

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

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16

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

36 Keywords: bottleneck; population density; fallback food; nutrition; seasonality

37

38 **Introduction**

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

49 Primates are ideal subjects to study both animal abundance and
50 feeding ecology. Since they are diurnal and standardized census methods are
51 established (National_Research_Council 1981; Whitesides et al. 1988),
52 comparable data on abundance are available for many species, often from a
53 number of populations. Furthermore, since most primates are diurnal and have
54 large body sizes, detailed behavioral observation is feasible and there have
55 been many studies of their feeding ecology (Clutton-Brock 1977; Hohmann et al.
56 2006). Primates are generalist consumers and are dependent on a diverse
57 array of resources, such as leaves, fruits/seeds, flowers, gum/sap, barks, and
58 insects (Kay 1984). These food resources vary in their nutritional and
59 distributional properties, thus comparative primate research can clarify various
60 mechanisms concerning how food affects abundance.

61 For primary consumers, the simplest mechanism of food resource
62 (resource, hereafter) limitation suggests that habitats can sustain an increasing

63 number of animals up to the point where the total consumption by the population
64 equals the production of food by the plant community. Coelho et al. (1976)
65 concluded that primates are unlikely to be limited by resource, based on two
66 months of behavioral observations of two species of primates (*Alouatta pigra*
67 and *Ateles geoffroy*). They estimated the primates' energy requirements
68 based on their activity budget and calculated the total energy requirement of the
69 populations of the two species to be 13,640 kcal/km²/day. This was lower than
70 the pulp production of only one species of their main food (*Brosimum alicastrum*;
71 716,000 kcal/km²/day). These calculations were used to suggest that this one
72 fruiting tree species could sustain 1,700 individuals/km² of primates, which is
73 implausibly high. This conclusion was criticized by Cant (1980) who pointed
74 out that (1) food availability changes both seasonally and supra-annually and
75 one cannot conclude that animals are free from resource limitation with only two
76 months of data and (2) food quality was not considered. He argued that even if
77 resources are super-abundant in most of the seasons, animals experience
78 'ecological crunches,' when resources are in short supply and their populations
79 can be limited by these periods. In the three decades since the publication of
80 these papers a great deal of data on primate feeding ecology and population
81 abundance has accumulated that can be matched to data on forest productivity
82 and food quality, thus now is the time to revisit Cant's (1980) question: 'What
83 limits primates?'

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

88 discuss future research directions.

89

90 **Approaches to study resource limitation at the population level**

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

104 Primates have largely been studied in static approach. If the animals
105 change their number rapidly, as seen with rodent population cycles or ungulate
106 migrations (Kaji et al. 1988; Wolff 1996), static approach may not be useful.
107 Although many primates change their number over time, the scale over the year
108 or the duration of most studies is much smaller than that of many other
109 mammals (Hanya 2009). Experiment on resource limitation in primates is
110 usually difficult because both spatial and time scales are too large for
111 researchers to mimic. For example, provisioning or food removal experiments
112 with rodents and pigeons were conducted at a scale of 1.7-3.5 ha and 1.8 ha,

113 respectively (Adler 1998; Moegenburg and Levey 2003), which is much smaller
114 than a home range of a single group of most diurnal primates (5 ha-24 km²)
115 (Mitani and Rodman 1979). Large-scale provisioning of free-ranging primates
116 is conducted mainly for tourism or for management of introduced colonies.
117 Although their effect on population changes has been confirmed (Mori 1979a;
118 Sugiyama and Ohsawa 1982; Watanabe et al. 1992), food abundance was
119 manipulated for management, not for the research on resource limitation.
120 These studies took several decades to observe population changes, which is
121 much longer than the response observed in rodent or pigeon studies (<1 year)
122 (Adler 1998; Moegenburg and Levey 2003). Therefore, although data on
123 provisioned populations directly tests whether primates are food limited, studies
124 based on the comparison of natural populations are indispensable in exploring
125 natural mechanism of resource limitation.

