit of weighing larger stems (and their larger associated fruit crops) more heavily. However, TBA calculations obscured the effects of lianas. Therefore, we also used the measure of stems/ha in order to incorporate the effects of lianas. There was no relationship between habitat-specific density and either food stems/ha ($r^2 = 0.06$, $p = 0.61$) or TBA of food trees ($r^2 = 0.18$, $p = 0.34$) in a habitat. Taken together, these tests showed that total food availability is uncorrelated with density, and that total abundance of food does not constrain gibbon population density. In our test of *H2* (gibbon density is limited by average food availability), mean food availability/month in a habitat was similarly unrelated to density ($n = 7$ habitats, RMA $r^2 = 0.0001$, $p = 0.98$, Kendall's Tau 0.05, $p = 0.88$), indicating that the average food availability in a habitat does not serve as the key limitation of gibbon population density.

To test *H3* and *H4* (gibbon density is limited by preferred and fallback foods, respectively), we used the data from the phenology plots to calculate the mean food availability/month in each habitat during each of the four categories of food availability. The mean food availability, regardless of category, did not predict gibbon density ($n = 7$ habitats, $r^2 < 0.15$, $p > 0.30$ for all tests). We also analyzed the relationship between gibbon density and the stem density and TBA/ha of preferred and non-preferred foods for each of the four seasons. Of the eight classes of foods formed by these combinations, only the preferred HFP foods were significant predictors of gibbon density (TBA/ha: $r^2 = 0.71$, $p = 0.01$; stems/ha $r^2 = 0.72$, $p = 0.02$).

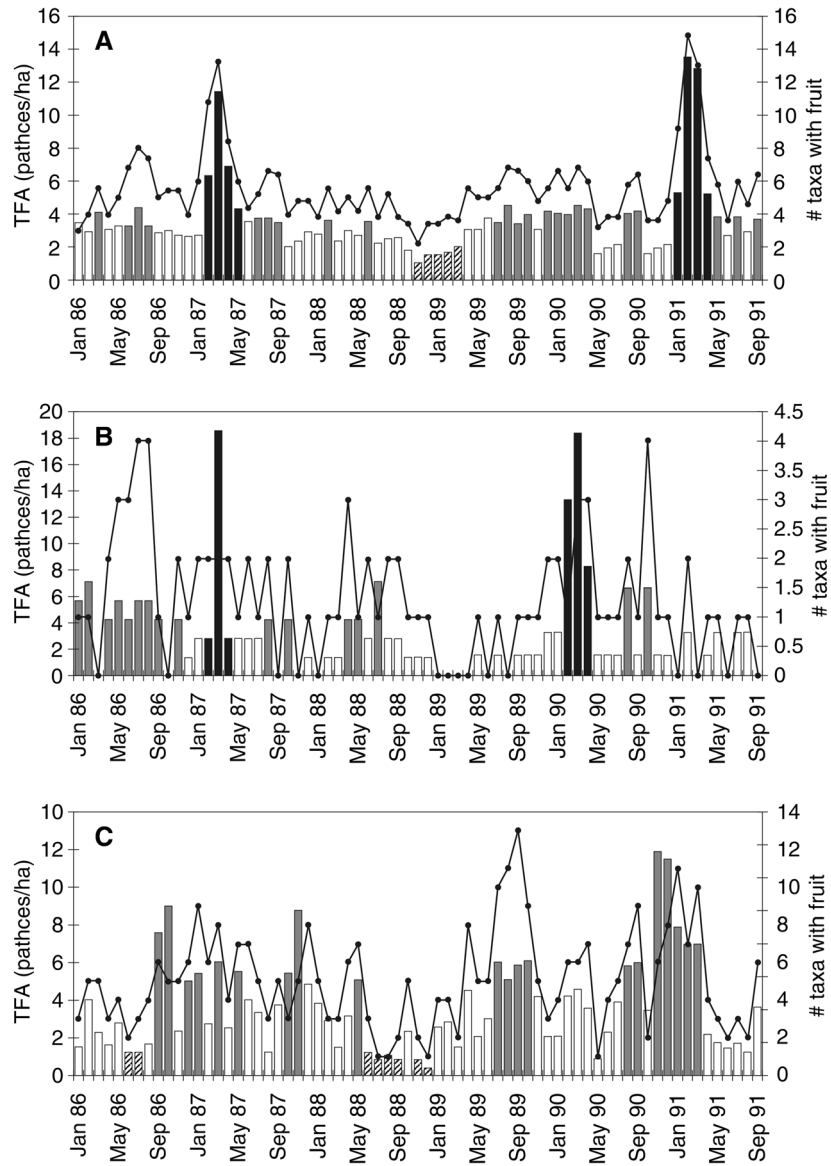


Figure 12.3. Phenological characterizations of gibbon food availability in lowland (A), montane (B), peat swamp (C) forest habitats. Line indicates the number of taxa with fruit in each month. Bars indicate mast (black), HFP (gray), LFP (white), and crunch (hatched).

Although the relationship between two measures of preferred HFP foods and gibbon density were significant, they were clearly strongly influenced by a single point, representing the montane forest. Using the logic that if gibbon densities are constrained by the availability of HFP preferred foods then the correlation between density and the availability of these food resources should remain if one habitat is removed, we removed the montane habitat and recalculated the correlations. Following the removal of the highly influential montane habitat datum from the analysis, both the strength and significance of both correlations dropped sharply ($n = 6$ habitats, $r^2 < 0.47$, $p > 0.14$ for both). This suggested that the availability of HFP preferred foods may not serve as the most important limiting factor on gibbon population density.

