Caribbean Journal of Science, Vol. 35, No. 3-4, 249-264, 1999

Pre- and Post-Hurricane Fruit Availability: Implications for Puerto Rican Parrots in the Luquillo Mountains

JOSEPH M. WUNDERLE, JR.

International Institute of Tropical Forestry, USDA Forest Service, P.O. Box 490, Palmer, Puerto Rico 00721 USA

ABSTRACT.—Fruit availability on 25 plant species, consumed or potentially consumed by the Puerto Rican Parrot (*Amazona vittata*), was studied to document the seasonal and annual variation in fruit production in the Luquillo Mountains. In the 33 months before Hurricane Hugo, an annual cycle in the number of species with ripe fruit was evident, with a peak in October-February and a trough during June-July. About half the plant species showed this annual fruiting cycle. Irregular noncyclic fruiting was found in the other half, and varied among species in annual duration. Fruit production reached its lowest point in October 1989, just after Hurricane Hugo, when 72% of the broadleaf foliage was lost and only one species had ripe fruit. The number of fruiting species subsequently increased, but the cyclic fruiting pattern, evident in the number of fruiting species before the storm, disappeared and was not observed during 27 months after the storm. This noncyclic pattern was attributed mostly to species with annual fruiting cycles in which annual fruiting shifted out of phase, was suppressed after the hurricane, or both. Parrot breeding was associated with fruiting, as breeding occurred during fruiting peaks before the storm, and was delayed in the first season after the storm, but returned to normal by the second season. Thus parrots faced considerable annual and year-to-year variation in fruit availability prior to the hurricane, and substantial fruit loss afterwards, followed by a recovery involving changes in fruiting phenology of individual species and the overall community.

INTRODUCTION

Frequent seasonal or nomadic movements are characteristic of many tropical frugivores and seedeaters. The Puerto Rican Parrot (*Amazona vittata*) is no exception, and its movements within the Luquillo Mountains are viewed as a response to food resources which are often separated in space and time (Snyder et al., 1987). The lack of a rigidly-defined pattern of movement within the forest is a logical outcome of the parrot's reliance on a wide range of acceptable food resources characterized by patchy distributions and year-to-year variation in production. Although many opportunistic field observations indicate that the Puerto Rican Parrot feeds on at least 60 plant species (Snyder et al., 1987), relatively little is known about the seasonal and annual variation in the seed or fruit production of these plants. Knowledge of the phenology of the parrot's main food items is useful for understanding movements as well as other aspects of its biology.

Several phenology studies have been conducted in various parts of the Luquillo forest. Most have been done in the lower elevations of the forest, particularly at El Verde (350 m), where fruit fall of the major forest trees has been studied (Estrada Pinto, 1970) and compared (Devoe, 1989) between closed canopy forest and forest openings. Also at El Verde, Bannister (1970) and Murphy (1970) described the phenology of sierra palm (*Prestoea montana*), an important fruit for the Puerto Rican Parrot. Others have studied palm fruit fall at higher forest altitudes (Frangi and Lugo, 1985, Lugo and Frangi, 1993). Rodríguez-Vidal (1959) presented fruiting seasons for 54 plant species fed upon by parrots. Snyder et al. (1987) note that 22 % of Rodríguez-Vidal's 117 parrot feeding observations and 22 % of their 87 feeding records occurred on dates outside the bounds of the stated fruiting dates. Similarly, they found that many feeding observations also fell outside the fruiting periods summarized by Estrada

Pinto (1970). This suggests that the extent of fruiting period variation, relevant to parrot foraging, has not been fully described in the Luquillo Mountains.

This study was initiated in January 1987 to describe the phenological variation of fruits or seeds used, or potentially used, by the Puerto Rican Parrot. Three trails were selected in parrot foraging areas near traditional nesting sites at 450-730 m in the Luquillo forest. The study was conducted for 33 months before the site was struck on 18 September 1989 by Hurricane Hugo, a class 3 hurricane responsible for substantial defoliation and structural damage to trees. Patterns of fruit production were expected to be disrupted by the storm, which in turn would affect parrot behavior. These expectations arose from previous hurricane studies which indicated that frugivore/seedeaters were vulnerable to hurricane impacts by the loss of food resources (reviewed in Wiley and Wunderle, 1993). Fruiting phenology was followed for 27 months after the storm to document recovery patterns. This paper describes pre- and post-hurricane fruiting phenology patterns in an effort to better understand its potential effects on Puerto Rican Parrot behavior.

Study Site And Methods

This study was conducted in the Luquillo Experimental Forest (LEF) in eastern Puerto Rico. The evergreen forest has been classified into four major types including tabonuco, colorado, palm, and dwarf forest (Wadsworth, 1951). These four forest types are approximately stratified by altitude. At the lowest level below 600 m, is the tabonuco forest named for the predominant tree (*Dacryodes excelsa*). This forest type covers approximately 70 % of the LEF and is found within the subtropical wet forest zone (Ewel and Whitmore, 1973). Above 600 m is the colorado forest which covers approximately 17 % of the LEF and is found within the subtropical lower montane wet forest zone (Ewel and Whitmore, 1973). This forest type is named for the common palo colorado tree (*Cyrilla racemiflora*). Above 750 m on the peaks and ridges is the dwarf forest, which covers approximately 2 % of the LEF. This forest type is named for the dwarf, gnarled stature of the forest trees. Interspersed between the dwarf and colorado forests are patches of palm-brake or palm forest characteristic of sites with steeper slopes, poor drainage and saturated soils. This forest type (covering about 11 % of the LEF) is made up of virtually pure stands of sierra palm (*Prestoea montana*).

Three phenology trails were established in traditional parrot foraging sites. The East Fork trail, 445 m long, spanned 450-550 m in altitude in the upper tabonuco zone. The Palo Hueco trail was approximately 1,100 m long and ranged from 550 to 650 m at the tabonuco-colorado forest boundary. The 1,930 m Caimitillo trail passed through colorado forest at an altitude range of 670-730 m. Plants along these trails were selected for observation on the basis of their potential or actual use by Puerto Rican Parrots (Snyder et al., 1987). Because the only "fruits" recorded on these trails are those that are potentially bird dispersed (i.e., mostly succulent fruits), the study does not fully characterize the phenology of the plant communities at these sites. With the exception of two vines (*Clusia gundlachii, Marcgravia sintenisii*) all marked plants were subcanopy or canopy trees (voucher specimens deposited in the Missouri Botanical Garden). Diameter at breast height (dbh) was measured 1.3 m from the base of all trees. Initially 342 plants of 30 species were marked with aluminum tags. However, due to mortality only 180 individuals of 25 species were studied, of which 64 % are known to produce fruits or seeds consumed by the parrot (Table 1). This included 57 individuals of 17 species in Caimitillo, 62 individuals of 16 species in Palo Hueco, and 61 individuals of 12 species in East Fork. Only plants that survived to the end of the study were included in the analysis. Species with 5 or more individuals are designated as common in the text and shown in Figure 2. Species with less than 5 individuals are designated as rare and are shown in Figure 3.

Fruiting phenology was monitored from January 1987 through January 1992 on a

TABLE 1. Tree and vine species monitored on three phenology trails with total labeled plants at start of study and total remaining alive at the end of the study.