126

127 **Previous studies on primate abundance**

128 Density has been estimated for many primate populations, but only a small
129 proportion of these studies have examined the environmental factors affecting
130 variation among populations (static) or within a population over time (dynamic).
131 Of those that do speculate on environmental drivers of density, the majority only
132 make qualitative comparison among vegetation types or study sites (Freese et al.
133 1982; Weisenseel et al. 1993; White 1994; Yoshihiro et al. 1999; Mathews and
134 Matthews 2002; McConkey and Chivers 2004). Other studies examined
135 vegetational correlates of primate abundance, such as tree density, basal area,
136 shrub cover, and tree species diversity (Butynski 1990; Chapman and Chapman
137 1999; Balcomb et al. 2000; Wiczowski 2004; Worman and Chapman 2006;

138 Hamard et al. 2010). While this is useful information regarding the habitat
139 preference, their ability to determine determinants of animal abundance is
140 limited. For example, vegetation structure only evaluates food quantity in the
141 most general way. Such studies do not evaluate the seasonal changes of food
142 availability, the importance of fallback foods (foods that are eaten during the
143 scarcity of preferred foods), or the type of the resource limiting the animal.

144 Such studies examining vegetational correlates of primate abundance
145 can be used in meta-analyses; however, since it is usually difficult to collect data
146 on both primate and habitat variables in comparable fashions, primate
147 abundance is usually correlated with indirect measure of forest productivity, such
148 as rainfall or forest type. Forest type can explain the difference in primate
149 abundance in a rudimentary fashion (Ganzhorn et al. 1999; Peres 1999; Peres
150 and Dolman 2000), but climate usually cannot (Chapman and Balcomb 1998;
151 Gupta and Chivers 1999; van Schaik et al. 2005). However, using direct
152 measures of food abundance, such as fruit fall, significant results are found
153 (Stevenson 2001).

154 Studies on folivorous primates are exceptional because a single habitat
155 parameter is known to correlate with their biomass. Milton (1979) proposed
156 that the protein-to-fiber ratio of leaves was an important criterion for leaf
157 selection by primates, whereby leaves with higher protein and low fiber ratios
158 were selected. This preference has been demonstrated for a large number of
159 primates (Chapman and Chapman 2002; Ganzhorn 2002; Hanya and Bernard
160 2012). Fiber is often considered an antifeedant because it requires
161 fermentation by symbiotic microbes and the cellulose and hemicellulose
162 components of the fiber is typically only partially digestible by folivores (McNab

163 2002). Furthermore, nitrogen is the limiting nutrient in many terrestrial
164 ecosystems and since it is primarily found in protein, herbivores should
165 compensate for this limitation by choosing high protein foods (White 1993).
166 These important ideas proposed by Milton have been applied at the population
167 level by others (McKey et al. 1981; Waterman et al. 1988; Oates et al. 1990;
168 Davies 1994; Chapman et al. 2002). For example, Waterman et al. (1988)
169 proposed that the weighted contributions of the protein-to-fiber ratios of the
170 mature leaves of the most abundant trees in a particular area could predict the
171 biomass of folivorous colobines. This index of dietary quality has been
172 successfully applied to predict the biomass of folivorous monkeys at local
173 (Chapman et al. 2002; Ganzhorn 2002) and regional scales (Waterman et al.
174 1988; Oates et al. 1990; Ganzhorn 1995; Chapman et al. 2004; Fashing et al.
175 2007). Davies (1994) suggested that the year-round availability of digestible
176 mature leaves with high protein-to-fiber ratios, which are used by colobus
177 species when other, more preferred foods are unavailable, serves to limit the
178 size of colobine populations (i.e., high protein-to-fiber mature leaves are
179 important fallback foods). However, some colobines rarely eat mature leaves
180 since young leaves are always available, yet their biomass can still be predicted
181 by this index (Chapman et al. 2004). Thus, the protein-to fiber ratio of mature
182 leaves in an area may be correlated with the protein-to-fiber ratio of foods in
183 general. This is supported by the fact that in a sample of leaves from Kibale
184 National Park, Uganda, it was documented that the protein-to-fiber ratio of
185 mature and young leaves were strongly correlated ($r=0.837$, $P<0.001$; Chapman
186 et al. 2004). Thus, measuring the protein-to-fiber ratio of mature leaves may be
187 useful because it correlates with the general availability of high-protein, low-fiber

188 foods, and thus is a useful index of habitat quality for colobus monkeys. The
189 mechanism on how this parameter affects primate abundance remains unclear
190 as this ratio may correlate with other leaf constituents that really drive the
191 relationship (Chapman et al. 2002). For example, Wallis et al. (2012) suggest
192 that available nitrogen concentration of leaves, which takes both fiber and tannin
193 content, is a real influencing factor on folivore leaf choice. More research is
194 needed to determine why the protein-to-fiber index predicts folivore biomass.

