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# TEMPORAL PATTERNS IN DIET OF NESTLING WHITE-CROWNED PIGEONS: IMPLICATIONS FOR CONSERVATION OF FRUGIVOROUS COLUMBIDS

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ABSTRACT.—The timing and production of crop milk are important to the reproductive tactics of granivorous columbids, but little is known about crop-milk production in frugivorous columbids. We examined the diet of nestling White-crowned Pigeons (*Columba leucocephala*) and the relative contributions of crop milk and fruit during different stages of nestling development. The diet was dominated by five species of plants: *Metopium toxiferum* (poisonwood), *Guapira discolor* (blolly), *Ficus citrifolia* (shortleaf fig), *F. aurea* (strangler fig), and *Erithalis fruticosa* (black torch). Fruit of *F. aurea* and *F. citrifolia* dominated the diet during May and June. Fruit of *M. toxiferum*, which began to ripen in early July, dominated the diet through September. *Guapira discolor* was found in the diet throughout the nesting season and, overall, ranked as the second-most-important food. *Erithalis fruticosa* was found in small amounts in samples collected throughout the season. Crop milk remained an important component of the diet throughout the nestling period. As nestlings grew, fruit was added to the diet. At ages 0 to 2 days, the diet was entirely crop milk. The proportion of the diet composed of fruit increased from 10% on day 3 to 65% at day 15. These data suggest that the reproductive tactics of frugivorous pigeons may differ from those of granivorous pigeons. We speculate that frugivorous columbids may continue to supplement the diet of nestlings and fledglings with crop milk. Although this behavior may enhance growth rates and survival of individual young, it also may lengthen the interclutch interval. These findings emphasize the conservation importance of protecting large feeding areas to maintain populations of threatened and endangered frugivorous pigeons. *Received 8 June 1992, accepted 15 March 1993.*

THE WHITE-CROWNED PIGEON (*Columba leucocephala*) nests throughout most of the Caribbean, in the Florida Keys, and along the Central American coast of the Caribbean (Arendt et al. 1979, AOU 1983, Strong et al. 1991). In Florida, White-crowned Pigeons nest from May through September on small mangrove islands in and around Florida Bay, but forage in the hardwood forests of the mainline Florida Keys (Strong et al. 1991), where they feed exclusively on fruits of hardwood trees (Wiley and Wiley 1979). These hardwood forests have been extensively cleared (Strong and Bancroft 1994a), thus threatening this pigeon species (Bancroft in press, Strong and Bancroft 1994b). The Florida Game and Freshwater Fish Commission has listed the White-crowned Pigeon as Threatened (Wood 1990). Understanding their food requirements is imperative for developing effective management practices to maintain and restore this population (Bancroft in press).

Pigeons and doves feed their nestlings crop milk (Beams and Meyer 1931, Patel 1936), which is high in protein and lipids, and promotes rapid growth (Pace et al. 1952, Hegde 1972). Consequently, columbid growth rates are extremely fast relative to similar-sized birds (Ricklefs 1968, Vandeputte-Poma 1980). However, physiological limitations on crop-milk production may limit the maximum clutch size of columbids to two eggs (Lack 1948, Burley 1980, Blockstein 1989). Instead of producing a large clutch, the reproductive strategy of many columbids is rapid production of multiple broods (Blockstein 1986, Westmoreland et al. 1986). In granivorous columbids, the production of crop milk by adults seems timed for rapid renesting (Mirarchi and Scanlon 1980, Mirarchi et al. 1982). The diets of nestling granivorous columbids gradually shift from all crop milk for the first few days posthatching to entirely seeds midway through the nestling period (Murton et al. 1964,

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Levi 1974, Burley 1980, Mirarchi and Scanlon 1980, Blockstein 1989). The weaning of older nestlings from crop milk may allow adults to overlap clutches and increase overall fecundity (Burley 1980, Westmoreland et al. 1986, Blockstein 1989). Prolactin, which stimulates crop-milk production, apparently inhibits gonadal activity (Bates et al. 1935, 1937). By decreasing the dependence of older nestlings on crop milk, adults may be able to reduce prolactin production and shorten the interval between clutches or even overlap nesting attempts (Burley 1980, Blockstein 1989, Westmoreland et al. 1986).

Fruit pulp generally is lower in protein than are seeds (Wainio and Forbes 1941, Short and Epps 1976, Johnson et al. 1985, Moermond and Denslow 1985, Lee et al. 1991, Bowman and Bancroft unpubl. data). The degree to which frugivorous pigeons digest seeds varies among species and by diet (Goodwin 1967, Crome 1975, Frith et al. 1976, Innis 1989, Bancroft and Bowman unpubl. data). Consumption of relatively low-protein fruit might necessitate longer nestling periods and slow growth rates in some frugivorous birds (Snow 1962, Morton 1973, Willson 1986), yet White-crowned Pigeons appear to have relatively short nestling periods (16–20 days) and rapid growth rates (Wiley and Wiley 1979, Bowman and Bancroft unpubl. data). In this paper we examine the diet of nestling White-crowned Pigeons and the relative contributions of crop milk and fruit during different stages of their development. We hypothesize that White-crowned Pigeons maintain crop-milk production throughout the nestling period to supplement the fruit diet.