Species	Parrot Observations[1]	Total	
		Start	End
Alchornea latifolia	Yes	10	6
Byrsonima coriacea	Yes	5	5
Casearia guinensis	Yes	1	1
Clusia gundlachii	Yes	7	1
Clusia clusioides	No	12	8
Cordia borinquensis	No	11	2
Cyrilla racemiflora	No	1	1
Dacryodes excelsa	Yes	21	14
Eugenia borinquensis	No	3	2
Eugenia stahalii	Yes	3	3
Ficus laeviagata	Yes	6	5
Ficus sintenisii	No	1	1
Guarea ramiflora	Yes	16	6
Haenianthus salicifolius	No	18	5
Inga laurina	Yes	20	8
Laplacea portoricensis	No	1	1
Magnolia splendens	No	28	11
Marcgravia sintenisii	Yes	29	8
Matayba dominguensis	Yes	5	3
Micropholis chrysophylloides	No	10	2
Micropholis garciniaefolia	Yes	29	19
Ocotea spathulata	Yes	8	2
Prestoea montana	Yes	34	27
Rheedia portoricensis	Yes	19	11
Sloanea berteriana	Yes	35	28

[1]Refers to data taken from Snyder et al. (1987: Appendix 10).

monthly basis, except for March, July, and August 1987. Each trail was walked once on the 10, 11, and 12th of each month, except on weekends and during rainy periods when trails were visited on the first nonrainy weekday. During each survey fruit quantity on each tagged plant was visually scored (with the aid of 10 × 40 binoculars) on a relative scale ranging from 0-4, and by estimating the percentage of ripe fruit. The score of 0-4 was relative to the fruit quantity on each monitored species and therefore a maximum score on a large-crowned species was not equivalent to the same score on a small-crowned species. This scheme enabled comparisons among months within a species but not between species. To facilitate comparisons of plants with ripe fruits, a plant was considered to have ripe fruit when ≥10% of the crop was ripe.

A test for runs above and below the median (Sokal and Rohlf, 1995) was used to determine if there was cyclic variation in fruiting before, and after the hurricane, in the number of species and number of individuals of a species. After dividing the data into pre- and post-hurricane samples, I calculated the median number of species or individuals with ripe fruit in each month. The sequence and number of months when the number of species or individuals fell above or below the median was tallied. The runs test was used to determine whether the monthly sequence of values above or below the median was random. The median values were not included in the analysis except in the cases where the median was 0. In that case, the analysis was based on the sequence of values above the median compared with the sequence of 0s. A type I probability error of 0.05 or less was accepted as significant. Standard deviations were used to describe variation.

To correct for relative abundance of each tree species, I used the number of stems of each tree species in a 4 ha palo colorado forest plot (Wadsworth, 1949: Table 23). To estimate the number of fruiting stems (>10% of fruit crop ripe) for each tree species, the proportion of tagged individuals with ripe fruit during the specified month was multiplied by the number of stems in the 4 ha plot (half the number of stems was used for dioecious species). This quantity was divided by 4 to standardize to 1 ha. All fruiting species were then summed to obtain an estimate of fruiting stems per ha for each month.

To evaluate hurricane damage to the marked plants on the first sample period following Hurricane Hugo (October 1989), estimates were made of the percentage defoliation and extent of structural damage to each broadleaf tree. Damage classes in broadleaf trees (from most to least severe) were: trunk broken; trunk down (uprooted with trunk or branches on the ground); trunk leaning (partially uprooted); and presence of major branch breaks (branches > 10 cm diameter). When a tree had more than one type of damage, only the most severe was used in the analysis. Damage was recorded in diameter (dbh) classes of 3-8 cm; 9-15 cm; 16-23 cm; 24-38 cm; and ≥ 39 cm.

Breeding periods of individual pairs of Puerto Rican Parrots were graphed to illustrate the timing of breeding relative to fruiting phenology (Figure 1). The probable date of clutch initiation for each pair was based on observation of the first time the female spent the night in the nest cavity as provided by the U.S. Fish and Wildlife Service. The nesting duration of each pair was assumed to be 92 days based on a range of 82-103 days (Snyder et al., 1987). This duration ignored instances where predation or accidents terminated breeding and consistently illustrate the 92-day period. Only the first breeding attempt is shown for a year and replacement clutches were not included.

RESULTS

Pre-hurricane fruiting patterns.—Monthly rainfall at East Peak, 3.5 km from the nearest phenology trail (East Fork) varied greatly during the study (Figure 1). The fruiting pattern, as measured by the number of fruiting species or individuals, was not correlated with monthly rainfall; although fruit production was sometimes lowest during the driest periods. Distinct fruiting peaks in number of fruiting species and individuals occurred at the end and beginning of each year (October - February) during 1987-1988 and 1988-1989. A smaller peak occurred early in 1987. The number of fruiting species was consistently lowest in June and July. The fruiting pattern of the assemblage of 25 species was nonrandom, as indicated by a significant sequence in the monthly number of fruiting species, which was greater than the monthly median (Median = 9) and was followed by a sequence below the median (Runs Test, $P = 0.01$). These cyclic patterns were consistent among the three phenology trails, indicating relatively little geographic variation in fruiting phenologies, at least in terms of the number of species or individuals in fruit.

Approximately half the species (56 %,14/25) showed an annual cycle of fruiting which approximately corresponded with two repetitions of the major October-February peak. An annual cycle was evident to varying degrees in common species (Figure 2), which displayed a fruiting peak just before the end of the year (*Haenianthus salicifolius*, $P = 0.02$; *Inga laurina*, $P = 0.05$; *Magnolia splendens*, $P = 0.02$; *Rheedia portoricensis*, $P = 0.05$); at the end of the year (*Ficus laeviagata,* $P = 0.05$; *Micropholis garciniifolia,* $P > 0.05$); or the beginning of a year (*Byrsonima coriacea,* $P = 0.02$; *Marcgravia sintenisii,* $P = 0.02$). Another common species with a peak in the October- February period was *Prestoea montana* ($P = 0.01$), which showed its highest peak every other year. Among rare species (Figure 3), an annual cycle with peaks in or near October-February was also apparent in *Eugenia stahlii, Cyrilla racemiflora, Laplacea portoricensis*, and *Micropholis chrysophylloides*. Finally, the common *Alchornea latifolia* ($P = 0.02$) showed an annual cycle which peaked in April-May just after the main October-February peak.

