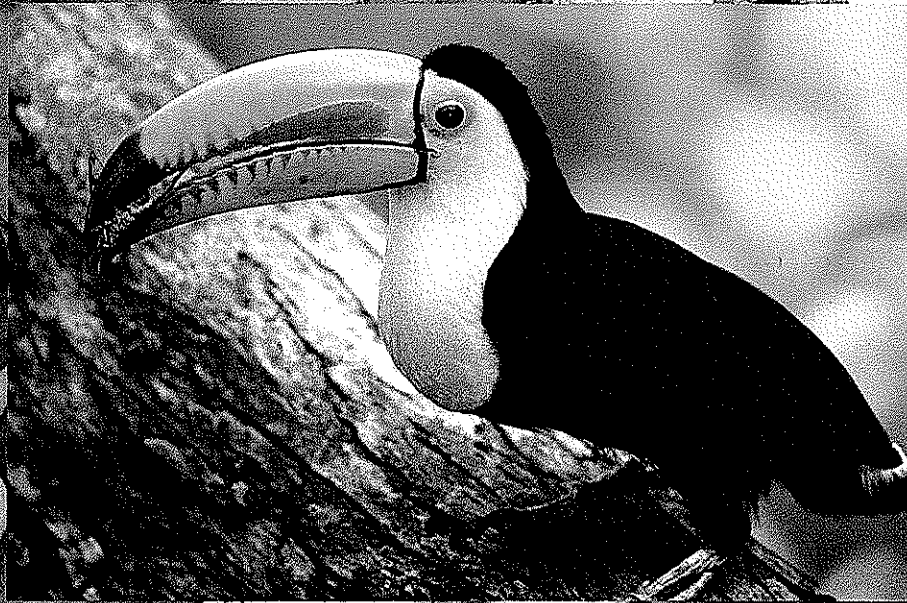




Tropical Fruits and Frugivores

The Search for Strong Interactors

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CHAPTER 2.

DO FRUGIVORE POPULATION FLUCTUATIONS REFLECT FRUIT PRODUCTION? EVIDENCE FROM PANAMA

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GRETCHEN STOCKMAYER

Abstract

To conserve tropical mammals, it is important to understand factors affecting the range of population fluctuations that normally occur over both the short and long term. Annual shifts in the population size of many species may be tied, at least in part, to phenological production patterns of plants, which in turn are often affected by climatic events. To examine the influence of annual fruit crop size on population dynamics of frugivorous mammals, we compared estimates of fruit production and the relative abundance of four frugivorous mammal species (agoutis, squirrels, capuchin monkeys, howler monkeys) for 15 years on Barro Colorado Island, Republic of Panama. Species differed in the magnitude of population fluctuation. Howler monkey population estimates showed little annual fluctuation and no significant relationship to fruit production. In contrast, population estimates for agoutis, squirrels and capuchin monkeys showed interannual fluctuations, at times dramatic, but these were not always concordant nor did they necessarily appear to relate to fruit production estimates, either within years or with a one- or two-year lag. Fruit production data suggest that, on average, in any given year only 20 to 30% of the mid-to-late rainy season species producing fruits important to frugivores will have an unusually good year; other species will have an average to sub-standard year. The next year, 20 to 30% of the other important fruit species in this temporal cohort will have an unusually good year—though one cannot predict in advance which species they will be. This oscillating production pattern makes it difficult to predict, except in extreme years, how the frugivore community or individual species will be affected by fruit availability. To draw conclusions on this topic, more detailed data are required on annual fruit production patterns of a representative sample of individuals of important fruit species as well as data on reproductive and other relevant traits of each mammal species. The possibility remains that many mammal populations may be affected more immediately by top-down factors such as predators, parasites or disease rather than by bottom-up factors such as fruit availability. As population parameters for each mammal species are likely influenced by a continuously varying combination of factors, barring effects of rare environmental events, the particular set of factors affecting the population dynamics of one frugivorous species in any given year may not necessarily impact similarly in that year on other frugivorous species at that same site.

Key words: Fruit production, population dynamics, tropical forests, Panama, mammals, monkeys, agoutis, squirrels, El Niño Southern Oscillation (ENSO)

INTRODUCTION

Tropical forests and their animal populations were once regarded as stable and unchanging (Karr & Freemark, 1983; Wikelski et al., 2000). Extensive research has shown, however, that tropical forests experience a wide range of climatic and other environmental fluctuations both within and between annual cycles, calling into question the hypothesized stability of their vertebrate populations (Foster, 1982a,b; Foster & Terborgh, 1998; Swaine et al., 1987; Whitmore, 1991; Wolda, 1983). It has been suggested that climatic fluctuations, particularly the timing and amount of rainfall received in a given region, may influence phenological production patterns, affecting fruit set (Alvin, 1960; Foster, 1982a,b; Matthews, 1963; Milton, 1982; Wright et al., 1999). In turn, the availability of edible fruits is hypothesized to play a critical role in the population dynamics of many frugivorous mammals inhabiting tropical forests (Foster, 1982a; Glanz et al., 1982; Leigh, 1999; Smythe et al., 1982; Van Schaik et al., 1993; Wright et al., 1999). It seems reasonable to assume that for any given site in years when fruit abundance is low many frugivore populations might decline due to a lack of suitable food. And in years when fruit abundance is high one might predict a corresponding increase in frugivore reproduction, survivorship, and total numbers.

Available evidence, however, suggests that the actual situation is neither as clear nor as linear and predictable as such assumptions imply. For example, it has been proposed that many tropical forest communities are characterized by the presence of *keystone* fruit resources (Gautier-Hion & Michaloud, 1989; Gilbert, 1980; Peres, 1994; Terborgh, 1983)—that is, resources available to a large component of the frugivore community during periods of forest-wide fruit scarcity which serve to buffer them until new crops of more preferred fruit species appear. In this scenario, keystone resources tide resident frugivores over during periods of forest-wide fruit scarcity, averting population declines. However, other data indicate that many frugivore species have specific “fallback” foods that can be relied on until better fruiting conditions prevail (Bodmer, 1990; Conklin-Brittain et al., 1998; Fragoso, 1998; Furuichi et al., 2001; Glanz et al., 1982; Milton, 1980; Smythe et al., 1982; Terborgh, 1987). How does the concept of community-wide keystone resources relate to observations of species-specific fallback foods?

Then there are long-standing demographic concepts such as density dependent mechanisms which imply that many animal populations have behavioral or other mechanisms (e.g., predators, parasites) that help maintain population size below levels at which food scarcity generally might pose a problem (Getz, 1996; Herre, 1993; Milton, 1982; but see Den Boer & Reddingius, 1996). Observations suggest that some frugivore populations oscillate notably in size over relatively short time periods whereas populations of other species appear stable for many generations (Giacalone-Madden et al., 1990; Milton, 1996). How can all of these concepts—keystone resources, fallback foods, density dependent mechanisms and so on—be reconciled with such disparate demographic observations?

Understanding factors which influence the population dynamics of tropical frugivores is clearly a problem of no small magnitude. It is also a problem of considerable current interest to ecologists and conservation biologists. Tropical moist forests are responsible for almost 32% of terrestrial net primary productivity and are a major resource of global importance (Leith & Whittaker, 1975). Seed dispersal by resident frugivores is believed to play a critical role in the continued maintenance of the high plant species diversity characteristic of tropical forests (Corlett, 2002; Dirzo & Miranda, 1991; Jordano & Godoy, 2002; Wright & Duber, 2001). Because of intensive habitat destruction and hunting pressures in many tropical regions, the opportunity to compile long-term data sets on plant-animal interactions over large expanses of undisturbed tropical forest may be running out. Yet a better understanding of such relationships is essential if we wish to make predictive statements about the causal factors which relate to natural shifts in frugivore densities and abundances at particular sites and the effects of such shifts on forest structure and composition (Andresen, 1994; Asquith et al., 1997, 1999; Dirzo & Miranda, 1991; 1999; Wright & Duber, 2001). The ability to accurately estimate the range of population fluctuations that normally occur over the short and long term also seems necessary for informed conservation decisions, which need to take into account the influence of reserve size and resource availability on the population dynamics of resident frugivores.

METHODS

In this paper, we compare 15 years of data (1987- 2001) on ripe fruit production with data on population censuses for four frugivorous mammal species living on Barro Colorado Island (BCI), Panama. Detailed descriptions of the history, flora and fauna of BCI are available in the literature (Foster & Brokaw, 1982; Leigh et al., 1982).

Study Site

To briefly review, BCI is a 1600 ha nature preserve, established in 1914. The entire island is densely covered in mature forest and old secondary growth (Foster & Brokaw, 1982; Milton, 1980). As BCI is a nature preserve, there is minimal interference in its ecology. Most animal species found on the island are the descendants of populations naturally occurring in the area prior to creation of the Panama Canal. Annual rainfall and fruit production patterns are presented later in the text.

Study Subjects

The four mammal species selected for examination were agoutis (*Dasyprocta punctata*), squirrels (*Sciurus granatensis*), capuchin monkeys (*Cebus capucinus*), and howler monkeys (*Alouatta palliata*). These four species are heavily dependent

on fruits in the diet (>40% of the annual diet from fruit in all cases) but differ in important ways in their life history strategies and uses of particular kinds of fruits.

