

TROPICAL FRUITS AND FRUGIVORES

Tropical Fruits and Frugivores

The Search for Strong Interactors

Edited by

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Preface

This book documents interactions between plants and animals that biologists consider particularly important for conserving the habitats that they study. Here we undertake a cross-continental comparison of the relationships between tropical plants and the frugivorous animal communities that depend on them. The chapters in this book originate from a symposium that brought together more than 30 biologists from around the world to share and compare their research on these interactions. The symposium was funded by the National Science Foundation, the Wildlife Conservation Society, and the Institute for the Conservation of Tropical Environments. It was held in Panama City, Panama, at a conference entitled “Tropical Forests, Past, Present, and Future” hosted by the Association for Tropical Biology and the Smithsonian Tropical Research Institute. The editors would like to thank everyone who helped bring the project to fruition.

CHAPTER 1.

INTRODUCTION: FRUGIVORY, PHENOLOGY, AND RAINFOREST CONSERVATION

J. LAWRENCE DEW

Species diversity on Earth is highest in the tropics, and if we are to protect as much of this diversity as possible from human-caused extinction then conserving the tropical rainforests is a top priority (Myers, 1984). In tropical rainforests much of the primary production is passed on to the second trophic level in the form of fruit pulp. Up to 90% of tropical forest tree species produce fleshy, nutritious fruits that are crucial food resources for large portions of the animal community (Frankie et al. 1974, Gentry, 1983). Some researchers have found that the resources produced by a few key taxa, such as the fruits of fig trees, sustain the bulk of tropical vertebrate communities during seasonal periods of low food availability (Peres, 2000; Terborgh, 1983, 1986). Likewise, particular frugivorous animals are known to serve as vital “mobile links” upon which many of these plants depend to disperse their seeds (Gilbert, 1980; Howe, 1983). The potential conservation applications of this phenomenon are great (Chapman, 1995; Simberloff, 1998).

Temporal patterns of the abundance and distribution of fruits and other plant resources help determine the biomass and diversity of consumers that can be sustained by the plant community. The chapters that follow examine these relationships in each major region of the tropics. The aims of this book are, first, to compare the varying phenological rhythms of different tropical forests; second, to identify key plant taxa that sustain tropical forest frugivores in different regions; third, to identify animals which are of particular significance to these plant communities; and finally, to examine the relevance of these interactions to conservation.

The first of these explorations takes place in Panama, where Katharine Milton and her coauthors examine vertebrate responses to seasonal variation in fruit availability. They demonstrate the complexity of accurately documenting these

patterns even in the best-studied tropical forests. In the following chapter Pablo Stevenson scrutinizes the issue of keystone resources in a Colombian forest. He finds that the search for such resources in Amazonia is not as clear-cut as it once might have seemed.

Tropical forests differ greatly in plant composition, with different sets of plants producing fleshy animal-dispersed fruits. One step towards understanding patterns of consumer abundance and diversity is to understand what governs the floristic composition of tropical forests (Phillips et al., 1994). Chapter 4 by Jean Philippe Boubli examines these relationships in a comparison of two forests within Amazonia that have different animal and plant assemblages.

The authors in this book clearly demonstrate the value of collecting long-term datasets on fruiting phenology. An excellent example of this is found in Chapter 5, by Colin Chapman and his colleagues. Their analysis of phenology at a Ugandan site shows that the tropical rainforests are not immune to the effects of global environmental change. In Chapter 6 An Bollen and her coauthors compare two forests in Madagascar, examining the potential evolutionary importance of frugivores on fruit traits. Patricia Wright and colleagues in Chapter 7 then turn the tables and illustrate the evolutionary effects of strong community-wide fruiting seasonality on a unique frugivore coterie.