Irregular noncyclic fruiting was apparent

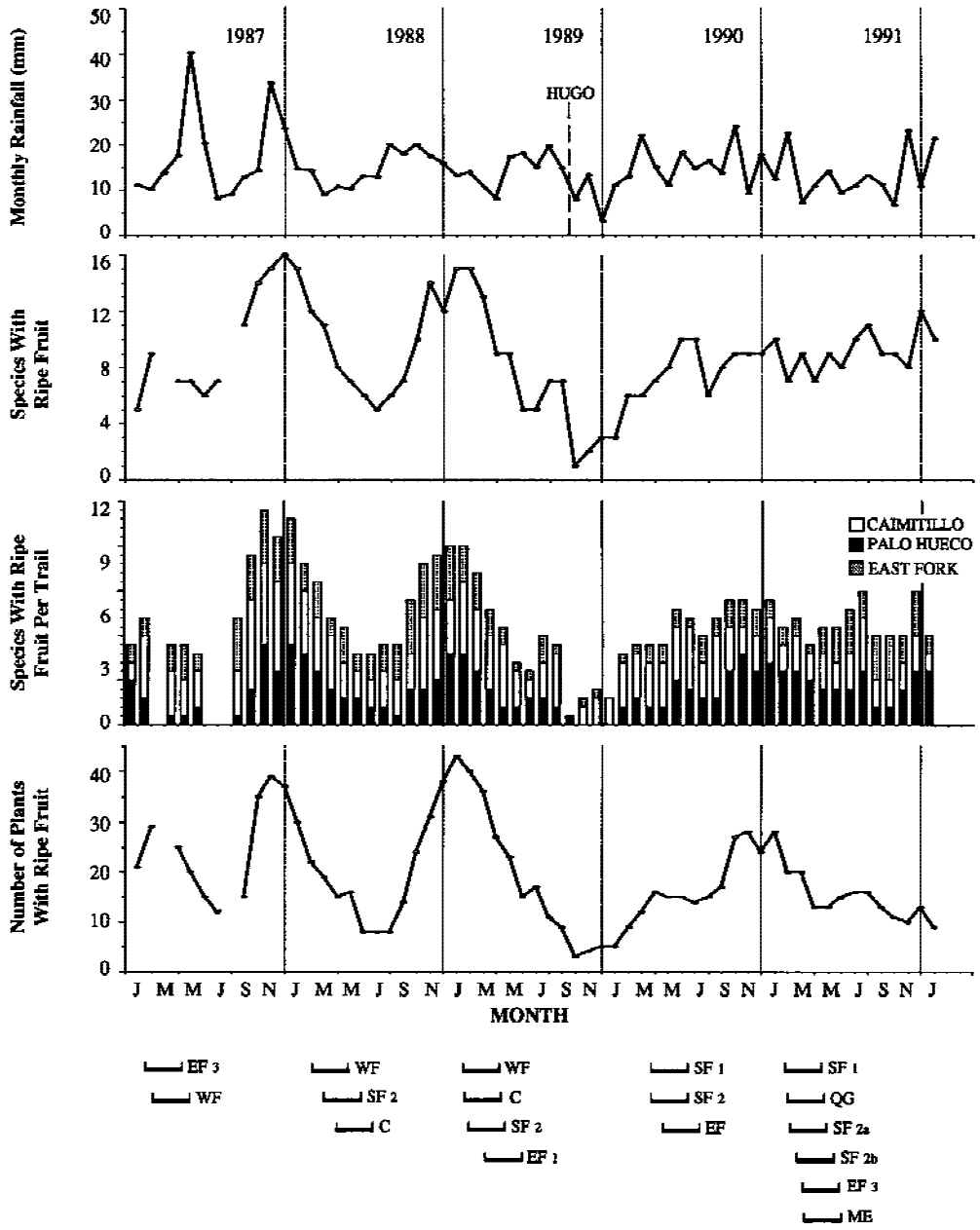

FIG. 1. Monthly rainfall, number of species with ripe fruit, number of species with ripe fruit per phenology trail, number of plants with ripe fruit and nesting chronology of the Puerto Rican Parrot from 1987 to 1991. Plants with ripe fruit are defined as plants in which ≥10% of the fruit crop is ripe. Hurricane Hugo struck the LEF on 18 September 1989. Parrot nesting chronology is shown at the bottom, where each horizontal bar indicates a 92-day nest period of a pair as indicated by the code at the end of the bar. The date of nest initiation (left side of each bar) is based on the first time the female spent the night in the nest cavity.

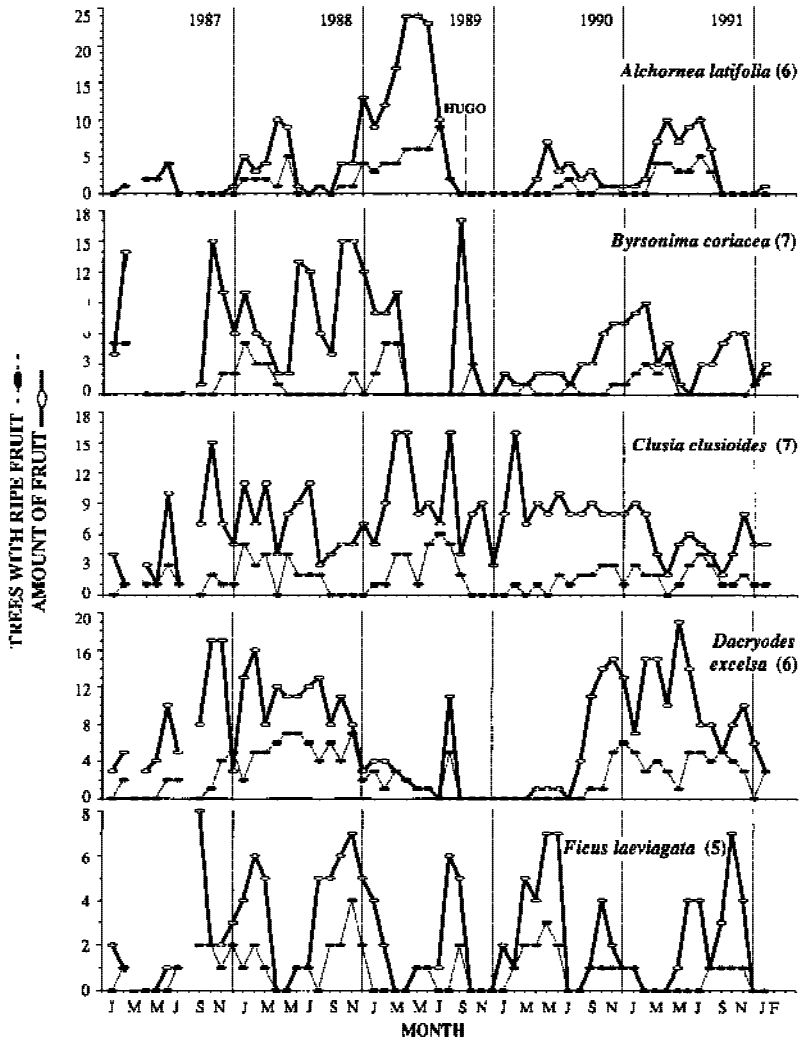

FIG. 2. Fruiting phenologies of marked common species (N ≥ 5 individuals) in the LEF from 1987 to 1991. Plants with ripe fruit are defined as plants in which ≥10% of the fruit crop is ripe. Amount of fruit was estimated on a scale of 0-4 for each plant and summed for all plants of that species. The number in parentheses is sample size.

in 44 % of the species (11/25). In these species the yearly duration of fruit production ranged from long to short. Irregular long-duration fruiting was characterized by species in which fruit was available for at least half the year. This pattern was evident in several common species including *Clusia clusioides* ($P > 0.05$), *Dacryodes excelsa* ($P > 0.05$), and *Guarea ramiflora* ($P = 0.02$) and in two rare species: *Ficus sintenisii* and *Matayba domingensis*. In contrast, irregularly short-duration fruiting species did not produce fruit in some years (*Cordia borinquensis, Ocotea spathulata*). Although the common *Sloanea berteriana* ($P > 0.05$) infrequently produced fruit, in some years fruit was present for over six months. This same pattern occurred in one rare species (*Eugenia borinquensis*), while *Casearia arborea* and *Clusia gundlachii* did not fruit before the hurricane.