195 Studies of frugivorous primates similarly indicate the importance of food
196 resources, but suggest that in addition to food quantity, seasonality is also
197 critical in regulating primate populations. For example, Hanya et al. (2004)
198 examined the effects of both total annual fruit production and the degree of
199 seasonality in fruiting (number of months when no fruit is available) on the
200 density of a Japanese macaque (*Macaca fuscata*) population in Yakushima.
201 They indicated that total annual fruit production, affected density more than
202 seasonality. Japanese macaques survive the lean season (winter) not only by
203 consuming the food available during that period (mature leaves) but also by
204 using the fat accumulated by eating fruits and seeds during the period of high
205 fruit availability (Hanya 2004). Therefore, in an altitudinal zone where fruit
206 production is low, macaques need to range over a large area to accumulate
207 sufficient fat stores and as a result, density is low. Hanya et al. (2006) tested
208 this idea through a meta-analysis across the species range and documented
209 that density was consistently higher in evergreen as compared to deciduous
210 habitats (Takasaki 1981b; Takasaki 1981a; Hanya et al. 2006). In winter,
211 Japanese macaques rely on mature leaves in evergreen forest and on buds and
212 barks in deciduous forest (Iwamoto 1982; Nakagawa 1989a; Hill 1997; Tsuji et al.

213 2008), thus food deficiency in winter is more severe in deciduous than in
214 evergreen forests (Nakagawa et al. 1996). Therefore, even if the total annual
215 fruit production is constant, macaques in deciduous forest need to range over a
216 larger area before winter to accumulate sufficient fat stores to last the winter. In
217 fact, home range size tends to be the largest in summer or autumn, not in winter
218 (Hanya et al. 2006). The combined influence of the seasonality and total
219 annual food abundance on primates is supported by the meta-analysis of 16
220 frugivorous primate communities in the Old and New Worlds (Hanya et al. 2011).
221 In this study, the best-fit model predicting primate abundance included both total
222 annual fruit fall (+) and its seasonality (-, assessed by coefficient of variation of
223 monthly fruit fall). This result suggests that, when food availability varies
224 seasonally, primates have access to less food or lower-quality food during the
225 food-scarce season than when food is equally available throughout the year.

226

227 **Coping with seasonality: two hypotheses on the resource limitation**

228 Primates primarily respond to seasonal variation of food availability by shifting
229 their diet (van Schaik et al. 1993). Recent studies on primate feeding ecology
230 have categorized foods into preferred and fallback foods (Lambert 2007;
231 Marshall and Wrangham 2007; Marshall et al. 2009). Preferred food is one
232 which is of high quality and is eaten more than the relative abundance in the
233 habitat. Availability of preferred foods is usually limited and its seasonal
234 consumption correlates with that of availability. Fallback food is one which is of
235 lower quality than preferred foods but available throughout a year and eaten
236 when preferred foods are less available. Among the above-mentioned
237 Japanese macaque foods, for example, fruit and seed are preferred foods and

238 mature leaf, bud, and bark are fallback foods (Hanya 2004; Tsuji et al. 2008).
239 Fallback foods can vary in quality from those that are sufficiently nutritious to
240 support the population to those that cannot (Lambert 2007).
241 Which is more important in limiting primate populations, preferred or
242 fallback foods? This question is central to the problem of how seasonality
243 affects primate abundance. Food may be sufficiently abundant most of the year,
244 but when it decreases dramatically in one season, it may act as an 'ecological
245 crunch,' or 'bottleneck', and primate density may be limited by food availability
246 only during this lean season (Cant 1980). From this view, fallback foods could
247 serve as limiting factors of primate abundance. Studies on Japanese
248 macaques indicate that both fallback food quality and total annual abundance of
249 preferred food affect macaque density (Hanya et al. 2004; Hanya et al. 2006).
250 However, three conditions influence the nature of how fallback food influence
251 populations: (1) animals cannot satisfy nutritional requirements only by fallback
252 foods, (2) animals are capable of 'saving' foods, such as fat accumulation or
253 scatter-hoarding, and (3) fallback food is superabundant. With regard to the
254 first condition, some primates rely on fallback foods which are of higher quality,
255 such as fig fruits, than those of Japanese macaques (Lambert 2007). Unlike
256 Japanese macaques, animals may be able to satisfy nutritional requirements
257 with these foods, but the availability are expected to be limited (Lambert 2007).
258 In fact, fig tree density correlates with orangutan (*Pongo abelii*) and gibbon
259 (*Hylobates* spp) density in some locations (Wich et al. 2004; Marshall and
260 Leighton 2006). Gibbon density was not correlated with the overall food tree
261 density, suggesting abundance of fallback food is more important than the total
262 annual food availability (Marshall and Leighton 2006). Concerning the second