Agoutis, which on BCI associate in pairs, are strictly terrestrial, relying on fallen fruits, often dropped by one of the other focal species in this study. They have specialized incisors that make it possible to feed on the large, hard seeds from genera such as *Dipteryx* (Fabaceae), *Astrocaryum* (Palmae), *Attalea* (Palmae), and *Socratea* (Palmae). Many such seeds are buried for storage, thus providing backup food supplies to help carry animals through shortages of fresh fruits (Smythe et al., 1982). Agoutis also feed heavily on a great variety of other fruits and flowers. They are relatively rapid breeders, since an adult female in good condition may breed up to three times per year, giving birth to one or two offspring each time. Mortality, hypothesized to relate to food shortages (Smythe et al., 1982), appears to affect immature individuals first, since adults defend territories and food caches.

Red-tailed squirrels, which are solitary, make use of the same hard seeds as agoutis, and may utilize stored supplies for many months after the fruits actually fall. Their diet is composed largely (ca. 99%) of plant material, mainly fruits, seeds, and some flowers (Giacalone-Madden et al., 1990; Glanz et al., 1982). In comparison with agoutis and monkeys, BCI squirrels have an extended season for use of these critical resources because they are arboreal, and can feed on seeds in trees before the pulp of the fruit is fully ripened. Squirrels often store seeds in tree cavities, out of reach of agoutis, and seeds comprise 50-90% or more of the diet, depending on time of year.

Squirrels on BCI may breed twice a year and produce litters with a mean size of just under two. Adult females, which may live for 8-9 years, defend territories (Giacalone, unpub.). Some data suggest a link between annual patterns of fruit abundance and the population dynamics of BCI squirrels. In times of poor fruit supply, for example, squirrels have been observed to drastically decrease breeding activity (Giacalone-Madden et al., 1990; Glanz et al., 1982). Squirrels rarely breed in the period August to December, a time of relatively low fruit availability on BCI (Foster, 1982; Milton, 1980, 1990, 1996; Wright et al., 1999) and usually begin breeding when *Dipteryx panamensis* fruits (considered an important dietary resource) begin to ripen in late December (Glanz et al., 1982).

White-faced monkeys (or capuchins) on BCI live in relatively closed social units averaging 8 individuals and composed of adults of both sexes and their immature offspring (Oppenheimer, 1982; Rowell & Mitchell, 1991). Capuchins rely heavily on small "bird fruits" in the diet as well as the soft parts of larger fruits. However, they cannot make use of seeds from some of the very hard fruits used by agoutis and squirrels, nor do they store seeds for later use. Capuchins are also seasonally dependent on invertebrates (10-40% of the diet, depending on time of year) and smaller vertebrates in the diet and these are consumed opportunistically on a daily basis along with ripe fruits (Oppenheimer, 1982; Rowell & Mitchell 1991). Capuchins usually produce one offspring every other year, but females are not reproductively active until their fourth or fifth year (Oppenheimer, 1982).

Howler monkeys on BCI live in relatively closed social units averaging 19 individuals and composed of adults of both sexes and their immature offspring

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Howler monkeys have no access to hard-shelled seeds, but feed heavily on softer ripe fruits whenever possible as well as portions of many immature fruits. Fruit-eating makes up $42.1 \pm 26.3\%$ of annual feeding time (Milton, 1980, mean ± 1 SD, $n = 9$ monthly values, covering all seasons). Howler monkeys, also rely heavily on leaves in the diet ($48.2 \pm 26.3\%$). Unlike the other three species in our sample, howler monkeys can live for weeks on diets composed largely or entirely of leaves (Milton, 1980). Female howlers typically give birth to a single offspring every 17-20 months and births can take place at any time of year (Milton, 1982).

The following analysis examines annual census data on these four mammal species to determine how successfully population declines or increases might be predicted based on annual fruit production data. Though we have an unusual wealth of comparative material on fruit production patterns, life histories, feeding records, and long-term censuses, our results emphasize nothing so much as the fact that much remains to be discovered about plant-animal interactions in tropical forests and how best to study them.

Data Sets: Rainfall and Fruitfall

Rainfall Patterns

As rainfall is believed to affect patterns of fruit production in tropical forests, we first examine rainfall data. BCI is characterized by an annual average of 2633 ± 462 mm of rainfall per year (mean ± 1 SD derived from 73 years of rainfall data, 1929-2001, provided by the Environmental Science Program, BCI). During the 15-year study period, rainfall showed considerable interannual variation (Fig. 1) and there were two El Niño Southern Oscillation (ENSO) years, 1992 and 1997.

The rainy season typically begins each year in mid-April and continues through November into December (Fig. 2). There is an approximately three-month-long dry season from January through March, when mean monthly rainfall averages 45 mm.

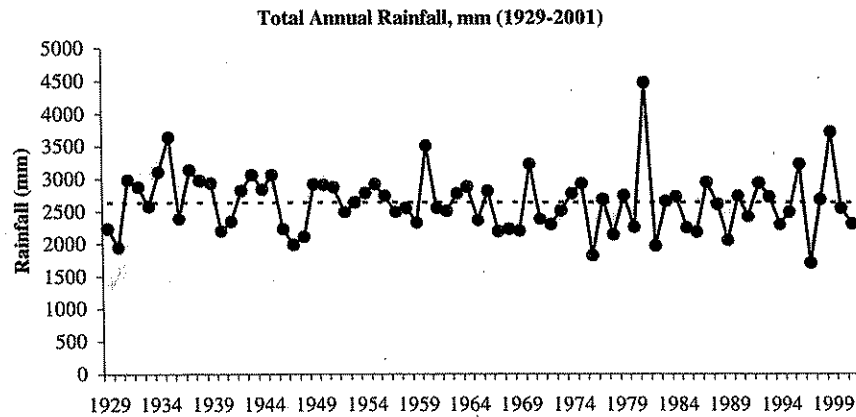


Figure 1. Total annual rainfall data for Barro Colorado Island (BCI) over a 73-yr period, 1929-2001. Annual average rainfall = 2633 ± 462 mm of rainfall. Dashed line at 2,633mm is the mean value for period 1929-2001.

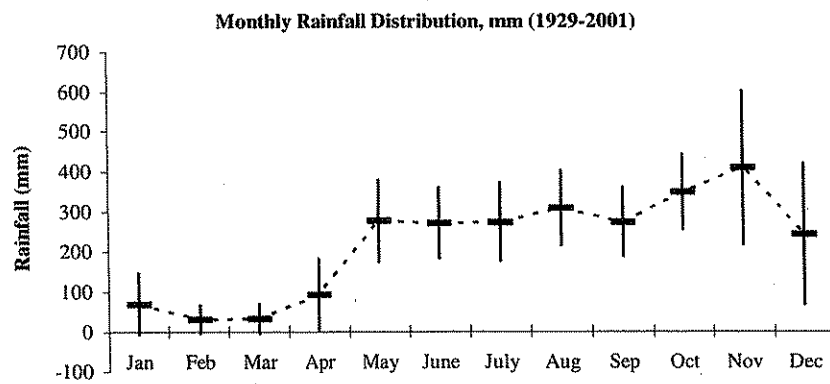


Figure 2. Average monthly rainfall in mm for BCI over a 73-yr period, 1929-2001. The solid lines and error bars represent mean monthly rainfall \pm one standard deviation.

Annual Fruit Production Patterns

Dry mass fruit production is considered perhaps the single best index of fruit availability for frugivores and granivores (Wright et al., 1999). This paper includes analysis of data collected from two sets of fruit traps. One data set is based on fruit dry mass, while the other relies on counts of seeds expressed as "seed equivalents."

Figure 3 shows summed monthly fruit dry mass production on BCI as determined weekly for 59 litter traps over 15-yr (1987-2001). Traps were randomly located in an area of older forest in the southwest section of the island known as Poachers' Peninsula (see Wright et al., 1999 for details of data collection). Monthly fruit production is more or less the inverse of monthly rainfall—in months when rainfall is low, fruitfall into traps is high, in months when rainfall is high, fruitfall into traps is low (Fig. 3). No bimodal annual pattern is detectable in fruit production or even oscillating peaks and valleys. Rather, dry mass fruit production typically rises to its annual peak around February of each year and stays elevated into April when, with one slight upward permutation in July, it gradually declines over the rest of the year (Fig. 3). Fruitfall typically reaches its annual low point during the two wettest months of the year, October and November.

