

RAINFALL, FRUITING PHENOLOGY, AND THE NESTING SEASON OF WHITE-CROWNED PIGEONS IN THE UPPER FLORIDA KEYS

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ABSTRACT.—White-crowned Pigeons (*Columba leucocephala*) varied their timing of breeding and nesting intensity in response to variation in production of the four most important fruit species in their breeding-season diet in the upper Florida Keys. From 1988 through 1990, we monitored fruit production year-round in five habitats in which pigeons foraged and monitored all pigeon nests along two transects on Middle Butternut Key. Annually, pigeon breeding was positively correlated with summer rains and with the peak in overall fruit production. However, within the breeding season, only the availability of *Metopium toxiferum* was positively correlated with rainfall and the number of new clutches initiated. Both the timing and magnitude of breeding varied annually. In 1988, when *Metopium* was more available, more pigeons nested, the nesting season started earlier and lasted longer, and a large peak in nesting occurred when *Metopium* fruit ripened. During 1989 and 1990, when the relative availability of *Metopium* was lower, fewer pigeons nested, the nesting season was shorter, and the seasonal peak in nesting associated with *Metopium* fruit was reduced or absent. Nesting patterns did not appear to vary with changes in the relative availability of other fruits. White-crowned Pigeons appear to prefer *Metopium* fruits to other species. Because pigeons do not supplement nestling diets with arthropods, but augment their diets with protein-rich crop milk, they may depend on lipid-rich fruits such as *Metopium* to provide the energy for breeding and crop-milk production. *Metopium* fruit production may be influenced by rainfall and climatic conditions, both of which may vary spatially within the range of White-crowned Pigeons in Florida. Evidence that pigeons shift foraging sites when *Metopium* availability varies emphasizes the need to preserve large tracts of seasonal deciduous forest in the Keys and to protect *Metopium* trees in suburban areas where they are removed because they cause contact dermatitis in humans. Received 11 December 1998, accepted 1 October 1999.

IN THE TROPICS and subtropics, the production of fleshy fruits tends to be highest early in the wet season (Foster 1982, Lieberman 1982, Guevara de Lampe et al. 1992). The timing of avian reproduction generally coincides with seasonal peaks in food supply (Lack 1968, Daan et al. 1988). Thus, most studies of frugivorous birds in the Neotropics or Australia have concluded that breeding activity is associated with periods of fruit abundance (Snow and Snow 1964, Frith et al. 1976, Worthington 1982; but see Herrera 1998). Variation in the number or density of breeding birds among sites or years reflects general patterns of fruit availability (Crome 1975a, Wiley and Wiley 1979), and many frugivores exhibit seasonal movements in response to fruit availability (Crome 1975b, Wheelwright 1983, Innis 1989, Powell

and Bjork 1995). Indeed, some birds appear to be able to track complex spatiotemporal patterns of fruit abundance (Rey 1995), suggesting that temporal variation in the abundance of frugivores reflects variation in the availability of their preferred food plants (Levey 1988, Innis 1989, Loiselle and Blake 1991).

Many studies that assert a relationship between fruit abundance and the breeding seasons (Fogden 1972, Morton 1973) or movement and abundance patterns (Karr 1976, Morton 1977, Greenberg 1981) of frugivores merely infer fruit abundance rather than sample it quantitatively. Few studies have examined the relationship between frugivore abundance or breeding activity and variation in the abundance and exploitation of food resources (Ward 1969, Boag and Grant 1984, Levey 1988, Poulin et al. 1992). Although avian frugivores may consume the fruits of many species, they often specialize on only a few (Crome 1975a, b; Bancroft and Bowman 1994), or augment their diet

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with arthropods (Levey 1988, Loiselle and Blake 1991, Poulin et al. 1992), during the breeding season. Variation in seasonal availability of these few species of fruits or arthropods may have a greater influence on timing of breeding than does overall fruit abundance.

White-crowned Pigeons (*Columba leucocephala*) are obligate frugivores and perhaps are the most important seed dispersers in the seasonal deciduous forests of the Florida Keys and adjacent mainland (Strong and Bancroft 1994a). In Florida, White-crowned Pigeons feed on fruits of at least 37 species of trees (G. Bancroft and R. Bowman unpubl. data). However, the nestling diet is dominated by fruit from only four species: *Metopium toxiferum* (poisonwood), *Guapira discolor* (blolly), *Ficus citrifolia* (short-leaf fig), and *F. aurea* (strangler fig; Bancroft and Bowman 1994). Nestling diets vary within the breeding season consistently among years. Nestlings reared early in the breeding season are fed predominantly *Ficus* spp., but nestlings reared later in the season are fed predominantly *Metopium* (Bancroft and Bowman 1994). White-crowned Pigeons do not supplement nestling diets with arthropods, but feed their young crop milk, which is a relatively high-protein, high-lipid secretion (Pace et al. 1952) from the epithelial tissues in the crop gland.