The final section of the book explores the patterns of Australasia. In Chapter 8 T. Ganesh and Priya Davidar examine the phenological patterns of a wet forest in southern India. Tim O'Brien and Margaret Kinnaird then compare two forests in Indonesia that show remarkable ecological differences despite close proximity. In chapters 10 and 11 Andrew Mack and Debra Wright search for keystone seed dispersers in New Guinea. David Westcott completes the tour in Chapter 12 by documenting interactions in a community of plants and frugivores in tropical Australia.

Our panel of experts revealed crucial roles played by some seed-dispersing frugivores and their food plants. Several new examples of possible keystone species were documented. Other studies found hyperdiverse systems like rainforests to be difficult places to find tightly coevolved fruit-frugivore relationships. One clear pattern that emerges from these papers is that tropical forests, whether they have one or two annual wet and dry seasons, or if they are ever-wet with aseasonal rainfall, all show regular, annual, community-wide fluctuations in fruit availability. Yet, the ecological importance of superannual variation in resource abundance was found by several authors to have been overlooked by scientists so far. Also underemphasized have been key plants that fruit during annual community-wide seasons of fruit abundance, providing important caloric resources that allow some animals to accumulate fat reserves. Several authors articulate clear and novel conservation implications of these ecological interactions, particularly in light of current rates of habitat fragmentation and global change.

Power et al. (1996) wrote, "Identifying keystone species is difficult--but essential to understanding how loss of species will affect ecosystems." By bringing together researchers to compare their study sites and address these issues, we have attempted to help focus the search. The scientists in this volume identify numerous tropical

taxa that are important to ecosystem structure and function in biomass, productivity, and/or functional role (Odum, 1971, Bond, 2001). These researchers reexamine the terms “strong interactors,” “keystone resources,” and “keystone mutualists,” describing promising directions for future research, and emphasizing the utility of these species interactions to conservation. As scientists and conservationists, we hope that this work will serve as an impetus for action in the tropics.

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CHAPTER 2.

DO FRUGIVORE POPULATION FLUCTUATIONS REFLECT FRUIT PRODUCTION? EVIDENCE FROM PANAMA

KATHARINE MILTON, JACALYN GIACALONE, S. JOSEPH WRIGHT,
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, fall back 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

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 \pm 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.

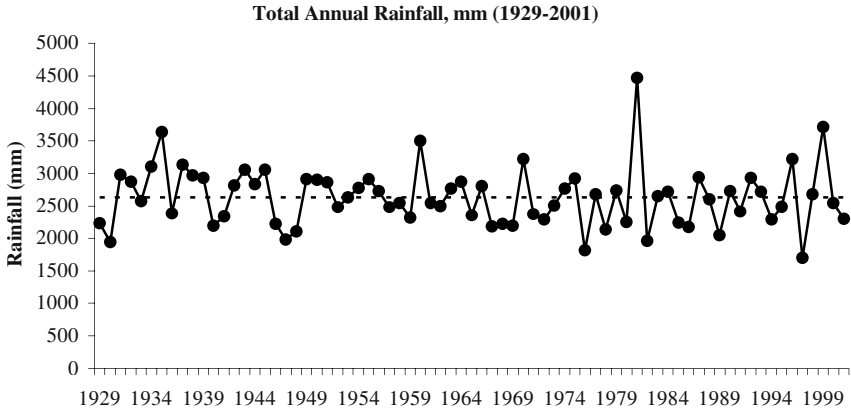


Figure 1. Total annual rainfall data for Barro Colorado Island (BCI) over a 73-yr period, 1929-2001. Annual average rainfall = 2633 ± 462 mm of rainfall. Dashed line at 2,633mm is the mean value for period 1929-2001.

