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**17. How variable is a primate`s world:  
Spatial and temporal variation in potential ecological drivers of behaviour?**

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32 **Abstract**

33           The field of primatology has reached the stage where there are sufficient long-term  
34 studies and many shorter investigations on the same species at many different locations, that we  
35 are able to appreciate how variable the behaviour of primates can be and how predictable their  
36 environment is over space and time. For example, redbtail monkeys (*Cercopithecus ascanius*)  
37 exhibit extreme flexibility in diet; i.e., within the same national park, the amount of time they  
38 spend eating fruit varies from 36 to 60% of their foraging time and among populations time spent  
39 eating fruit ranges from 13 to 61%. Similarly, long-term phenological data from the same area  
40 encompassing over two decades illustrate that fruit availability can vary among years by as much  
41 as eight-fold. While data have steadily accumulated on how variable primate behaviour and  
42 proposed environmental predictors of behaviour can be, this information has not been used to  
43 effectively re-evaluate theory. For example, current primate socioecological theory has derived  
44 general frameworks using the average behavioural traits of species or genera, but these new data  
45 suggest it is inappropriate to use such averages. Similarly, environments have often been  
46 characterized by single studies of two years or less, which does not sufficiently account for  
47 environmental variation. Here, we present examples of behavioural and ecological variation and  
48 consider ways that our field could advance in the future by considering this variation.

49  
50 **Keywords:** Diet, Social organization, Ecological determinants, Group size, Standardized  
51 methods

52

## 53 **17.1 Introduction**

54           Socioecological research has traditionally been a central theme in behavioural studies of  
55 primates (Eisenberg et al. 1972, Clutton-Brock and Harvey 1977, Wrangham 1980, Terborgh  
56 1983, Janson and van Schaik 1988, Sterck et al. 1997). In the broadest sense, this research has  
57 involved investigations into how primate behaviour, social structure, and organization are  
58 influenced by a species' or population's environment. Such research has also been used to  
59 develop theories concerning groups size (Chapman et al. 1995, Gogarten et al. 2015), feeding  
60 strategies and competition (Janson 2000, Clutton-Brock and Janson 2012), and dominance  
61 relationships (Wright 1999), just to name a few. Thus, this is one area of research where primate  
62 studies have contributed most to the development of general theoretical models and gathering  
63 empirical data to test these models has stimulated extensive primate research and involved the  
64 quantification of their environment (Clutton-Brock and Janson 2012).

65           Perhaps one area of such research that deserves special mention is the development of  
66 what has become known as the "Primate Socioecological Model" (Clutton-Brock and Harvey  
67 1977, Isbell 1991, Koenig and Borries 2006, Snaith and Chapman 2007). Since the early 1980s  
68 researchers have built theories concerning the consequences of feeding competition on group  
69 size and social relationships (Wrangham 1979, 1980, van Schaik 1983, van Schaik 1989). In  
70 brief, it became widely accepted that if food resources were uniformly distributed in small  
71 patches of even quality that could not be defended and monopolized, or in very large patches  
72 where the whole group could simultaneously feed, then food competition would not occur  
73 through outright contest. Rather, animals would scramble to acquire the food items first. Under  
74 these ecological conditions, it is suggested that female fitness would be affected primarily by  
75 group size, and individuals would not be able to increase food acquisition through aggression. In

76 contrast, when food resources occurred in well-defined, defensible patches that varied in quality  
77 and were not large enough for all group members to feed simultaneously, then aggression over  
78 food would occur among group members. This logic lead to a series of predictions regarding  
79 female dispersal and social relationships under various competitive regimes (Janson and  
80 van Schaik 1988, Isbell 1991, Sterck et al. 1997, Koenig 2002, Snaith and Chapman 2007, 2008).

81 A second area of research on how the environment influences primate groups that  
82 deserves special mention deals with the expression of atypical patterns in social and sexual  
83 behavior and morphology in the lemurs of Madagascar. It is suggested that Madagascar has an  
84 unpredictable climate, causing unreliable fruiting patterns, which results in these atypical  
85 patterns because female lemurs have an elevated energy need associated with reproduction  
86 compared to female primates from other geographical areas. This explanation has been called the  
87 Energy Frugality Model (EFH; Wright 1999). To support this hypothesis, it is necessary to  
88 demonstrate that Madagascar, where female dominance is common, has a more unpredictable  
89 climate and fruiting patterns than other tropical regions where male dominance is the norm. To  
90 fully assess resource availability and predictability for testing the EFH hypothesis the data must  
91 result from long-term phenology studies that span multiple cycles of climatic variation; but how  
92 many cycles? So, a question that needs to be asked is: How many years of monitoring is needed  
93 to assess inter-annual variability in fruiting?