Because of their relatively long period of fruit production, the irregular long-duration fruiting species (common and

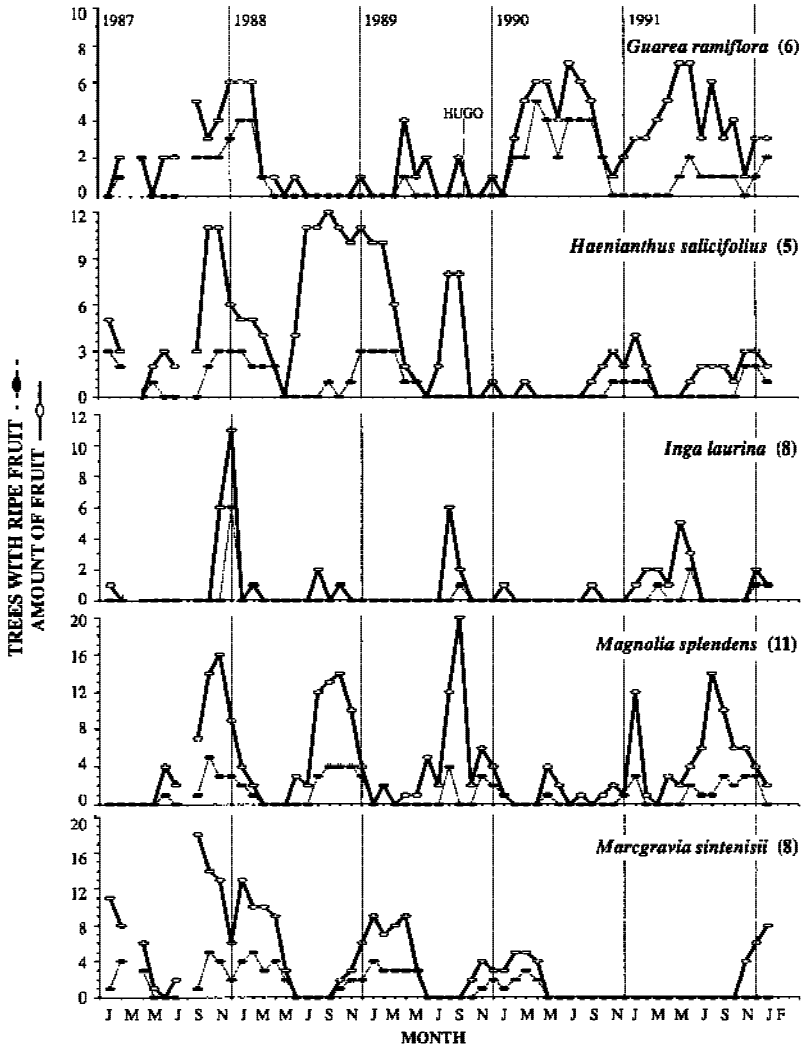

FIG. 2b.

rare) had fruit present in both October-February peaks, as well as during the three troughs between peaks. These troughs in the number of species bearing fruit occurred in April-June 1987, June-August 1988, and June-July 1989. Thirty-six percent (5/14) of the species with an annual cycle of fruiting consistently had some fruit present in the three troughs (*Haenianthus salicifolius, Magnolia splendens, Prestoea montana, Alchornea latifolia*, and *Ficus laevigata*.)

Hurricane Damage.—Defoliation of broadleaf trees on the three trails was severe, as indicated by an average estimated defoliation per tree of 72.2 % ± 33.6 in the 172 trees which survived in an upright position. Average defoliation per tree varied among the trails from a high of 82.4 % ± 23.7 defoliation per tree in Palo Hueco (N = 59 trees) to a low of 60.6 % ± 39.4 defoliation per tree in East Fork (N = 59 trees). Caimitillo (N = 54 trees) suffered an intermediate level of defoliation per tree (71.9 % ± 28.3). Palm defoliation averaged 61.2 % ± 21.3 (N = 27 palms) and the variation among trails mirrored the pattern found in broadleaf trees: that is, average defoliation per palm was highest in Palo Hueco (79.3 % ± 21.7, N = 9),

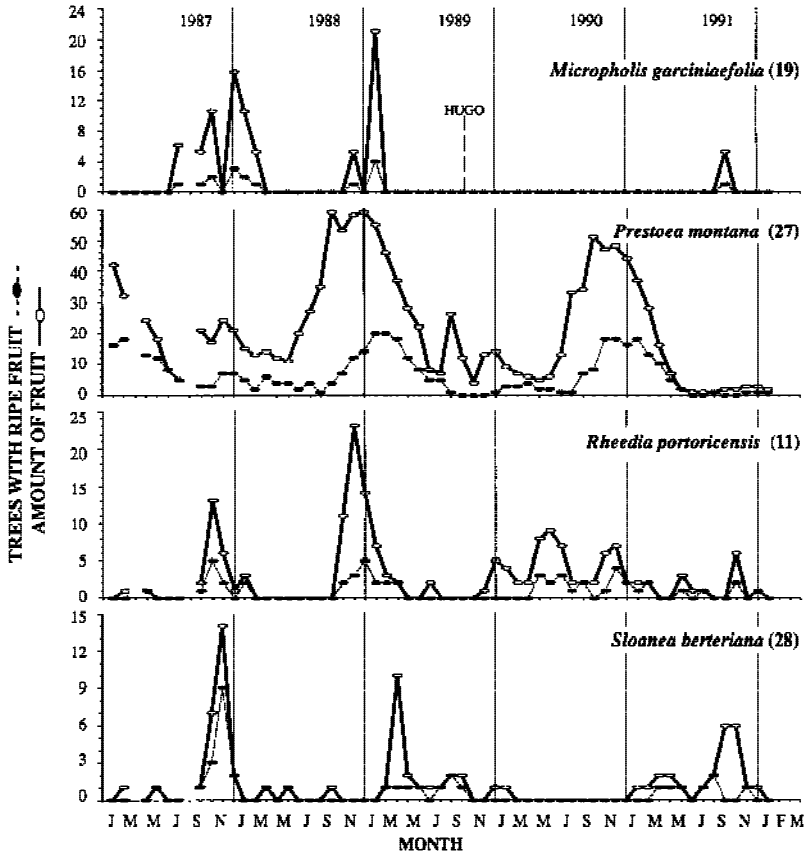

FIG. 2c.

lowest in East Fork (36.2 % ± 11.4, N = 8), and intermediate in Caimitillo (68.2 % ± 28.0, N = 10).

Overall structural damage to broadleaf trees was partially related to tree size; the smallest DBH stems were the least damaged (Figure 4). The likelihood of major branch breakage was also directly related to size; the largest trees were most likely to lose major limbs (e.g., 66 % of 82 trees ≥39 cm vs. 6 % of 38 trees 3 - 8 cm). The more severe classes of damage (i.e., trunk leaning, down, or broken) were not directly related to tree size. Variation in tree structural damage among the three trails corresponded with the defoliation pattern with the greatest amount of structural damage in Palo Hueco (79 % of the trees damaged), then Caimitillo (77 % of the trees damaged), and least in East Fork (56 % of the trees damaged). The most severe structural damage, as tabulated in the categories of trunk lean, trunk down or trunk break, occurred in Caimitillo.

Hurricane damage accounted for virtually all the plant mortality observed in this study. Only one of the tagged plants (*Prestoea montana*) died before the hurricane, compared with 47 % of the tagged plants (162/342) which died after the hurricane. Mortality rates were highest in vines (75 %, 27/36), intermediate in broadleaf trees (47 %, 128/272), and lowest in palms (20 %, 7/34). Variation in the mortality rates of broadleaf trees corresponded to the damage pattern variation, with the highest mortality in Palo Hueco (54 %, 59/109), then Camitillo (51 %, 45/88), and least in East Fork (33 %, 25/76).