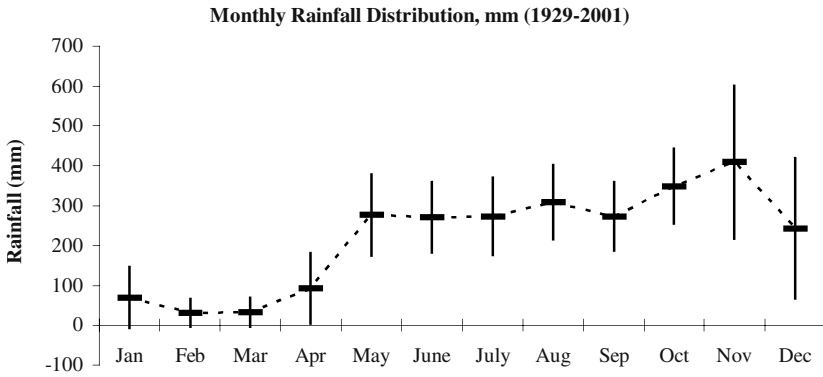


Figure 2. Average monthly rainfall in mm for BCI over a 73-yr period, 1929-2001. The solid lines and error bars represent mean monthly rainfall \pm one standard deviation.

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.

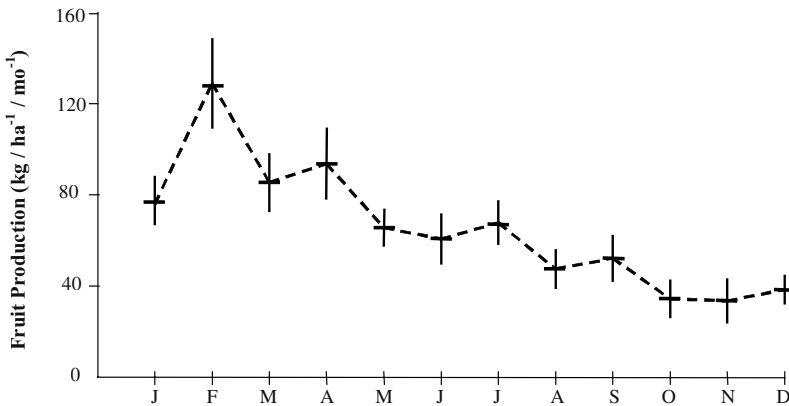


Figure 3. Monthly dry mass fruit production summed over all species for BCI over a 15-yr period. The solid lines and error bars represent mean productivity ± 1 SD (calculated from 1 Jan. 1987-31 Dec. 2001). Data derive from 59 fruit traps; see text for details of data collection.

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.

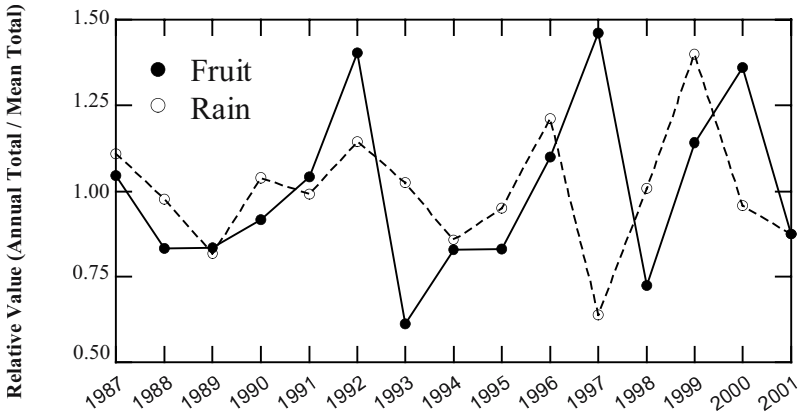


Figure 4. Relative annual rainfall expressed against relative annual fruit production over a 15-yr period on BCI. The dashed line represents rainfall while the solid line represents dry mass fruit production. Data derive from 200 fruit traps, see text for details of data collection.

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.