In this study, we evaluate the relationship between rainfall, the relative availability of the four fruits most preferred by White-crowned Pigeons during the breeding season, and pigeon breeding phenology over three years, 1988 through 1990, in the upper Florida Keys. We examine whether annual variation in fruit availability influences the timing of pigeon breeding and if variation in fruit availability within the breeding season influences the magnitude of the breeding effort. We predict that because pigeons do not supplement the nestling diet with arthropods, breeding activity should be correlated with peak fruit abundance. Because White-crowned Pigeons preferentially exploit *Metopium* even when *Ficus* and *Guapira* are relatively abundant (Bancroft and Bowman 1994), we predict that both within and among years, breeding patterns will be more strongly influenced by the relative availability of *Metopium* than by that of *Ficus* or *Guapira*.

STUDY AREA AND METHODS

Study area.—In the upper Florida Keys, White-crowned Pigeons nest primarily on small mangrove islands in Florida Bay (Strong et al. 1991). We monitored nesting activity on Middle Butternut Key (25°05'N, 80°31'W) in eastern Florida Bay (Fig. 1). Middle Butternut Key is similar in structure to many of the keys used by breeding pigeons (Strong et al. 1991). The key was fringed with red mangroves (*Rhizophora mangle*) that graded into black mangroves (*Avicennia germinans*) of various heights and canopy closure. Inside the mangrove fringe, a shell-sand berm supported a variety of plant species, many of which are typical of the seasonal deciduous forests on the main islands of the Keys archipelago. These included *Bursera simaruba*, *Coccoloba uvifera*, *Conocarpus erectus*, *Erithalis fruticosa*, several species of *Eugenia*, *Metopium toxiferum*, and two species of *Pithecellobium*. The interior of the island consisted of relatively open stands of low-growing black mangrove in shallow water and a deeper lagoon fringed with taller red mangroves. Pigeons nested throughout Middle Butternut Key.

Breeding White-crowned Pigeons fly daily to the seasonal deciduous forests of the larger keys and the mainland to feed (pers. obs.). White-crowned Pigeons forage in forests of different successional stages and in a variety of disturbed forest habitats in which fruit production might vary (G. Bancroft and R. Bowman unpubl. data). To control for this heterogeneity in foraging habitat, we surveyed fruit phenology at five locations in the upper Florida Keys that were typical of the foraging habitats available to pigeons (Fig. 1). Lignumvitae Key, a state botanical preserve, was mature uncut forest similar to the hardwood forests of the larger keys prior to human development. Chastain Hammock and Dynamite Dock were mature second-growth forests. Forests on Plantation Key and northern Key Largo were younger second-growth forests in a suburban setting and along a discrete forest edge (roadside), respectively. All sites were 5 to 20 km from our nesting study sites (Fig. 1) and were well within the observed foraging radius of breeding pigeons (G. Bancroft and A. Strong unpubl. data). We collected rainfall data with an automatic rain gage stationed on Middle Butternut Key. For missing days, daily rainfall was taken from the United States Weather Service station at Tavernier, Florida.

Nesting phenology.—We walked each of two nesting transects on Middle Butternut Key three times weekly from early May through October. We found no evidence of nesting outside of this period. Transects meandered throughout the key and were situated to cover most of the available nesting habitat for pigeons. All new pigeon nests that could be visibly detected from the transect were marked with numbered surveyor's tape, and the nest contents were re-