94 To answer such questions, description of changing patterns of resource availability must  
95 be carefully considered. For example, a system could be highly variable (wet one season, dry the  
96 next), but highly predictable (the seasons occur at same time every year, and the amount of rain  
97 is similar from year to year), or it could exhibit the same variability, but be unpredictable (rains  
98 come at any time of the year and with varying amounts). It is when resource conditions are

99 predictable that we most likely expect to observe strategies develop for resource acquisition. Of  
100 course, the timeframe over which the data are available influences this characterization. For  
101 example, a system could have wet and dry seasons occurring at the same time every year, but a  
102 20-year study could document the same annual rainfall for four years, that are followed by a  
103 period of slowly decreasing rainfall for eight years, followed by five years of stable rainfall, and  
104 three years of slowly increasing rainfall. Examining any pair of adjacent years (many ecological  
105 studies are two years or less) would suggest that the rainfall was predictable, but over the two  
106 decades, it is evident that the rainfall is unpredictable. Colwell (1974) presents a detailed  
107 consideration of these terms with respect to plant phenology.

108         Testing any general theories such as these, points to the importance of understanding how  
109 well the proposed ecological determinants can be assessed. Any such assessment depends on  
110 how well the variables of interest are represented by the sampling, both from temporal and  
111 spatial perspectives, and on the accuracy with which the ecological variable proposed as a  
112 selective force is measured. The field of primatology has reached the stage where there are  
113 sufficient long-term studies and many shorter investigations on the same species at many  
114 different locations, that we are able to appreciate how variable the behaviour of primates can be  
115 and how predictable their environment is over space and time. Over the last three decades there  
116 has been an impressive accumulation of data on the diets and behaviour of wild primates,  
117 enabling more informed intraspecific comparisons (Butynski 1990, Davies et al. 1999, Chapman  
118 and Rothman 2009). Similarly, there are now a growing number of long-term studies available to  
119 examine year to year variation in ecological variables used in theoretical arguments (Chapman et  
120 al. 2005b, Alberts and Altmann 2012, Fedigan and Jack 2012, Kappeler and Watts 2012,  
121 Campos et al. 2017, Chapman et al. 2017, Hogan and Melin, this Volume).

122           Based on the perspective that the variation and predictability of ecological factors is  
123 important for understanding of the evolution of a trait, our objective is to address three issues:

124           **1)** At what temporal scale must monitoring be conducted to adequately represent the  
125 variability and predictability that systems typically experience? How often are any one or two  
126 years of sampling, as is typically done when developing theory, representative of reality?

127           **2)** At what spatial scale must monitoring be conducted to adequately represent the  
128 variability and predictability that the system experiences? How often is the sampling of one or  
129 two sites, as is typically done when developing theory, representative of reality?

130           **3)** Do the indices used to measure the ecological variables of interest represent reality?

131

132           This evaluation is done within a relatively simple evolutionary framework. We believe it  
133 may be helpful to state our framework because it is the basis with which ecological factors can  
134 influence behaviour and because the framework is very frequently not considered. Within the  
135 ecological time frame that is used to test ideas, this framework assumes that if a trait within a  
136 population at one time or location is being favored by a specific selective force, it cannot be  
137 countered by an opposing selective pressure at another point in time or at another location, if  
138 directional selection is to occur. Stated with respect to the situation under consideration, if one  
139 population at a specific location or time (ecological timeframe) is experiencing selection for a  
140 behaviour, and interbreeds with another population experiencing a very different or opposing  
141 selection of similar magnitude, no change in behaviour will occur. When studies are made only  
142 at one location or at one point in time and evolutionary conclusion are drawn, we are assuming  
143 that selection is operating in the same way for all members of the population which may be  
144 spread across hundreds or thousands of square kilometers and it is occurring over a meaningful

145 duration. Is this a reasonable assumption? A meaningful duration from an evolutionary  
146 perspective will involve multiple generations, and given that chimpanzee generation time is 24.6  
147 year (Langergraber et al. 2012), we are typically looking at consistent selection pressures over  
148 decades or centuries.