## METHODS

We studied the reproductive ecology of White-crowned Pigeons at three keys in northeastern Florida Bay (within the boundaries of Everglades National Park): Middle Butternut Key, West Butternut Key, and Bottle Key (25°04.70′N, 80°32.02′W). We investigated food habits through samples collected from live squabs during 1986 through 1989. Most samples were collected on West Butternut and Bottle Keys, but a few were collected from fledging-age young on Middle Butternut Key. Samples were obtained by gently massaging the crop and throat of nestlings 3 to 15 days old. We attempted to completely empty the crop. For each day of age from 4 to 14, at least 10 samples were collected. Nestlings older than 14 days often fledged prematurely, so we did not try to collect many samples from older young. Crops of nestlings less than three days old appeared to contain only crop milk (pers. obs.) and, therefore, were not sampled. In all years, we attempted to obtain a few samples from all age classes. To minimize the influence on nestling survival, individual squabs were sampled only once. We do not think that crop sampling negatively influenced survival.

Crop samples were frozen and later sorted by food species. Individual items were counted; their mass was determined by weighing and volume by displacement. To measure the importance of each fruit species in the diet, we calculated the aggregate percent mass and aggregate percent volume for each species (Swanson et al. 1974).

We used multiple linear regression to examine the influence of nestling age and seasonal diet period on crop mass and volume, as well as on the proportion, mass, and volume of both fruit and crop-milk components of the diet. We examined seasonal trends in fruit use by calculating the average proportion a species comprised of the fruit portion for all samples collected during each week. All proportional data were arcsin transformed, and seasonal trends were analyzed by Pearson product-moment correlations on weekly means. We used ANOVA and a Kruskal-Wallis nonparametric analysis of variance to examine among-year patterns in crop mass, crop volume, and the ratio of crop milk to fruit. To examine shifts in the consumption of different fruit species between years, we used two-way contingency table analysis and the G-statistic (Sokal and Rohlf 1981).

## RESULTS

From 1986 through 1989, we collected 207 crop samples from pigeon nestlings: 51 in 1986, 53 in 1987, 68 in 1988, and 35 in 1989. Crop milk was present in 206 of the 207 samples (Table 1). Based on aggregate percent mass and volume, crop milk accounted for more than 52% of the nestling diet. We found fruits of 12 species in crop samples, as well as the flowers of 1 species. The results for aggregate percent volume and aggregate percent mass differed little. For brevity, we use only aggregate percent mass in the text. All percent masses are based on the aggregate approach.

Five plant species accounted for over 97% by mass of the fruit found in the crop samples from nestlings. *Metopium toxiferum* (poisonwood) was the most important, occurring in 78% of the samples and comprising 61% of the mass of the fruit diet (Table 1). *Guapira discolor* (blolly) was the second-most-important fruit, occurring in 46% of the samples and representing 19% of the mass. Fruits of *Ficus aurea* (strangler fig) and *F.*

TABLE 1. Analysis of food items from 207 crop samples taken from nestling White-crowned Pigeons in Florida Bay during 1986-1989.

| Food species | Samples[a] | Items[a] | Total mass (g) | Aggregate percent mass: With milk | Aggregate percent mass: Without milk | Total volume (cc) | Aggregate percent volume: With milk | Aggregate percent volume: Without milk |
|---|---|---|---|---|---|---|---|---|
| Crop milk | 206 (99.5) | — | 1,262.97 | 52.55 | — | 1,201.9 | 52.93 | — |
| *Metopium toxiferum* | 162 (77.9) | 2,420 (40.05) | 749.89 | 28.70 | 61.30 | 689.9 | 28.03 | 60.76 |
| *Guapira discolor* | 95 (45.7) | 2,189 (36.23) | 240.60 | 9.57 | 19.01 | 221.2 | 9.50 | 19.14 |
| *Ficus* spp. | 35 (16.8) | 316 (5.23) | 150.17 | 5.48 | 9.41 | 149.4 | 5.57 | 9.58 |
| *Erithalis fruticosa* | 54 (26.0) | 816 (13.51) | 58.82 | 2.52 | 6.31 | 63.0 | 2.82 | 7.22 |
| *Avicennia germinans* | 11 (5.3) | 93 (1.54) | 5.13 | 0.20 | 0.70 | 6.9 | 0.31 | 1.12 |
| *Bumelia salicifolia* | 2 (1.0) | 5 (0.08) | 0.91 | 0.05 | 0.10 | 1.3 | 0.07 | 0.16 |
| *Krugiodendron ferreum* | 2 (1.0) | 2 (0.03) | 0.95 | 0.03 | 0.04 | 0.9 | 0.03 | 0.04 |
| *Simarouba glauca* | 1 (0.5) | 2 (0.03) | 3.47 | 0.09 | 0.12 | 4.2 | 0.12 | 0.18 |
| *Chrysobalanus icaco* | 1 (0.5) | 1 (0.02) | 1.79 | 0.07 | 0.10 | 1.8 | 0.08 | 0.10 |
| *Cocoloba diversifolia* | 1 (0.5) | 1 (0.02) | 0.92 | 0.08 | 0.10 | 1.0 | 0.09 | 0.11 |
| *Bourreria ovata* | 1 (0.5) | 1 (0.02) | 0.69 | 0.02 | 0.02 | 0.6 | 0.02 | 0.02 |
| *Trema* spp. | 1 (0.5) | 18 (0.30) | 0.44 | 0.02 | 0.03 | 0.5 | 0.02 | 0.03 |
| Fruit pulp | 2 (1.0) | 4 (0.07) | 0.95 | 0.03 | 0.08 | 0.8 | 0.03 | 0.08 |
| Seed | 2 (1.0) | 3 (0.05) | 0.18 | 0.01 | 0.01 | 0.3 | 0.01 | 0.02 |
| Leafy material | 1 (0.5) | 1 (0.02) | 0.48 | 0.01 | 0.03 | 0.5 | 0.02 | 0.03 |
| Unknown | 16 (7.7) | 132 (2.18) | 7.65 | 0.23 | 5.04 | 7.5 | 0.24 | 1.12 |
| Grit | 5 (2.4) | 38 (0.63) | 0.25 | 0.01 | 0.01 | 0.5 | 0.02 | 0.04 |
| Total | 207 | 6,042 | 2,486.26 | — | — | 2,352.2 | — | — |