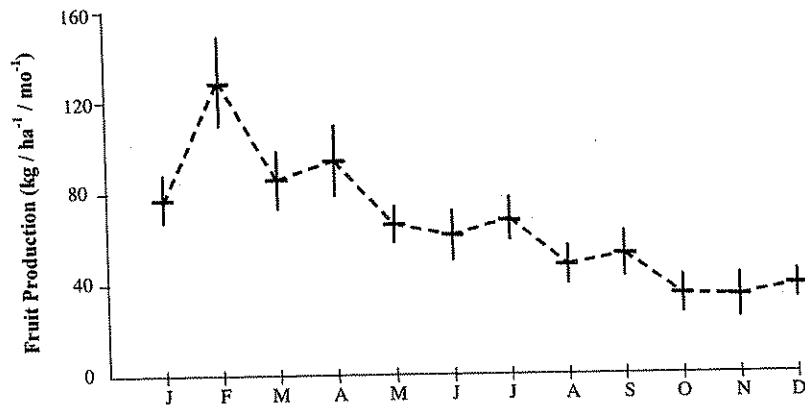


Figure 3. Monthly dry mass fruit production summed over all species for BCI over a 15-yr period. The solid lines and error bars represent mean productivity ± 1 SD (calculated from 1 Jan. 1987-31 Dec. 2001). Data derive from 59 fruit traps; see text for details of data collection.

The second data set uses data on "seed equivalents" derived from counts of fruits, seeds and other fruit parts falling into 200 litter traps placed in old growth

forest on the central plateau of the island (details of fruit trap placement and fruit collection are found in Wright et al., 1999). "Seed equivalents" for each species are expressed as the sum of seeds plus mature fruits of a species multiplied by the average seed-to-fruit ratio for each species. Seed equivalents could be divided by the seed-to-fruit ratio to estimate "fruit equivalents" or the number of fruits represented. We use seed equivalents as a relative index of fruit production throughout this paper because traps capture many more seeds than fruits.

The number of traps containing seeds or fruits of a species each week provides a measure of how widespread fruit production by that species was. The average number of fruit species per fruit trap per week provides a measure of how many species were maturing fruit and is useful for monthly and seasonal comparisons. Intact fruits falling into traps were also divided into two categories, mature or immature fruits, providing an additional data set on whole fruits in traps by species and their stage of maturation.

Subsample of Fruits Used by Focal Mammal Species

Seeds in traps come from all fruit types produced in the BCI forest and many of these species are not eaten by mammals. From all species in traps, we selected 60 species known to produce fruits of importance in the diet of one or more of our focal mammal species and examined annual fruit production patterns for these 60 species. For inclusion in analyses a species had to have at least one weekly sample in the 15-yr period with more than 50 seeds and more than five traps containing fruit of that species. Only 39 of the 60 species met these requirements. Unless otherwise noted, all production estimates discussed below derive from these 39 edible fruit species.¹

RESULTS

Patterns and Correlations

Fruit Production and Rainfall

When relative annual mature fruit production is compared with relative annual rainfall over the 15-yr study period (Fig. 4), no clear pattern emerges. No correlation was found between rainfall and mature fruit production either within years (Pearson correlation coefficient, $r=0.041$) or when annual rainfall was lagged back one ($r=0.461$) or two years ($r=-0.308$) relative to the year of fruit production.

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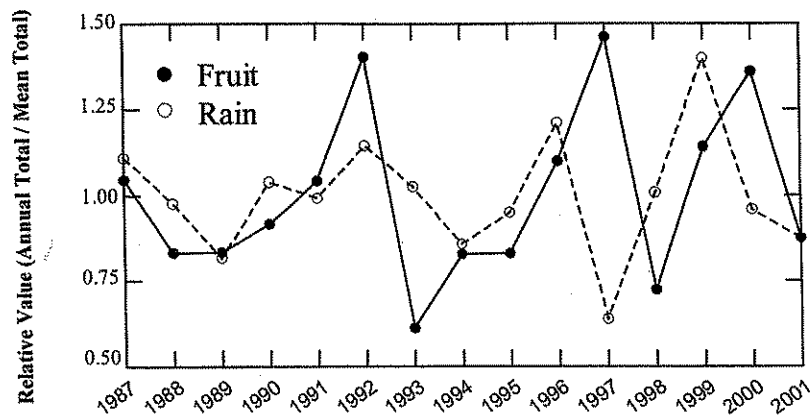


Figure 4. Relative annual rainfall expressed against relative annual fruit production over a 15-yr period on BCI. The dashed line represents rainfall while the solid line represents dry mass fruit production. Data derive from 200 fruit traps, see text for details of data collection.

Fruit Production for 39 Edible Species

Summed annual production data for the 39 edible species (Fig. 5a) as well as number of traps with fruits (Fig. 5b) showed interannual fluctuation. Annual fluctuations are best appreciated by viewing data on individual species. Fig. 6a and b shows annual fruit production patterns for *Quararibea asterolepis* (Bombacaceae) and *Coccoloba parimensis* (Polygonaceae), respectively, over the 15 yrs of the study. Such annual fluctuation was highly characteristic of most other species in this sample as well.

The pattern of monthly fruit production for the 39 edible species (Fig. 7a) is very similar to that shown in Fig. 3 for monthly fruit dry mass production for all species but the single broad peak for the 39 species, April and May, comes slightly later in the year than that for fruit production as a whole (Feb-April). The number of traps with fruit of one or more of the 39 species (Fig. 7b), in contrast, shows a peak in Aug-Oct. This August-October peak is largely attributable to *Trichilia tuberculata* (Meliaceae) and *Quararibea asterolepis*, which are the first and fifth most common canopy tree species in old growth forest on BCI. These very abundant species ripen fruit between August and October and seeds from these species reach most traps. Other fruit species in the diets of our four frugivore species are notably less abundant or produce far fewer seeds.

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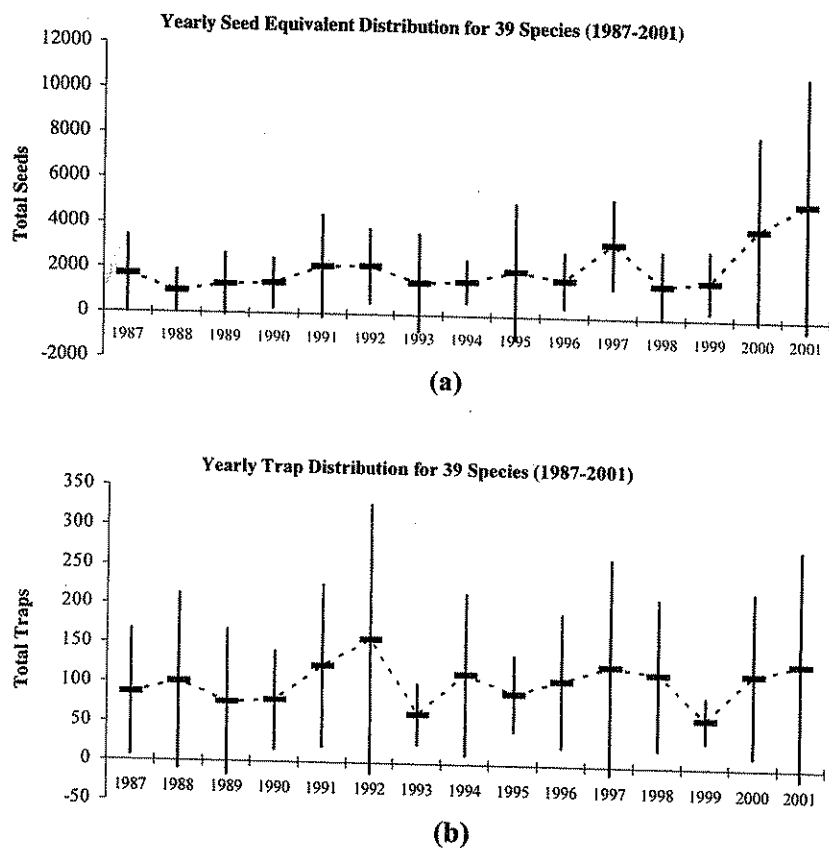


Figure 5. a) Summed annual fruit production (seed equivalent) data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal species. b) Summed annual fruit trap data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal species. For both figures, the solid lines and error bars represent mean values \pm one standard deviation.

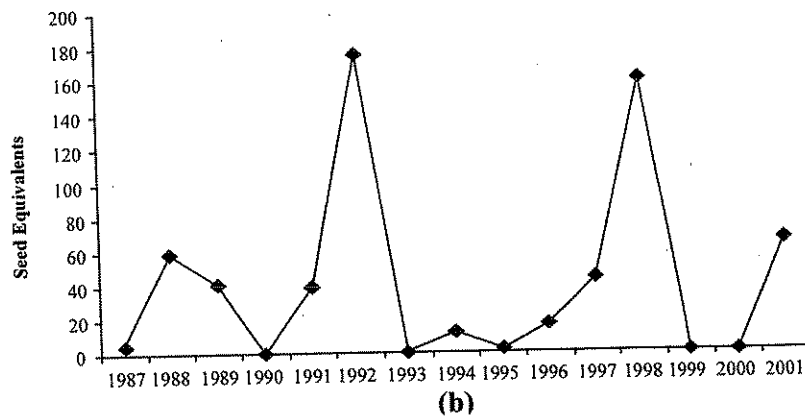
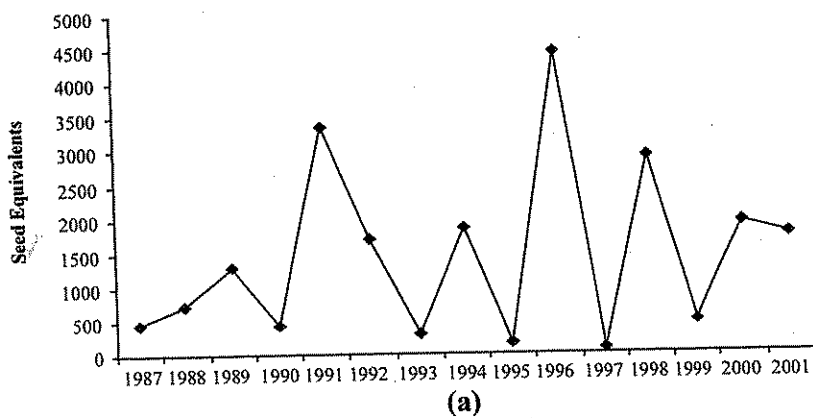
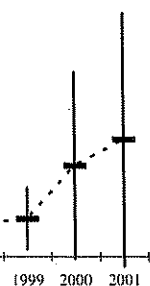


Figure 6. Annual fruit production data for a) *Quararibea asterolepis* and b) *Coccoloba paraensis* over a 15-yr period.