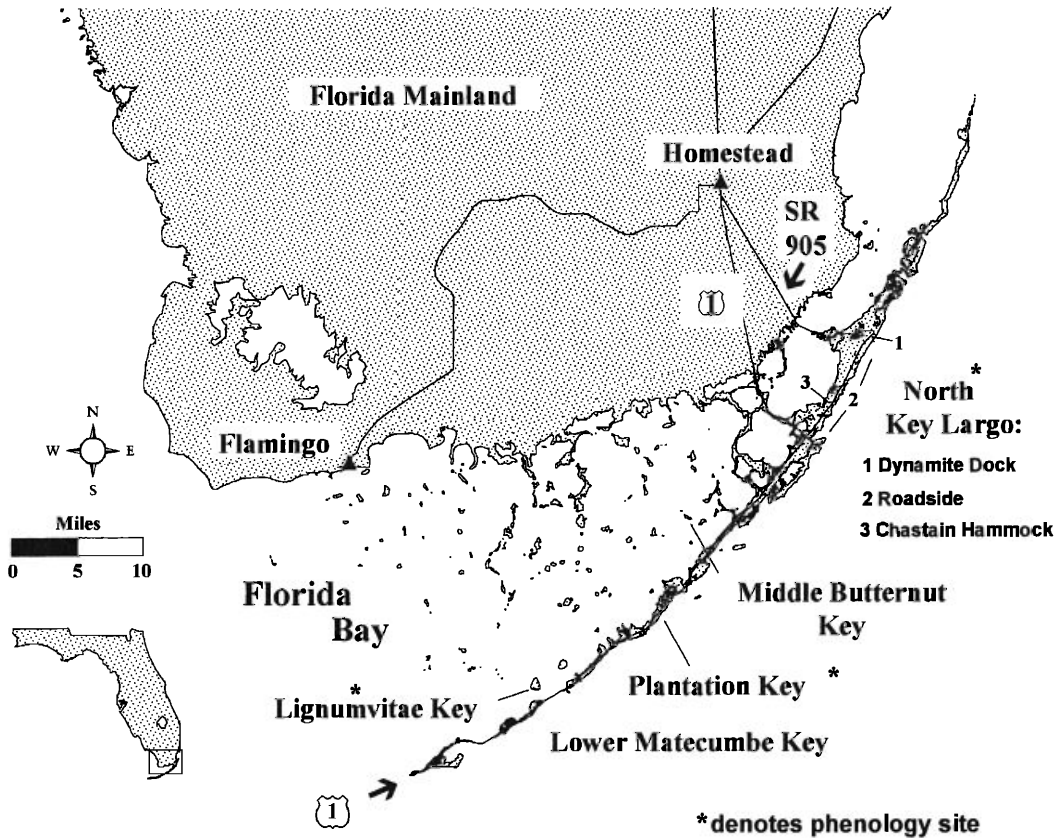


FIG. 1. Locations of fruiting phenology sites (Lignumvitae Key, Plantation Key, North Key Largo) and pigeon breeding sites (Middle Butternut Key) in the upper Florida Keys.

corded at each visit. White-crowned Pigeons typically lay two-egg clutches and begin incubation with the laying of the first egg. Incubation lasts 14 days and chicks hatch on successive days (Wiley and Wiley 1979). For nests found after laying was completed, we backdated 14 days from the date on which the first egg hatched. When nests failed before hatching, we assumed the second egg had been laid one day before the nest was first located and backdated two days. When nests were found after hatching, we estimated the age of nestlings by comparing their measurements with those of known-age nestlings and then backdated from the estimated hatching date.

Fruiting phenology.—We studied the fruiting phenology of *Metopium*, *Guapira*, and the two *Ficus* species by conducting twice-monthly fruiting censuses at three sites from January 1988 through December 1990 (Lignumvitae Key, Plantation Key, northern Key Largo) and monthly censuses at two sites from March 1988 through December 1990 (Chastain Hammock and Dynamite Dock). At each site, a random sample of trees was marked. Each marked tree was visited during each census. *Metopium* is dioecious,

and we present results only from female trees. In total, we censused 34 female *Metopium*, 48 *Guapira*, 25 *F. aurea*, and 16 *F. citrifolia*.

At each tree visited during censuses, we used Wheelwright's (1985) technique to record fruiting intensity by determining the proportion of each tree's canopy that was bearing fruit: no fruit present = 0; 1% of canopy bearing fruit = 0.5; 2 to 25% = 1; 26 to 75% = 2; and 76 to 100% = 3. We estimated the developmental stage of fruit by recording the stage of the most advanced fruit on the tree: 0 = no fruit; 1 = recently fertilized (very small); 2 = partially developed but not full sized; 3 = full grown fruit but not ripe; 4 = ripe fruit.

To provide a relative measure of fruit availability at each site, we calculated a relative availability index (RI) for each tree species (Wheelwright 1985). We multiplied the proportion of individuals bearing ripe fruit during each month's census by the mean fruiting intensity of those individuals to determine the fruiting RI. For example, during the first census, 70% of *Metopium* had ripe fruit with a mean intensity of 1.14. The RI, the product of these two variables,

was 0.80. This method, although providing only a relative measure of fruit availability, is correlated with absolute fruit counts (Wheelwright 1986) and provides a measure of fruiting effort unbiased by differences in the size of surveyed individuals. One limitation of this technique is that some trees could be categorized as bearing ripe fruit (developmental stage 4) based on the observation of only a single ripe fruit.

Data analysis.—We calculated the mean relative availability of ripe fruit for each plant species at each phenology census site for each month from 1988 to 1990. We used a repeated-measures ANOVA on fruiting data from all 12 months, pooled by site, with month as the within-subject factor and year as the between-subject factor to examine if the relative availability of fruit varied seasonally and/or annually. When assumptions of sphericity were violated, we corrected *P*-values with the Greenhouse-Geisser adjustment (Beal and Khamis 1990, Quinn and Keough 1991). We used a paired *t*-test to compare fruit availability in the same sample of trees during the wet season (May to September) and the dry season (October to April). To determine if variation in fruit availability throughout the year influenced the timing of pigeon breeding, we examined the correlation coefficients between rainfall, relative availability of fruit (for each species and for all four species combined), and the number of new nests initiated each month. Because rainfall was not measured at each of the different census sites, we pooled fruit availability from each site and examined correlations between monthly means of the above data.

