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THE EL NIÑO SOUTHERN OSCILLATION, VARIABLE FRUIT PRODUCTION, AND FAMINE IN A TROPICAL FOREST

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Abstract. We tested the hypothesis that the El Niño Southern Oscillation influences forest-wide fruit production, which, in turn, limits frugivorous and granivorous mammals on Barro Colorado Island (BCI), Panamá. Observations of BCI mammals have been compiled for 49 years. Frugivorous mammals experienced famine between September and January in 1931–1932, 1958–1959, 1970–1971, and 1993–1994. The most recent famine is evident from an 11-yr record of natural deaths of mammals and a 2-yr record of population densities. Famine occurred every time a mild dry season followed an El Niño event in the 49-yr record. This coincidence is statistically improbable, as demonstrated by a randomization test.

A 2-yr cycle of high, then low community-level fruit production has been observed twice for BCI when a mild dry season followed an El Niño event. We used 260 litter traps to monitor community- and species-level fruit production from 1 January 1987 through 30 June 1996. Community-level fruit production was greatest during the 1992 El Niño event and lowest one year later, after the mild 1993 dry season. We also reinterpret an earlier 2-yr record of fruit production in light of our 9.5-yr record of fruit production. Community-level fruit production was elevated during the 1969 El Niño event and was very low one year later, after the mild 1970 dry season. We hypothesize that (1) El Niño conditions enhance fruit production; (2) high fruit production consumes stored reserves, limiting the next reproductive event; and (3) mild dry seasons reduce fruit production. Each plant species may respond to any combination of the three components of this hypothesis. Community-level fruit production is extremely low when species sensitive to components 1 and 2 are entrained with species sensitive to component 3, or when a mild dry season follows one year after an El Niño event.

El Niño events bring dry, sunny conditions to BCI and a large portion of the wet tropics. Drought and sun may both favor fruit production in wet tropical forests. Drought is known to synchronize flowering, and sunny conditions may relieve light limitation. The El Niño Southern Oscillation has a strong 24-mo periodicity. This creates a strong tendency for dry, sunny years to alternate with wet, cloudy years in Central America and elsewhere in the tropics. We present evidence that this alternately enhances and reduces fruit production on BCI.

Terborgh hypothesized that predators regulate frugivorous mammals in tropical forests. As a corollary, he further hypothesized that famines occur on BCI because several large predators are absent and frugivores escape predation. We extended censuses to the nearby mainland to evaluate this hypothesis. Poachers, who are active on the mainland, reduce the abundances of game species below levels maintained in the presence of large felids and raptors. There was evidence for famine in poached, mainland populations, and we rejected the hypothesis that reduced predation pressure is a prerequisite for famine.

Key words: Barro Colorado Island, Republic of Panamá; *Dasyprocta punctata*; *El Niño Southern Oscillation*; *famine*; *fruit and seed production*; *Mazama americana*; *Nasua narica*; *Odocoileus virginianus*; *Panama*; *Sciurus granatensis*; *Tayassu tajacu*; *tropical forest*.

INTRODUCTION

We hypothesize that the El Niño Southern Oscillation influences fruit production which, in turn, limits frugivorous and granivorous mammals on Barro Colorado Island (BCI), Panamá. El Niño events bring warm, dry, sunny conditions to BCI and to a large portion of the wet tropics (see *Introduction: El Niño Southern Os-*

cillation). If these conditions generally favor fruit production, then similar effects may be expected wherever fruit production limits frugivores in wet tropical forests.

At least two attributes of El Niño events might favor fruit production. Drought affects most of the wet tropics during El Niño events (Ropelewski and Halpert 1987). Threshold levels of drought synchronize flowering and enhance seed set in selected tropical forest plants (Alvim 1960). If threshold drought responses were widespread, then drought would enhance com-

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munity-level fruit production during El Niño events. Reduced cloudiness is the second attribute of El Niño events that might favor fruit production. Clouds absorb photosynthetically active radiation (PAR), and low PAR may limit many tropical forest plants, including trees and lianas (Van Schaik et al. 1993, Wright and Van Schaik 1994). El Niño events, high levels of PAR and mast fruiting may be associated in peninsular Malaysia. Here, members of 41 plant families reproduce in synchronized mast-fruiting events at irregular, multiyear intervals (Appanah 1985). These masting events coincide with unusually sunny years and also with El Niño events (Van Schaik 1986, Ashton et al. 1988). Associations between fruit production and El Niño events are unknown outside Malesia.

Seasonally variable fruit production limits frugivores and granivores in many tropical forests (reviewed by Van Schaik et al. 1993). Many frugivores reproduce, grow rapidly, store fat, and/or cache seeds during the season of greatest fruit production. Many of the same species lose body mass, suffer increased mortality, and/or emigrate during the season of scarcity. Interannual variation in fruit production may also limit frugivores. Janzen (1974), for example, hypothesized that prolonged scarcity limits frugivores and granivores during nonmast years in Malesian dipterocarp forests. This hypothesis remains untested, perhaps because few tropical studies span enough years to evaluate population fluctuations.

One of the longest ecological records from tropical forest concerns the mammals of BCI. Frugivorous mammals experienced famine in 1931–1932, 1958–1959, and 1970–1971. The famines all occurred between September and January. In 1931–1932, coatis (*Nasua narica*), peccaries, and brocket deer (*Mazama americana*) were emaciated, and collared and white-lipped peccaries (*Tayassu tajacu* and *T. pecari*) foraged in the laboratory clearing (Enders 1935, Chapman 1938). In 1958–1959, collared peccaries and deer were again emaciated, and more than half of the individuals in a marked population of coatis died (Kaufman 1962). At the height of the 1970–1971 famine, corpses of frugivores occurred, on average, every 300 m along forest trails (Foster 1982a). Foster (1982a) analyzed 18 years of BCI mammal observations and noted that the famines each followed a mild dry season. Foster also documented fruit production for two years, including the 1970–1971 famine. Many plant species failed to fruit after the mild 1970 dry season, suggesting a link between dry-season rains, failed fruit production, and famine. Foster hypothesized that dry-season rains prevent many species from attaining the threshold levels of drought required to initiate flowering. Recent events indicate that this hypothesis is, at best, partly correct. The two rainiest dry seasons yet recorded on BCI (1981 and 1996) were not followed by fruit failure or by famine.

We re-evaluate the relationships among climate, fruit

production, and mammal populations. Observations of BCI mammals have been compiled for 49 years, and fruit production has been monitored for 10 years. A fourth famine in 1993–1994 is evident from an 11-yr record of natural deaths of mammals and a 2-yr record of population densities. The famines of 1930–1931, 1958–1959, 1970–1971, and 1993–1994 each followed one year after an El Niño event when the intervening dry season was mild. We evaluate the following hypotheses for 138 plant species: (1) El Niño conditions enhance fruit production; (2) high fruit production consumes stored reserves, limiting the next reproductive event; and (3) mild dry seasons reduce fruit production.

Terborgh (1992) hypothesized that large felids and raptors regulate populations of frugivorous and granivorous mammals in tropical forests. The three largest raptors and two largest felids recorded in central Panama are no longer resident on BCI. Terborgh (1992) hypothesized that reduced predation pressure has permitted the population densities of prey species to increase on BCI. As a corollary, he suggested that famines occur because the population densities of frugivores and granivores are not regulated by predation on BCI. We extended censuses to the nearby mainland, where poachers are active, to evaluate this hypothesis. Poachers reduce the abundances of game species below levels maintained in the presence of large felids and raptors (Freese et al. 1982, Peres 1990, 1996, Redford 1992). If there is evidence for famine in poached populations, we will reject the hypothesis that reduced predation pressure is a prerequisite for famine.

THE EL NIÑO SOUTHERN OSCILLATION

The El Niño Southern Oscillation (ENSO) is the major cause of interannual climate variation in the tropics. Atmospheric pressure oscillates across the equatorial Pacific with a pronounced 24-mo periodicity (Rasmusson et al. 1990). The Southern Oscillation Index (SOI) quantifies this oscillation as the difference in standardized atmospheric pressures between Tahiti and Darwin, Australia. Extreme values of the SOI occur at irregular multi-year intervals and are associated with El Niño (negative SOI) and La Niña (positive SOI) events. During El Niño events, atmospheric pressure is unusually low in the eastern Pacific, the westerly tradewinds weaken or even change direction, upwelling fails along western South America, and sea surface temperatures (SSTs) rise throughout the eastern equatorial Pacific. El Niño events are identified by extreme and persistent values of the SOI and SST anomalies (Kiladis and Diaz 1989). The El Niño events of 1923, 1925, 1930, 1932, 1939, 1951, 1953, 1957, 1963, 1965, 1969, 1972, 1976, 1982, 1986, and 1992 have occurred since BCI became a biological station (Kiladis and Diaz 1989, Trenberth and Hoar 1996).