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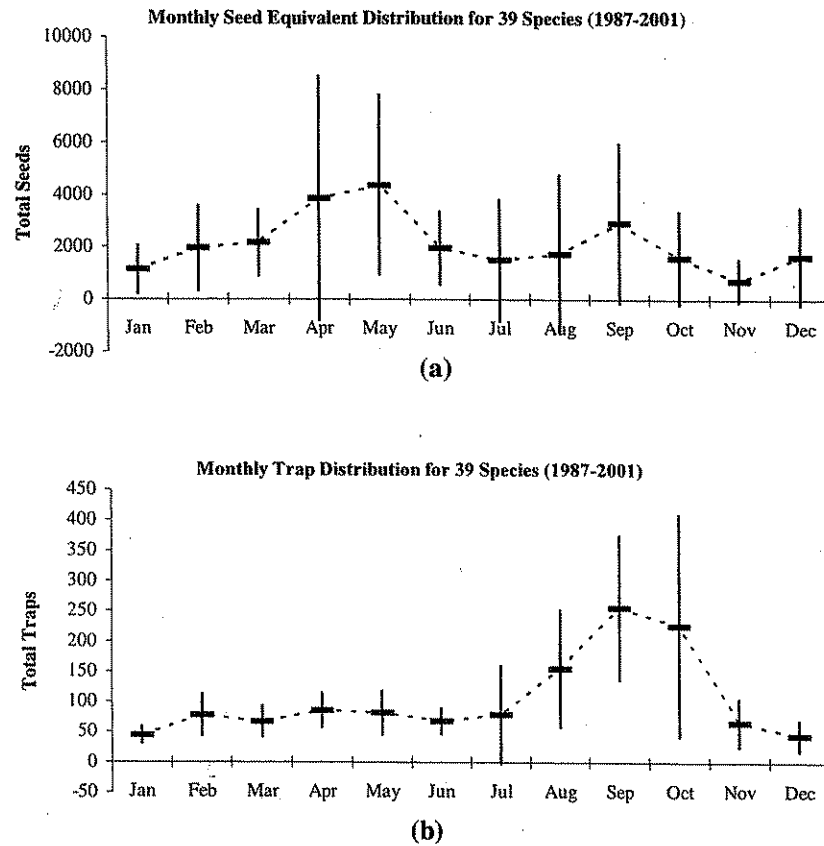


Figure 7. a) Summed monthly fruit production (seed equivalent) data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal species. b) Summed monthly fruit trap data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal species. The solid lines and error bars represent the mean of the 15 annual values \pm one standard deviation.

Species-specific Production Patterns

Each year, the seasonal timing of fruit production by a given species typically showed high predictability while the amount of fruit produced did not. Three examples help illustrate this point. *Spondias mombin* (Anacardiaceae) is a species whose fruits are eaten by a wide range of frugivores on BCI. The population-wide

timing of annual fruit production by *S. mombin* is highly predictable (Fig. 8a). Ripe fruits invariably become available to frugivores in September—occasionally appearing as early as July–August and extend through September into October. Fruit was produced by *S. mombin* in all 15 years of the sample (Fig. 8b).

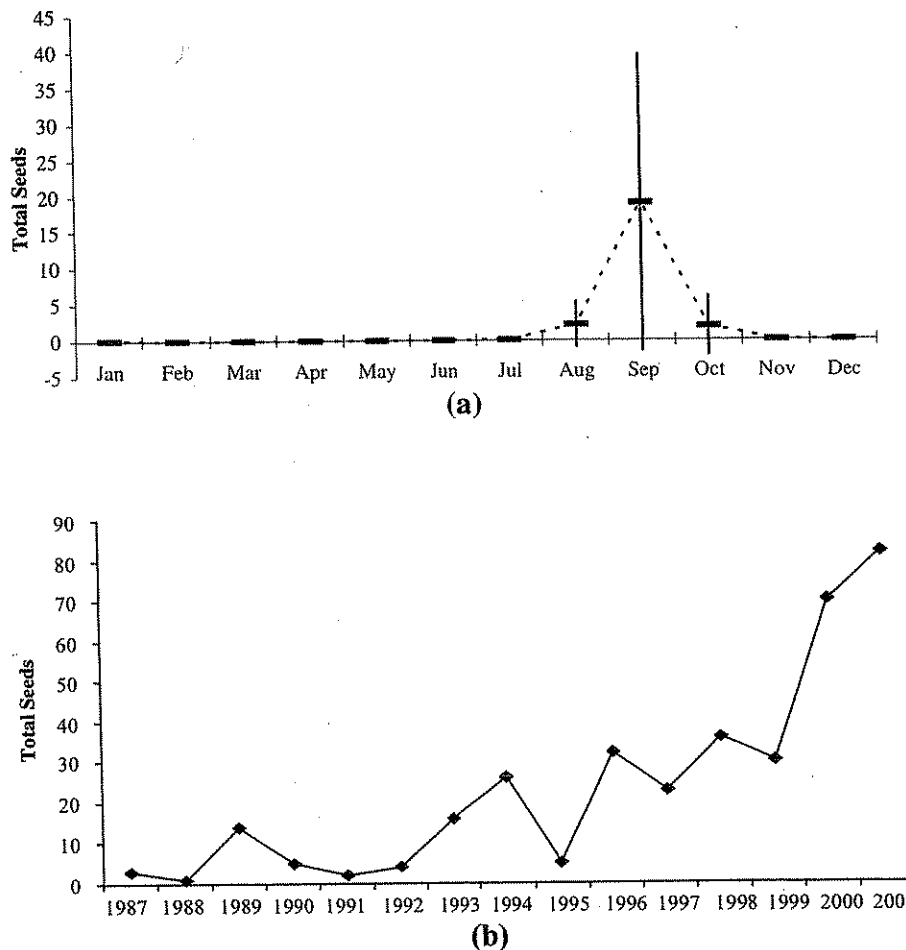


Figure 8. a) Pattern of monthly ripe fruit production by *Spondias mombin* on BCI over a 15-yr period. The solid lines and error bars represent the mean of the 15 annual values \pm one standard deviation. b) Pattern of yearly ripe fruit production by *Spondias mombin* on BCI over a 15-yr period.

This element of predictability vanishes when considering the amount of fruit produced by *S. mombin* in different years (Fig. 8b, range 1–82 seed equivalents, depending on year). Likewise, in some years, more traps contained *S. mombin* fruits

(range 1 to 14 traps) than in other years. No temporal autocorrelation was evident for annual fruit crop size --a year of low fruit production by *S. mombin* might be followed by one to several years of higher, lower or similar fruit production (Fig. 8b).

Dipteryx panamensis, a critical early dry season resource for many BCI frugivores, presents a very similar picture (Fig. 9a, b). The annual timing of ripe fruit production is highly predictable, beginning in Nov-Dec, peaking in Jan-Feb and ending in March.