149

150 **17.2.1 At what temporal scale must monitoring be conducted to adequately represent the**  
151 **variability that systems typically experience?**

152 The availability of food resources is frequently the basis of hypotheses used to explain  
153 variation in primate behavioural and even anatomical characteristics. Numerous hypotheses have  
154 proposed that ecological variables, such as overall habitat wide food availability, seasonal  
155 shortages, and month to month variability in food are important selective forces (Oates et al.  
156 1990, Janson and Chapman 1999, Lambert 2009, Marshall et al. 2009). Testing such hypotheses  
157 involves evaluating food availability over time and thus involves the quantification of  
158 phenological patterns of plants. Proposed drivers of phenological patterns of tropical rain forests  
159 include rainfall, day length, irradiance, and temperature (Opler et al. 1976, Ashton et al. 1988,  
160 van Schaik et al. 1993, Newbery et al. 1998, but see Polansky and Boesch 2013, Chapman et al.  
161 In press), mode of seed dispersal (Smythe 1970, Wheelwright 1985), activity of pollinators or  
162 seed dispersers (Snow 1965, Frankie et al. 1974, Rathke and Lacey 1985), variation in  
163 germination conditions (Janzen 1967, Frankie et al. 1974), the potential to swamp the ability of  
164 seed predators to destroy seeds (Visser et al. 2011), life history traits (Davies and Ashton 1999,  
165 Pau et al. 2011), and relative abundance of the trees themselves (van Schaik et al. 1993). Each of  
166 these interacting drivers have the potential to be highly variable, thus it is not surprising that  
167 phenological parameters, like fruiting, have been documented to vary between weeks, months,

168 years, and even longer periods (e.g., El Nino cycles, Wright and Calderón 2006, Hogan and  
169 Melin, this Volume).

170 To investigate at what temporal scale primatologists typically need to consider, we will  
171 evaluate one theoretical argument in detail and subsequently briefly reflect on a number of other  
172 examples. A number of theories have been put forward to explain why lemurs characteristically  
173 differ from anthropoids with respect to features like female dominance, lack of sexual  
174 dimorphism regardless of mating system, sperm competition coupled with male-male aggression,  
175 high infant mortality, and strict seasonal breeding (Kappeler and Fichtel 2015). The most widely  
176 accepted hypothesis to explain such differences is the Energy Frugality Hypothesis (EFH) and  
177 the article naming the hypothesis has been cited 422 times as of March 5, 2018 (Wright 1999).  
178 This hypothesis claims that these lemur traits are adaptations to conserve energy or maximize use  
179 of scarce resources that were selected for to efficiently deal with the severe and unpredictable  
180 environment of Madagascar and the particularly high costs to females of food scarcity (Wright  
181 1999, Pochron et al. 2003, Dewar and Richard 2007, Dunham 2008).

182 An assumption of this hypothesis is that food resource availability is less predictable in  
183 Madagascar as compared to areas where these “lemur traits” are not found, like mainland Africa.  
184 Support for this hypothesis is largely derived from the study of Overdorff and colleagues  
185 (Overdorff 1996a, b) that monitored for 24 months 104 trees belonging to 26 species that  
186 contributed to the diet of brown lemurs (*Eulemur fulvus* and *E. rubriventer*) in Ranomafana  
187 National Park. Over those two years there were five months when fruit resources were  
188 considered to be scarce. Based on these observations, Overdorff (1996a, b) concluded that  
189 fruiting phenology is unpredictable and resources are unreliable for primates in Malagasy forests,  
190 supporting the EFH.



191           These wet forest studies have been influential in subsequent research in Madagascar,  
192 despite their limited duration, small sample sizes, and importantly, the lack of direct comparisons  
193 to tropical wet forests elsewhere. To test this difference in resource predictability between  
194 Madagascar and mainland Africa, Federman et al. (2017) analyzed phenology datasets and their  
195 environmental correlates from two tropical wet forests, the Réserve Naturelle Intégrale  
196 Betampona, Madagascar and Kibale National Park, Uganda. Temperature was a significant  
197 environmental predictor of fruit availability at both sites. However, contrary to what would be  
198 predicted by the EFH, long-term temperature data from both sites (15 years from Kibale and 14  
199 from Betampona) indicated that temperature was more predictable at Betampona than at Kibale.  
200 Most importantly, however, they found no evidence of a significant difference in the  
201 predictability of fruit between the two sites, which would be essential as support for the EFH.  
202 Since this theory is largely based on the two-year study of Overdorff, Federman et al. (2017) also  
203 analyzed the Kibale data at two-year intervals. Over a two-year period, Betampona experienced  
204 no months when fruiting was lower than 10% of the maximum observed amount of available  
205 fruit, while over a 15-year time frame Kibale experienced seven such months. When scarcity is  
206 defined as less than 25% of the maximum observed amount of fruit, Betampona experienced  
207 three consecutive months of scarcity (12.5% of the total period), while in the 15-year Kibale  
208 study there were 71 months of at least 25% scarcity (39.4% of the total period); also there were  
209 nine times where periods of scarcity constituted three or more consecutive months. This amounts  
210 to a period of scarcity at Kibale roughly every 1.5 years. Thus, when comparing two-year  
211 intervals at Kibale to the monitoring period at Betampona, fruiting predictability at Betampona  
212 falls within the range of two-year intervals from Kibale. Further, during the two years examined  
213 at each site, Betampona showed no long periods of fruit scarcity analogous to those observed by