The ENSO influences global climate (Ropelewski and Halpert 1987, Aceituno 1988, Kiladis and Diaz 1989). El Niño events bring below-average rainfall and

above-average temperatures to Central America, northern South America, the Amazon, Malesia, New Guinea, northern Australia, and parts of equatorial west Africa and India (Ropelewski and Halpert 1987, Aceituno 1988, Kiladis and Diaz 1989, Diaz and Kiladis 1992). Reduced cloudiness and increased incident radiation contribute to above-average temperatures during El Niño events (Aceituno 1988, Kiladis and Diaz 1989, Diaz and Kiladis 1992). The global teleconnections of La Niña events are generally opposite to those of El Niño events. The 24-mo periodicity of the ENSO creates a strong tendency for dry, sunny, and warm years to alternate with wet, cloudy, and cool years over large parts of the tropics (Ropelewski and Halpert 1987, Aceituno 1988, Kiladis and Diaz 1989). We hypothesize that fruit production is enhanced by El Niño conditions and constrained by La Niña conditions for plants that are limited by light and for plants that require threshold drought to synchronize flowering.

STUDY SITES

Barro Colorado Island (BCI; 9°9' N, 79°51' W) supports tropical moist forest with a 35-m tall canopy (Croat 1978). Annual rainfall averages 2600 mm. A 4-mo dry season most often begins in December and ends in April. BCI became an island (16 km²) in 1914 when Gatun Lake was flooded to complete the Panama Canal. Several large predators are now absent. The Harpy Eagle (*Harpyia harpyia*) and possibly the Crested Eagle (*Morphnus guianensis*) have been extirpated from central Panama. The puma (*Felis concolor*) was once abundant on BCI, where it has not been recorded since 1965 (Enders 1935; M. Moynihan, *personal communication*). The jaguar (*Panthera onca*) and Ornate Hawk Eagle (*Spizaetus ornatus*) are resident on the adjacent mainland and visit BCI. The next largest predators, ocelots (*F. pardalis*) and Black Hawk Eagles (*S. tyrannus*), are resident on BCI, as are all smaller predators of mammals recorded in central Panama (Glanz 1982, Karr 1982). Eighteen forest wardens exclude poachers.

The Gigante Peninsula is immediately to the south of BCI and was incorporated into the Barro Colorado Nature Monument (BCNM) in 1979. Soils and climate are similar to those of BCI. The forest is largely secondary, with old-growth remnants along ridges and more extensively to the southwest. Poachers are active on Gigante and hunt coatis, agouti (*Dasyprocta punctata*), paca (*Agouti paca*), white-tailed deer (*Odocoileus virginianus*), and collared peccary, but shun monkeys and red-tailed squirrels (*Sciurus granatensis*) (Glanz 1991; Security Services of the BCNM, *unpublished data*). Non-indigenous hunters select similar prey throughout the Neotropics (Redford and Robinson 1987).

METHODS

We conducted three censuses of fruit production and two censuses of mammals. The first three censuses provide a 10-yr perspective for BCI. The final two permit

detailed comparisons of BCI and Gigante from August or September 1993 through July 1995.

Census 1: Fruit dry mass.—Fruit dry mass productivity (in grams per square meter per week) was determined weekly for 60 litter traps between 18 November 1985 and 30 June 1996. Traps were randomly located in old-growth forest on BCI, were constructed of plastic screening (1.2-mm mesh), had a surface area of 0.25 m², and were mounted 40 cm above the ground. Plant reproductive parts were identified to species and were dried to constant mass at 60°C. Analyses are restricted to the 25 most productive species and to community-level production (i.e., fruit dry mass summed over all species). Wright and Cornejo (1990a, b) provide further details.

Census 2: Seed set and flowering activity.—Seed set and flowering activity were determined weekly for 200 litter traps between 1 January 1987 and 30 June 1996. Traps were randomly located in old-growth forest on BCI (2 km from census 1), had a surface area of 0.5 m², were mounted 80 cm above the ground, and were otherwise as for census 1. Plant reproductive parts were identified to species, the presence of flowers was recorded, and seeds and mature fruit were counted. Flower activity (traps per week) equalled the number of traps in which flowers were recorded. Seed set (number of seeds per square meter per week) equalled the number of seeds captured plus the number of mature fruit captured multiplied by the mean number of seeds per fruit for each species (Croat 1978, S. J. Wright, *unpublished data*). Wright and Calderón (1995) provide further details.

Analyses were restricted to species encountered in five or more traps in at least one calendar year. This insures that multiple individuals were sampled. Analyses of interannual variation were further restricted to species with ≥ 50 seed or flower records. Epiphytes were excluded because identifications were problematic before 1991. Epiphytes made up just 0.024% of fruit dry mass in census 1 (S. J. Wright and O. Calderón, *unpublished data*). Censuses 1 and 2 permit evaluation of long-term fruit production for two sites within BCI and for two indices of production.

Census 3: Mammal deaths.—The skulls of dead mammals were collected every 2 wk from 6.7 km of BCI trails from January 1987 through November 1996. The observer covered 3 km/h, with frequent stops to evaluate the phenological status of selected trees. Corpses were detected by odor and the presence of vultures. Skulls were also collected during mammal transect censuses on Gigante (see *Methods: Census 5: Mammal densities*). Primate skulls were given to Katherine Milton and are not considered here.

Census 4: Fallen seeds and fruit.—Seed plus fruit density (number per square meter) was determined from September 1993 through August 1995 for transects located randomly along the permanent trail systems of BCI and Gigante. Each transect was 50 cm

wide and 100 m long. The number of transects examined at each site each month varied from 10 (six in October 1993 for BCI) to 21. Numbers were estimated for the seed shadows beneath fruiting canopies by multiplying a mean density by the area of the transect within the seed shadow. The mean density was determined for 10 0.11-m² plots randomly located within the transect and seed shadow.

Units for the three fruit censuses differ in two important ways. Seeds and fruit were converted to common units for censuses 1 (dry mass) and 2 (seeds). Seeds and fruit had to be equated for census 4 because dry masses and seed-to-fruit ratios were unknown for a number of species unique to Gigante. The second difference concerns time. Traps were emptied each week, and censuses 1 and 2 quantify production per unit area per unit time (a flux density). Transects were never cleared, seeds and fruit accumulated and disappeared at unknown rates, and census 4 quantifies the standing density of fallen seeds plus fruit. Fruit production will be used as a convenient shorthand to describe all three censuses.

Census 5: Mammal densities.—Mammals were counted along eight 5-km transects each on BCI and Gigante. Transects followed permanent trails, excluding trails within 1 km of the laboratory clearing on BCI (Wright et al. 1994). Each transect was censused once each month from August 1993 through March 1994 (40 km per month per site) and once each two months from April 1994 through July 1995 (20 km per month per site). Censuses were conducted between 0600 and 1130 and between 1600 and 1830 when it was not raining. The observer covered 1.2 km/h and noted the species, sex, age (juvenile or adult), and initial detection distance between mammal and observer.

The King estimator is frequently used to estimate population densities of neotropical forest mammals from transect counts (e.g., Freese et al. 1982, Glanz 1982, Peres 1996). The King estimator is $D = N/(2LR)$, where D is the estimated population density, N is the number of individuals encountered, L is the length of the transect, and R is the mean detection distance. Population densities were estimated using 40 km of transects for each site (1-mo intervals before April 1994 and 2-mo intervals thereafter), and again using 80 km of transects for each site (2-mo intervals before April 1994 and 4-mo intervals thereafter).

For social species, N is often estimated by multiplying the number of social groups encountered by mean group size (Freese et al. 1982, Glanz 1982). This convention was avoided because group size varied during this study (Matthew Gompper, unpublished data). For coatis and collared peccaries, N was estimated directly by counting each animal in each social group. For primates, the time required to count the individuals in a troop precluded an ongoing transect census. The densities of primates were therefore not estimated.