Post-hurricane Fruiting Patterns.—Hurricane Hugo was a relatively dry storm (Figure 1). A dry period of several weeks fol-

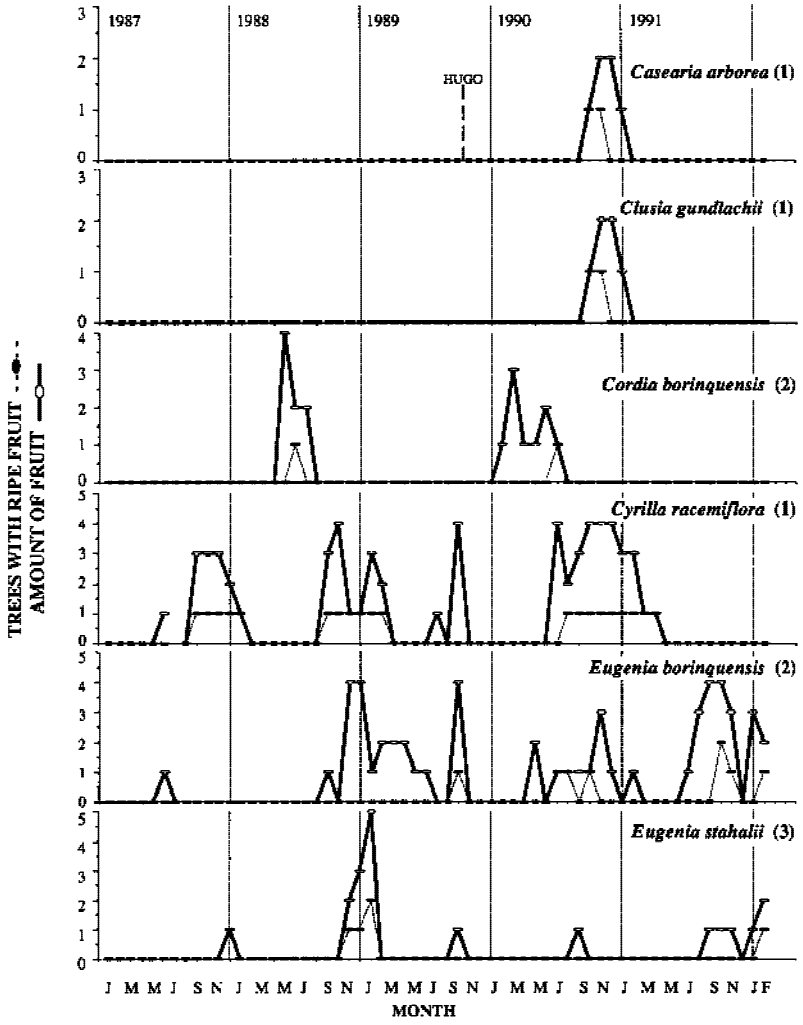

FIG. 3. Fruiting phenologies of marked rare species (N < 5 individuals) in the LEF from 1987 to 1991. Plants with ripe fruit are defined as plants in which ≥10% of the fruit crop is ripe. Amount of fruit was estimated on a scale of 0-4 for each plant and summed for all plants of that species. The number in parentheses is sample size.

lowed the storm, and Scatena and Larsen (1991) note that monthly rainfall totals were below long-term means within the LEF at El Verde until the end of the year.

Fruit production reached its lowest point in October 1989, just after the passage of Hurricane Hugo (Figure 1). Only two individuals of *Byrsonima coriacea* remained with ripe fruit. Following this low, the number of species bearing fruit increased and peaked in June and July 1990. Although there was evidence of a slight peak during December-January, the overall pattern of fruit production in the monitored species remained non-cyclic until the end of the study (Median = 8.5 species; Runs Test, $P > 0.05$), in contrast to the significant cyclic pattern in number of fruiting species before the hurricane.

The non-cyclic pattern in number of species bearing fruit after the hurricane was mostly attributable to the species with annual cycles, which had their normal pre-hurricane fruiting pattern shift out of

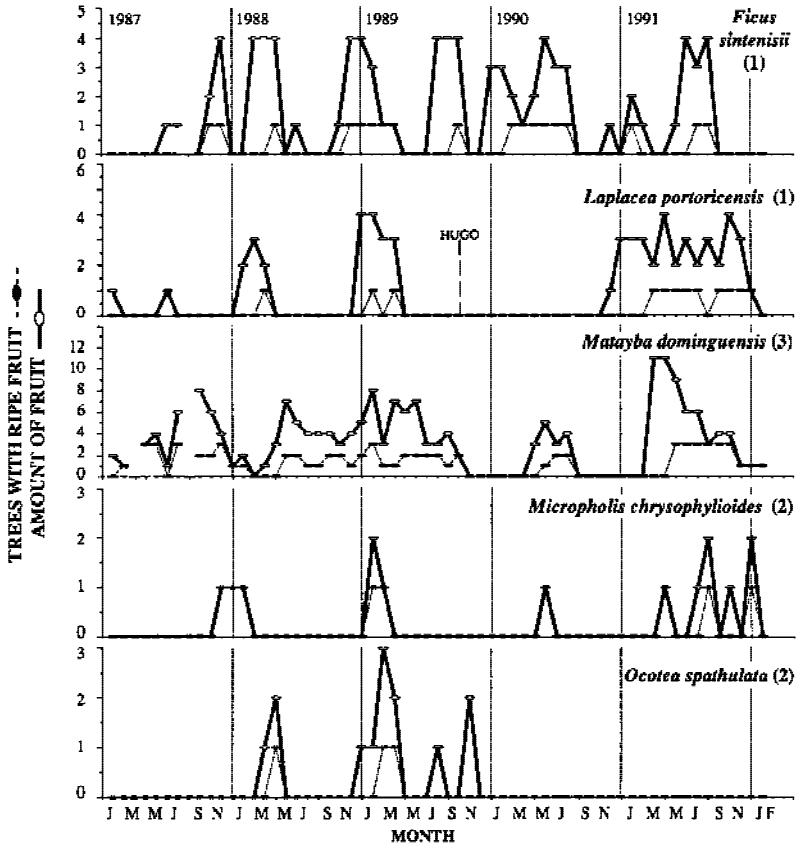

FIG. 3b.

phase, suppressed after the hurricane, or both. Only two species retained their normal annual fruiting cycle and fruiting intensity after Hugo (*Magnolia splendens*, P = 0.05; *Ficus laevigata*, P = 0.01). Another common cyclic species maintained its normal annual cycle, but fruiting intensity was suppressed (*Alchornea latifolia*, P = 0.01). Although this may have also been the case in the common *Prestoa montana* (P = 0.01), it is equally likely that the post-hurricane peak was normally suppressed due to increased fruit production every other year. *Marcgravia sintenisii* (P = 0.01) produced fruit as expected, but quantity diminished in late 1989 and early 1990, and afterwards fruit production was suppressed for 17 months. Four cyclic species missed their normal end/beginning of the year fruiting peak after Hugo, but the normal pattern returned by the end of 1990, although with a suppression in quantity (*Byrsonima coriacea*, P= 0.02; *Eugenia stahlii, Haenianthus salicifolius*, P =0.01; *Microphilus garciniifolia*, P > 0.05). In the single individual of *Laplacea portoricensis* the annual peak was delayed for a year before an extended flush of fruiting. The normal annual cycle of the common *Rheedia portoricensis* (P > 0.05) disappeared after the hurricane and its fruiting period extended throughout the year. There was no consistent pattern of response to the hurricane by species that typically have cyclic fruiting.