[a] Number with percent in parentheses.

*citrifolia* (shortleaf fig) were found in almost 17% of the samples. Often we could not distinguish the fruit of these two species in crop samples and, therefore, the data were pooled. *Ficus* spp. fruit represented slightly less than 10% by mass of the fruit diet. *Erithalis fruticosa* (black torch) was found in 26% of the samples and comprised 6% of the mass. Flowers of *Avicennia germinans* (black mangroves) were found in 11 samples and represented about 1% of the fruit diet. Other fruit species each represented less than 1% of the diet and were found only in a few samples.

The diet of nestlings gradually shifted from 100% crop milk at days 0-2 to less than 35% crop milk by volume at day 15 (Fig. 1). Mean crop mass and volume varied significantly with age, independent of time of season ($F$ = 5.30 and 5.70, respectively, $P < 0.01$, multiple linear regression), tending to increase with age ($R^2 = 0.192$, $P = 0.006$). Mean crop-milk volume also varied significantly with age (Fig. 1, $F = 1.92$, $P = 0.034$, linear regression); however, it significantly declined with age ($r = -0.281$, $P < 0.05$). As a result, the proportion of the diet composed of crop milk decreased significantly with increasing nestling age ($r = -0.585$, $P < 0.01$, Pearson product-moment correlation). Crop milk appears to be replaced gradually by fruit as the nestlings grow, rather than simply having more fruit added to a constant supply of crop milk.

*Within-year variation.*—The fruit content of the nestling diet demonstrated seasonal variation. We divided the season into two periods based on food habits. The first half (through mid-July) was dominated by *Ficus* spp. and the second half by *M. toxiferum*. Early in the breeding season (May and June), *Ficus* spp. fruits comprised as much as 60% of the fruit content by volume (Fig. 2). The proportion of *Ficus* spp. in the diet declined throughout the season (Fig. 2, $r = -0.653$, $P < 0.01$, $n = 205$). By the second week in July, *Ficus* spp. comprised less than 2% of the fruit diet and remained a small part of the diet for the rest of the season. In contrast, the proportion of *M. toxiferum* in the diet increased throughout the breeding season (Fig. 2, $r = 0.613$, $P < 0.01$, $n = 205$). After the second week of July, *M. toxiferum* comprised, on average, 73.8% of the fruit diet.

*Guapira discolor* was consumed throughout the breeding season; however, its relative importance in the diet varied considerably (Fig. 2). It comprised as much as 30% of the fruit diet in early June to as little as 2% in early July. *Erithalis*

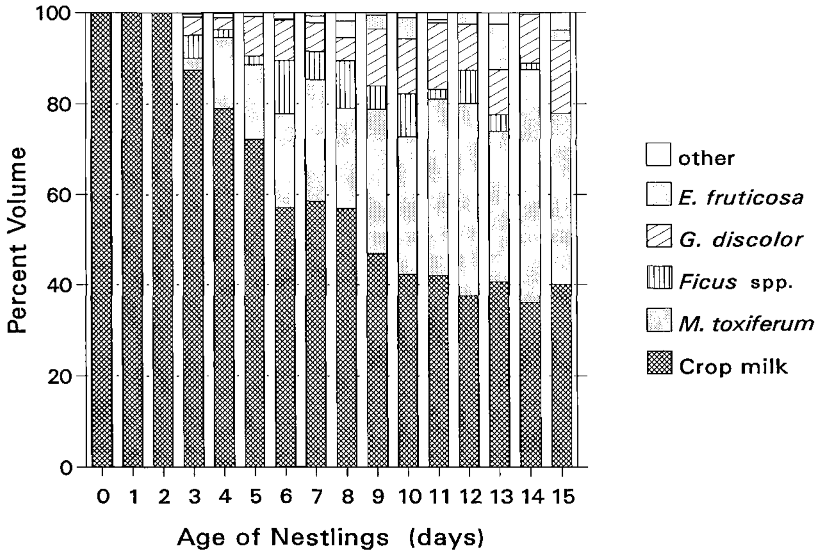


Fig. 1. Percent volume of individual food items in crop samples collected from nestling White-crowned Pigeons relative to age.