The reliability of transect estimates of BCI mammal

densities has been evaluated by Eisenberg and Thorington (1973), Glanz (1982), and Gompper (1996). Density estimates from transect counts and from more intensive census methods are very similar for agoutis, coatis, and collared peccaries. Transect counts consistently underestimate red-tailed squirrel densities. The efficiency of transect counts cannot be assessed for deer, because more intensive census methods have not been used for neotropical forest deer.

Plant reproduction

The analyses of fruit production had four objectives: (1) describe seasonal variation in fruit production; (2) compare fruit production between BCI and Gigante; (3) identify extreme interannual fluctuations in fruit production; and (4) evaluate factors contributing to those extremes.

Seasonal variation in fruit production.—Seasonality was described in two ways. Mean (± 1 SD) monthly fruit dry mass production summed over all species was calculated for December 1985 through June 1996 using census 1. When census weeks bridged months, fruit dry mass was partitioned in proportion to the number of days in each month.

Seasonality was also described by the number of species with mean dates of seed set (flower activity) falling in each month. The Julian date of each census was converted to an angle and weighted by seed set (flower activity) to calculate a mean vector for each species, using census 2. The angle and length of the mean vector equal the mean date and temporal concentration of seed set (flower activity), respectively. Temporal concentration equals zero when production is equal for all census dates (modulo 360°) and equals one when production is limited to a single date. Wright and Calderón (1995) describe mean vectors in greater detail.

Mean vectors are problematic when distributions are bimodal or multimodal within years (Batschelet 1981). Autocorrelations of the time series of weekly seed set were performed to identify species with multimodal production within years. Significant autocorrelations for lags of <52 wk indicated multimodal production within years. This occurred for just two species. *Heronima laxiflora* and *Havetiopsis flexilis* reproduced twice each year, and their mean vectors were calculated separately for each reproductive event. Seed production was unimodal within years for all remaining species (analyses not shown).

Spatial variation in fruit production.—A log-linear contingency analysis was performed to evaluate spatial variation in fruit production. Each fruit transect was characterized by site (BCI vs. Gigante), time interval (12 intervals of two consecutive months each), and a dichotomous index of fruit production (0 vs. ≥ 1 fallen seeds plus fruit). Two fruit production categories and 12 time intervals were used to maintain expected frequencies. ANOVA could not be used because many

transects lacked fallen seeds plus fruit; this introduced heteroscedasticity that could not be removed by transformation (see *Results: Spatial variation in fruit production*).

Interannual variation in fruit production.—We created a 9.5-yr time series of the proportion of flowering events followed by high levels of seed set, using census 2. Total seed set was ranked for each reproductive event and species. Ranks ranged from 1 to 9, with 1 and 9 being the respective highest and lowest levels of seed set observed for each species for the nine annual reproductive events between 1 January 1987 and 30 June 1996. Ranks for *Hyeronima laxiflora* and *Havetiopsis flexilis* ranged from 1 to 18 (two reproductive events each year), and were standardized by dividing by two. Mean ranks were assigned in the case of ties. Ranked seed set was associated with the mean flowering month appropriate for the species and year. The final time series was for the proportion of species flowering each month that subsequently had high levels of seed set, where high levels of seed set were defined by ranks ≤ 3.5 (expected for $\sim 33\%$ of species, given nine ranked events). The time series was subjected to a 3-mo smooth.

Fruit dry mass production summed over all plant species is perhaps the best index of fruit availability for frugivores and granivores. We used the 10.5-yr record provided by census 1 to identify extreme values of this index for all intervals of x consecutive weeks, for $x \leq 26$.

Factors contributing to extreme fruit production.—Three descriptive and two causal factors were evaluated that might contribute to extreme interannual fluctuations in fruit production. Extreme community-level production may be most likely (1) at a time of year when relatively few species mature fruit. Unusual production by just a few species could cause a community-level extreme at such times. Extreme community-level production may also occur when (2) many species have similar atypical levels of production, and/or (3) many species shift the timing of reproduction. Our causal hypotheses were that (4) seed set is dependent between years, and (5) dry-season rains reduce seed set. These possibilities could co-occur, reinforcing one another. The five possibilities were evaluated using census 2 to contrast periods of extreme production (see *Results: Plant reproduction: Interannual variation in fruit production*) with the remainder of the 9.5-yr record.

1) A contingency analysis compared the number of species with mean dates of seed set falling in two 6-mo intervals, with the null expectation of equal numbers of species. The 6-mo intervals were chosen to isolate the period of lowest observed community-level production.

2) A contingency analysis compared numbers of species with high, medium, and low seed set (flowering activity), with the null expectation of equal numbers of species for the period of greatest community-level

production. High, medium, and low production were defined for ranked seed production for $1 \leq \text{rank} \leq 3.5$, $3.5 < \text{rank} \leq 6.5$, and $\text{rank} > 6.5$, respectively (for the definition of ranks, see *Methods: Plant reproduction: Interannual variation in fruit production*). A similar analysis for the period of lowest community-level fruit production is implicit to the analysis for dependent seed set between years.

3) Circular correlation analyses contrasted mean dates, and paired t tests contrasted temporal concentration for seed set for periods of extreme production vs. all other censuses. Batschelet (1981) describes circular correlation analyses.

4) A contingency analysis evaluated dependence between years. Species were assigned to high, medium, and low seed set categories for two consecutive years with contrasting community-level production. A McNemar symmetry chi-square contrasted counts in cells above and below the diagonal to evaluate dependence between years.

5) A final contingency analysis evaluated the hypothesis, proposed by Foster (1982a), that failure to fruit after a mild dry season falls disproportionately among species that flower in May, June, and July because these species require threshold levels of drought to initiate flowering. Species were assigned to two seasons (May through July vs. the nine remaining months) by mean flowering dates, and were assigned to high, medium, and low seed set categories for a year with a mild dry season and low community-level fruit production.

Mammals

A contingency analysis was performed to contrast the number of corpses found from September 1993 through February 1994 with the remaining 113 census months. The six critical months were shifted back three weeks relative to the period of lowest community-level fruit production (10 August 1993 through 7 February 1994; see *Results: Plant reproduction: Interannual variation in fruit production*) because deaths were expected to lag behind low fruit production. The analysis was restricted to species with >20 corpses, to maintain expected frequencies.

A repeated-measures ANOVA was used to evaluate mammal densities. Main effects were site (BCI vs. Gigante), species and census interval, with repeated measures on census interval. The analysis was repeated for census intervals that included 40 and 80 km of transects for each site. Nonprimate species with >100 individuals registered were included. Brocket and white-tailed deer were pooled for these analyses because brocket deer inhabit older forest and were only recorded on BCI, and white-tailed deer inhabit younger forest and were only recorded on Gigante. The ANOVA model omitted species \times site and species \times site \times month interactions because there was a single density estimate for each species, site, and month. The Huynh-Feldt

procedure was used to correct for a mild violation of the compound symmetry assumption of repeated-measures ANOVA (Huynh-Feldt epsilon > 0.6; Wilkinson 1990).

The long-term record

Mammals.—There are 49 years of published records of population fluctuations of BCI mammals or of field observations for the critical period between September and January. This includes 1926 through 1937, 1951, 1955, 1958, 1959, 1961, and 1966 through 1997 (Enders 1935, 1939, Chapman 1938, Ingles 1953, Altmann 1959, Kaufman 1962, Bernstein 1964, Hladik and Hladik 1969, Eisenberg and Thorington 1973, Foster 1982a, Glanz 1982, 1990, Giacalone-Madden et al. 1990, Wright et al. 1994; J. Giacalone-Madden et al., unpublished data).

The timing of famines was evaluated relative to El Niño events and dry-season rainfall deficits for these 49 years. Dry-season rainfall deficits were defined to equal the smallest cumulative value of daily rainfall (recorded since January 1929) minus mean daily dry-season potential evapotranspiration, where positive values (surplus rainfall) were reset to zero. More sophisticated estimates of dry-season severity were precluded because only rainfall was recorded before 1971 (Windsor 1990). Dry-season rainfall deficits were divided into three categories, each including 22 or 23 years. Mild, intermediate, and severe dry seasons corresponded to dry-season rainfall deficits ≥ -449 mm, between -450 mm and -542 mm, and < -542 mm, respectively. The 1992 dry season was severe, with a rainfall deficit of -596 mm. The 1993 dry season was mild, with a rainfall deficit of only -392 mm.