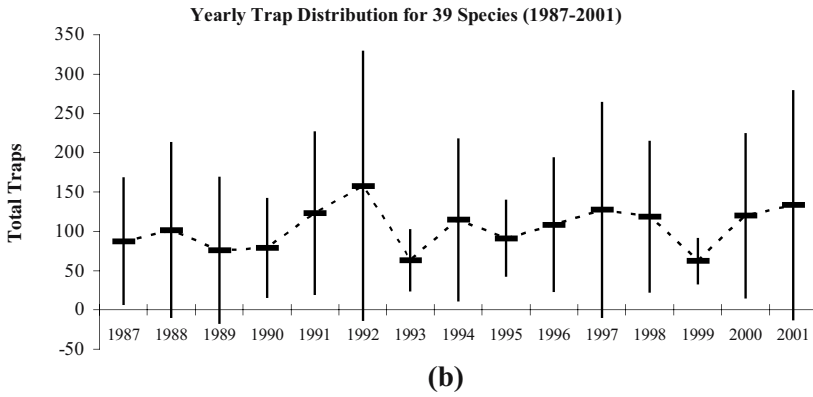
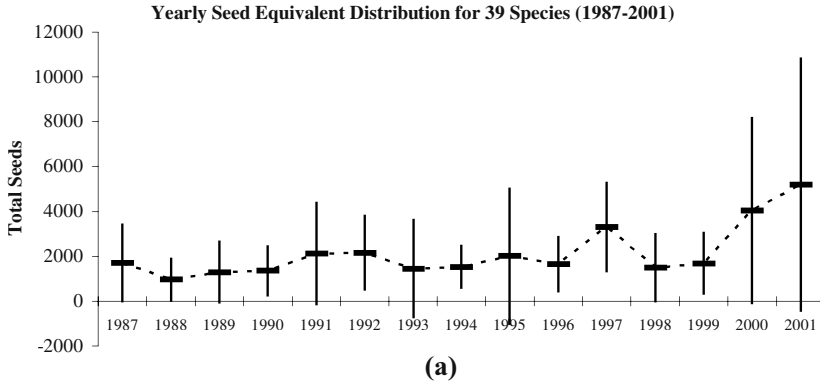
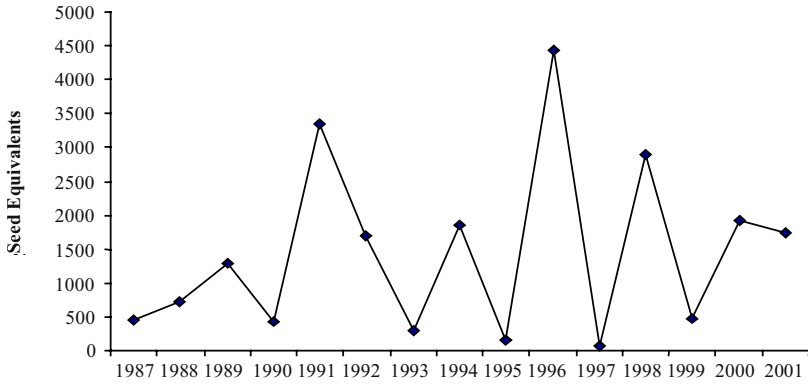
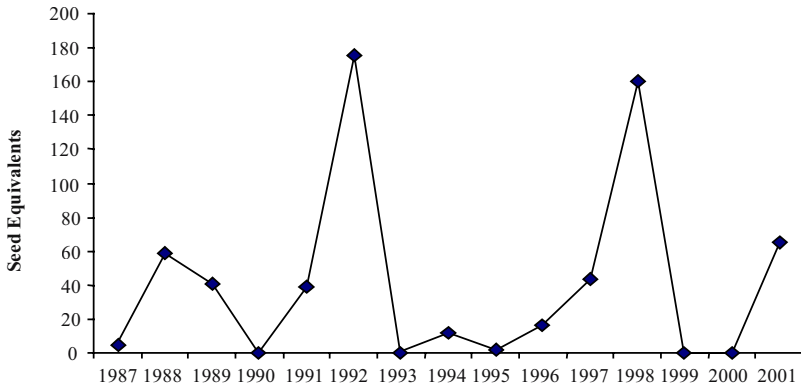