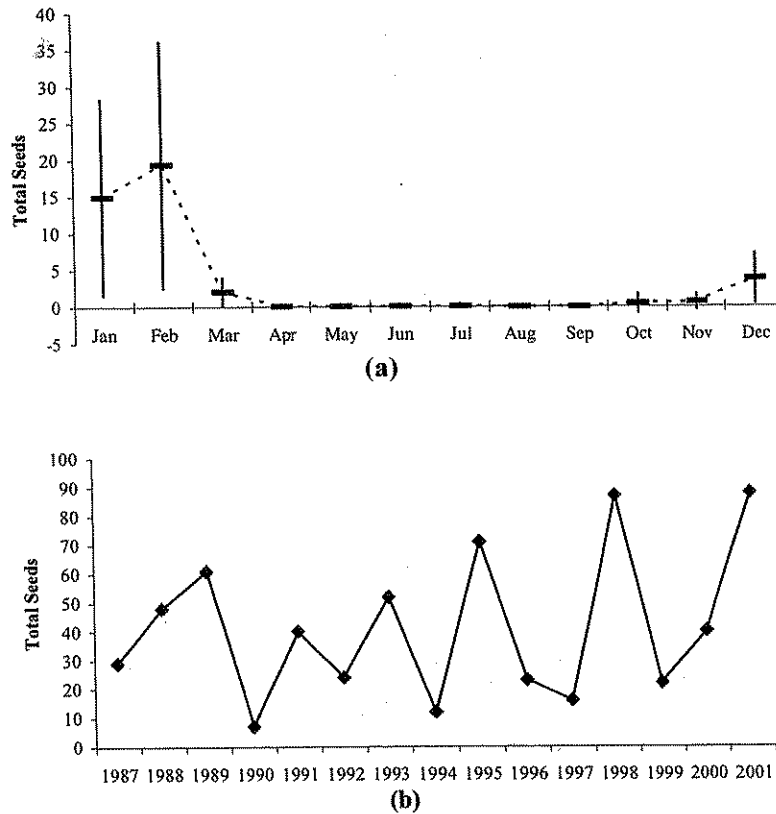


Figure 9. a) Pattern of monthly ripe fruit production for *Dipteryx panamensis* on BCI over a 15-yr period. The solid line and error bars represent the mean of the 15 annual values \pm one standard deviation. b) Pattern of yearly ripe fruit production for *Dipteryx panamensis* over a 15-yr period.

Fruit was produced by *D. panamensis* in all 15 sample years. But the amount of fruit produced per year was highly variable (range 7 to 88 seed equivalents depending on year) as were the number of traps with fruit (range 6 to 51 traps). A

see-saw effect was noted between most pairs of years but the time series autocorrelation with a one-year lag was not quite significant ($r=0.51$, $p=0.053$) (Fig. 9b).

A final species, *Brosimum alicastrum* (Moraceae), also an important fruit resource, produces ripe fruit most heavily in May – July each year (Fig. 10 a, b). Fruit was produced by *B. alicastrum* in all 15 years of the sample. However, the amount of fruit produced varied notably between years (76-1406 seed equivalents, depending on year) as did the number of traps with fruit (range 19-75 traps). In some years, ripe fruit from *B. alicastrum* was available to frugivores over a period of two or more months, whereas in other years, fruit production by this species was noted for only two or three weeks.

Based on these patterns, which seem representative of the majority of species in our sample, we conclude that a BCI frugivore can rely confidently on some fruit from most of these species at predictable times each year, excepting species from genera such as *Ficus* (Moraceae), which generally show intraspecific asynchrony in phenology and can produce fruit in any month of the year (e.g., Milton, 1991). How much fruit a given species will produce and how long this fruit will be available in any given year, however, seem highly unpredictable.

Mammal Census Results

Howler Monkeys

To compile data, KM walked the BCI trail system, usually over a period of 7-10 days per sample month, and counted all members of any howler troop encountered, noting down the sex of each adult animal and assigning immature animals to juvenile or infant classes. All areas of the island were covered in censuses. Further descriptions of this census protocol can be found in Milton 1982 and 1996. In some years howler troops were censused in several different months whereas in other years only a single monthly census was taken. Because of this variability, annual data were smoothed for analysis using a LOWESS smoother.

One might assume that many new howler troops were formed over the 15-yr sample period. However, several island-wide estimates of the total number of howler troops (~ 60 troops) on BCI did not indicate that new troops were being formed to any detectable degree (Milton, 1982, 1996 and unpublished data). Rather, the island appears to be well saturated with howler monkeys, each troop and its descendants occupying the same basic home range generation after generation. For this reason, mean troop size for a given year can be used as an indication of howler population size for that year.

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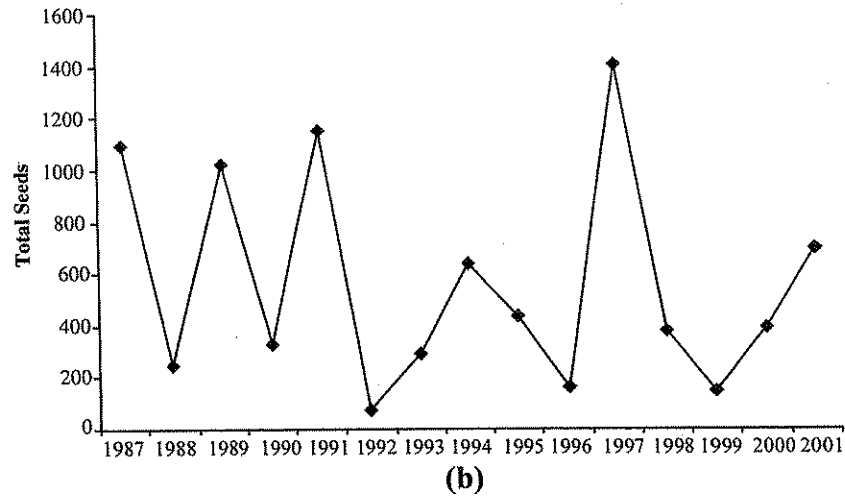
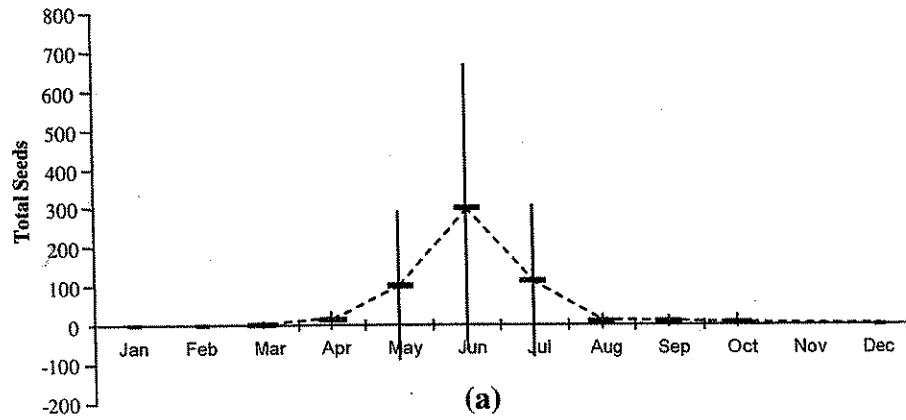


Figure 10. a) Pattern of monthly ripe fruit production by *Brosimum alicastrum* over a 15-yr period. The solid lines and error bars represent the mean of the 15 annual values \pm one standard deviation. b) Pattern of yearly ripe fruit production for *Brosimum alicastrum* over a 15-yr period.

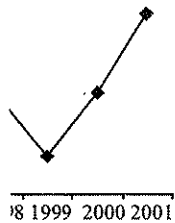
No significant difference in mean annual troop size for howlers was detected over the 15-yr period (ANOVA, $F = 1.63$, $P > F = 0.07$, $df = 14, 244$). This result is not what one would predict if variability in annual fruit production showed a direct

relationship to howler population size. KM has long contended that howler troop size on BCI tends to decline as the rainy season progresses and census data suggest such a trend. In addition, significantly more howler monkeys are found dead between July-December than January-June (Mann-Whitney U-test; $Z = 3.323$, $P \leq 0.009$, $n = 43$ months Jan-June, 48 months Jul-Dec). This is a persistent annual pattern (Milton, 1982, 1990, 1996).

However, troop counts for the 15-yr sample did not support the assumption of significantly smaller troop size in howlers in the rainy half of the year. No significant seasonal difference in mean troop size could be found for howler monkeys in the first relative to the second half of the year regardless of the test employed (t-test, Mann-Whitney U-test and an ANOVA were run on these data). Results were the same whether all 15 years of data were analyzed or only those eight years for which there were troop counts in both seasons of that year.

We then examined monthly means for troop size for the 15-yr sample (Fig. 11). Mean troop size in January and in June differed significantly from all other months (Wilcoxon rank sum test: January, $Z = -2.19$, $n = 257$, $P > Z = 0.03$; June, $Z = -2.36$, $n = 259$, $P > Z = 0.02$; the same results were obtained for both months using a t-test). Testing for differences between mean number of individuals in each age class by month showed significantly more adult monkeys present in troops in January and June (Jan: Mann-Whitney U, $Z = -2.17$, $n = 259$, $P > Z = 0.03$; June, Mann-Whitney U, $Z = -2.70$, $n = 259$, $P > Z = 0.01$). Significantly more infants were also present in troops in January (Mann-Whitney U, $Z = -2.05$, $n = 259$, $P > Z = 0.04$) and June ($Z = -1.76$, $n = 259$, $P > Z = 0.08$). Results suggest two intra-annual population cycles for howlers per year, a peak and a trough followed by a peak and a trough. Neither January nor June stand out on BCI in terms of monthly fruit production or amount of rainfall received.