*fruticosa* also was consumed throughout the season, rarely comprising more than 10% of the fruit diet. It had the highest percent mass in early July. Other fruits and *A. germinans* flowers were most abundant in the diet early in the season.

Neither total crop mass nor volume differed between the two seasonal diet periods (Table 2). The crop-milk content of the diet, however, did vary seasonally. The proportion, mass, and volume of crop milk increased between the first half and second half of the season, independent of nestling age ($F = 61.26$, $P = 0.001$, multiple linear regression). Because the proportion of

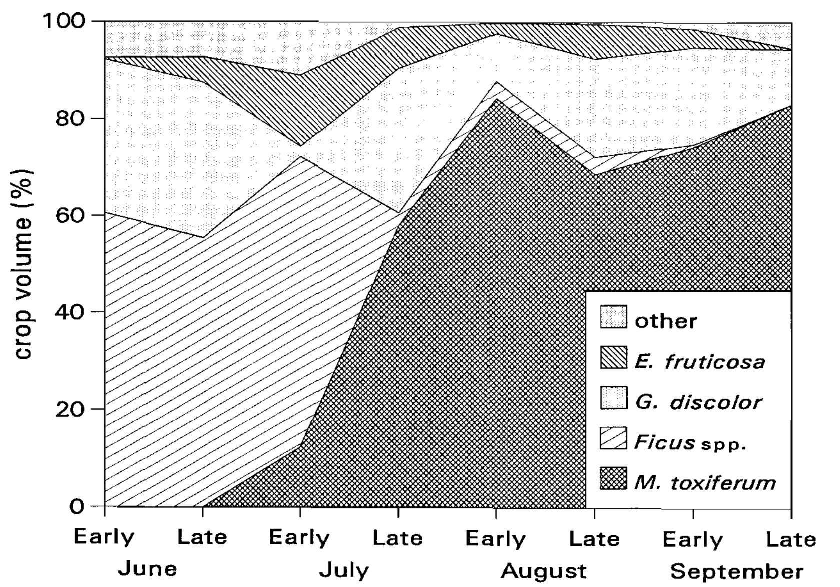


Fig. 2. Percent volume of food items other than crop milk in samples collected from nestling White-crowned Pigeons relative to half-month periods.

TABLE 2. Seasonal variation in crop size and amount of crop milk fed 7- to 10-day-old nestling White-crowned Pigeons ($\bar{x} \pm$ SD, two-tailed independent $t$-test).

| Variable | Early | Late | $t^a$ |
|---|---|---|---|
| Crop mass (g) | 13.9 ± 4.6 | 12.9 ± 4.8 | $-1.34^{ns}$ |
| Crop volume (cc) | 13.7 ± 4.5 | 12.2 ± 4.7 | $-1.85^{ns}$ |
| Percent crop milk | 40.4 ± 19.4 | 54.4 ± 17.7 | 2.91** |
| Crop-milk mass (g) | 4.5 ± 2.6 | 6.6 ± 3.1 | 2.72** |
| Crop-milk volume (cc) | 4.6 ± 2.3 | 6.2 ± 2.9 | 2.26* |

$^{a}$ $^{ns}$, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$.

crop milk in the diet also varied with nestling age, we controlled for age effects by comparing only 7- to 10-day-olds. Before mid-July, these nestlings were fed, on average, 40.4% crop milk. After mid-July, the percent volume of crop milk increased to 54.4%. Mean volume and mass of crop milk in crops increased significantly between the early and late parts of the season (Table 2), suggesting that parents are actually producing and feeding nestlings more crop milk late in the season than they are earlier.

*Among-year variation.*—The mean mass of crop samples collected did not vary significantly among years ($F = 1.41$, $P = 0.239$, one-way ANOVA). Crop samples averaged 12.4 g in 1986, 12.3 g in 1987, 12.6 g in 1988, and 10.3 g in 1989. The proportion of the samples composed of crop milk also did not vary significantly among years ($X^2 = 5.99$, $P = 0.1121$, Kruskal-Wallis test). Crop milk averaged 52.1% of the total mass in 1986, 57.4% in 1987, 52.7% in 1988, and 45.5% in 1989.