Figure 5. a) Summed annual fruit production (seed equivalent) data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal species. b) Summed annual fruit trap data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal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



(a)



(b)

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

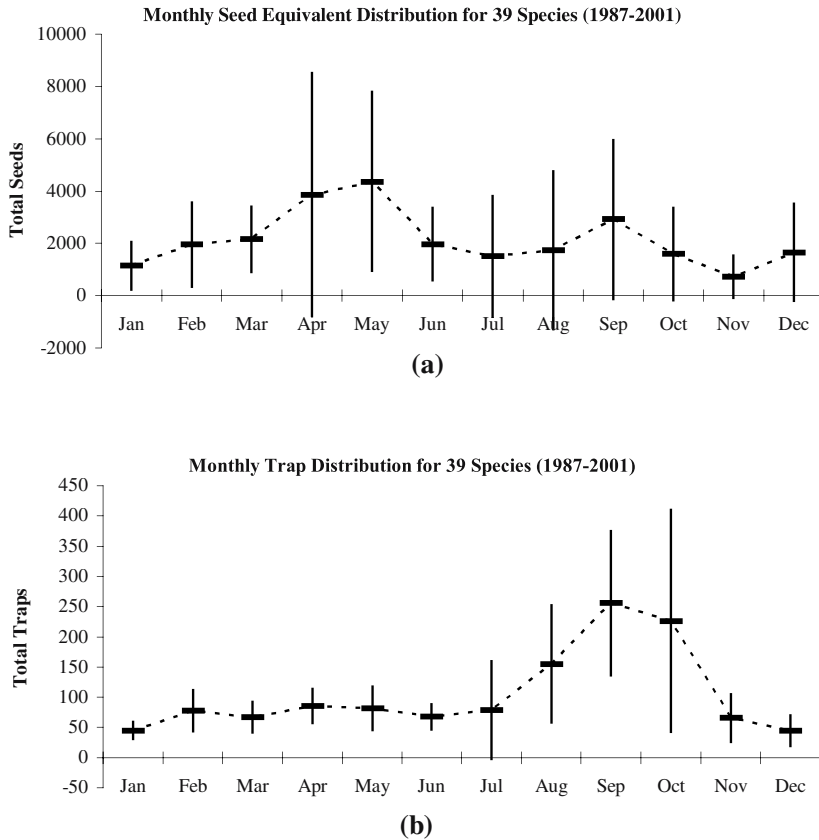
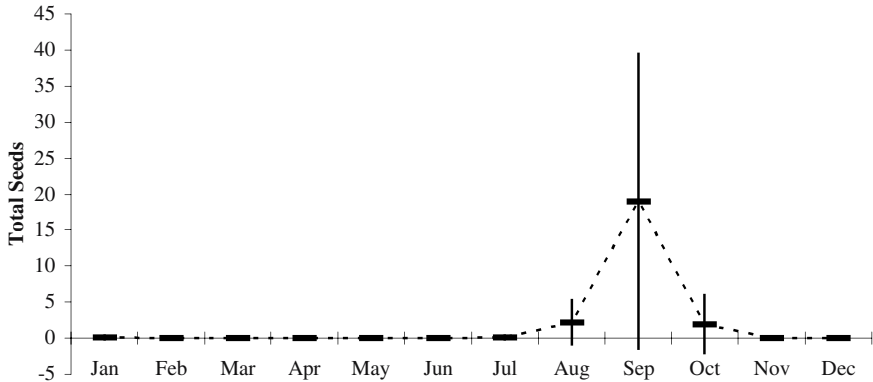


Figure 7. a) Summed monthly fruit production (seed equivalent) data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal species. b) Summed monthly fruit trap data over a 15-yr period on BCI for 39 fruit species important in the diet of one or more focal mammal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