Some of the irregularly fruiting species shifted their pattern or intensity of fruiting after the hurricane. However, since these species were not responsible for the community pattern of cyclic fruiting prior to the hurricane, their post-hurricane response did not produce the shift from cyclic to noncyclic fruiting in the assemblage of

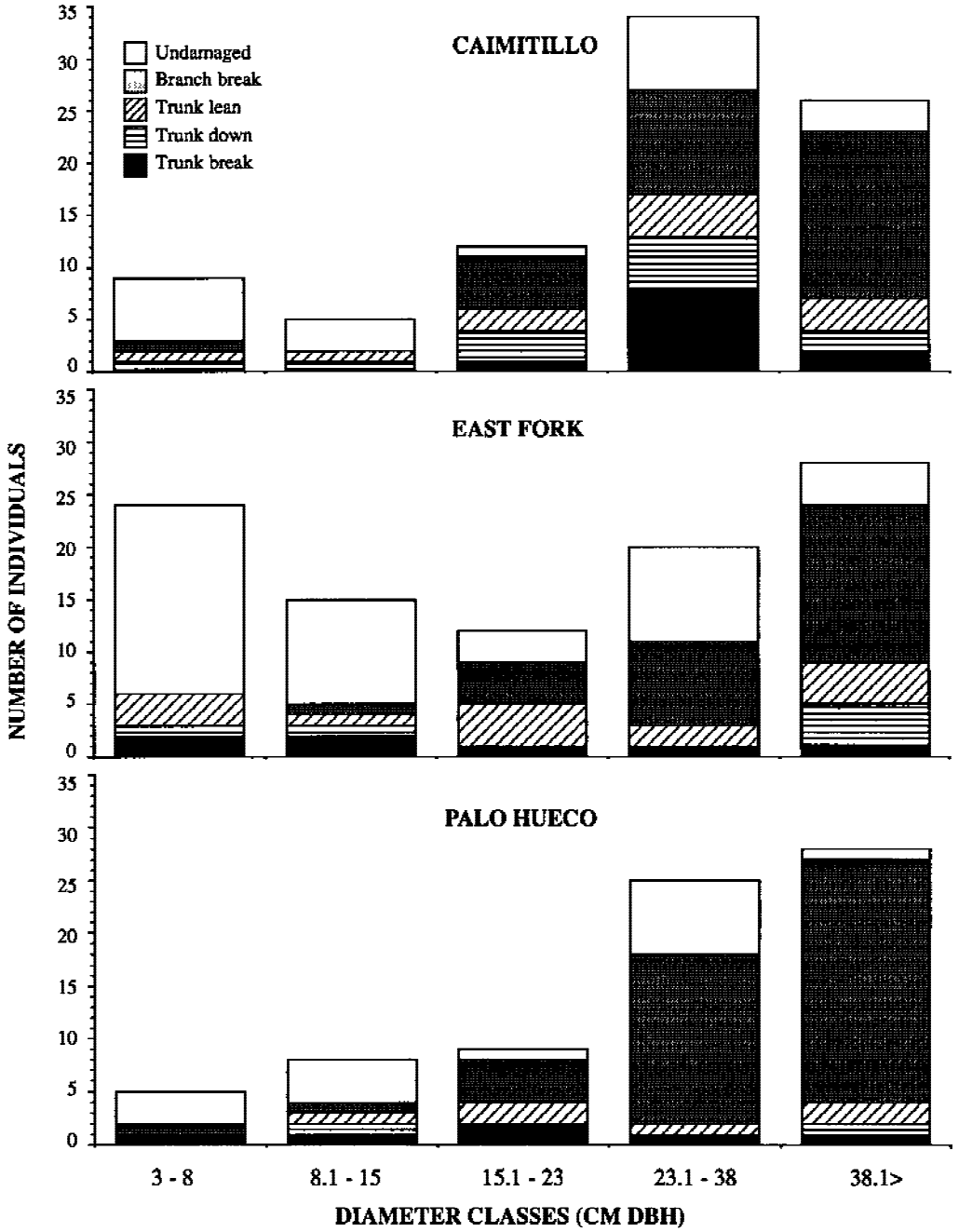

FIG. 4. Major structural damage to broadleaf trees by diameter class along three phenology trails in the LEF caused by Hurricane Hugo. Trees classified by most severe damage sustained in the following order: trunk break; trunk down (completely uprooted); trunk lean (partially uprooted); branch breaks; and undamaged. Number of trees on Y-axis shows pooled sample sizes of trees in each diameter class.

monitored species. In some irregular species the normal fruiting peak was delayed after Hugo, but when it resumed fruit production was lower (*Sloanea berteriana*, $P > 0.05$), normal (*Dacryodes excelsa*, $P = 0.01$), or increased in the second year after Hugo (*Matayba domingensis*). An increase in the abundance of fruit and duration of fruiting occurred in the common *Guarea ramiflora* ($P = 0.02$). The rare *Ocotea spathulata* failed to produce fruit after the hurricane.

For many irregular fruiting species it was difficult to detect a post-hurricane shift in pattern or intensity of fruit production. No obvious hurricane response was found in the common *Clusia clusioides* ($P > 0.05$) and *Inga laurina* ($P > 0.05$), as well as in the rare *Eugenia borinquensis, Ficus sintenisii* and *Micropholis chrysophylloides*.

Timing of Parrot Breeding.—The probable dates of clutch initiation ranged from 15 February to 15 May, as determined by the first time the female spent the night in the cavity (Figure 1). Before the hurricane, the probable dates of clutch initiation ranged from 15 February to 29 April (Median = 29 February). In 1990, after the hurricane, breeding was delayed as illustrated by the range of starting dates (18 April-15 May; Median = 19 April). However, by 1991 (the second breeding season after the hurricane) clutch initiation dates (20 February-3 April; Median = 12 March) had partially returned to the dates of previous years.

Before the hurricane, parrot nesting started during a period when many plant species had ripe fruit, whereas actual or potential fledging occurred when fewer plant species had ripe fruit (Figure 1). After the hurricane, in the absence of a marked annual cycle in number of fruiting species, parrot clutch initiation and fledging occurred during periods when equivalent numbers of plant species were fruiting.

DISCUSSION

Pre-hurricane.—The observed cyclic pattern in number of species fruiting with an October-February peak and a trough in June-July, suggests that seasonal fruit abundance may vary correspondingly. An annual cycle in the total number of individual plants with ripe fruit coincided with the cycle in the total number of species, supporting the likelihood of seasonal variation in fruit abundance. However, the number of tagged individuals of each species was not representative of their relative abundance in the forest.

The estimates of the number of stems with ripe fruit per ha indicate that at a particular site the abundance of fruiting trees in a peak can differ from a trough by a factor as great as 26.5. Although considerable year-to-year variation exists in these estimates, the year-to-year variation was not equal to the estimated difference between the peaks and troughs within a year. For example, at the fruiting peak in December 1987 an estimated 68 stems had ripe fruit, in contrast to 212 stems in the January 1989 peak. In contrast, the number of stems with ripe fruit per ha in troughs were 30 (June 1987), 8 (July 1988), and 23 (June 1989).

A more conservative analysis, based only on the fruiting species from which parrots are known to feed (Snyder et al., 1987), reveals a similar pattern, but the magnitude of the difference between lowest trough and highest peak was not as great (a factor of 12.8). For example, the peak of stems with ripe fruit per ha was 61 (December 1987) and 103 (January 1989), compared with the troughs of 27 (June 1987), 8 (July 1988), and 23 (June 1989). The actual difference between peak and troughs is probably greater than these estimates. The common vine (*Marcgravia sintenisii*) was excluded from the analysis because no estimates of relative abundance were available. Because *Marcgravia* produced fruit during the peaks and not in the troughs it would be expected to intensify the difference between peaks and troughs. It is likely that frugivores in the lower palo colorado forest and upper tabonuco forest are normally faced with considerable seasonal and year-to-year variation in fruit availability.