214 Overdorff (Overdorff 1996a, b) at Ranomafana. Thus, these results conflict with the prevailing  
215 Energy Frugality Hypothesis, which proposes that the selective force behind many of lemurs  
216 unique features is the unpredictable resource availability or temperature in Madagascar.

217 Other examples of ideas being refuted when the data is sampled at different temporal  
218 scales are not difficult to find. For example, figs (*Ficus* spp.) have frequently been presented as  
219 examples of keystone plant resources in tropical forests (Terborgh 1986, Power et al. 1996) and  
220 textbooks have presented figs as a clear case of the keystone species concept (Bush 2000). Yet,  
221 to our knowledge whenever the concept has been tested using data at longer temporal scale than  
222 the original study by Terborgh (1986), figs were not found to be keystone resources (Gautier-  
223 Hion and Michaloud 1989, Peres 2000, Chapman et al. 2005a). If figs served as a keystone food  
224 resource they must be available during months when few trees were fruiting, which long-term  
225 data indicates does not occur (Chapman et al. 2005a).

226 The answer to our original question - at what temporal scale must monitoring be  
227 conducted to adequately represent the variability that systems typically experience? – is we do  
228 not know. The answer will depend on the question asked, the ecological variable of interest, and  
229 the primate species. With respect to questions involving the assessment of fruit availability, we  
230 have data from one location that provides some indication. Fruiting data from six species  
231 collected over the last 47 years from Kibale suggest that only after a decade does the assessment  
232 include times close (10%) of the overall maximum and minimum and include patterns of  
233 abundant and scarce years (Chapman unpublished data). Of course, researchers cannot wait a  
234 decade to publish!

235 As for solutions, we encourage updates to be presented and with online publishing this  
236 has become possible. Given the growing difficulty of maintaining funding over a decade, updates

237 should not be required to obtain the original intensity of sampling, but casual observations  
238 should be allowed to be posted (e.g., long-term researchers who have worked in the area for 30  
239 years say they have never seen a time with such fruit scarcity). Similarly, additions to online data  
240 sets should be encouraged. We strongly encourage that whenever possible researchers re-  
241 evaluate hypotheses that have become generally accepted, but were developed from limited data  
242 sets. We must critically evaluate what our academic community wants to consider a valuable  
243 contribution. For example, many journals do not publish case studies, but long-term data often  
244 involve case studies (Chapman and Peres 2001).

245

246 **17.2.2 At what spatial scale must monitoring be conducted to adequately represent the**  
247 **variability that the system experiences?**

248 Many theoretical arguments have used a dietary classification to assess interspecific  
249 differences in diet to predict evolution of traits, such as day range (Clutton-Brock and Harvey  
250 1977), brain size and intelligence (Dunbar 2003), morphology and physiology (Teaford and  
251 Walker 1984, McNab 2002), and life history (Leigh 1994). Such interspecific comparisons have  
252 been a foundation on which many primate theories have been advanced; however, there has been  
253 an accumulation of data on primate diets over the last four decades that has led to a growing  
254 appreciation of the magnitude of dietary variation within species (Butynski 1990, Chapman and  
255 Fedigan 1990, Davies et al. 1999, Chapman et al. 2002b). For example, redbelt monkey groups  
256 (*Cercopithecus ascanius*) within the same national park varied in the amount of time they spent  
257 foraging on leaves (13-35%), fruit (36-60%), and insects (15-31%; Chapman et al. 2002a). On a  
258 larger spatial scale, contrasting the diets of 11 groups of redbelt monkeys across a number of  
259 countries documented that the proportion of time spent eating different plant parts varies

260 dramatically (leaves 7–74%, fruit 13–61%, and insects 1–16%; Chapman et al. 2002a). Even  
261 greater levels of variation were found in blue monkeys (*Cercopithecus mitis*). Butynski (1990)  
262 studied four groups of blue monkeys at the same site and found that the amount of time feeding  
263 on fruit varied from 22 to 35%. Fruit intake varied among populations from 26% to 91%, and  
264 leaf intake varied from 3% to 47% (Chapman et al. 2002a). One population of blue monkeys has  
265 even been described to rely on bamboo (*Arundinaria alpina*) for 60% of its foraging time  
266 (Twinomugisha and Chapman 2008). Similar differences can be found when folivores are  
267 considered (Davies et al. 1999, Chapman et al. 2002b). When the scientific community only has  
268 one study, of one population, at one location, there is no way to evaluate if values used in  
269 interspecific comparisons are good representatives of the species or extreme outliers.