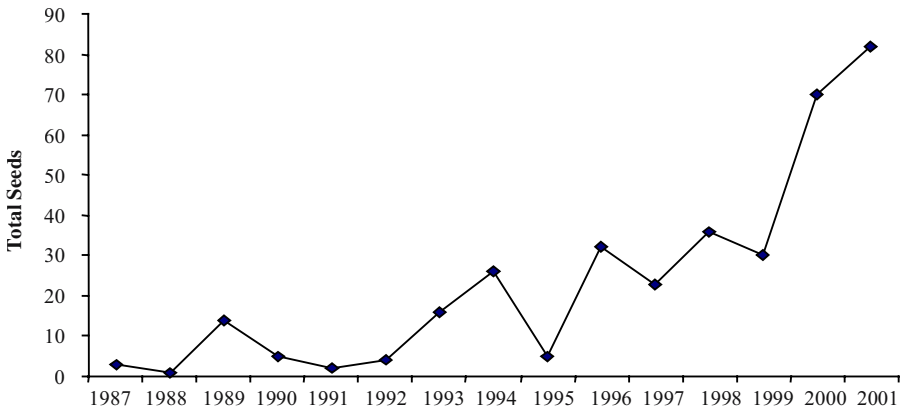
Species-specific Production Patterns

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).



(a)



(b)

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.

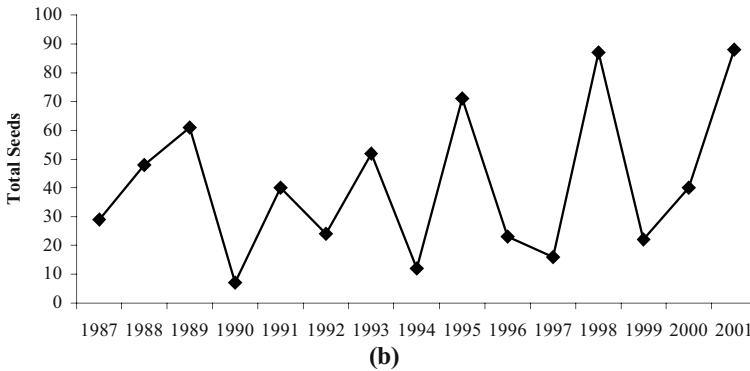
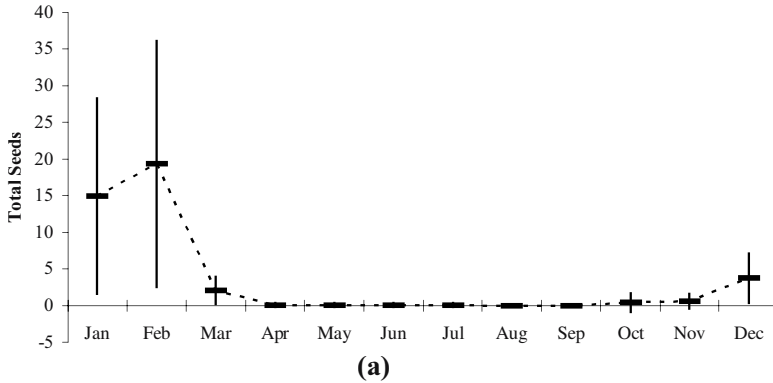


Figure 9. a) Pattern of monthly ripe fruit production for *Dipteryx panamensis* on BCI over a 15-yr period. The solid line and error bars represent the mean of the 15 annual values \pm one standard deviation. b) Pattern of yearly ripe fruit production for *Dipteryx panamensis* over a 15-yr period.

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 descendents 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.