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Monthly Howler Troop Size Distribution (1987-2001)

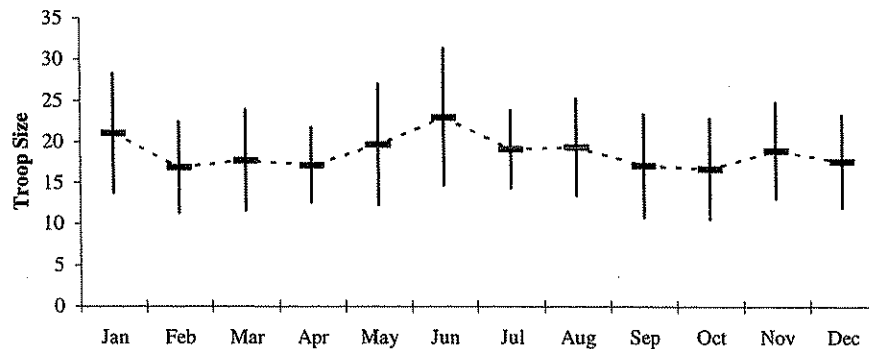


Figure 11. Monthly howler troop size distribution 1987-2001. The solid lines and error bars represent the mean of the 15 annual values +/- one standard deviation.

Squirrels, Agoutis, Capuchin Monkeys

The other focal mammal species, squirrels, agoutis and capuchin monkeys, were censused annually in December-January by J. Giacalone and G. Willis. Censuses were conducted in the morning, largely between 7 and 10 am by an observer who walked along the island trail system at a speed of approximately 1 km/h, noting down the species, height above ground, distance from the trail and initial detection distance from the observer of all animals encountered, along with the time and location of the encounter. Each annual census included over 100 km and covered all trail segments on BCI at least once. Data presented here represent the number of sightings of individuals of each species for each sample year adjusted by the number of km of trail walked in that year; these results can be used to estimate population size for each species for each sample year. For analysis, all estimates were assigned to the December year of that census. We present only 14 yrs of data for the three species (1987–2000) as the 2001–2002 census data were not available for analysis.

Each species showed notable interannual variation in estimated numbers; extreme estimates for a particular species differed by more than 100% (Fig. 12). The direction of change for one species did not necessarily track the direction of change for the other species (Fig. 12). This lack of concordance is not what one would predict if variability in annual fruit production showed a direct relationship to frugivore population estimates.

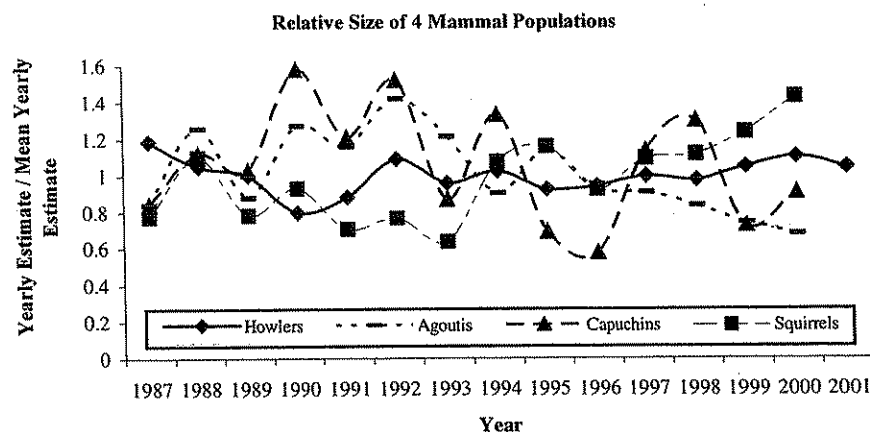


Figure 12. Relative annual size of each of the 4 frugivore populations (15 yrs for howler monkeys; 14 yrs for the other three species).

Squirrels and agoutis have specialized dentition to exploit hard-shelled seeds and for this reason might be viewed as members of a guild. As such, their populations might be expected to track together in response to the relative availability of such seeds. As shown in Fig. 12, the agouti and squirrel populations on BCI might show

concordance for two or three years but then one species increases in numbers and the other declines. This pattern suggests that absolute fruit abundance does not explain population fluctuations for the two species. Perhaps, for example, each species relies on a somewhat different set of primary fruit species, including those producing hard-shelled seeds.

To investigate this possibility, we tested for significant correlations between annual population estimates for each of the four mammal species and annual fruit production estimates for each of the 39 edible fruit species. We used a t-test to evaluate the significance of Pearson product-moment correlation coefficients. This is justified if the distribution of the two variables is bivariate normal. While it is difficult to verify a bivariate normal distribution with the number of data points we have, examination of the data did not find strong evidence that the normality assumption was inappropriate.

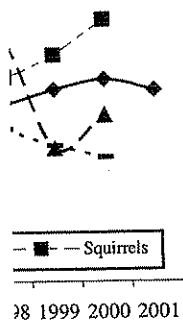
Squirrel numbers showed a significant positive within-year correlation (≤ 0.05 level of significance) with fruit production (seed equivalent) data for six fruit species, capuchin numbers with four, agouti numbers with two and howler numbers with one. Given feeding records for each species on BCI, most such correlations appeared plausible.

Time-lag Effects

We then tested for a one- or two-year lag effect between fruit production and population size of each mammal species (i.e., one year lag = abundance of a fruit species in year A relative to abundance of a given frugivore species in year A + 1; two-year lag = abundance of a fruit species in year A relative to abundance of a given frugivore in year A + 2). Squirrel population estimates showed a significant correlation at a one year lag in relation to fruit production for four fruit species and a significant correlation at a two year lag for eight species; capuchin population estimates showed a significant correlation at a one-year lag with zero species and a significant correlation at a 2-yr lag with two species; agouti population estimates showed a significant correlation at a 1-yr lag with three fruit species and a significant correlation at a two year lag with zero species; howler monkeys showed no correlations with any fruit species at a one year lag and a significant correlation at a 2-yr lag for two species.

Our 39 fruit species contained various species placed in the same genera. From these, we selected 10 genera (the 10 most speciose or best represented in seed equivalent data) and summed total production data for each genus for each sample year. We used these estimates to test for correlations with annual population size for each mammal species (looking within years and with a one-year or two-year lag). Squirrels showed three significant correlations – all within-year, with the genera *Miconia* (Melastomataceae), *Spondias* and *Dolioscarpus* (Dilleniaceae). Capuchins showed one significant correlation, a within-year correlation with fruits of the genus *Coccoloba*. Agoutis showed one significant correlation, within-year, with fruits of the genus *Chrysophyllum* (Sapotaceae). Howlers showed no correlation with any

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Because of the large number of tests employed, some of the significant results are likely spurious. To control for this, we re-evaluated the significance of each correlation using a sequential Bonferroni technique. This more rigorous test produced just one significant correlation between the abundance of any of the four mammal populations at any of the three time lags (0, 1, and 2 years) and considered several indices of fruit production (total immature fruit, total mature fruit, total number of fruit species in traps, the 39 important fruit species as a group, each of the 39 fruit species separately, each of the 10 important fruit genera separately). The single significant correlation was between squirrels and *Spondias mombin* at a one-year lag.

Yet, when we compare population patterns for a given mammal species against patterns for some highly preferred fruit species, results, at times, seemed suggestive in spite of the lack of significant correlation indicated by the Bonferroni technique. In Fig. 13, for example, we show annual estimates for capuchin numbers and fruit production by *Doliocarpus major* over a 15 yr period. The two patterns seem to track fairly well. All of the tests we employed measured linear associations between variables. The relationship between the population estimates of a given frugivore species and estimates of the abundance of a given fruit species may, however, not be linear. As we have only 15 data points for three of the four mammal species, we are limited in our ability to do more with data at present.

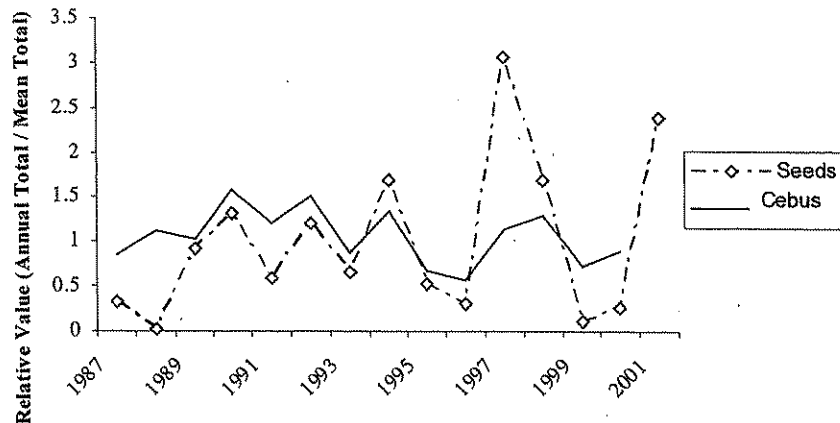


Figure 13. Relative annual estimates for population size of *Cebus capucinus* and total mature fruit production by *Doliocarpus major* over a 15-yr period.

We also noted that some fruit species long regarded as tightly associated with the reproductive biology of one or more of our focal mammal species, for example,

Dipteryx, *Astrocaryum*, *Gustavia* (Lecythidaceae) and *Attalea* for squirrels (Glanz et al., 1982), showed no correlation with population estimates for that species using either the Pearson product-moment correlation coefficient or the Bonferroni technique. However, judging from sample size, of these four species only *Dipteryx* was well represented in trap data. Ripe fruits of these four species are either large relative to most fruits on BCI or, in the case of the palm species, generally occur on only one infructescence in one area of the tree at any given time. The size and placement patterns of traps may not have accurately sampled production in these four important fruit species. Very small-seeded fruits such as those of *Ficus*, a genus of strong dietary importance to howlers, may likewise not be accurately reflected in trap data as seeds are minute, variable in number and difficult to identify as to species.