270         Yet again we cannot answer our question what is the needed spatial scale to sample to  
271 represent the variability of a system and again it will be dependent on the question, ecological  
272 variable of interest, and species. Of course, increasing the sample size will likely make it more  
273 representative and having sampled several distinct sites should result in insights if more variation  
274 is to be expected. Also, for many questions other mammals will be influenced in the same way as  
275 primates and therefore considering non-primate models will be useful (Clutton-Brock and Janson  
276 2012)

277

### 278 **17.2.3 Do the indices used to measure the ecological variables of interest represent reality?**

279         Lastly, we feel that it is important to emphasize that if the scientific community is to rely  
280 on indices to represent the ecological variables hypothesized to be selective pressures on primate  
281 behavior, these indices must accurately represent the ecological variable of interest.  
282 Unfortunately, very little research exists to evaluate the methods used to quantify many of the

283 variables of interest. Much of the theory that is central to primatological thinking was conceived  
284 and published prior to any significant quantification of the proposed driving ecological variables  
285 (Clutton-Brock and Janson 2012). At this time researchers used natural history observations to  
286 state, for instance, the time of the year when food was scarce. For example, it was often assumed  
287 that the dry season was the period of low food availability; however, recent phenological studies  
288 have shown that this is often not the case (Wright and Calderón 2006, Melin et al. 2014,  
289 Mosdossy et al. 2015, Chapman et al. In press). These natural history observations were used to  
290 develop theory, but have they been subsequently substantiated with rigorous methods? Here we  
291 address the reliability of methods to quantify of food abundance.

292         For many questions the first question must be considered when quantifying food  
293 availability is “what is food?” Tropical rain forests are extraordinarily species-rich, often with  
294 over 1000 woody species in an area of a few square kilometers (Croat 1978). Only a fraction of  
295 this diversity is consumed by any one primate species but knowing exactly which plants are  
296 potential foods is extremely difficult. Typical lists of plant foods for a single primate species  
297 vary from 60 to 200 species, and often these lists grow even after several years of study. Figure  
298 17.1 illustrates the number of food items (species and part, e.g., *Prunus africana* bark) that we  
299 identified as being eaten by a long-term red colobus study group over 9 years in Kibale. The  
300 expectation would be that as the duration of the study increased the rate of accumulation of new  
301 foods would decline and reach an asymptote. Researcher may debate when the asymptote should  
302 be reached, but most field researchers would view that this should occur well before 9 years. But  
303 it does not (Figure 17.1).

304         For most theoretical questions not *all foods* are important for the question being asked, as  
305 they are rarely eaten. Furthermore, it is a logistic impossibility to measure temporal changes in

306 the availability of *all foods*. As a result, researchers usually employ an operational definition of  
307 food, but there is no consistent operational definition of what is food, which is likely one of the  
308 most basic questions. At one extreme, some studies of frugivores assume that any fleshy fruit is a  
309 potential food, even when the study species has not been observed to eat that fruit (Terborgh  
310 1983). This assumption is partly justified by the fact that there is relatively little differentiation in  
311 the fruit parts of the diets of coexisting primate species (Terborgh 1983) and the fact that  
312 primates eat many species of fruit that are evolved to be dispersed by other animals (Janson  
313 1983). At the other extreme, some studies consider only those plant species the animals were  
314 seen to eat as food. Thus, possibly the top X number of food items eaten in a particular month is  
315 used as that month's index of food abundance. However, the operational definition of the X  
316 number can dramatically alter the estimate of the ecological parameter of interest. For example,  
317 during the first five years of research on spider monkey (*Ateles geoffroyi*) in Costa Rica  
318 (Chapman 1990), the animals were rarely seen to eat the fruits of *Bursera simaruba* (< 0.1 of  
319 their feeding time); however in the sixth year, the community fed on this fruit extensively  
320 (22.8%) during a month when little else was available. *Bursera simaruba* is a very common tree  
321 and including it in the diet of spider monkeys for the month that it was eaten increases the food  
322 density estimates by 20.3 food trees / ha. If the observations of feeding on *B. simaruba* fruit had  
323 not been made in the sixth year, it would not have been considered a food source. Similarly,  
324 using nine years of red colobus foraging data provides a second more robust example. The  
325 species to be included in a species diet can be indexed as including various indices of the 'top  
326 species', for example, only the top species eaten for the most time (species 1), the top two most  
327 eaten species (species 1+2), top three eaten species (species 1+2+3), or top X eaten species  
328 (species 1+2+3+4...X). Figure 17.2a depicts the 10 most frequently eaten species by red