The relative contributions of various fruit species varied among years. In all years *M. toxiferum* had the highest percent mass. The percent mass of *M. toxiferum* varied from 44.8 and 47.7% of the total fruit content in 1989 and 1987, respectively, to 69.7% in 1986 and 74.2% in 1988. The proportion of samples containing *M. toxiferum* did not vary significantly among years ($G = 5.46$, $P > 0.10$). *Guapira discolor* had the second highest percent mass in all years. It had lower percent mass in years that *M. toxiferum* had higher percent mass. The percent mass of *G. discolor* varied from 11.4% in 1988 and 13.6% in 1986 to 25.5% in 1987 and 31.5% in 1989. The proportion of crop samples with *G. discolor* fruit varied significantly among years ($G = 14.27$, $P < 0.01$). In 1986 and 1988 less than one-half the samples contained *G. discolor*, whereas in 1987 and 1989 more than one-half contained it. The relative importance of *Ficus* spp. fruit varied substantially among years. Although the proportion of samples containing *Ficus* spp. fruit did not vary significantly among years 1987, 1988, and 1989 ($G = 4.76$, $P > 0.05$), the percent mass was almost twice as high in 1987 (16.5%) and 1989 (15.7%) as it was in 1988 (7.1%). In 1986, *Ficus* spp. were practically nonexistent in the diet. However, in 1986 we did not begin to collect samples until late July, and by then *M. toxiferum* had become ripe. Had we collected samples in June, *Ficus* spp. would likely have been present in crops (unpubl. data). The importance of *E. fruticosa* also varied among years. The percent mass of *E. fruticosa* was 3.4% in 1988, 4.9% in 1987, 8.4% in 1989, and 10.1% in 1986. The proportion of samples containing *E. fruticosa* did not vary significantly among years ($G = 0.85$, $P > 0.05$).

## DISCUSSION

In this study we have shown that: (1) the diet of nestling White-crowned Pigeons in the upper Florida Keys is dominated by the fruit of five species of plants; (2) a distinctive seasonal shift occurs in the dominant species consumed; (3) crop milk remains an important component of the diet throughout the nestling period; and (4) as nestlings grow, the volume of fruit in their diet increases, while the volume of crop milk decreases.

*Fruit-consumption patterns.*—Five species of plants made up 97% of the fruit in the diet of nestling White-crowned Pigeons. Most of the other seven species recorded occurred in samples collected during the first half of the season. *Metopium toxiferum*, *G. discolor*, both *Ficus* species, and *E. fruticosa* were the most common fruits. *Erithalis fruticosa* is probably not an important fruit in the diet of nestling White-crowned Pigeons throughout their Florida range because this plant is relatively rare, found primarily on the berms of a few nesting keys and rarely on the mainland where adult pigeons forage. It may have been exploited opportunistically by birds nesting on the keys where we collected samples. Some nests were built in *E. fruticosa* shrubs on our study keys. These shrubs fruited sporadically throughout the nesting season. The other four species, however, do appear to be very important.

*Metopium toxiferum* was the most abundant fruit in the diet of nestling White-crowned Pigeons on Mona Island, Puerto Rico (Wiley and Wiley 1979). On mainland Puerto Rico, *M. toxiferum* does not grow abundantly and is less common in nestling diets; Wiley and Wiley (1979) reported that in Puerto Rico *Ficus citrifolia* was most common by volume. A species of *Guapira* not found in Florida also was important. Additional fruits that are not found in Florida also were prominent in the diet of Puerto Rican White-crowned Pigeons.

Seasonal patterns of fruit consumption may reflect, in part, differences in patterns of fruiting phenology of the various plant species. Foraging habits of fruit pigeons in subtropical rainforests of Australia seem to be largely opportunistic, using whatever fruits are available at particular times (Innis 1989). Throughout the pigeon breeding season, some individual *G. discolor* and *Ficus* spp. trees in the Florida Keys can be found in fruit. *Metopium toxiferum* fruit begins to ripen by mid-July in Florida (unpubl. data). The shift in nestling diet seems directly related to this seasonal pattern of ripening; *M. toxiferum* dominated the fruit component of the diet after the second week in July. Even when *M. toxiferum* is available, *G. discolor* still remains important in the diet, but *Ficus* even if common is consumed only in tiny amounts, if at all, when *M. toxiferum* is ripe.

The relative importance of each plant species in the pigeon diet also may reflect the relative abundance of these plants in the Keys. The hardwood forest canopy in the northern Florida Keys is comprised of 5 to 18% *M. toxiferum* and 1 to 7% *G. discolor*, as well as less than 1% of the two *Ficus* species (M. Ross pers. comm.). The shift in diet may reflect a foraging decision to feed on a more abundant food source. However, factors other than fruit abundance or phenological patterns may influence the foraging decisions of White-crowned Pigeons. These birds digest the seeds of *M. toxiferum* and *G. discolor* fruits, but pass unharmed the seeds of *Ficus* fruits (unpubl. data). In addition *M. toxiferum* fruits contain significantly more lipids and less water than do those of *Ficus* spp. and have significantly higher amounts of energy per gram dry mass (unpubl. data). Our work supports the suggestions of other studies that nutritional contents of fruits play a role in foraging decisions of birds (Stiles 1980, Stiles and White 1982, Johnson et al. 1985; but see Borowicz 1988).

Flowers of *A. germinans* were found in some crop samples during the early part of the season. *Avicennia germinans* flowers were higher in energy content than many of the fruits eaten by White-crowned Pigeons (unpubl. data). Their consumption during the early part of the breeding season may be an effort to supplement the relatively poor energetic content of *Ficus* spp., the dominant food item during this period. Similar foraging behavior has been recorded in Common Wood-Pigeons (*C. palumbus*) in England, which when cereal grains and mast are scarce supplement their diet by eating leaves, buds, and flowers (Murton et al. 1964).