We used repeated-measures ANOVA, again with month as the within-subject factor and species and year as the between-subject factors, to determine if the relative availability of fruit varied from May to September and if annual variation existed during this period. A significant month \times species interaction existed, so we repeated the analyses for each individual species. Within this period, all data except rainfall were normally distributed; thus, we used Spearman rank correlation for all comparisons with rainfall data and Pearson correlation to evaluate the relationship between fruit availability and the number of new clutches.

RESULTS

Rainfall.—Rainfall in the upper Florida Keys was highly seasonal (Fig. 2) and varied significantly by month (Kruskal-Wallis, $\chi^2 = 24.8$, $df = 11$, $P < 0.01$). On average, 1,179 mm of rain falls annually (National Weather Service), with about 60% of it occurring from mid-May through September. Although average monthly rainfall (for all 12 months) did not differ among

years ($\chi^2 = 0.15$, $df = 2$, $P > 0.05$), total annual rainfall varied among years (1988, 1,255 mm; 1989, 706 mm; 1990, 732 mm). Within the pigeon breeding season (May to September), average monthly rainfall varied significantly among years ($\chi^2 = 6.74$, $df = 2$, $P < 0.05$) and was significantly higher in 1988 than in 1989 or 1990 (Student-Newman-Keuls test).

Fruiting phenology.—For all fruits combined, the relative availability of fruit varied significantly among months ($F = 9.01$, $df = 11$ and 110 , $P < 0.001$) but not among years ($F = 1.74$, $df = 2$ and 10 , $P = 0.224$; Fig. 2). The relative availability of fruit was significantly higher during May to September (wet season) than during the rest of the year ($\bar{x} = 1.1 \pm \text{SE of } 0.16$ vs. 0.53 ± 0.08 ; paired $t = 5.64$, $df = 64$, $P < 0.001$). In all years, the availability of ripe fruit was low or decreasing from January through April or May, increasing in May or June, highest in July or August, and decreasing from September to October (Fig. 2). The relative availability of *Metopium* fruit ($F = 7.86$, $df = 11$ and 132 , $P < 0.002$) and *Guapira* fruit ($F = 12.70$, $df = 11$ and 132 , $P < 0.001$) varied significantly by month (Fig. 2). Monthly variation in *F. aurea* was close to significant ($F = 2.47$, $df = 11$ and 132 , $P = 0.061$), but *F. citrifolia* did not vary significantly among months ($F = 2.21$, $df = 11$ and 132 , $P < 0.11$). None of these species exhibited annual variation in the relative availability of fruits.

The timing of fruiting in *Metopium* and *Guapira* was very predictable from year to year. Ripe *Metopium* fruit appeared in late June or early July, peaked in July and August, and then declined steadily until just before ripe fruit appeared the following year (Fig. 2). Ripe *Guapira* fruit was available only during summer and fall. In contrast, some *Ficus* of both species bore ripe fruit during any given month of the year. For *F. aurea*, fruit production was higher from May through August, and for *F. citrifolia*, fruit production tended to increase in May and June.

Fruiting patterns within the five-month breeding season of pigeons (May to September) differed from annual patterns of fruiting. *Ficus aurea* and *F. citrifolia* bore fruit throughout the pigeon nesting season (Fig. 3). Within this five-month period, neither species of *Ficus* showed significant monthly or yearly variation in the relative availability of fruit (Table 1). Ripe *Guapira* fruit was available from June until the end