Fisher's Exact Tests were used to evaluate associations between famine and (1) an El Niño event in the previous year, (2) a mild dry-season rainfall deficit in the current year, and (3) a severe dry-season rainfall deficit in the previous year. Intermediate dry seasons were pooled with mild or severe dry seasons for these Exact Tests. This analysis assumes that years are independent. In fact, years are dependent (consider the alternation of El Niño and La Niña conditions).

A randomization test was therefore performed to validate the contingency analyses. The 68-yr record was treated as a torus by wrapping 1997 around to precede 1929. The record of famine and nonfamine years was fixed, including years that lacked an observation. The temporal order of meteorological events was also fixed, but the beginning point of the meteorological record was advanced one year at a time around the torus. The number of matches between famine and each meteorological event was recorded for each of the 67 possible beginning points (discounting the observed beginning point). The 67 simulated numbers of matches were compared to the single observed number of matches.

In addition to validating the three contingency analyses previously mentioned, the randomization test was

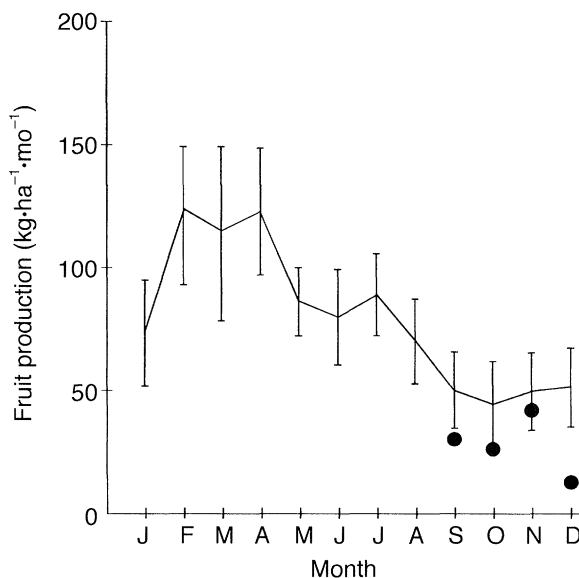


FIG. 1. Monthly fruit dry mass production summed over all species. The solid line and error bars represent mean productivity ± 1 SD (calculated from December 1985 through June 1996). Solid circles represent September through December 1993. Data are from census 1.

used to evaluate associations between famine and meteorological events that spanned two consecutive years. These compound meteorological events included a mild dry season in the current year combined with (4) a severe dry season in the previous year, and (5) an El Niño event in the previous year.

Plant reproduction.—Observations of plant reproduction across famines and El Niño events are limited. Foster (1982a) scored fruit production on a three-point scale (failed, poor, successful) for 58 species during the 1970–1971 famine. Our census 2 included 46 of these species. We performed a contingency analysis to evaluate the null hypothesis that fruit production during the 1970–1971 and 1993–1994 famines was unrelated for these 46 species. The poor and successful categories of Foster were pooled, and failure to produce fruit was contrasted with at least some fruit production.

Analyses

All analyses were performed using SYSTAT 5.0 (Wilkinson 1990). The circular correlation analysis was programmed in SYSTAT BASIC and was checked against sample data sets provided by Batschelet (1981).

RESULTS

Plant reproduction

Seasonal variation in fruit production.—Census 1 (60 litter traps) included 326 species and 15.58 kg dry mass of fruit and seeds in 552 weekly censuses. Community-level fruit dry mass productivity had a single broad peak between February and April (Fig. 1). Fruit dry mass productivity was consistently low between

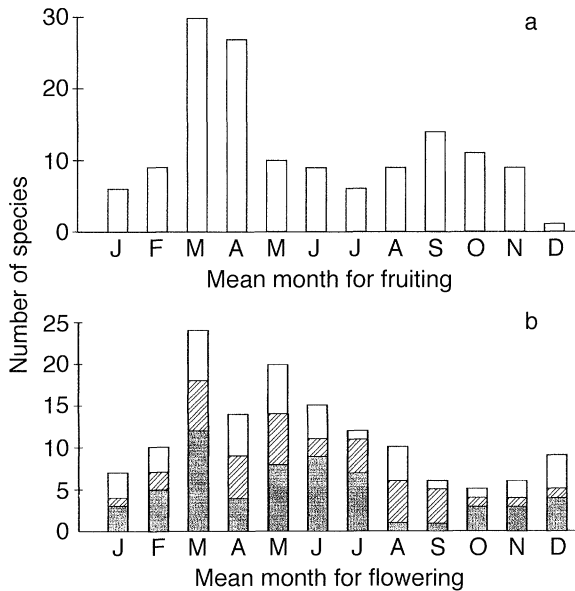


FIG. 2. Number of species with (a) mean fruiting dates and (b) mean flowering dates falling in each month. In panel b, the shaded, diagonally slashed, and open portions of each bar represent species with low, intermediate, and high levels of seed set following 1993 flowering. The levels of seed set are defined in the caption to Table 2. Data are from census 2.

September and December, averaging just 40.5% of February–April levels.

Census 2 (200 litter traps) included 478 species in 499 weekly censuses; 138 species had ≥ 50 seed records and were encountered in five or more traps in at least one calendar year. Represented were 48 families, including trees (81 species), lianas (45), hemiepiphytes (3), shrubs (7), and parasitic shrubs (2). Mean dates for seed set fell in March and April for 57 of the 138 species (Fig. 2a). The species-level analysis reinforces the single peak observed for community-level fruit productivity. 127 species also had ≥ 50 flower records. There was a broader peak for mean dates of flowering activity between March and June (Fig. 2b).

The seasonality of BCI fruit production has previ-

ously been reported as the number of species in fruit each month (Croat 1975, 1978, Foster 1982b). This metric confounds the timing and duration of fruit production. Many species have asymmetric fruit production within a fruiting season, with a quick peak followed by persistent low fruit fall (S. J. Wright and O. Calderón, unpublished data). The number of species in fruit therefore broadens and shifts community-level fruiting peaks back in time. The metrics presented here describe the seasonality of fruit production with greater temporal resolution (Figs. 1 and 2).

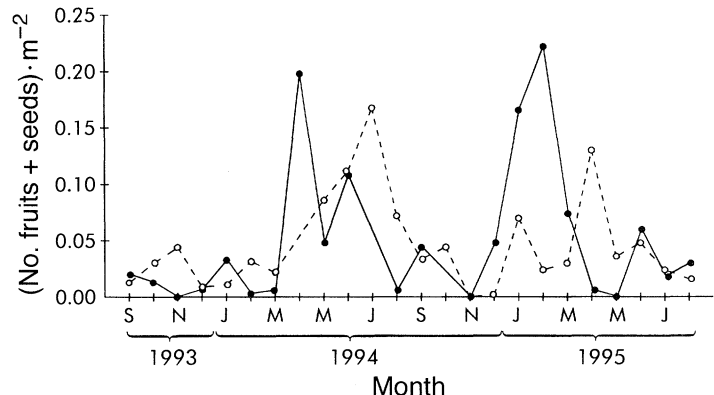
Spatial variation in fruit production.—Census 4 (seed and fruit transects) included seeds and fruit of 86 species in 576 transects. The interaction among site, time interval, and fruit production was insignificant ($\chi^2 = 18.8$, $df = 12$, $P = 0.094$). Fruit production reached its annual low between September and December and was consistently low from September 1993 through March 1994 at both sites (Fig. 3).

Seeds and fruit were present in more transects on Gigante (140 of 301) than on BCI (98 of 275), leading to a significant interaction between site and apparent fruit production ($\chi^2 = 6.41$, $df = 1$, $P < 0.05$). This may actually reflect more complete removal of fallen seeds and fruit by terrestrial mammals on BCI (see *Results: Mammals*).

Interannual variation in fruit production.—The proportion of species with high levels of seed set was consistently greatest for flowering events that occurred from February 1992 through October 1992 (Fig. 4). The complete distributions of species-level ranks of flowering activity and subsequent seed set for these nine months confirm high levels of reproductive activity for most species (Table 1).