In order to conduct our final test of *H4*, we examined the relationship between feeding observations on various food taxa and overall food availability. Our analysis showed that the percentage of gibbon feeding observations on figs was significantly negatively correlated to overall food availability ($n = 21$ 3-month periods, $r^2 = 0.36$, $p = 0.003$, Marshall, 2004). This indicated that figs served as fallback foods for gibbons at GPNP. This conclusion is supported by substantial evidence from a range of tropical sites that figs serve as important fallback foods for other vertebrate frugivores during periods of resource scarcity (e.g., Leighton & Leighton, 1983; Terborgh, 1986; Wrangham *et al.*, 1993; O'Brien *et al.*, 1998).

Gibbon densities were highly correlated with the density of figs ($n = 7$ habitats, $r^2 = 0.93$, $p = 0.0005$, Figure 12.4). In order to establish that this relationship was not driven by a single, overly influential outlier, we removed the montane habitat and reran this analysis. In contrast to the results for HFP preferred foods, figs remained a strong and significant predictor of gibbon density when the montane habitat was removed ($n = 6$ habitats, $r^2 = 0.90$, $p = 0.004$). These analyses suggest that fig density is the key constraint on gibbon density, and that the density of preferred HFP foods is merely correlated with fig density, with little independent explanatory power.

Discussion

In this chapter we tested hypotheses about the role of various types of food resources in limiting gibbon population density. We systematically classified food resources based on their phenology, preference, and importance for gibbons and examined how variation in different classes of food was related to differences in population density across seven different habitat types. We found that gibbon population density was highly correlated with the

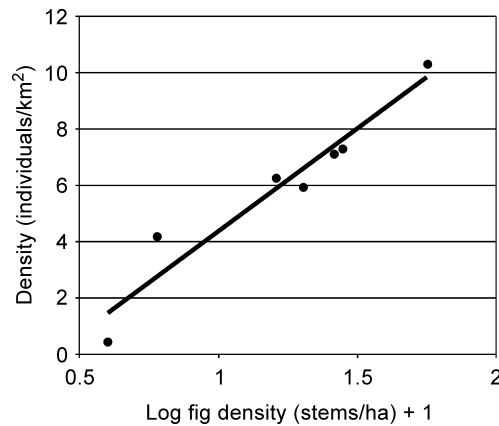


Figure 12.4. The relationship between gibbon density and the density of figs in seven habitats ($r^2 = 0.93$, $p = 0.0005$). Fig density was logged to reduce non-normality.

abundance of figs. This result suggests that gibbon populations are constrained by the availability of their most important fallback food, figs. Thus, gibbons conform to the classic view that primate populations are primarily limited by food availability during periods of overall low resource availability.

Gibbons exhibit relatively risk-averse life history strategies (i.e., low inter-birth intervals, high infant and juvenile survivorship), suggesting that there has been strong selection in this species on traits that promote survivorship. Figs may provide female gibbons with the energy required to maintain body condition during food-poor times when the intense obligate investment required to insure offspring survival is metabolically costly. In habitats with high densities of figs, gibbon females may be able to maintain better health and physical condition during LFP and crunches than they could in habitats with low fig densities. This would allow them to recover faster from costly periods of pregnancy and lactation and thus reproduce more frequently. Under this scenario, fig densities limit gibbon populations through their effects on female condition during periods of low food availability, which in turn affect birth rates.

The results provided in this chapter are based on small sample sizes ($n = 7$), and therefore preclude the use of multivariate models required to simultaneously test the effects of different types of food resources. In addition, these small sample sizes reduce the power of statistical tests to reject our null hypotheses. Several refinements are possible that would allow us to more fully address this question. First, subdividing the habitats into smaller sections and comparing gibbon density to the food availability within each smaller section

would increase our sample size and might provide sufficient data to conduct multivariate tests. Second, long-term demographic monitoring of groups of both species across the range of habitats found at GPNP would uncover temporal variation in birth and death rates that would shed light on the factors constraining population density. Third, formal demographic modeling would provide an opportunity to examine the actions of various regulatory mechanisms and their theoretical implications in more depth. Finally, the predictive power of the models proposed here could be tested using data from other sites.

Broader applications and implications

Although there is broad general interest in identifying the factors that limit primate population density, attempts to do so have to date met with limited success. This is primarily due to the fact that the theoretical framework from which we examine these questions is underdeveloped. Few general hypotheses have been proposed about the role of various ecological variables as limiting factors on primate populations, and formal models that explicitly consider the effects of temporal and spatial variation in resource availability have yet to be developed for primates. In this chapter we suggest a conceptual approach that explicitly considers the importance of different classes of foods and stresses the importance of classifying food resources relative to overall resource availability. Although temporal variation in food availability is unusually pronounced at our site, and despite the fact that the importance of temporal fluctuations in resource availability is strongly related to the dietary adaptations of a species, this approach could be profitably applied at a wide range of sites. This methodology requires that one have long-term data on both primate population density and food availability. Fortunately, these data are collected regularly by primate fieldworkers, suggesting that data are available from a wide range of sites that could be used to test the general applicability of the hypotheses we propose here. Ideally, studies would examine the correlates of population density of the same species at several sites that are close in proximity but variable in quality (e.g., Chapman & Chapman, 1999).

Studies that advance our understanding of the ultimate constraints on primate populations have the potential for providing important information to conservation managers. For example, if the key food resources that regulate primate populations can be identified, then these tree and liana taxa can be spared during selective logging operations (Wasserman & Chapman, 2003). In addition, techniques that rapidly assess the quality of habitat for primates can be developed and used to either identify areas that deserve special

conservation attention or to determine which of several areas are the most deserving of limited conservation funds. Finally, an understanding of the key factors constraining primate populations would suggest valuable ways to artificially manipulate carrying capacity in forests that have been degraded or are being specifically managed to maximize primate population size.

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