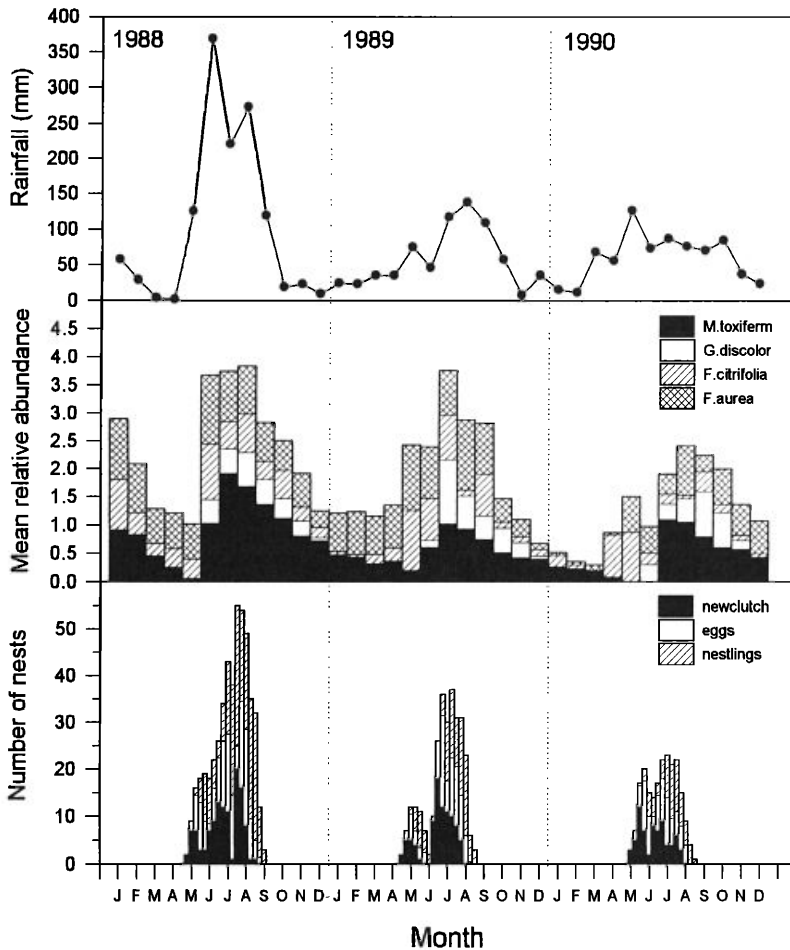


FIG. 2. Rainfall, fruit availability, and nest initiations of White-crowned Pigeons in the upper Florida Keys between 1988 and 1990. Rainfall and fruit phenology were recorded monthly, and the number of pigeon nests was recorded weekly. The top of the stacked bar histograms indicates the overall availability of fruit and the total number of active pigeon nests weekly.

of the pigeon breeding season (Fig. 3). The relative availability of *Guapira* fruit varied significantly among months but not among years; however, the monthly pattern of availability of *Guapira* fruit varied among years (month \times year interaction; Table 1). Ripe *Metopium* fruit was available from late June or early July until nearly the end of May the following year (Fig. 3). During most years, a few *Metopium* trees still bore fruits from the previous year just prior to flowering of the next fruit crop. The relative availability of *Metopium* fruit varied significantly among months but not among years, and no interactions between months and years existed (Table 1). The relative availability of *Me-*

topium fruit was higher from July through September than earlier in the year, and *Metopium* was usually the most available fruit to breeding pigeons from July until the end of the breeding season (Fig. 3). Within the pigeon nesting season, total fruit availability increased to a peak in July and August (Fig. 2), but the repeated-measures ANOVA interaction between month and species ($F = 4.96$, $df = 12$ and 192 , $P < 0.001$) indicated that fruit availability across the breeding season varied with species (Fig. 3).

Nesting phenology.—White-crowned Pigeon breeding was highly seasonal (Fig. 2), occurring only from May through August or early September. The earliest clutch was initiated on

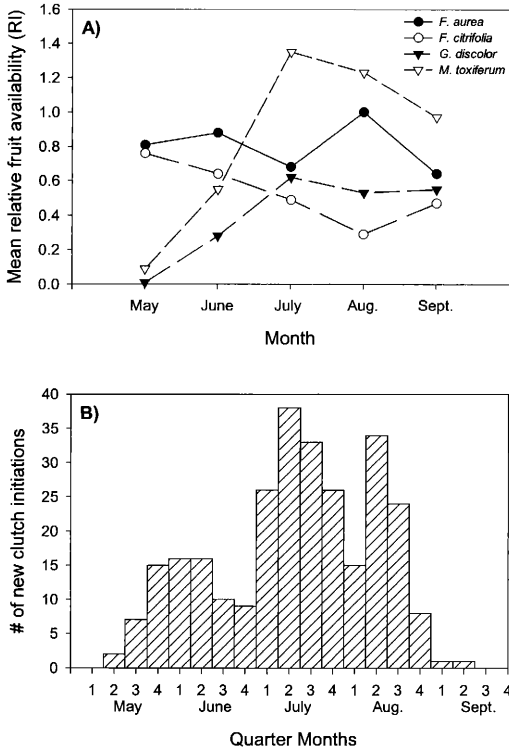


FIG. 3. Mean monthly relative availability of fruit (A) and the timing and magnitude of pigeon breeding (B) pooled for 1988 to 1990.

12 May (1989), and the latest clutch that successfully fledged young was initiated on 2 September (1988). The length of the nesting season varied from 15 weeks in 1990 to 18 weeks in 1988.

The number of nesting attempts within our study area varied substantially among years. In 1988, 121 nesting attempts occurred, whereas in 1989 and 1990, 89 and 70 nesting attempts occurred, respectively. Although the number of nest initiations per week did not differ among

years ($\chi^2 = 0.64$, $df = 2$, $P > 0.05$), the number of active nests each week was significantly higher in 1988 than in 1989 or 1990 ($\chi^2 = 4.32$, $df = 2$, $P < 0.05$, Student-Newman-Keuls test; Fig. 2). This was especially true in July and August, after ripe *Metopium* fruit was available. For all years combined, clutch initiations varied within the breeding season, resulting in several peaks in nesting activity (Fig. 3). An early peak of nesting occurred from the fourth week of May through the second week of June. During this period, 46 (16.5%) of the 280 new clutches were initiated. This peak was followed by a lull in late June and then a second, larger nesting peak that occurred during July when 123 (43.9%) of the total number of new clutches were started. A third peak occurred in the second and third weeks of August, when 58 (20.7%) clutches were produced.