Community-level fruit dry mass production was lowest from 10 August 1993 through 7 February 1994. This was true for all intervals from 17 through 26 consecutive weeks in the 10.5-yr record. Community-level fruit dry mass production reaches its annual low between September and December, and, in 1993, averaged 43% below those already low mean levels (Fig. 1). All three fruit censuses identified extremely low

FIG. 3. Number of fruit plus seeds per square meter on the ground from September 1993 through August 1995 for BCI (open circles, dashed lines) and Gigante (closed circles, solid lines). Data are from census 4.



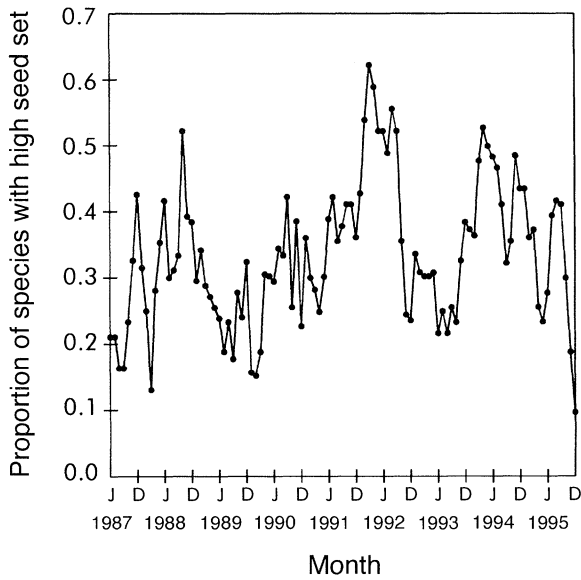


FIG. 4. Time series summarizing 9.5 yr of fruit production for 138 species. The time series is for the proportion of species that flowered each month and subsequently had high seed set. High seed set is defined for ranks ≤ 3.5 , where ranks are defined in the caption to Table 1 (also see *Methods: Plant reproduction: 3. Interannual variation in fruit production*). Ticks marks represent each December (D) and June (J) along the abscissa. Data are from census 2.

TABLE 1. Flowering activity from February 1992 through October 1992 and subsequent seed set. Entries are numbers of plant species.

Rank	Flowering activity	Seed set
1	24	28
2	23	18
3	11	20
4	14	13
5	19	7
6	7	8
7	4	5
8	3	15
9	2	2

Notes: Ranks 1 and 9 refer to the highest and lowest levels of production observed for each species for the nine annual reproductive events between 1 January 1987 and 30 June 1996. There are fewer species for flowering activity because several species met the criterion for analyses of interannual variation (≥ 50 trap records) for seeds only. Data are from census 2.

levels of fruit production in late 1993 (Figs. 1, 3, 4, and 5).

Factors contributing to extreme fruit production.—

1) Mean dates of fruit production fell between August and January for 48 species, and between February and July for 90 species (Fig. 2a; $\chi^2 = 12.8$, $df = 1$, $P < 0.01$). The four famines all occurred at the time of year when fewest species have mean dates of fruit production. This also coincided with the lowest observed community-level fruit production.

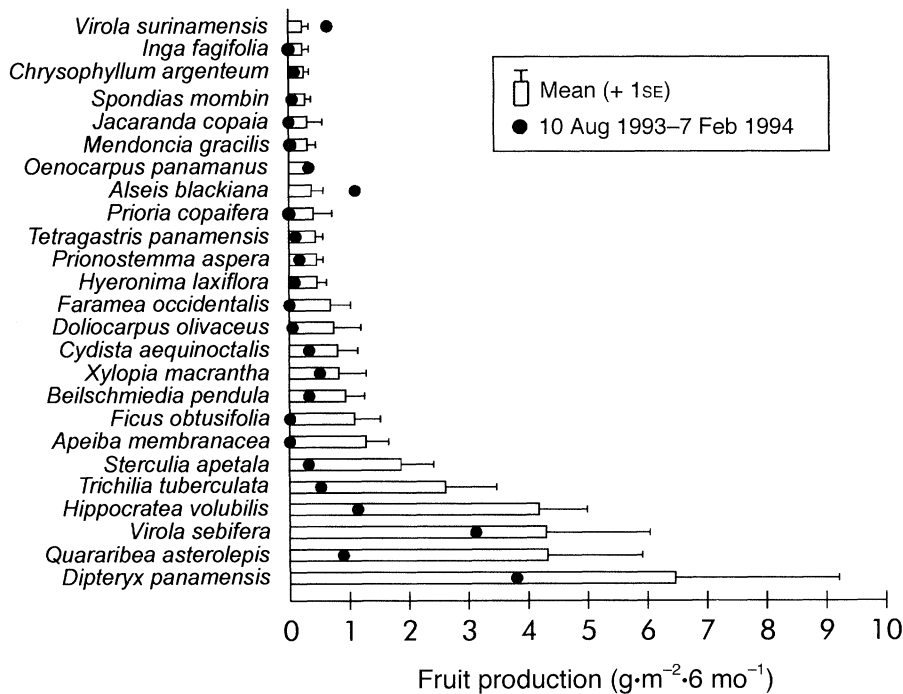


FIG. 5. Mean (and 1 SE) fruit dry mass production (horizontal histogram) between 10 August and 7 February from 1986–1987 through 1995–1996 for the 25 species with the greatest mean production for these 26 wk. Solid circles represent production between 10 August 1993 and 7 February 1994. Data are from census 1.

TABLE 2. Dependent seed set between 1992 and 1993. Entries are numbers of plant species.

	Seed set for 1993		
	High	Medium	Low
Seed set for 1992			
High	11	21	34
Medium	12	6	10
Low	8	8	6

Notes: All species flowered from February through October. High, medium and low seed set were defined for ranks for $1 \leq \text{rank} \leq 3.5$, $3.5 < \text{rank} \leq 6.5$, and $\text{rank} > 6.5$, respectively. Ranks are defined in the caption to Table 1 (also see *Methods*; *Plant reproduction*, 3. *Interannual variation in fruit production*).

2) Many species had similar atypical levels of fruit production during community-level extremes. Most species had high levels of flowering activity and subsequent high levels of seed set during the period of highest community-level production from February 1992 through October 1992 (Table 1; $\chi^2 = 34.4$ and $\chi^2 = 23.6$ for flowering and seed set, respectively; $df = 2$, $P < 0.001$). In contrast, 22 of the 25 most productive species had below-average fruit production during the period of lowest community-level production from 10 August 1993 through 7 February 1994 (Fig. 5). Fruit production was more than two standard errors below mean levels for 17 of these 25 species (Fig. 5).

3) Shifts in timing did not contribute to periods of extreme community-level fruit production. Mean angular dates of seed production were highly correlated for the extreme reproductive events of 1992 and 1993–1994 vs. all other years (circular correlation coefficients > 0.55 , $P < 0.0001$). The temporal concentration of seed set was indistinguishable for 1992 and 1993 vs. all other years ($t = -0.63$ and -1.49 , respectively, $P > 0.15$).

4) Levels of fruit production were dependent between years (Table 2, McNemar chi-square = 18.8, $P < 0.001$). Species that had high levels of seed set following flowering between February 1992 and October 1992 tended to have reduced seed set one year later.

5) In 1993, levels of seed set did not differ significantly for species that flowered in May, June, and July vs. the nine remaining months of the year (Fig. 2b; $\chi^2 = 1.81$, $df = 2$, $P = 0.40$).

Mammals

Census 3 registered 132 dead mammals (excluding primates) in 1730 km of censuses on BCI and four dead mammals in 510 km on Gigante. Disproportionate numbers of corpses were encountered between September 1993 and February 1994. Agouti, collared peccary, and brocket deer died at rates 5–8 times above background levels on BCI (Table 3). This increase was highly significant for collared peccary and brocket deer (Table 3). On Gigante, two collared peccary and two coati corpses were encountered between November 1993 and February 1994, and then no corpses were encountered in the next 17 mo. Natural deaths were concentrated during the period of extremely low fruit production at both sites.

Census 5 registered 2406 mammals (excluding primates) in 524.8 km and 510 km of transects on BCI and Gigante, respectively (Table 4). The six species encountered more than 100 times (red-tailed squirrel, agouti, coati, collared peccary, and the pooled brocket and white-tailed deer) all consume large amounts of fruit and/or seeds (Enders 1935, Kiltie 1981, Smythe et al. 1982, Brannan et al. 1985, Giacalone-Madden et al. 1990, Gompper 1996).