Interannual differences in fruit consumption appear related to the relative abundance of these fruits. During 1988, *M. toxiferum* fruit production was high (unpubl. data). Pigeons began feeding on *M. toxiferum* earlier in 1988 than in the other years, and this fruit represented a greater percent mass of the nestling fruit diet than in any other year. During 1989, the Florida Keys experienced a drought and *M. toxiferum* fruit production declined. During 1990, drought conditions continued and *M. toxiferum* fruit production remained low in the Keys. A freeze during December 1989 damaged large numbers of *M. toxiferum* trees on the mainland and reduced fruit production even further. We did not systematically collect crop samples in 1990, but sporadic checks suggested that *M. toxiferum* was not as important in the diet as in previous years, even during the later part of the breeding season (A. Strong and M. Carrington unpubl. data).

*Crop-milk production.*—Regression of crop-gland activity varies greatly within the columbids (Levi 1974). The crop-gland cycle appears to be timed for rapid renesting in several granivorous columbids (Mirarchi and Scanlon 1980, Mirarchi et al. 1982, Mirarchi 1993a). In granivorous columbids crop-milk production ceases before young fledge and nestling growth is sustained by seeds (Burley 1980, Blockstein 1989, Mirarchi 1993b). Ziegler (1971), however, found that crop milk was produced by Band-tailed Pigeons (*C. fasciata*), which eat both fruits and seeds, for up to 30 days after hatching. White-crowned Pigeons produce crop milk for at least 16 days posthatching. Samples collected from a few fledglings over 20 days old also contained crop milk. Fledglings remain on the breeding keys for up to 40 days posthatching (unpubl. data) and depend on the adults for much of their food (pers. obs.), suggesting that adult White-crowned Pigeons may produce crop milk throughout this period.

Differences in the timing of crop-milk production may be related to nutritional differences between granivorous and frugivorous diets. Most columbids—frugivores and granivores alike—are fed only crop milk during the first three to four days after hatching, and then a mixture of crop milk and seeds or fruit. Crop milk is high in protein and lipids and contains an unknown growth-promoting factor (perhaps digestive microflora; Pace et al. 1952, Hegde 1972). When young are receiving crop milk, they grow extremely rapidly (Riddle 1928), and this rapid growth period is apparently critical for reaching normal adult size (Westmoreland and Best 1987). Once the period of crop-milk dependence is passed, a granivorous diet may provide sufficient protein for nestling development. This allows adults to cease crop-milk production (Blockstein and Westmoreland 1993), which because of hormonal changes may increase the speed with which a second clutch can be initiated (Burley 1980, Westmoreland et al. 1986). Clutch overlap and rapid production of multiple broods may be tactics by which granivorous columbids achieve high reproductive potential despite being limited to a clutch size of two eggs (Burley 1980, Blockstein 1986, Westmoreland et al. 1986). A frugivorous diet may lack sufficient protein for nestling development through fledging and may require supplemental protein, in the form of crop milk, throughout the nestling period. The hormones required to maintain crop-milk production may restrict gonadal development (see Mirarchi 1993b) and, therefore, increase the interclutch interval.

Adult White-crowned Pigeons forage up to 44 km from the breeding keys and normally make a single foraging trip each day (A. M. Strong and G. T. Bancroft unpubl. data). This may limit the volume of fruit adults can feed young. It also may impose a nutritional constraint so that the chicks' diet requires supplementation with crop milk. The gradual increase in the volume of fruit in the diet of nestlings may reflect, in part, the ability of nestlings to process a greater volume of food as they grow larger. The importance of crop milk in the diet also may necessitate biparental care throughout the nestling period. Haas (1980) and Blockstein (pers. comm.) found that biparental care was essential for Mourning Doves (*Zenaida macroura*) to successfully fledge young. Single adults could only successfully fledge young if they were assisted by a mate during the first several days posthatching. Crop-milk dependence throughout the nestling and into the postfledging period may necessitate extended parental care in frugivorous pigeons. Thus, the number of successful nesting attempts frugivorous pigeons can have in a season is limited, but the extended period of crop milk in the diet may increase the growth rate and survival of young.

Frugivorous columbids in the tropical Old World genera *Ptilinopus* and *Ducula* lay single-egg clutches (Goodwin 1967). Some of these species feed extensively on the fruit of *Ficus* species and may have reduced crop-milk production as do White-crowned Pigeons when feeding on *Ficus* fruit. If they, like the frugivorous White-crowned Pigeon, supplement the diet with crop milk throughout the nestling period and even during the postfledging period, the rapid production of multiple broods might be less common than for pigeons who stop producing crop milk earlier in the nesting cycle. Combined with a smaller clutch size, the reproductive potential of frugivorous columbids may be lower than that of granivorous columbids. African Green Pigeons (*Treron* spp.), which are fig specialists, lay two-egg clutches and may have higher reproductive potential because they apparently digest the seeds of figs as well as pulp (Cowles and Goodwin 1959).