Correlations between rainfall, fruit availability, and nesting.—The availability of fruit of the four important species was significantly correlated with rainfall throughout the year ($r_s = 0.47$ to 0.53 , $P < 0.01$). Rainfall ($r_s = 0.66$, $P < 0.001$) and the relative availability of fruit on the four species combined ($r_s = 0.65$, $P < 0.001$) also were highly correlated with the number of clutches initiated per month; however, the correlation coefficients between fruiting and nesting activity varied with tree species. The relative availability of *F. citrifolia* fruit throughout the year was not significantly correlated ($r_s = 0.32$, $P > 0.05$), and that of *F. aurea* was only weakly correlated ($r_s = 0.36$, $P < 0.05$), with the monthly initiation of pigeon clutches. In contrast, clutch initiation was highly correlated with the relative availability of *Guapira* fruits ($r_s = 0.60$, $P < 0.001$) and of *Metopium* fruits ($r_s = 0.57$, $P < 0.001$) throughout the year.

Within the pigeon breeding season (May to September), only the availability of *Metopium*

TABLE 1. Repeated-measures ANOVA of the relative availability of fruits by species, with month as the within-subject factor and year as the between-subject factor, during the breeding season of White-crowned Pigeons in the Florida Keys (May to September), 1988 to 1990.

Species	Month effect (df = 4 and 48)		Year effect (df = 2 and 12)		Month × year effect (df = 8 and 48)	
	F	P	F	P	F	P
<i>Metopium toxiferum</i>	10.04	0.001	1.00	0.396	0.79	0.547
<i>Guapira discolor</i>	9.17	0.001	0.12	0.888	3.24	0.009
<i>Ficus aurea</i>	1.34	0.275	0.55	0.592	0.90	0.511
<i>Ficus citrifolia</i>	1.07	0.356	0.46	0.642	1.14	0.360

fruit was correlated with clutch initiations by pigeons ($r = 0.53$, $P < 0.05$). Although pigeon nesting also was correlated with the overall availability of fruit ($r = 0.53$, $P < 0.05$), the availability of *Metopium* fruit had the largest relative influence (highest correlation coefficient) on overall fruit availability ($r = 0.01$ to 0.49 for the other three species, $P > 0.05$). *Metopium* also was the only species in which fruit production during the breeding season of pigeons was correlated with rainfall ($r_s = 0.51$, $P < 0.05$).

DISCUSSION

Variation within and among years in the nesting patterns of White-crowned Pigeons suggested a strong relationship with the relative availability of four fruits that are important in the diets of pigeons. Most White-crowned Pigeons are migratory and return in large numbers to the Florida Keys in April and early May (Bancroft 1996). A small percentage of the population is resident in the Keys throughout the year. Breeding activity begins during the late dry and early wet season but ends well before the end of the wet season. Although three of the four fruits important in the diet of breeding White-crowned Pigeons are present during the dry season, they increase in relative availability at the start of the wet season. Pigeon nesting begins in mid-May when the seasonal availability of both species of *Ficus* is increasing. Ripe fruits of *Metopium* and *Guapira* are not available until mid-June or July. A larger peak in nesting activity coincides with the availability of ripe *Metopium* fruits, and to a lesser extent, ripe *Guapira* fruits. Variation in the timing and intensity of fruiting appears to influence the number of pigeons that nest during the May-to-June and July-to-August periods.

Fruiting phenology.—The relative availability of fruit of all four species was correlated with annual rainfall. The seasonal deciduous forests of the Florida Keys are relatively dry (1,000 to 1,200 mm rain annually) and, as in many other studies in seasonal dry forests (Janzen 1967, Foster 1982, Garwood 1983; but see Lieberman 1982, Guevara de Lampe et al. 1992), most fruiting occurred during the late-dry/early-wet season. In the Florida Keys, the phenological patterns in response to rainfall varied among the four species. Although rainfall var-

ied among years, only *Metopium* showed significant annual variation in fruit production that also was correlated with rainfall. During 1988, rainfall patterns were similar to the long-term average for the upper Florida Keys, and overall fruit availability was higher than in any other year. Most *Metopium* fruit ripened two to three weeks earlier than during other years, and fruit remained abundant later in the summer. During 1989 and 1990, which were drought years in southern Florida, *Metopium* fruit ripened later and was less abundant than in 1988. The significant interaction among months and years for *Guapira* fruit availability suggested that fruit production varied with rainfall. In 1988, the relative availability of *Guapira* fruit showed a major peak in July, whereas in 1989 and 1990, the availability of *Guapira* fruit was more constant and low throughout the fruiting season. The relative availability of fruit of both species of *Ficus* did not appear to be adversely affected by low rainfall. Although flower and fruit production in figs may, in part, be explained by seasonal availability of resources (Bronstein and Patel 1992), continual fruiting at the population level appears to be a characteristic of the obligatory mutualism between figs and their pollinators (Janzen 1979, Bronstein 1992).