329 colobus, while Figure 17.2b depicts the density of food trees including the top 1, top 2, and so on  
330 up to the top 10 species, and Figure 17.2c depicts the same species included in an index of food  
331 abundance, but weighting density by Diameter of Breast Height (DBH). It is evident that an  
332 increase in the number of species used in the index can cause a small or large increase in the  
333 density or basal area of what are considered resources. This is because some species frequently  
334 consumed by the red colobus are very rare, while other species are common. Furthermore, the  
335 pattern of increase is different if the density is weighted by DBH or not, which is simply a result  
336 that some commonly eaten species are large as adults, while others are not.

337         Unfortunately, once food has been defined, determining its abundance and value are both  
338 very difficult. Ideally a researcher would be able know the number of food items and their value  
339 to the primate in question in terms of how they regulate their population. Even for food items  
340 that occur in discrete patches such as trees, estimating abundance has proven extremely difficult.  
341 A number of indices have been proposed, but each varies in its accuracy and ease of measure  
342 (Chapman et al. 1995, Anderson et al. 2005, Bortolamiol et al. 2014). Estimates include a  
343 number of indices of the abundance of food item on a tree (e.g., DBH, basal area, modified basal  
344 area, ranked abundance) with DBH being the most common. With respect to evaluating the  
345 accuracy of DBH in predicting fruit biomass, Chapman et al. (1992) evaluated this relationship  
346 for four species of primate consumed trees in Kibale and found that *within a species* DBH  
347 explained an average of 47.2% of the variance in fruit biomass. However, generalizing this study  
348 to all primate foods should be done with extreme caution as it is limited to just four small  
349 understory species that one of the authors (CAC) could climb. Yet the limitations of this study  
350 have not been well considered and it has been cited 369 times, typically as a suitable way to  
351 measure food availability (as of September 21, 2017- google scholar). Such estimates of per tree

352 fruit abundance are then combined with estimates of the density of food trees calculated from  
353 vegetation plots (e.g., sum of the DBHs of all suitable food trees) and then weighted by the  
354 temporal variation in the abundance of the items (e.g., phenology trails, plots, fruit traps). In  
355 statistical terms, we only estimate the variable of interest once (e.g., fruit abundance in a  
356 particular month). If the index used only explains approximately 50% of the variance, as is the  
357 case with DBH and fruit biomass, and there are say 3 variables used to predict fruit abundance  
358 (e.g., DBH, density, and phenology) and each has even a small random error associated with  
359 measurement, then the accuracy of the estimate of fruit availability is low. Considering this, we  
360 are very surprised that primatologist have found statistically significant relationships as often as  
361 they have, which may imply that the relationships being examined are actually robust.

362         Lastly there is the question of the nutritional value of foods, which is very difficult to  
363 measure (Rothman et al. 2012), yet extremely important. The animal may be attempting to  
364 maximize energy (Rothman et al. 2011), protein to fiber balance (Chapman et al. 2004) or  
365 nutrients and minerals (Rode et al. 2003) and without a comprehensives study it is not possible to  
366 know which. Ideally a researcher would like to know the nutrient that is limiting the populations  
367 growth and consider it in detail; however, this requires a detailed nutritional analysis over a  
368 sufficiently long period where that nutrient's availability and the population abundance changed.  
369 Such data are rarely available.

370         Given such error and difficulties of defining food, it is not surprising that some of these  
371 measures do not even correlate. For example, estimates of fruit abundance derived from  
372 cumulative DBH of monthly fruiting trees do not correlate with estimates derived from fruit traps  
373 (Chapman et al. 1994). What this mean for advancing theory needs much more careful attention.