Basically, with data in hand, of the four mammal species, it appears that squirrels, with by far the smallest body size, show the highest number of suggestive links with particular fruit species. We predict that squirrel population dynamics will be found to be more closely tied to a wider range of fruit species than is the case for our other three mammal species, followed by capuchins and agoutis, who have almost identical body size and finally by the considerably larger-bodied howler monkeys. Howler monkey population dynamics do not appear closely tied to any fruit species, perhaps because, unlike the other three species, howler monkeys can also depend on leaves as food.

Effects of Unusual Years

Though our data failed to show any simple direct correlation between annual fruit production and frugivore numbers on BCI, other researchers have detected such an association under specific conditions. In 1982, Foster suggested that excessive rain out of season might be highly disruptive to the forest frugivore community in terms of fruit set. A weak dry season (unusually short and wet) was hypothesized to lead to fruit failure in the rainy season of that year, causing island-wide famine and unusually high frugivore mortality (Foster, 1982).

In 1999, Wright and his associates refined Foster's observations and presented a 2-yr cycle model related to El Niño years. This model predicted that a warm sunny El Niño year, immediately followed by a year with "a mild dry season" (which they defined quantitatively and which was unusually short and wet) would result in fruit failure by many species that same year, extending into the early months of the subsequent year. Such fruit failure during the mid-to-late rainy season and subsequent early dry season, was predicted to lead to island-wide famine, causing unusually high mortality in frugivorous mammals (Wright et al., 1999).

Only one El Niño year (1992) followed by the requisite "mild dry season" year (1993) occurred in our 15-yr sample. Wright et al. (1999) speculated that frugivore populations may have increased in size during the 1992 El Niño year when community-wide fruit production was unusually high (Fig. 4). Indeed, our data show that all four of the frugivores studied here increased in abundance between

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December 1991 and December 1992 (Fig. 12). After the mild dry season of 1993, also as predicted by the model, many tree species on BCI produced fruit crops well below mean size and some species failed to set fruit (Wright et al., 1999). Cadaver recovery showed that two mammal species, collared peccaries and white-tailed deer, suffered significantly higher than average mortality in late 1993 (Wright et al., 1999). Census data compiled by Wright et al. (1999) indicated some other mammal species (e.g., coatis; Gompper, 1996) also declined in numbers between December 1992 and December 1993, apparently due to famine caused by fruit shortage. All four of our focal mammal species, using three independent estimates, showed a decline in numbers in 1993.

Typical Years

We then compared the full 15 years of data on mammal densities and fruit production with information for 1992-1993 to see if these two unusual years might provide insight into factors affecting population fluctuations in other years. Though population size for all of our focal species declined in 1993, only the squirrel population seemed unusually low and squirrel population size was also depressed in 1991 and 1992 (Fig. 12). Squirrel numbers did recover slightly in 1992, the El Niño year, only to sink to their lowest level in 1993. However, it was not unusual for our focal mammal species to show concurrent population declines or increases. Three out of four of our focal species also fell below their relative means in 1987, 1989, and 1996 while all four species were elevated above their relative means in 1988 and three out of four were elevated in 1994 and 1997 (Fig. 12). In general, the overall pattern for these species (howlers to a less dramatic extent) over the 15-yr period was one of constant oscillation.

The 1997 El Niño year (the only other El Niño year in our 15-yr data set) produced the highest peak in overall fruit abundance on BCI in the 15-yr sample (Fig. 4). Similar to 1992, three out of four of our focal mammal species showed an increase in population size in 1997. The following year, 1998, did not have a "mild dry season" and therefore did not meet conditions of the Wright et al. (1999) model. In 1998, two of our four species increased and two declined in population size relative to their population size in 1997. However, only agouti population size was below its relative mean in 1998 and it was also below the mean in the El Niño year, 1997, and in 1999 and 2000.

Data on annual fruit production (each of the 15 years expressed in relation to the 15-yr mean) showed that 1993 and 1998 were the two lowest years in overall fruit production on BCI in the 15-yr sample. Both years followed warm, sunny El Niño years (1992 and 1997) with overall high fruit production (Fig. 4). Of particular interest, however, in terms of the El Niño famine model are species producing edible ripe fruit crops in the mid-to-late rainy season. As noted, the late rainy season is the time of year when overall fruit production on BCI declines to its lowest level (Fig. 3), and when overall mammal mortality is highest (Milton, 1982, 1990, 1996; Wright et al., 1996).

In their 1999 paper, Wright et al. presented a figure of the 25 fruit species on BCI showing "greatest mean dry mass fruit production" between 10 August of one year and 7 February of the following year (this evaluation based on 10 1/2 years of data on dry mass fruit production from 59 fruit traps, 18 November 1985-30 June 1996). Only fourteen of these 25 species produce fruit of known importance to mammalian frugivores on BCI. The other 11 species: (1) produce wind-dispersed fruits, (2) were not known to KM and JG and likely are not important foods for mammalian frugivores on BCI or (3) also produce fruit during other months. Following predictions of the Wright et al. model, 13 of these 14 edible species showed fruit production depressed below the mean, often well below the mean between 10 August 1993-7 February 1994 (Wright et al., 1999).

However, examination of seed equivalent data for 8 of these 14 species over our 15-yr sample suggests that it is not uncommon for a number of important species to show low fruit production in the same year (Fig. 14). Only one of these 8 species, *Trichilea tuberculata*, actually had its single worst year of fruit production in 1993 (the year following the 1992 El Niño yr); *Hyeronima laxiflora* (Euphorbiaceae) had its single worst year in 1992, an el Niño year; *Quararibea asterolepis* had its single worst year in 1997, another el Niño year; *Dipteryx panamensis* had its single worst year in 1990, *Spondias mombin* in 1991 and so on (Fig. 14). The fruit production patterns presented in Figure 14 suggest that it would be difficult to predict the strength of annual fruit production for these species as there is considerable interannual variability.

What Can Be Predicted?

Using these species as an example, what can be predicted about annual fruit production from the 15 years of seed equivalent data? If any pattern is apparent in Figure 14, it is one indicating that, in any given year, the probability is high that only 20 to 30% of the important mid rainy to early dry season species will have an unusually good year in terms of fruit production; other species will have an average to sub-standard year (Fig. 14). The next year, 20 to 30% of the *other* species in this temporal cohort can be predicted to have an unusually good year though one cannot predict in advance exactly which species these will be. This oscillating production pattern makes it difficult to predict, except in extreme circumstances, how the frugivore community or particular frugivore species will be affected by fruit availability in any given year.

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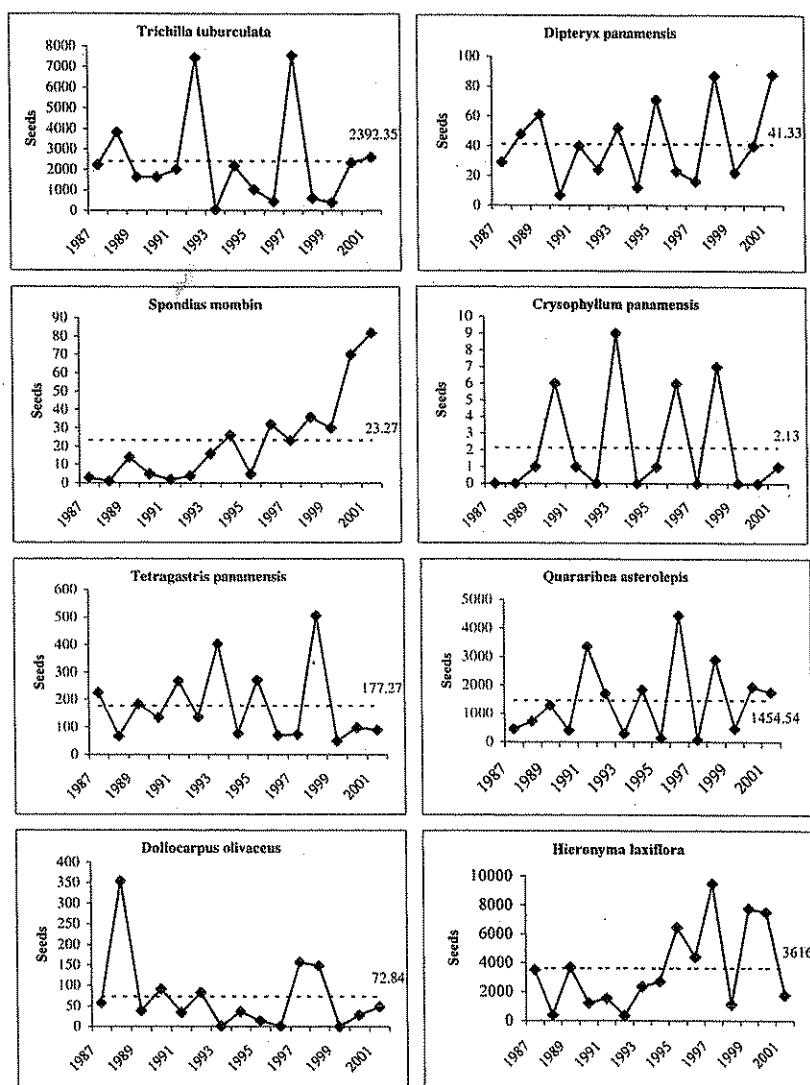


Figure 14. Annual total fruit production (as estimated from seed equivalents) for 8 tree species fruiting in the mid-to-late rainy season on BCI. For each species, the solid line graphs the annual total. The dashed line graphs the mean value for the 15-yr period. All species are important mid-to-late rainy season food species for many mammals on BCI, including one or more focal mammal species.