Although our statistical analyses suggested that the relative availability of fruit of these four species did not vary among years (Table 1), we suspect that, at least for *Metopium*, this may have been an artifact of our survey technique. Our impression was that the availability of *Metopium* fruit was highest in 1988, lowest in 1990, and intermediate in 1989. The average fruit availability for *Metopium* suggested that more fruit was available in 1988 (mean RI = 1.21) than in 1989 (mean RI = 0.70) or 1990 (mean RI = 0.59). Furthermore, the relative availability of *Metopium* fruit in 1988 remained high over a longer period than in the other years (Fig. 2). In addition, the average proportion of trees with ripe fruit in July and August was 83% in 1988 but only 59 to 65% in 1989 and 1990. In December 1989, a severe freeze killed most of the *Metopium* on the mainland and damaged many trees in the upper Florida Keys, reducing the amount of fruit available in both locations during the following summer. Thus, although the proportion of trees with ripe fruit might have been similar, we suspect the absolute amount

of fruit was greatly reduced. In summary, although our statistics did not show significant variation in *Metopium* fruit production among years, we suspect that a real difference existed.

Nesting phenology.—The relative availability of ripe *Metopium* fruit appeared to influence the timing and magnitude of breeding by White-crowned Pigeons. Within the breeding season, *Metopium* was the only fruit whose relative availability was positively correlated with the number of nest initiations. In 1988, more pigeons started clutches in July and August than in other years. They laid 83 clutches in the second half of the 1988 breeding season when *Metopium* fruits were ripe, whereas in 1989 and 1990, only 64 and 32 clutches were initiated during this same period. In 1990, breeding was later than in previous years, and virtually no increase in nest initiations occurred during the second half of the breeding season. During 1990, when less *Metopium* may have been available to nesting pigeons than our data implied, the proportion of *Metopium* fruit in the nestling diet was considerably lower than in previous years (G. Bancroft unpubl. data).

It is possible that the cumulative availability of all four fruit species also may influence the nesting phenology of pigeons. Although *Metopium* fruit production was low in 1989, overall fruit availability remained relatively high owing to the availability of *Ficus* and *Guapira* fruit. In 1990, when production of all fruits was relatively poor, the lowest number of pigeons bred for the shortest period of time. Although the availability of *Ficus* fruit during May and June varied among years, we observed little variation in the magnitude of early nesting, suggesting that pigeons did not respond in a major way to differences in the relative availability of *Ficus*.

Considerable variation existed among sites in the timing of breeding by White-crowned Pigeons in Puerto Rico (Wiley and Wiley 1979). Where fruit was abundant year-round, pigeons began nesting in February, and the breeding season spanned 192 days; where fruit was seasonally available, nesting began later in April or May, and breeding spanned only 92 days. Elsewhere in Puerto Rico, White-crowned Pigeons have bred outside the normal nesting season when fruit was abundant (Wiley and Wiley 1979).

Variation in the timing and duration of the

breeding season in a wide variety of birds has been attributed to food availability. Within the Columbidae, the nesting phenology of Wood Pigeons (*Columba palumbus*) in Europe varied with the availability of mast crops (Cramp 1972). In the moist and wet zones of Puerto Rico, the abundance of fruits from several species known to be important in the diet of columbids explained more of the variation in nesting density between seasons than did rainfall (Rivera-Milán 1996). In some species, variation in breeding attributes may be linked to the availability of specific types of fruit. Year-to-year variation in the breeding effort of New Zealand Pigeons (*Hemiphaga novaeseelandiae*) has been linked to annual variation in fruit availability of two species of trees (Powlesland et al. 1997). The breeding season of the Torres Strait Pigeon (*Ducula spilorrhoa*) in Australia coincided with peak fruit production in one family of plants, the Lauraceae (Crome 1975a). Nesting density of *Ducula spilorrhoa* also was higher in years when more Lauraceae fruit was available (Crome 1975a). Similarly, the availability of Lauraceae fruit influenced movements and the timing of breeding of Resplendent Quetzals (*Pharomachrus mocinno*; Wheelwright 1983). Peak breeding of quetzals corresponded to the period of highest availability and species richness of fruiting Lauraceae, and breeding was delayed in years when the availability of fruit was relatively low (Wheelwright 1983).