## CONSERVATION IMPLICATIONS

Fecundity is an important demographic variable in estimating the viability of populations (Goodman 1987), and reliable estimates, including environmentally-induced variation, are critical to effective management of small, endangered populations (Soulé and Kohm 1989). Many of the frugivorous columbids of the genera *Ptilinopus* and *Ducula* are island endemics and critically endangered. In the New World, many tropical pigeons in the genus *Columba* feed exclusively on fruit and many of these also are threatened or endangered. Little is known about annual reproductive performance and demographic patterns of these columbids, but our study suggests that their reproductive tactics may differ from granivorous columbids. Further research on the demography of frugivorous columbids could be critical for their effective management.

White-crowned Pigeons are a Threatened species (Wood 1990, Bancroft in press) in Florida as well as through much of their range (Arendt et al. 1979). The destruction of tropical forests in Florida represents a serious threat to the status of this species because it eliminates many fruit-producing trees (Strong and Bancroft 1994a, b). Furthermore, *M. toxiferum* is often removed in remaining forest fragments in suburban areas because its sap can cause dermatitis in humans (Scurlock 1987). Conservation of White-crowned Pigeons in Florida will require the maintenance of abundant populations of *M. toxiferum* and other fruit producing trees.

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## Literature Cited

American Ornithologists' Union. 1983. Check-list of North American birds, 6th ed. Am. Ornithol. Union, Washington, D.C.

Arendt, W. J., T. A. Vargas Mora, and J. W. Wiley. 1979. White-crowned Pigeon: Status rangewide and in the Dominican Republic. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 33:111–122.

Bancroft, G. T. In press. White-crowned Pigeon. *In* Rare and endangered biota of Florida Birds, vol. 2 (J. Rodgers, Ed.). Univ. Presses of Florida, Gainesville.

Bates, R. W., E. L. Lahr, and O. Riddle. 1935. The gross action of prolactin and follicle-stimulating hormone on the mature ovary and sex accessories of the fowl. Am. J. Physiol. 111:361-368.

Bates, R. W., O. Riddle, and E. L. Lahr. 1937. The mechanism of the anti-gonad action of prolactin in adult pigeons. Am. J. Physiol. 119:610-614.

Beams, H. W., and R. K. Meyer. 1931. The formation of pigeon milk. Physiol. Zool. 4:486-500.

Blockstein, D. 1986. Reproductive behavior and parental investment of Mourning Doves (*Zenaida macroura*). Ph.D. dissertation, Univ. Minnesota, Minneapolis.

Blockstein, D. 1989. Crop milk and clutch size in Mourning Doves. Wilson Bull. 101:11-25.

Blockstein, D. E., and D. Westmoreland. 1993. Reproductive strategy. Pages 105-116 *in* Ecology and management of the Mourning Dove (T. S. Baskett, M. W. Sayre, R. E. Tomlinson, and R. E. Mirarchi, Eds.). Stackpole Books, Harrisburg, Pennsylvania.

Borowicz, V. A. 1988. Fruit consumption by birds in relation to fat content of pulp. Am. Midl. Nat. 119:121-127.

Burley, N. 1980. Clutch overlap and clutch size: Alternative and complementary reproductive tactics. Am. Nat. 115:223-246.

Cowles, G. S., and D. Goodwin. 1959. Seed digestion by fruit-eating pigeons, *Treron*. Ibis 101:253–254.

Crome, F. H. J. 1975. The ecology of fruit pigeons in tropical northern Queensland. Aust. Wildl. Res. 2:155-185.

Frith, H. J., F. H. J. Crome, and T. O. Wolfe. 1976. Food of fruit-pigeons in New Guinea. Emu 76: 49-58.

Goodman, D. 1987. The demography of chance extinction. Pages 11-34 *in* Viable populations for conservation (M. E. Soulé, Ed.). Cambridge Univ. Press, Cambridge.

Goodwin, D. 1967. Pigeons and doves of the world. Trustees of the British Museum (Nat. Hist.), London.

Haas, G. H. 1980. Success of single-parent Mourning Dove nests. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 34:426-429.

Hegde, S. N. 1972. Composition of pigeon milk and its effect on growth of chicks. Indian J. Exp. Biol. 11:238-239.

Innis, G. J. 1989. Feeding ecology of fruit pigeons in subtropical rainforests of south-eastern Queensland. Aust. Wildl. Res. 16:365-394.

Johnson, R. A., M. F. Willson, J. N. Thompson, and R. I. Bertin. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. Ecology 66:819-827.

Lack, D. 1948. The significance of clutch size. Ibis 90:25-45.

Lee, W. G., P. J. Grubb, and J. B. Wilson. 1991. Patterns of resource allocation in fleshy fruits of nine European tall-shrub species. Oikos 61:307-315.

LEVI, W. M. 1974. The pigeon, 3rd ed. Levi Publishing Co., Sumter, South Carolina.

MIRARCHI, R. E. 1993a. The crop gland. Pages 117–128 *in* Ecology and management of the Mourning Dove (T. S. Baskett, M. W. Sayre, R. E. Tomlinson, and R. E. Mirarchi, Eds). Stackpole Books, Harrisburg, Pennsylvania.