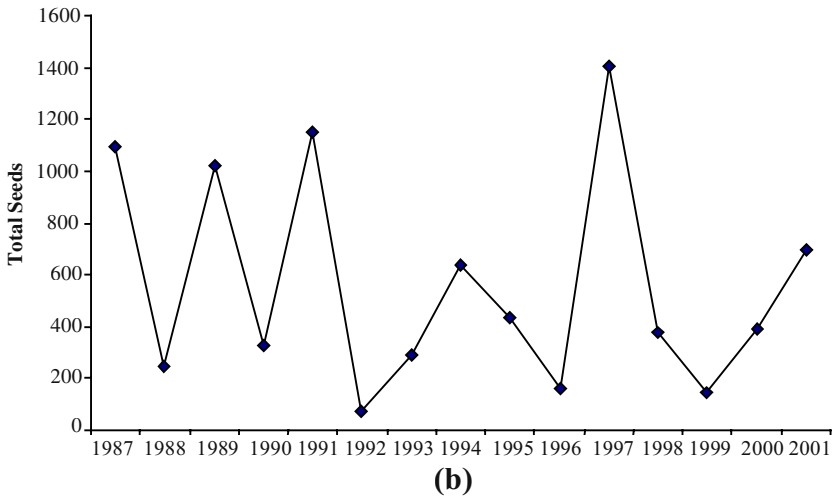
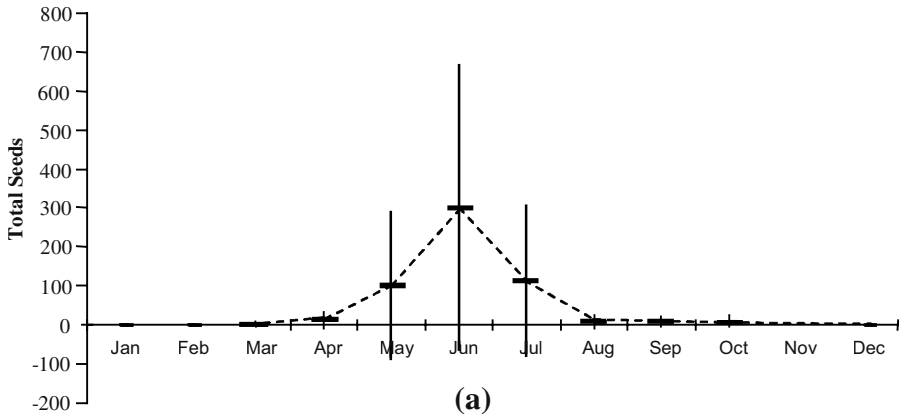


Figure 10. a) Pattern of monthly ripe fruit production by *Brosimum alicastrum* over a 15-yr period. The solid lines and error bars represent the mean of the 15 annual values \pm one standard deviation. b) Pattern of yearly ripe fruit production for *Brosimum alicastrum* over a 15-yr period.

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.

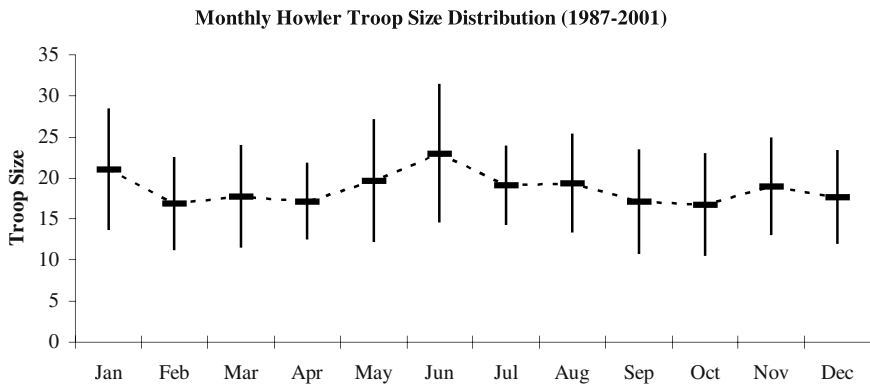


Figure 11. Monthly howler troop size distribution 1987-2001. The solid lines and error bars represent the mean of the 15 annual values \pm one standard deviation.