Because breeding is energetically expensive and egg production requires large amounts of protein, frugivorous birds may supplement their breeding-season diet with arthropods (Ward 1969, Boag and Grant 1984, Poulin et al. 1992). Studies that have simultaneously examined the breeding phenology of frugivorous birds, their food exploitation, and fruit availability have concluded that arthropod availability may have a stronger influence on the timing of breeding than does fruit availability (Levey 1988, Loiselle and Blake 1991, Poulin et al. 1992). In contrast to these frugivores, White-crowned Pigeons do not supplement their diet with arthropods during the breeding season (Bancroft and Bowman 1994). Instead, they produce crop milk, which is physiologically expensive to produce (Patel 1936) and requires inputs of energy and protein by breeding adults. *Metopium* fruit is relatively energy-dense com-

pared with *Ficus* and *Guapira* fruit (R. Bowman and G. Bancroft unpubl. data). In addition, White-crowned Pigeons digest the protein-rich seeds of *Metopium* fruits but defecate seeds of *Ficus*. Adult pigeons produce more crop milk, and feed more of it to their nestlings, when they are feeding on *Metopium* than when feeding on *Ficus* (Bancroft and Bowman 1994). In addition, pigeons cease feeding on *Ficus* when *Metopium* fruit ripens, even though *Ficus* fruit is still readily available (Bancroft and Bowman 1994). These patterns support the conclusion that *Metopium* may provide energy and protein that are essential to reproduction in White-crowned Pigeons and that pigeons appear to prefer *Metopium* fruit even when other fruits are available. Thus, the relative availability of *Metopium* may have an important influence on the timing and magnitude of breeding.

The termination of nesting by White-crowned Pigeons may not be completely explained by the availability of *Metopium* fruit. Although overall fruit availability remains high through September, breeding typically ceases by the end of August. Ripe *Metopium* fruits usually persist throughout the fall and winter, although the relative availability is lower than during the pigeon breeding season. Furthermore, fruits of several other species (*Bourreria ovata*, *Nectandra coriacea*) in the pigeon diet begin to ripen in early fall. Why don't some White-crowned Pigeons breed into the fall? First, pigeons may be faced with conflicting energy demands that must be met while overall fruit availability, especially of high-energy fruits like *Metopium*, is still relatively high. Although we know little about molt in White-crowned Pigeons, molt should occur before pigeons migrate. Most White-crowned Pigeons migrate from the Keys in late September through October. The first prebasal molt in most pigeons occurs 50 to 100 days postfledging (Skutch and Gardner 1991); thus, adults may terminate nesting early enough to allow juveniles to exploit abundant energy-rich fruits to facilitate molt well before migration. In other species, molt occurs during periods of fruit abundance (Snow and Snow 1964, Fogden 1972, Worthington 1982, Poulin et al. 1992). Second, we suspect that the palatability of *Metopium* fruit may decrease in the fall. In late August and September, *Metopium* fruits darken and develop black, oily spots. The frequency with

which we have observed pigeons feeding on *Metopium* generally decreases in September. *Metopium*, which is in the Anacardiaceae, contains volatile phenols that may be distasteful. In some species in the Anacardiaceae, the concentration of volatile oils changes with fruit stage (Alencar et al. 1996). Thus, although we observed substantial amounts of *Metopium* fruit in September, it may not actually be available to pigeons. Third, in contrast to *Metopium*, which comprise 15 to 20% of the canopy, many of the fall-fruiting species comprise a relatively small percentage of the total canopy in seasonal deciduous forests in the Keys (M. Ross pers. comm.).

Conservation implications.—During the nesting season, White-crowned Pigeons are dependent upon relatively few plant species for food, one of which, *Metopium toxiferum*, appears to be especially important for successful breeding. Fruit production by *Metopium* seems to vary substantially both temporally and spatially in response to rainfall. Adult White-crowned Pigeons often fly more than 20 km on foraging trips in the Florida Keys (G. Bancroft and A. Strong unpubl. data), and they may fly considerably farther during periods of relative fruit scarcity. Many frugivorous columbids are known to be nomadic during periods of low fruit availability (Frith 1982). Maintaining numerous tracts of forest over large spatial scales may be important for breeding pigeons. The seasonally deciduous forests of the Florida Keys have become increasingly fragmented by human development (Strong and Bancroft 1994b). In the Keys, *Ficus* trees often are removed from residential areas because their extensive root systems interfere with septic systems. *Metopium* trees are removed because their sap causes contact dermatitis in humans (Scurlock 1987). Loss of critical foraging habitat and important food species in the Keys could have serious long-term implications for the persistence of White-crowned Pigeons.

Seed dispersal among isolated forest fragments may be critical to preserving long-term biodiversity in the Florida Keys (Strong and Bancroft 1994a, b). Because White-crowned Pigeons tend to be important medium- and long-distance seed dispersers, maintaining viable populations of pigeons may contribute to the conservation of a large fraction of an entire community (Terborgh 1986). Currently, the

White-crowned Pigeon is listed as Threatened by the state of Florida and is threatened or endangered throughout much of its range (Arendt et al. 1979). Understanding the relationship between resource availability and breeding patterns may be critical in developing effective management plans for this species.

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