263 condition, fat accumulation has been reported in temperate macaques,
264 orangutans, many lemurs, and humans (Wada 1975; Zhao 1994; Knott 1998;
265 Atsalis 1999; Muroyama et al. 2006), but it has not been carefully examined for
266 most species. As for the third condition, leaves are often considered a
267 superabundant fallback food; however, the quality of leaves is quite variable and
268 primates are very selective with respect to leaf quality (Milton 1979; Ganzhorn
269 1992; Chapman and Chapman 2002; Hanya and Bernard 2012) . To determine
270 if leaves can be a superabundant fallback food, we need to know if the leaf
271 quality that is required for the animal's digestive ability to extract sufficient
272 nutrients is suitable and that leaf production of this required quality is sufficiently
273 high to maintain the primate population. This information is generally
274 unavailable, but there is a growing body of evidence that even folivorous
275 primates experience food competition (Snaith and Chapman 2007; Tombak et al.
276 2012).

277 Based on this, we propose two hypotheses concerning mechanisms of
278 resource limitation (Table 1). First, when fallback food quality is too low to
279 satisfy nutritional requirement but it is superabundant, total annual food quantity
280 of preferred foods should affect animal abundance. This relationship can be
281 modified by the quality (condition C in Table 1) of fallback foods. Fat
282 accumulating Japanese macaques are one example (Hanya et al. 2004) for the
283 hypothesis, but an example of folivorous sportive lemur (*Lepilemur ruficaudatus*)
284 may tell that another mechanism is feasible for this hypothesis to work. This
285 species eat nutrient-rich young leaves and reproduce in wet season and fall
286 back to mature leaves in dry season, when young leaves are not available.
287 They survive the lean season by keeping the extremely low metabolic rate and

288 low levels of activity (Schmid and Ganzhorn 1996). Their abundance correlates
289 with the product of quantity (number of food trees) and quality (protein to fiber
290 ratio) of young leaves during the food-abundant wet season (Ganzhorn 2002).
291 This index would likely correlate with the quantity of young leaves that is above a
292 certain level of nutritional quality, thus the findings of this species support our
293 hypothesis.

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

302 In addition to the above two conditions, two more conditions are
303 conceivable. When fallback food quality is too low to satisfy nutritional
304 requirement, and its quantity is limited (condition D), we cannot make
305 predictions because in principle both preferred and fallback food quantity can
306 affect animal abundance. We expect that the animal abundance would be
307 determined by the food which is more limited (i.e., the one that requires larger
308 home range to secure the species requirements). When fallback food quality
309 is high enough to satisfy nutritional requirement and quantity is superabundant,
310 animals are, in principle, not limited by food (conditions A). It is not clear
311 whether this last condition occurs naturally, but colobines living at extremely
312 high density, exceeding 200 individuals/km² (Watanabe 1981), may be included

313 in this category. In fact, Yeager and Kirkpatrick (1998) consider the
314 abundance of Asian colobines are limited by non-food factors, such as social
315 stress. However, the assumed quantity and quality of fallback foods available
316 to colobines has recently been questioned (Snaith and Chapman 2007).