Population densities differed significantly with time and site (Table 5, within-subjects interaction). Densities were highest between August and October 1993 and declined sharply by April/May 1994 for all species on BCI (Fig. 6). Similar declines occurred among red-tailed squirrels, agoutis, and collared peccaries on Gigante. Two observations substantiate the population declines observed between August 1993 and March 1994. First, disproportionate numbers of natural deaths occurred at the same time (Table 3). Second, the low population densities attained by March 1994 were subsequently sustained for ≥ 1 yr (Fig. 6).

Fig. 6 also presents earlier population density esti-

TABLE 3. Number of natural deaths recorded in 1730 km of censuses equally distributed between 1 January 1987 and 30 November 1996 on BCI and the proportion that occurred from September 1993 through February 1994.

Species	Total no. dead animals, Jan 1987 through Nov 1996	Proportion of total, Sep 1993 through Feb 1994	χ^2
<i>Dasyprocta punctata</i>	11	0.364	
<i>Nasua narica</i>	15	0.067	
<i>Tayassu tajacu</i>	25	0.320	40.5***
<i>Mazama americana</i>	23	0.261	22.9***

Notes: The six months that included the 1993–1994 fruit shortage make up 4.7% of the censuses. The contingency analysis tests the null hypothesis that deaths were equally likely per month during these six months and during the remaining 113 mo. The analysis was limited to species with > 20 corpses to maintain minimum expected frequencies > 1 .

*** $P < 0.001$.

TABLE 4. Numbers of individual mammals registered on BCI (524.8 km of transects) and Gigante (510.0 km).

Species	Common name	BCI	Gigante
<i>Alouatta palliata</i>	howler monkey	620	510
<i>Cebus capucinus</i>	white-faced monkey	306	387
<i>Saguinus geoffroyi</i>	tamarin	38	46
<i>Bradypus variegatus</i>	three-toed sloth	2	0
<i>Choloepus hoffmanni</i>	two-toed sloth	1	1
<i>Tamandua mexicana</i>	anteater	10	19
<i>Dasybus novemcinctus</i>	nine-banded armadillo	1	0
<i>Sylvilagus brasiliensis</i>	rabbit	1	1
<i>Sciurus granatensis</i>	red-tailed squirrel	71 (60)	87 (77)
<i>Dasyprocta punctata</i>	agouti	737 (651)	459 (428)
<i>Agouti paca</i>	paca	1	0
<i>Nasua narica</i>	coati	422 (127)	136 (60)
<i>Eira barbara</i>	tayra	4	1
<i>Tapirus bairdii</i>	tapir	0	1
<i>Tayassu tajacu</i>	collared peccary	204 (107)	69 (35)
<i>Mazama americana</i>	brocket deer	95 (89)	0
<i>Odocoileus virginianus</i>	white-tailed deer	0	44 (43)
unidentified		4	0

Note: Numbers in parentheses are numbers of encounters with one or more individuals for selected species.

mates based on transect censuses for BCI. The population densities of red-tailed squirrel, coati, brocket deer, and collared peccary were unusually high in August and September 1993, and then declined to levels observed in earlier studies. Population densities of agouti declined from the high end to the low end of the range of values observed previously. Frugivores and granivores had high population densities when fruit production fell to low levels in August 1993 (cf. Figs. 1, 5, and 6).

Relative population densities on BCI and Gigante parallel poaching pressure. Poachers are active on Gigante but not on BCI. They take agouti, coati, collared peccary, and deer, but not red-tailed squirrels (Security Services of the BCNM, unpublished data). Population densities were generally greater on BCI for the four poached species, but not for red-tailed squirrels (Fig. 6). Natural deaths substantiate the site difference for the four poached species, nearly four times as many corpses being found per month on BCI as on Gigante (74 corpses in 119 mo vs. 4 corpses in 24 mo). Squirrel corpses were rarely found ($N = 2$).

The physical condition of all six species had dete-

riorated by December 1993 (C. Carrasco and S. J. Wright, *personal observation*). Many individuals were emaciated, with protruding hip bones. Coatis searched the leaf litter ceaselessly. Collared peccaries were in particularly poor condition, and several individuals were unable to escape a slowly walking observer.

These changes in physical condition may have increased detectability. This, compounded by low population densities and low numbers of encounters, in turn, may have contributed to an ephemeral increase in the apparent population densities of coatis and white-tailed deer on Gigante between December 1993 and February/March 1994 (Fig. 6). To increase numbers of encounters and the reliability of population density estimates, population densities were also calculated for census intervals that included 80 km of transects at each site. Results of the repeated-measures ANOVA were quantitatively similar and qualitatively identical for census intervals including 40 km or 80 km of transects, and only the results for census intervals including 40 km of transects have been presented (Table 5, Fig. 6).

The long-term record

Mammals.—Famine was associated with a mild dry season in the current year, a severe dry season in the previous year, and an El Niño event in the previous year (Fisher's Exact Test, $P = 0.013$, $P = 0.005$, $P = 0.002$, respectively). The randomization test validated the statistical significance of each of these associations ($P \leq 0.03$). Their predictive value was limited, however. Famine occurred in the same year for four of 16 mild dry seasons, one year after four of 13 severe dry seasons, and one year after four of 10 El Niño events. The dry-season rainfall deficits corresponding to famines also suggest limited predictive power. Famines

TABLE 5. Repeated-measures ANOVA of mammal densities.

Source	SS	df	MS	F
Between subjects				
Species	41 501	4	10 375	7.14*
Site	5939	1	5938	4.08
Error	5817	4	1454	
Within subjects				
Census	6218	15	414	4.51**
Census × Species	8067	60	134	1.46
Census × Site	4786	15	319	3.47**
Error	5520	60	91	

* $P < 0.05$, ** $P < 0.001$.