374           Of the three questions we posed at the start, it pleases us to be able to state that we can  
375 clearly answer this question. To the question “Do the indices used to measure the ecological  
376 variables of interest represent reality?” the answer is clearly NO. This means there are clear  
377 opportunities to advance the field by evaluating and comparing different methods. However,  
378 conducting the needed studies will take time. In the meantime, it only seems logical, IF the goal  
379 is to advance knowledge about primates, and NOT to advance personal CVs, researcher should  
380 be encouraged to use the mostly commonly agreed upon method and provide the results of each  
381 of these methods on in supplementary material, until the time that the “best” method is agreed  
382 upon. A classic, and unfortunate example involves how to estimate the number of primate  
383 species. It is our humble impression that a year does not go by without one or two papers are  
384 published.

385

386 Many of which are statistically elegant, but biologically naïve.

387

388

### 389 **17.3 Conclusions**

390           Our intent is not to be critical of the theories or studies we have mentioned, rather it is to  
391 use this example to illustrate that science is a process where ideas grow and are modified with  
392 the inclusion of new investigations, the use of new methods, and the maturation of the particular  
393 field. Early primate socioecological studies arrived at some very interesting concepts that have  
394 proven to be useful to advance our understanding of these intriguing animals. With the gradual  
395 accumulation of research on the same species at many different locations and of a few long-term  
396 studies, it has become apparent that there is a great deal of variability in both ecological variables

397 that potentially influence primates, and in primate behaviour. Thus, there is a need to assess this  
398 variability, evaluate the flexibility of primates over time, and to constantly re-evaluate our past  
399 theoretical advancements. Associated with this is a clear need to continue to improve the  
400 methods that we use to assess the ecology of primates.

401

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413

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605 **Figure Legends**

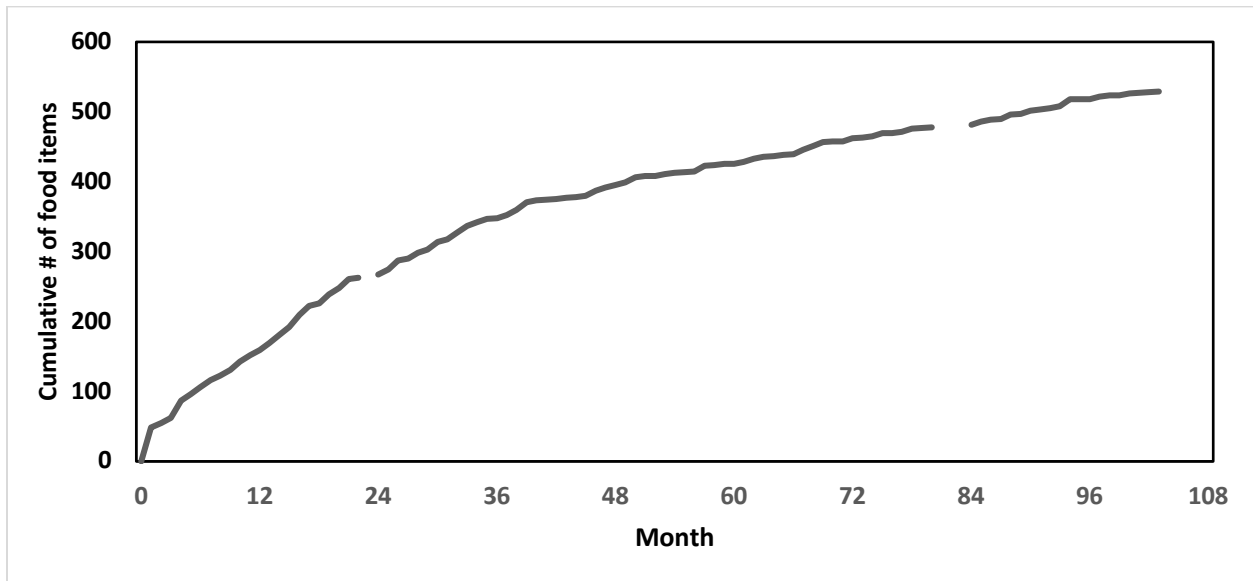
606

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608 Figure 17.1:

609 The number of food items (species and part) that we identified as being eaten by a long-term red  
610 colobus study group over 9 years in Kibale National Park, Uganda.