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Fruit Trap

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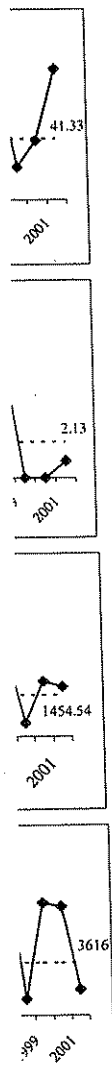
DISCUSSION

It is a simple matter to state our major conclusion: namely that, though strong relationships likely exist between animal numbers and fruit production patterns on some level, with data in hand we can find no clear evidence to support this assumption except in extreme years. Our data suggest that the frugivore community can depend on at least some ripe fruit from most edible species at predictable times each year but in any given year, data also suggest that only a small subset of such species will show high productivity; other species will generally show average to low productivity. This pattern appears to be relatively constant and largely unpredictable in terms of which particular species will have an unusually good fruit crop in any given year (except to say that it generally will *not* be species or individuals which produced an unusually good crop in the preceding year). This fruiting pattern likely reflects the interplay of the particular top down and bottom up factors impinging on tree species (or individual trees) at any given time. It is possible that animal numbers are affected more by predators, parasites or disease than by fruit availability or by a complex and constantly oscillating combination of top-down and bottom-up factors (Milton, 1986). However, the lack of correlation we noted for animal numbers and fruit production patterns may also reflect, at least in part, limitations inherent in our sampling methods and data. A brief discussion of some of these perceived limitations may prove helpful for those interested in carrying out similar long-term studies.

Fruit Trap Data

The trap data utilized for this analysis were not compiled to study factors affecting the population dynamics of frugivorous mammals. Rather, these data were compiled to monitor interannual variation in seed set for the more abundant tree and liana species on BCI and to provide input for demographic studies of plants (Harms et al., 2000; Hubbell et al., 1999). The study design of randomly located seed traps provides large overall sample sizes and reliable estimates of production by the plant community as a whole. Randomly located traps also provide reliable production estimates for abundant plant species and those producing copious numbers of small seeds.

However, randomly located traps are far less reliable for rare plant species and for plant species that produce smaller numbers of large seeds or fruits produced in few large infructescences. Many tree species in areas of older forest on BCI can be regarded as rare (Milton, 1980) and various of the important food species for one or more of our focal mammal species produce small numbers of large seeds or seeds in clusters. The use of random fruit traps for general collection needs to be combined with traps that focus on a number of individuals of particular fruit species important in the diet of particular mammal species. This approach might provide data more



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useful for examination of fruit-mammal relationships though this method could overlook the possible importance of many secondary food species.

Mammal Census Data

The accuracy of mammal census protocols deserves further study. Different census techniques need to be modified and calibrated such that they reliably produce similar results. For example, JG's strip census method and KM's troop count census method at times showed little annual concordance in terms of howler monkey numbers (Fig. 15). Techniques are required that produce estimates in basic agreement.

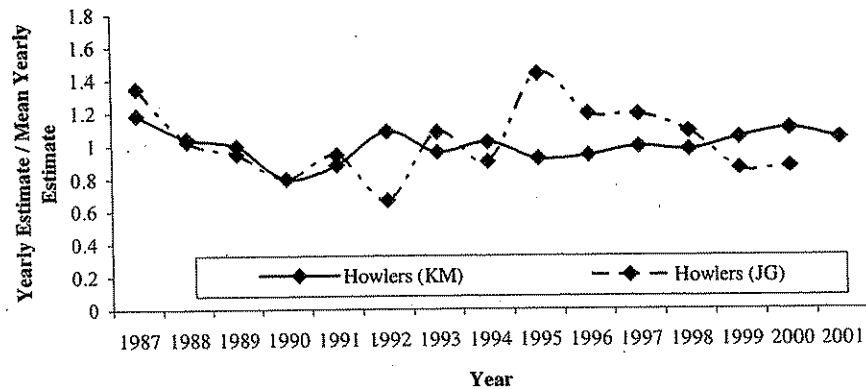
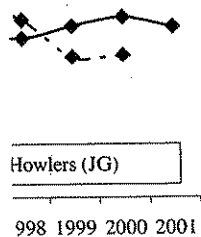


Figure 15. A comparison of results of annual howler monkey population estimates derived by using a strip censusing method (JG) or an individual troop count method (KM). See text for details of each sampling technique.

Standard mammal strip census methods are used widely now in tropical forests but our data suggest that such methods may work well only for certain species. Solitary or paired species such as squirrels or agoutis are likely to be accurately counted. Social species such as capuchin monkeys, however, which live in closed social units but which tend to forage spread out over a wide area, may be greatly under- or over-estimated. Social species such as spider monkeys, which live at relatively low densities, have a fission-fusion pattern of social organization and range over a large area pose special censusing difficulties.

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Integration of Fruit and Mammal Data

Another area deserving study is how to relate fruit production data to animal population data most meaningfully. Annual troop and/or population composition data, reproductive data and other relevant information for each mammal species need to be integrated in a biologically meaningful manner with fruit production data. Island-wide famines are rare events but some mammals of most species on BCI die every year, particularly during the mid-to-late rainy season (Foster, 1982; Milton, 1982, 1990, 1996; Wright et al., 1996, 1999). In some years, not necessarily a year following an El Niño year, animals from one or more species may die in far higher numbers than in other years. For example, in 1989, significantly more howler monkeys were found dead in the BCI forest than in any other year in KM's 28 years of work on BCI (Milton, 1993). Howler mortality in 1989 showed no correlation with island-wide fruit production estimates for 1989, 1988 or 1990 (Milton, 1993).

Looking at an earlier data set, we also noted that from January 1981 through January 1982, the BCI squirrel population suffered its greatest decline in 20 years. The *Dipteryx* crop, which is extremely important to squirrels on BCI, failed in January 1981 and *Gustavia*, another critical fruit species for squirrels (Glanz et al., 1982), also failed later that same year at what would have been the height of the squirrel breeding season (Giacalone-Madden et al., 1990). However, no El Niño year occurred immediately prior to these events and the very pronounced El Niño of 1982 did not appear to have a widespread impact on BCI mammal populations. It seems that particular fruit species of key dietary importance to particular mammal species may need to be monitored in relation to one another rather than--or in addition to-- broader sampling of the floral and faunal communities before we will begin to better understand the complexities of this ecosystem. Too, though fruit production may be an important factor affecting population size for many mammal species, data from this and other sites suggest that population fluctuations of some species can also be influenced by predator and parasite pressures (Gadgil & Prasad, 1984; Milton, 1993, 1996).

Tropical forests, which comprise the most complicated ecosystem on earth, are not proving amenable to facile analysis, even at sites as well studied as BCI. Eventually, however, as we continue to refine and improve our questions and methods of data collection, we are confident that the population dynamics of particular mammal species and their relationships, if any, to the production patterns of particular plant species will be better understood.

ACKNOWLEDGEMENTS

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NOTE

1) In this paper we adopted three conventions that differ from earlier treatment of the same fruit production data by Wright et al. (1999). Our goal was to evaluate possible relationships between annual mature fruit production by particular plant species and population fluctuations of particular frugivore species. In contrast, Wright et al. (1999) sought to evaluate the consequences of a sustained period of very low community-level fruit production for a range of frugivore species. In terms of differences in our analytical treatments, first, for data series that are the sum of seed equivalents, we weight each seed found in frugivore diets equally regardless of the fruit species. Wright et al. (1999) considered all plant species with fruits or seeds in traps (not just species known to be in frugivore diets) and weighted all fruit species equally rather than weighting individual seeds equally. However, as most analyses presented in this paper deal with data series that are sums of seed equivalents for individual fruit species only, they are not affected by this difference in treatment. Second, we report untransformed values of fruit production. Wright et al. (1999) reported logarithms of annual fruit production because untransformed values are strongly skewed (unpublished analyses of J. Wright). This is of minor concern in our paper because we are interested in *relative* levels of production. Third, we associated fruit production with the calendar year or month mature fruits were captured in traps. Wright et al. (1999) associated annual fruit production with the meteorological year of the appropriate flowering event. This difference explains discrepancies in the timing of fruit production reported here and by Wright et al. (1999).

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