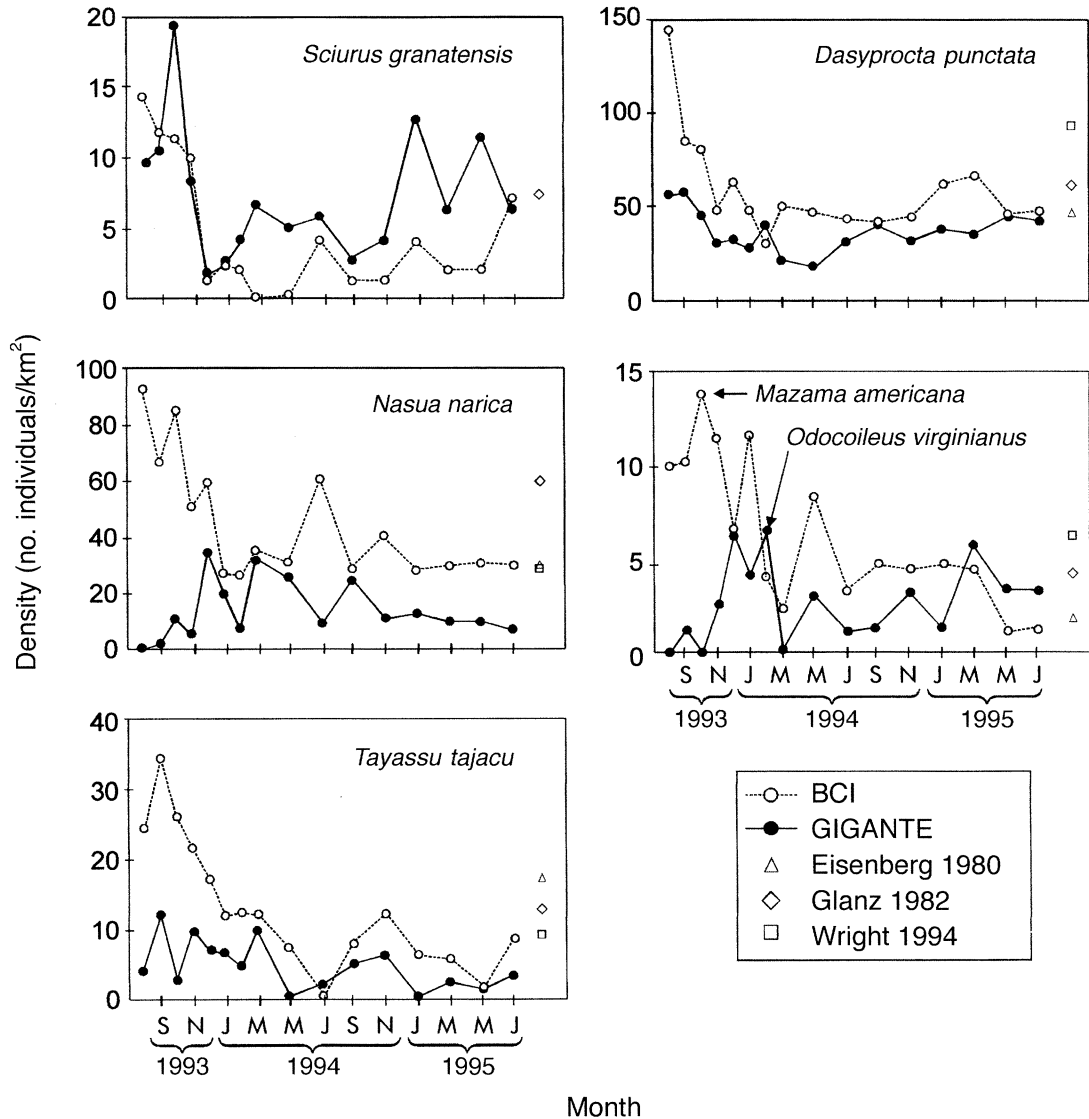


FIG. 6. Population densities (no. individuals/km²) for mammals from BCI (open circles, dashed lines) and Gigante (closed circles, solid lines) for August 1993 through July 1995. Data are from census 5. Triangles, diamonds, and squares represent additional density estimates from BCI (from Eisenberg and Thorington [1973] and Eisenberg [1980], Glanz [1982], and Wright et al. [1994], respectively).

coincided with the first, fourth, eighth, and ninth mildest dry seasons and occurred one year after the first, eighth, 11th, and 13th most severe dry seasons. Most mild dry seasons, most severe dry seasons, and most El Niño events were not followed by famine.

Meteorological events spanning two years had much greater predictive power. Famine occurred four of seven times when a mild dry season followed a severe dry season. Finally, famine occurred every time a mild dry season followed an El Niño event (Fig. 7). The randomization test confirmed the significance of both of these associations ($P = 0.015$).

Plant reproduction.—Species that failed to fruit during the 1970–1971 famine tended to fail to fruit again

during the 1993–1994 famine (Table 6; $\chi^2 = 6.76$, $df = 1$, $P < 0.01$). Anecdotal observations from 1931–1932 and 1958–1959 also suggest similar levels of fruit production by particular plant species. *Dipteryx panamensis* failed or fruited very poorly during all four famines, whereas *Apeiba membranacea* fruited reasonably well (Enders 1935, Chapman 1938, Kaufman 1962, Foster 1982a). *Coussarea curvigemma* and *Spondias mombin* also fruited well in 1958–1959, 1970–1971, and 1993–1994 (not mentioned for 1931–1932). Many species had similar fruit production in different famine years.

Other species had dissimilar production across famine years. *Quararibea asterolepis* had a successful fruit

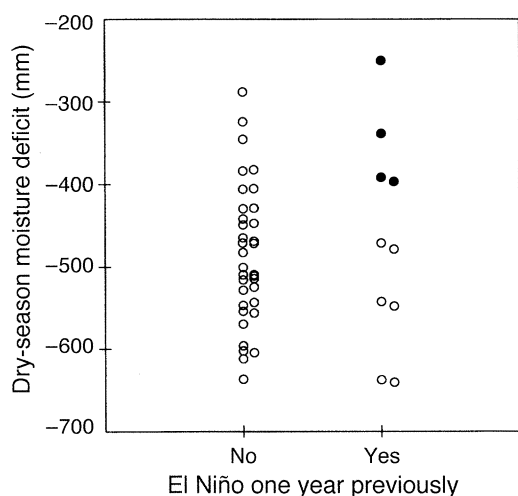


FIG. 7. Famine affects the frugivorous and granivorous mammals of BCI when the current dry season is mild and an El Niño event occurred in the previous year. Each symbol represents a year. Famine occurred between September and January for years represented by solid symbols. Dry-season moisture deficits equal the smallest cumulative value of daily rainfall minus mean daily dry-season potential evapotranspiration (see *Methods: The long-term record: Mammals*).

crop in 1970 and initiated a large crop in 1993; however, an outbreak of a defoliating caterpillar reduced the 1993 seed set dramatically (Wong et al. 1990; S. J. Wright, unpublished data). *Astrocaryum standleyanum* failed to flower in 1958 and 1970, but initiated a large seed crop in 1993; however, white-faced monkeys and coatis destroyed most of the seeds, drinking the proto-endosperm. Additional species with dissimilar production in 1970–1971 and 1993–1994 are evident in Table 6. A variety of species-specific and year-specific factors contribute to community-level variation in fruit production.

DISCUSSION

A 2-yr cycle of high and then low community-level fruit production has been documented twice for BCI (by Foster [1982a, b] and by the present study). Both times, high production occurred during an El Niño event and low production followed a mild dry season one year later. El Niño events occurred in 1969 and 1992. Foster (1982a, b) lacked a long-term record of fruit production for comparison, and considered the levels of fruit production observed during the wet season in 1969 to be the norm. Comparison with a new 9.5-yr record indicates that production was actually elevated in 1969 (compare our Fig. 1 with Foster 1982a: Fig. 1). The dry seasons of 1970 and 1993 were both mild. The same low level of fruit production, 18.7 g dry mass·m⁻²·6 mo⁻¹, was observed from August through January following both mild dry seasons. The parallels between the 1969–1971 and 1992–1994 records of fruit production are striking.

TABLE 6. Dependence of fruit production between famine years. Entries are numbers of plant species.

1970–1971 fruit production†	1993–1994 fruit production‡ (no. plant species)	
	Fruited	Failed
Fruited	20	5
Failed	9	12

† Data are from Foster (1982a: Table 2), with his subjective categories “poor fruit crop” and “successful fruit crop” pooled under “frUITed.”

‡ Data are from census 2 of the present study.

We hypothesize that (1) El Niño conditions stimulate fruit production; (2) high fruit production consumes stored reserves, limiting the next reproductive event; and (3) mild dry seasons reduce fruit production. Each plant species may respond to any combination of the three components of this hypothesis. The lowest community-level fruit production occurs when species sensitive to components 1 and 2 are entrained with species sensitive to component 3, or when a mild dry season follows one year after an El Niño event. Over 49 years, these conditions were invariably associated with famine among frugivorous mammals, substantiating the link to low community-level fruit production (Fig 7). This hypothesis will now be evaluated, beginning with the second component.

Fruit production in a variable environment

Elevated fruit production consumes reserves and limits future production for many fruit and timber trees (Matthews 1963). This is consistent with the negative dependence in fruit production observed between years (Table 2). The second component of the hypothesis is likely to be valid for many species.

One or more proximal cues must relate fruit production to El Niño conditions and to mild dry seasons, the first and third components of our hypothesis. Species with mean flowering dates between February and October had high levels of fruit production in 1992 (Table 1, Fig. 4), and species with mean flowering dates in every calendar month had low levels of fruit production in 1993–1994 (Fig. 2b). This suggests a cue common to many species and/or a variety of cues. Three possibilities will be evaluated.

Low minimum temperatures cue the development of reproductive buds during El Niño events in peninsular Malaysia and in Sarawak (Ashton et al. 1988; T. Inoue, personal communication). The minimum temperature recorded just above the forest canopy on BCI was 21°C between 1 January 1987 and 31 December 1996. The 46 nights with minimum temperatures under 22°C were unrelated to the extreme levels of fruit production observed between 1992 and 1994 (S. Paton, unpublished data). Low minimum temperatures can be discounted as a cue for community-level variation in fruit production on BCI.

Dry-season severity may be an important cue. Many tropical forest plant species require a threshold level of drought before flowering successfully (Alvim 1960; reviewed by Van Schaik et al. 1993). This threshold may be achieved during an initial severe dry season, but not during a subsequent mild dry season, enhancing and then reducing fruit production. If large numbers of species required threshold levels of drought to flower successfully, then the alternation of severe and then mild dry seasons could explain the alternation of high and then low community-level fruit production.