The sierra palm (*Prestoea montana*) is the most abundant tree in the LEF and variation in its fruit production may have important consequences for the Puerto Rican Parrot, since its fruit dominates the parrot's diet (Snyder et al., 1987). Banister (1970) in-

dicates that some palms fruit throughout the year, although more than half of the palms have fruit between November and February. Banister noted a large year-to-year variation in this pattern. Lugo and Frangi (1993) indicate that fruit fall peaks in June to August. Although they found a palm fruiting peak in 1980, by June of 1981 there was no evidence of the increase in fruiting found in previous years. This is consistent with my study, in which peak fruiting appeared to occur approximately every other year, at least in this altitude range. These observations suggest that although sierra palms may fruit throughout the year, most fruiting occurs during November-February, with differences between years in the quantity of fruit production.

Snyder et al. (1987) noted that Puerto Rican Parrots feed heavily on sierra palm fruit from January to May. During this period movements of parrots between the palo colorado zone and palm forest were most conspicuous. The dark purple stain observed on the bills of breeding parrots suggest that palm fruits were an important food item and that reliance on palm fruit might explain the timing of parrot breeding. Snyder et al. found that parrot nests were initiated in late February or early March, just as palm fruiting peaked. They speculated that the fruiting increase just before breeding could trigger parrot breeding. Nevertheless, they note that the timing of breeding also coincided with the dry season, which increases the availability of dry cavities required for reproductive success.

As observed in my study, it is unlikely that parrot breeding is timed specifically to the sierra palm fruiting peak, since the peak varies from year-to-year. Parrot breeding was initiated during or shortly after the greatest number of tree species bear fruit (presumably the period of greatest fruit availability). Reliance on the period with the greatest diversity of fruit might also help buffer parrot reproduction from the year-to-year variation in fruit availability associated with the use of a single plant species. For example, in 1974 Snyder et al. found an absence of sierra palm fruiting on the west side of the LEF. However, a pair successfully bred there, presumably relying on other fruits to rear their young.

The seasonal movements of Puerto Rican Parrots are probably associated with seasonal changes in food availability in the LEF (Snyder et al., 1987). These authors noted that at the end of 1968-1971 breeding seasons (May-June) parrots showed a dramatic increase in the number of flights between the east and west sides of the LEF. At this time parrots increased their use of *Clusia clusioides* fruit, particularly on mid-elevation ridges in the eastern LEF. The use of these fruits declined in the summer and the parrots eventually disappeared from middle and higher elevations of the forest. Although fruiting of *C. clusioides* on the phenology trails was irregular and noncyclic, some fruit was available for six months or longer during the summer. Parrot movements coincided approximately with the observed June-August fruiting troughs, when fewest species had fruit. During the June-August period in the 1970s and 1980s, researchers observed parrots moving to the lowlands, where they believe the parrots used the tabonuco forest during summer and early fall (Snyder et al., 1987). This observation was supported by Rodríguez-Vidal (1959), who indicated that the parrots consumed fruits known to be available only in the tabonuco forest during late summer.

The fruiting peak of tabonuco (*Dacryodes excelsa*) in the tabonuco zone occurs in July to October (Murphy, 1970); although some fruiting occurs throughout the year (Estrada Pinto, 1970; Devoe, 1989). My observations also indicate considerable year-to-year variation, with 1988 being a peak year in which fruits were abundant from January through October, followed by decreased fruit production in 1989. Tabonuco fruit production may be synchronized among different stands, since years of high and low production coincided on our two trails with tabonuco (East Fork, Palo Hueco). Scatena (pers. comm.) has noted synchrony between El Verde and Bisley tabonuco fruiting. It is possible that tabonuco fruits are available to parrots during most of the year, at least in peak years. Given the seasonal duration of tabonuco fruit avail-

ability and the abundance of tabonuco trees it is not surprising that these were the second most common fruit observed in the parrot's diet (Snyder et al., 1987).

The parrot feeding observations summarized by season by Snyder et al., 1987: Appendix 11 coincided with the monthly fruiting seasons of 10 of 11 plant species in my study. Only 1.3 % of their 151 feeding observations, summarized by month, fell outside the fruiting periods of the 11 plant species common to both studies. The lack of absolute congruence may be attributed to small sample size due to two September feeding observations which fell outside the fruiting period observed in two *Ocotea spathulata*. In some instances, the dates of parrot feeding observations coincided with the fruiting peaks recorded in my study. For example, most feeding records on sierra palm occurred in January through March, corresponding with observed fruiting peaks. There were fewer records in March and April. Fruit/seeds of the vine *Marcgravia sintenisii* were taken in January-March and October-November, corresponding with the fruiting peak observed between September-May. In other instances, feeding records were concentrated in a few months, although fruits of these plants were available for a long time. For instance, most tabonuco feeding observations occurred in July-October, although tabonuco fruits were sometimes available throughout the year. Also, most fruits/seeds of *Byrsonima coriacea* were consumed in January-February, which corresponds with some fruiting peaks in this species, although its fruits are sometimes available throughout the year.

Post-hurricane.—The distribution and extent of hurricane damage in the LEF after Hurricane Hugo was variable depending on exposure, elevation, and vegetation type (Walker et al., 1991, Boose et al., 1994). Hurricane damage was substantial in the parrot foraging sites sampled on our three phenology trails. The storm winds, which removed approximately 72 percent of the foliage per broadleaf tree, also removed most fruits, as noted after other hurricanes (e.g., Lynch, 1991). In addition, structural damage, particularly trunk and branch breakage, immediately contributed to fruit loss as well as having long-term effects on fruit production. Immediately after the hurricane only two *Byrsonima coriacea* had ripe fruit, although small quantities of unripe fruit were found on five other species. Fruit loss occurred in a season when at least 10 species were expected to bear ripe fruit. Although it was difficult to estimate the amount of fruit available on the phenology trails just after the hurricane, it was well below the quantity found during the lowest annual fruiting troughs.

Although high defoliation rates and structural damage caused by hurricanes may not always cause high rates of plant mortality (Bellingham et al., 1992), approximately half the marked plants died as a result of the storm. Mortality rates associated with the hurricane were highest in vines, which fell from supporting branches and trunks. On average, broadleaf trees showed intermediate levels of mortality, although species differences were marked, as described by Zimmerman et al. (1994). For example, *Cordia borinquensis* (N = 11) and *Haenianthus salicifolius* (N = 18) appeared to be very vulnerable with mortality rates of 81 % and 72 % respectively, in contrast to the 20 % mortality of *Sloanea berteriana* (N = 35). The latter rate was similar to that observed in the palm *Prestoea montana*, noted for its ability to survive hurricane impacts (Frangi and Lugo, 1985, Francis and Gillespie, 1993).

The most important hurricane effect on overall fruiting phenology was the loss of a distinct seasonal fruiting cycle, which was evident in the number of species bearing ripe fruit in the 33 months before the hurricane. It took approximately four months after the hurricane for the number of fruiting species to reach a level equivalent to the normal yearly low. Then, the number of species bearing ripe fruit fluctuated around 6-12 species until the end of the study. This contrasted with the trough to peak range of 4-16 species with ripe fruit before the hurricane. The cause of this loss of seasonal cycling is mostly attributed to the fact that 57 percent of the species with annual cycles prior to the hurricane stopped fruiting in synchrony during the October-February

period. This may have been caused by a variety of factors, including the post-hurricane drought, type and extent of hurricane damage, change in nutrient pulses, loss of apical dominance, and increased solar radiation.