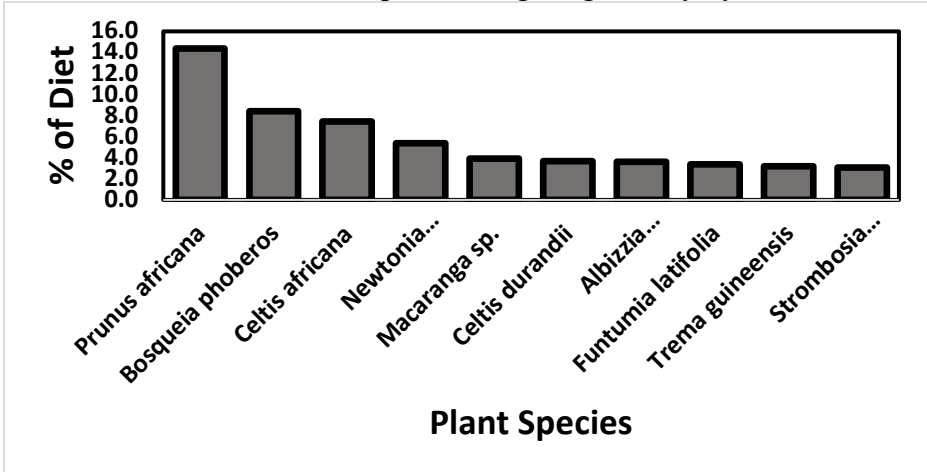
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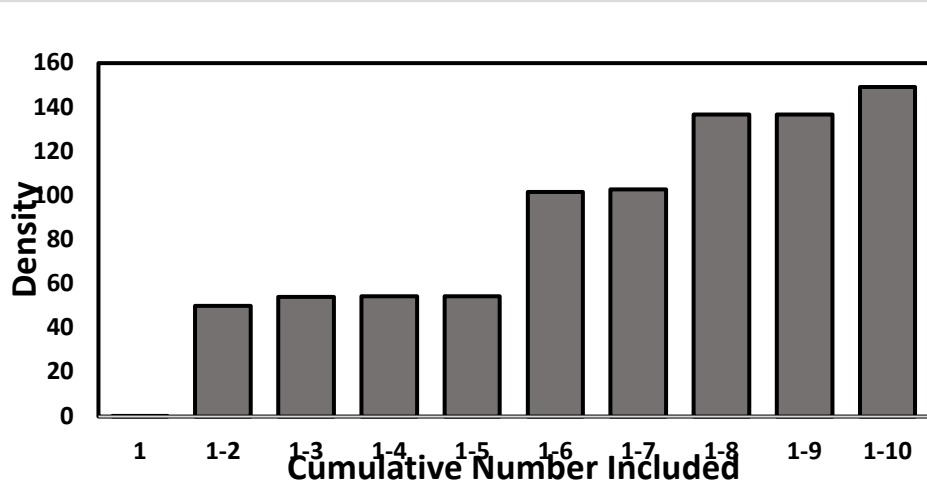
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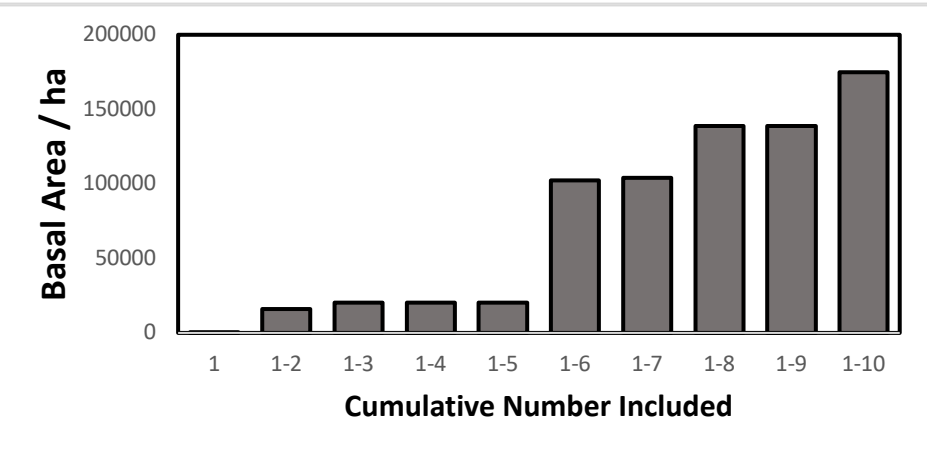
614 Figure 17.2:  
 615 Foraging behaviour of red colobus monkeys in Kibale National Park, Uganda. a) the 10 most  
 616 frequently eaten species in their diet as an index of food abundance, b) the cumulative density of  
 617 the red colobus food trees in Kibale National Park, Uganda including the top 1 species, top 1 and  
 618 2 species, top 1, top 2, top 3... top 10 as an index of food abundance, c) the cumulating density  
 619 of the red colobus food trees species weighting density by DBH as an index of food abundance.



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