317

318 **Studies on resource limitation at the behavioral level**

319 It is important to know whether animals can satisfy their nutritional requirements
320 by the consumption of fallback foods. The simplest means of examining this is
321 to quantify if the animals intake is lower than their requirements. For Japanese
322 macaques, their energy intake becomes only 60-90% of the requirement in
323 winter, when they fall back to mature leaves, buds, and barks (Iwamoto 1982;
324 Nakagawa 1989a; Tsuji et al. 2008). They become energy deficiency in two
325 ways (Nakagawa et al. 1996). First, energy content of mature leaves that are
326 their fallback foods is sometimes so low that animals cannot extract sufficient
327 nutrients even if they eat up to their gut capacity (Mori 1979b). Second, some
328 foods, such as buds, are so small that animals cannot eat enough even if they
329 spend most of their day feeding (Nakagawa et al. 1996). In fact, Japanese
330 macaques in deciduous forest spend almost 70% of their day feeding in the
331 winter (Nakagawa 1989b).

332 Deficiency in macronutrients can also be shown by urinalysis that
333 quantify ketone and c-peptide concentrations as indices of energy balance
334 (Harris et al. 2009; Harrison et al. 2010; MacIntosh et al. 2012) and urea and
335 $\delta^{15}\text{N}$ for protein balance (Vogel et al. 2012a). Using these techniques, Bornean
336 orangutans (*Pongo pygmaeus*) are shown to suffer from severe energy and
337 protein deficiencies during periods of fruit scarcity (Knott 1998; Vogel et al.

338 2012b).

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

355 In addition to macronutrients, animals may also be limited by
356 micronutrients, such as minerals or vitamins (Janson and Chapman 1999).
357 Currently very little is known about micronutrient limitation in primates, but
358 several lines of evidence indicates its importance. First, sodium (Na) makes up
359 90% of total blood cations and is necessary for animal muscle contraction, nerve
360 impulse transmission, acid-base balance, and metabolism (Robbins 1993), but
361 plants do not require it. Thus, animals eating only plants typically need a
362 sodium source other than their main food. Second, some primates select food

363 with high mineral content (Magliocca and Gautier-Hion 2002; Rode et al. 2003).
364 Third, some primates obtain sodium from unusual feeding locations, such as
365 swamp plants, salt licks, or eucalyptus plantations, and the availability of these
366 locations is often limited (Oates 1978; Harris and Chapman 2007; Matsubayashi
367 et al. 2011). Fourth, mineral availability is known to affect spatial distribution of
368 herbivorous African ungulates (McNaughton 1988) and a colobine monkey
369 (*Colobus guereza*) (Harris and Chapman 2007). To our knowledge, there is
370 only one study that examines the effect of minerals on primate abundance (Rode
371 et al. 2006). Among the four sites within the Kibale National Park, the density
372 of redtail monkeys (*Cercopithecus ascanius*) was associated with the copper
373 intake level (mg/day); however, copper availability was not quantified, thus it is
374 difficult to judge what limits this population.

375

376 **Linking feeding ecology and primate abundance: future perspectives**

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

385 Given the time it typically takes for primate populations to respond to a
386 change in the nature of their food resources, there are only a few study sites
387 where the data will be likely to be available to study determinants of primate

388 populations in the way that we have just suggested. However, a convenient
389 alternative means of examining this issue is to analyze seasonal variation in
390 home range size. Population density is the inverse of per capita home range
391 size and is modified by the degree of overlap of home range between
392 neighboring groups (Whitesides et al. 1988). Thus, an index of population
393 density can be obtained during the season when the animal range most
394 extensively, which is likely the season that limits animal abundance. Hanya et
395 al. (2006) suggests that the limiting season for Japanese macaques is summer
396 and autumn because home range size becomes largest at that time. Based on
397 our hypotheses concerning the effect of seasonality on animal abundance,
398 animals that are limited by fallback foods are predicted to have a largest home
399 range in the food-scarce period. In contrast, animals that rely on fat
400 accumulated by eating preferred foods are predicted to range most extensively
401 during the food-rich period.

402

403 In conclusion, we propose two mechanisms concerning how resource
404 availability and its seasonality determine animal abundance. When fallback
405 food quality is too low to satisfy nutritional requirement, total annual food quantity
406 affect animal abundance, and this relationship is modified by the quality of
407 fallback foods. When fallback food quality is high enough to satisfy nutritional
408 requirement but quantity is limited, quantity of fallback food is a limiting factor.
409 Examinations of seasonal variations of home range size will be useful to
410 determine the limiting season. For a direct test of the hypotheses, we need to
411 know the threshold value of quality of food that satisfies the animal's nutritional
412 requirement, and the quantity of production in the habitat that supplies nutrients

413 to animals.

414

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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	-

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