After the hurricane, a "flush" of fruit production was noted in some plants although the magnitude relative to pre-hurricane values was small and difficult to assess due to small samples. The maximum fruit quantity in monthly sampling periods was higher after the hurricane in only three species (*Dacryodes excelsa, Guarea ramiflora, Matayba dominguensis*). Two rare species (*Casearia arborea, Clusia gundlachii*), represented by one individual each fruited only after the hurricane. The duration of the fruiting period increased after the hurricane in eight species (*Alchornea latifolia, Cyrilla racemiflora, Guarea ramiflora, Inga laurina, Laplacea portoricensis, Micropholis chrysophyloides, Rheedia portoricensis, Cordia borinquensis*). In contrast, most of the 25 monitored species showed no evidence of increased fruit production, and 11 species had lower values for the maximum fruit quantity in monthly sampling periods after the hurricane. However, fruit production appeared to increase in edge or second growth species (e.g., Melastomataceae), and a distinct fruiting flush was documented in treefall gaps in the tabonuco forest 3-5 months after the hurricane (Wunderle, 1995).

Avian population declines observed after hurricanes are often related to diet; suggesting that the greatest hurricane stress on bird populations occurs after its passage rather than during its impact (Wiley and Wunderle, 1993). This may apply to the Puerto Rican Parrot suggesting that most of the mortality associated with the hurricane was related to food loss rather than to storm exposure. A combination of reduced food abundance, irregular fruiting periods, and increased patchiness of food resources may have stressed parrots by increasing the difficulty of locating food. Furthermore, foraging in storm-damaged forest canopies with limited cover may have increased parrot exposure to predation by Red-tailed Hawks (*Buteo jamaicensis*). It appeared that Red-tailed Hawk populations were unaffected by the storm, and raptor populations elsewhere have survived major hurricane impacts with little effect (Wauer and Wunderle, 1992).

Given the extent of hurricane damage and associated fruit loss in its traditional foraging areas it was not surprising that Puerto Rican Parrot breeding was delayed by almost a month and a half in the first breeding season after the storm. Although various factors may have contributed to this delay, food availability was probably most important. This seems likely, given the increased energy requirements of reproduction associated with egg formation and provisioning the young. Breeding was probably initiated after fruit abundance reached a minimal threshold. By April, when two pairs initiated breeding, seven plant species had ripe fruit on the phenology trails (*Clusia clusioides, Ficus laeviagata, F. sintenisii, Guraea ramiflora, Marcgravia sintenisii, Prestoea montana, Rheedia portoricensis*).

It is evident that parrots routinely face considerable seasonal and annual variation in fruit production, even in the absence of hurricanes. Similar levels of within and between year variation in fruit production have been observed in lauraceous fruits in a montane site in Costa Rica (Wheelwright, 1986). There, shortages of lauraceous fruits contributed to diet shifts, delayed breeding, and altitudinal migration in frugivorous birds (Wheelwright, 1983, 1986). My results are consistent with these findings and suggest that Puerto Rican Parrots may show similar responses to food variation.

Acknowledgments.—I thank Oscar Diaz and Esteban Terranova for conducting the monthly phenology surveys. Esteban also assisted with the analysis and preparation of figures. The study was designed and initiated by Jan Kalina. The U. S. Fish and Wildlife Service and Francisco Vilella provided parrot breeding data. The manuscript benefited from the constructive comments of Jean Lodge, Ariel Lugo, Noel Snyder, Charlotte Taylor, Jess Zimmerman, and two anonymous reviewers. This research was conducted in cooperation with the University of Puerto Rico.

LITERATURE CITED

Bannister, B. 1970. Ecological life cycle of *Euterpe globosa* Gaert. *In* H. T. Odum and R. F. Pigeon. (eds.), A tropical rain forest, pp. B-299 - B-323. National Technical Information Service, Springfield, Virginia.

Bellingham, P. J., et al. 1992. Hurricanes need not cause high mortality: the effects of Hurricane Gilbert on forests in Jamaica. J. Trop. Ecol. 8: 217-223.

Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecol. Mongr. 64: 369-400.

Devoe, N. N.1989. Differential seeding and regeneration in openings and beneath closed canopy in a sub-tropical wet forest. Dissertation, Yale University, New Haven, Connecticut. 307 pp.

Estrada Pinto, A. 1970. Phenological studies of trees at El Verde. *In* H. T. Odum and R. F. Pigeon. (eds.), A tropical rain forest, pp. D-14 - D-269. National Technical Information Service, Springfield, Virginia.

Ewel, J. J. and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA Forest Service, Res. Pap. ITF-18. 72 pp.

Francis, J. K. and A. J. R. Gillespie. 1993. Relating gust speed to tree damage in Hurricane Hugo. 1989. J. Arboculture 19: 368-373.

Frangi, J. L. and A. E. Lugo. 1985. Ecosystem dynamics of a subtropical floodplain forest. Ecol. Monogr. 55: 351-369.

Lugo, A. E. and J. L. Frangi. 1993. Fruit fall in the Luquillo Experimental Forest, Puerto Rico. Biotropica 25: 73-84.

Lynch, J. F. 1991. Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. Biotropica 23: 488-496.

Murphy, P. G.1970. Tree growth at El Verde and the effects of ionizing radiation. *In* H. T. Odum and R. F. Pigeon. (eds.), A tropical rain forest, pp. D-141 - D-171. National Technical Information Service, Springfield, Virginia.

Rodríguez-Vidal, J. A. 1959. Puerto Rican Parrot study. Monogr. Dep. Agric. Comm. Puerto Rico No. 1. 173 pp.

Scatena, F. N. and M. C. Larsen.1991. Physical aspects of Hurricane Hugo in Puerto Rico. Biotropica 23: 317-323.

Snyder, N. F. R., J. W. Wiley, and C. B. Kepler. 1987. The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles, California. 384 pp.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. W. H. Freeman and Co., New York. 859 pp.

Wadsworth, F. H. 1949. The development of the forest land resources of the Luquillo Mountains, Puerto Rico. Dissertation, University of Michigan. 481 pp.

Wadsworth, F. H. 1951. Forest management in the Luquillo Mountains. I. The setting. Carib. For. 12: 93-114.

Walker, L. R., N. V. L. Brokaw, D. J. Lodge, and R. B. Waide. (Eds.). 1991. Special issue: ecosystem, plant, and animal responses to hurricanes in the Caribbean. Biotropica 23: 313-521.

Wauer, R. H. and J. M. Wunderle, Jr. 1992. The effect of Hurricane Hugo on bird populations on St. Croix, U.S. Virgin Islands. Wilson Bull. 104: 656-673.

Wheelwright, N. T. 1983. Fruits and ecology of Resplendent Quetzals. Auk 100: 286-301.

Wheelwright, N. T. 1986. A seven-year study of individual variation in fruit production in tropical bird-dispersed tree species in the family Lauraceae. *In* A. Estrada and T. H. Fleming (eds.), Frugivores and seed dispersal. pp. 19 - 35. Dr. W. Junk Publishers, Dordrecht.

Wiley, J. W. and J. M. Wunderle, Jr., 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. Bird Cons. Internat. 3: 319-349.

Wunderle, Jr. J. M. 1995. Responses of bird populations in a Puerto Rican forest to Hurricane Hugo: the first 18 months. Condor 97: 879-896.

Zimmerman, J. K., et al. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life history. J. of Ecology 82: 911-922.