We evaluate the role of drought thresholds separately for mild and severe dry seasons. Failure to achieve a threshold level of drought during a mild dry season is not a sufficient cue for low community-level fruit production, as indicated by three lines of evidence. First, drought thresholds are most likely among species that flower early in the wet season from May through July (Foster 1982a); however, species that flower in all months contributed to low community-level fruit production in 1993–1994 (Fig. 2b). Second, flowering was unaffected by heavy dry-season irrigation for 49 of 50 tree and liana species on BCI (Wright and Cornejo 1990a, b). Third, fruit production was not unusually low following the two rainiest dry seasons yet recorded on BCI (1981 and 1996; S. J. Wright, *unpublished data*). We conclude that failure to achieve a threshold level of drought during a mild dry season has little effect on subsequent community-level fruit production. The third component of our hypothesis must be rejected. Some other attribute of the year following an El Niño event may reduce fruit production.

Only indirect evidence bears on the role of severe dry seasons. The long-term record indicates that a severe dry season is not sufficient to initiate the 2-yr cycle of fruit production that ends in famine. Specifically, famine did not occur on three occasions when a mild dry season followed a severe dry season (see *Results: Long-term record*). An initial severe dry season may still be an important cue, however. The four famines each followed a mild dry season that was preceded one year earlier by an El Niño event that *included a severe dry season*. The role of an initial severe dry season would be demonstrated if famine had failed to occur after a mild dry season preceded by an El Niño event that included an intermediate or mild dry season. This combination of events has not occurred since mammal observations began on BCI. We tentatively conclude that threshold drought, during an initial severe dry season, remains a viable cue that may contribute to the 2-yr cycle of fruit production that ends with famine. However, some other attribute of El Niño events is also essential.

Incident radiation is a possibility. Reduced cloud cover permits increased insolation over large areas of the tropics during El Niño events (Aceituno 1988, Diaz and Kiladis 1992). Light limits many tropical forest plants, even in the canopy (Van Schaik et al. 1993,

Wright and Van Schaik 1994). Above-average radiation may stimulate fruit production during El Niño events. The strong 24-mo periodicity of the El Niño Southern Oscillation causes sunny and cloudy years to alternate over many neotropical forests (Aceituno 1988). Cloudy conditions may reduce fruit production in the year following an El Niño event (replacing the third component of our hypothesis). Long-term radiation records are needed to evaluate the relationship between insolation and interannual variation in fruit production.

The many species with similar levels of fruit production in different famine years suggest that similar proximal cues acted across famine years (Table 6). Likely candidates include threshold dry-season drought and variable incident radiation. Each plant species may have a unique response to a variable environment, however, and many other possible cues remain to be explored.

Ecological implications

Terborgh (1992) hypothesized that population regulation by large felids and raptors precludes famine among their prey. We reject this hypothesis for two reasons. First, the 1931–1932 famine occurred when puma were considered to be abundant on BCI (Enders 1935, Chapman 1938). The comparison of BCI and Gigante provides a second reason to reject the hypothesis that predators preclude famine. Poachers take agouti, coati, collared peccary, and white-tailed deer from Gigante. Nonetheless, population declines for agouti and collared peccary, and natural deaths for coati and collared peccary, coincided with the six months of low fruit production on Gigante (cf. Figs. 3 and 6). We conclude that low fruit availability can limit tropical forest frugivores even when they are exposed to poachers.

El Niño events have occurred 21 times in this century and bring low rainfall, high incident radiation, and high temperatures to most tropical forest regions (see *Introduction: El Niño Southern Oscillation*). Models of both global climate change and regional deforestation predict decreased precipitation, increased temperatures, and more intense seasonality in the tropics (Shukla et al. 1990, Scholes and van Breemen 1997). El Niño events share these attributes and may provide a window on the future for a large part of the tropics. Despite the frequent and widespread impact of El Niño on tropical climates and the relevance to global climate change, just a handful of studies have examined the impact of El Niño events for wet tropical forests.

Five studies suggest that plant performance may improve during mild El Niño events and decline during severe El Niño events in wet tropical forests. High levels of fruit production are associated with El Niño events in peninsular Malaysia and on BCI (Ashton et al. 1988). For *Cordia alliodora* from the Barro Colorado Nature Monument (BCNM), annual tree rings spanned eight El Niño events (Devall et al. 1996). The

six largest growth increments occurred during mild El Niño events. The two remaining El Niño events, 1976 and 1982, corresponded to the two most severe dry seasons recorded for the BCNM. Finally, the most extreme El Niño event of this century occurred in 1982–1983. Elevated tree mortality followed in old-growth forest on BCI, and widespread forest fires followed in selectively logged forests in Borneo (Leighton and Wirawan 1986, Leigh et al. 1990, Condit et al. 1996). Additional studies that span multiple El Niño events are required to evaluate the hypothesis that plant performance is enhanced by mild El Niño events and reduced by severe El Niño events in wet tropical forests.

Even fewer studies consider tropical forest animals and El Niño events. Terricolous arthropods delay their annual ascent into the canopies of Amazonian flood plain forests during El Niño events (Adis and Latif 1996). The severe 1982–1983 El Niño event had little impact on the animals of BCI (Wheeler and Levings 1988, Leigh et al. 1990). We speculate that enhanced community-level fruit production may improve the condition of frugivorous mammals during El Niño events. Death rates of frugivorous mammals are greatest on BCI between September and December, when fruit production is at its annual low (Milton 1990). Enhanced fruit production at this time of year may sustain vulnerable frugivores during El Niño events. This is consistent with the unusually high population densities of frugivores following the 1992 El Niño event (Fig. 6). Elevated densities would exacerbate a famine if a mild dry season, low insolation, and extremely low community-level fruit production followed in the next year.

Evolutionary implications

Community-level fruit production may vary simply because fruit production by different plant species responds similarly to climatic variation (see *Discussion: Fruit production in a variable environment*). Selection may, however, further reinforce variable community-level fruit production for at least two reasons.

Selection may adjust reproductive effort to anticipate conditions favorable for future seedling establishment. This hypothesis posits a climatic signal that anticipates seedling environments by a full reproductive season. No such signal has yet been identified (Kelly 1994); however, the strong tendency for ENSO to alternate between El Niño and La Niña conditions suggests a possibility. Dry-season drought limits seedling establishment in seasonal tropical forests (Garwood 1983). We speculate that selection might favor enhanced reproduction during El Niño events, because La Niña conditions and a mild dry season that would favor seedling establishment are likely in the following year.

Selection may also favor variable fruit production when seed predators are alternately starved and satiated (Janzen 1974, Kelly 1994). Mammals are potent seed and seedling predators in tropical forests (Osunkoya

et al. 1992, Asquith et al. 1997). Seed survivorship would improve if high community-level fruit production satiated generalist mammals during El Niño events, or if low community-level fruit production starved and reduced populations of generalist mammals. Subsequent selection would synchronize seed set both within and among species (Janzen 1974, Kelly 1994).

Interspecific synchrony is extreme in Malesia where species from at least 41 families mast synchronously at irregular, multiyear intervals (Appanah 1985). Mast fruit production in peninsular Malaysia and enhanced community-level fruit production on BCI both coincide with El Niño events (Ashton et al. 1988). The two phenomena are fundamentally different, however. Although many species mast synchronously in Malesia, just one species is known to mast on BCI (Foster 1977; S. J. Wright, *unpublished analyses*). Why did synchronous masting evolve in Malesia but not in Panama?

Phylogenetic constraints and dominant plant families with very different biologies might provide the answer. Closely related species share similar reproductive phenologies by common descent (Kochmer and Handel 1986, Wright and Calderón 1995). The Dipterocarpaceae dominate Malesian forests, whereas the Leguminosae dominate Panamanian forests and most other tropical forests (Gentry 1988). Dipterocarpaceae is a small family (680 species), with many closely related species (only 16 genera) that share wind-dispersed seeds and pollination by generalist thrips and leaf beetles (Ashton et al. 1988; T. Inoue, *personal communication*). Leguminosae is a huge (18 000 species) and phylogenetically diverse family (642 genera), with member species requiring a diverse array of animal pollinators and seed dispersers. The evolution of synchronous masting may have been favored in Malesia because the dominant Dipterocarps initially shared similar reproductive phenologies and lacked the constraint imposed by the need to sustain specialist pollinators and seed dispersers.

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