MIRARCHI, R. E. 1993b. Energetics, metabolism and reproductive physiology. Pages 143-160 *in* Ecology and management of the Mourning Dove (T. S. Baskett, M. W. Sayre, R. E. Tomlinson, and R. E. Mirarchi, Eds.). Stackpole Books, Harrisburg, Pennsylvania.

MIRARCHI, R. E., AND P. F. SCANLON. 1980. Duration of Mourning Dove crop gland activity during the nesting cycle. J. Wildl. Manage. 44:209-213.

MIRARCHI, R. E., P. F. SCANLON, F. C. GWAZDAUSKAS, AND R. L. KIRKPATRICK. 1982. Gonadal and hormonal characteristics of captive adult Mourning Doves during the nesting cycle. Theriogenology 18:683–695.

MOERMOND, T. C., AND J. S. DENSLOW. 1985. Neotropical avian frugivores: Patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Ornithol. Monogr. 36:865–897.

MORTON, E. S. 1973. On the evolutionary advantages and disadvantages of fruit-eating in tropical birds. Am. Nat. 107:8–22.

MURTON, R. K., N. J. WESTWOOD, AND A. J. ISAACSON. 1964. The feeding habits of the Woodpigeon (*Columba palumbus*), Stock Dove (*C. oenas*) and Turtle Dove (*Streptopelia turtur*). Ibis 106:174–188.

PACE, D. M., P. A. LANDOLT, AND F. E. MUSSEHL. 1952. The effect of pigeon crop-milk on growth in chickens. Growth 16:279–285.

PATEL, M. D. 1936. The physiology of the formation of "pigeon's milk." Physiol. Zool. 9:129–152.

RICKLEFS, R. E. 1968. Patterns of growth in birds. Ibis 110:419–451.

RIDDLE, O. 1928. Studies on the physiology of reproduction in birds XXIII. Growth of gonads and bursa Fabricii in doves, with data for body growth and age at maturity. Am. J. Physiol. 86:248–265.

SCURLOCK, J. P. 1987. Native trees and shrubs of the Florida Keys. Laurel Press, Pittsburgh, Pennsylvania.

SHORT, H. L., AND R. A. EPPS. 1976. Nutrient quality and digestibility of seeds and fruit from southern forests. J. Wildl. Manage. 40:283–289.

SNOW, D. W. 1962. The natural history of the Oilbird, *Streatornis caripensis*, in Trinidad, W.I. Part 2: Population, breeding ecology, and food. Zoologica 47:199–221.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. W. H. Freeman, San Francisco.

SOULÉ, M. E., AND K. A. KOHM. 1989. Research priorities for conservation biology. Island Press, Washington, D.C.

STILES, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. Am. Nat. 116: 670–688.

STILES, E. W., AND D. WHITE. 1982. Additional information on temperate bird-disseminated fruits: Response to Herrera's comments. Am. Nat. 120: 823–827.

STRONG, A. M., AND G. T. BANCROFT. 1994a. Patterns of deforestation and fragmentation of mangrove and deciduous seasonal forests in the upper Florida Keys. Bull. Mar. Sci. In press.

STRONG, A. M., AND G. T. BANCROFT. 1994b. Postfledging dispersal of White-crowned Pigeons: Implications for conservation of deciduous seasonal forests in the Florida Keys. Conserv. Biol. In press.

STRONG, A. M., R. J. SAWICKI, AND G. T. BANCROFT. 1991. Effects of predator presence on the nesting distribution of White-crowned Pigeons in Florida Bay. Wilson Bull. 103:415- 425.

SWANSON, G. A., G. L. KRAPU, J. C. BARTONEK, J. R. SERIE, AND D. H. JOHNSON. 1974. Advantages in mathematically weighting waterfowl food habits data. J. Wildl. Manage. 38:302–307.

VANDEPUTTE-POMA, J. 1980. Feeding growth and metabolism of the pigeon, *Columba livia*: Duration and role of crop milk feeding. J. Comp. Physiol. 135:97–99.

WAINIO, W. W., AND E. B. FORBES. 1941. The chemical composition of forest fruits and nuts from Pennsylvania. J. Agric. Res. 62:627–635.

WESTMORELAND, D., AND L. B. BEST. 1987. What limits Mourning Doves to a clutch of two eggs? Condor 89:486–493.

WESTMORELAND, D., L. B. BEST, AND D. BLOCKSTEIN. 1986. Multiple brooding as a reproductive strategy: Time-conserving adaptations in Mourning Doves. Auk 103:196–203.

WILEY, J. W., AND B. N. WILEY. 1979. The biology of the White-crowned Pigeon. Wildl. Monogr. 64.

WILLSON, M. F. 1986. Avian frugivory and seed dispersal in eastern North America. Curr. Ornithol. 3:223–279.

WOOD, D. A. 1990. Official lists of endangered and potentially endangered fauna and flora in Florida. Florida Game and Fresh Water Fish Commission, Tallahassee.

ZIEGLER, D. L. 1971. Crop milk cycles in Band-tailed Pigeons and losses of squabs due to hunting pigeons in September. M.S. thesis, Oregon State Univ., Corvallis.