

**Relationship Between the Reproductive Ecology
of the White-crowned Pigeon and the Fruiting
Phenology of Tropical Hardwood Hammock Trees**

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ABSTRACT

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The ecology of White-crowned Pigeons in Florida is tightly tied to the abundance of fruits in the tropical forests. Four species, *Metopium toxiferum*, *Guapira discolor*, *Ficus aurea*, and *F. citrifolia* dominated the diet of birds during the nesting season. The two *Ficus* species produced fruit during all months of the year but fruit production tended to be greatest during the summer. *G. discolor* produced ripe fruit from late May through early fall and its production was closely associated with recent rainfall. *M. toxiferum* fruit began to ripen in July and ripe fruit remained on the trees through the winter although fruit loss was often substantial by early fall. The number of pigeons in the keys increased in April with increasing fruit abundance, reached a plateau extending from June through August and attained the annual peak in September. Pigeon numbers in Florida dropped precipitously each October when over 90% of the pigeons migrated out of Florida for the winter. The September peak included a large number of flying young from the preceding nesting season. Pigeons nested on half the mangrove islands in Florida Bay and on a few islands in Card and Barnes Sound. No pigeons were found nesting on mainland Florida and only one nest was found on the mainline Keys in 6 years. Nesting distribution in Florida Bay was nearly non-overlapping with the distribution of raccoons. Raccoons presumably restrict pigeon distribution by preying on nest contents or adults. Pigeons laid clutches of eggs from early May through early September. The onset of nesting and especially the termination of nesting were linked to fruit availability. The number of clutches laid during the season was also linked to fruit availability. Fruit was especially abundant in 1988 and more clutches were laid than in any other year. The number of new clutches laid per week showed a bimodal pattern during the season. An initial peak occurred in late May to mid June. The number of new starts per week decreased during late June to early July before increasing to the seasonal peak in late July-early August. The second major wave of nesting was tied to the ripening of *M. toxiferum* fruit. In 1988, when *M. toxiferum* ripened earlier and was extremely abundant, the second nesting wave began earlier and lasted longer. The availability of *M. toxiferum* fruit also had an impact on nesting success. Within a season, nesting success increased after *M. toxiferum* became available. The highest nesting success was recorded in 1988 when *M. toxiferum* was very abundant. Egg size, growth rates of young and young survivorship within nests increased when *M. toxiferum* became available. Two factors seem to explain the importance of *M. toxiferum*. First, the tree is still relatively abundant in the Upper Keys. Second, its fruit is extremely high in lipid content and low in water content resulting in substantially more energy content in a given volume of this fruit than any other fruit species available to pigeons.

White-crowned Pigeons remain threatened in Florida because of human developmental pressures on their foraging habitats. *M. toxiferum* trees are generally removed from suburban areas because they cause severe skin rashes on most people. We recommend that the FGFWFC work with Monroe County to develop a series of criteria for encouraging or requiring the planting of alternative fruit sources. We strongly recommend that *G. discolor* and *B. ovata* be planted whenever possible. We also recommend that a network of hammocks be maintained throughout the Keys to provide a range of foraging areas, especially for recently independent young.

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INTRODUCTION

The White-crowned Pigeon (*Columba leucocephala*) is a relatively large columbid nesting south from the southern tip of Florida through the Bahamas to the Lesser Antilles and west to the Cayman Islands, on cays off Belize, and possibly south to Panama (AOU 1983). They typically nest on offshore islands and feed in the lowland hardwood forests of adjacent large islands (Goodwin 1967, Wiley and Wiley 1979). Fruit from trees are their primary food. Over much of their range, White-crowned Pigeon populations have decreased dramatically. Decreases have resulted from destruction of nesting and feeding habitats as well as excessive hunting and collecting of squabs (Wetmore 1931, Bent 1932, Biegii 1970, Wiley and Wiley 1979).

In Florida, White-crowned Pigeons nest on small mangrove keys from Elliott Key south to the Marquesas Keys (AOU 1983). Many of these keys fall within the boundaries of Everglades National Park and are thus protected. The birds typically fly into the hardwood hammocks on the large keys to feed. Breeding populations are clearly tied to the existence of sufficient hammocks for the production of food, but since these hammocks occupy high ground, they have been extensively developed for human habitation. The destruction of these hammocks is a major factor in the listing of the White-crowned Pigeon as a threatened species in Florida (Kale 1978, Wood 1990).

The habitat requirements for White-crowned Pigeons are not known in detail (Owre 1978). The relationship between pigeon populations in the keys and the availability of food and of safe nesting sites seems critical to the development of a management plan for this threatened species. We, therefore, undertook a detailed study of the relationship between the nesting ecology of White-crowned Pigeons in the keys and the fruiting phenology of their food sources.

STUDY AREA

Our study area encompassed an approximately 1850 km² area which included Florida Bay, Barnes and Card sounds, the southern coast of mainland Florida, and the mainline Keys from Elliott Key south to Long Key (Fig. 1). Most of the study area is within Everglades National Park. Additional field work was conducted over a 63 km² portion of Whitewater Bay in mainland Everglades National Park.

Florida Bay is a large, shallow estuary. The eastern bay is characterized by relatively deep (1-2 m) basins divided by narrow (often < 200 m), shallow (< 30 cm) banks (Schomer and Drew 1982, Powell 1987). Most of the keys within the eastern bay are situated along these banks (Fig. 1). Areas of higher elevations on the banks support red mangroves (*Rhizophora mangle*) which over time may develop into keys. In the western bay, the banks are larger, with a maximum width of greater than 10 km (Powell 1987).

In the upper Florida Keys, White-crowned Pigeons nest on mangrove islands in Florida Bay. We studied the reproductive ecology of pigeons at three keys in the northeast corner of the bay (Fig. 2): Middle Butternut, West Butternut, and Bottle keys (25° 04 70' N, 80° 32 02' W). All three keys fall within the boundaries of Everglades National Park.

Our three study keys are physiographically similar, comprised of a perimeter berm of mangrove peat and shell sand that forms an embankment 30-60 cm above normal high tides. This berm is typically fringed with *R. mangle* and *Avicennia germinans* and the well-drained soil of the embankment supports tropical hammock vegetation similar to the hammocks on the larger keys (Craighead 1971). Plants typical of the shrub/strand community (Schomer and Drew 1982) such as *Suriana maritima*, *Batis* spp., and *Borrchia frutescens* are often interspersed with plants normally associated with the hammock/strand community: *Conocarpus erectus*, *Erithalis fruticosa*, *Eugenia* spp., *Metopium toxiferum*, and *Pithecellobium* spp. The presence of plants such as *Guapira discolor*, *Coccoloba uvifera*, and *Exothea paniculata* is more suggestive of the well-developed hammocks.

The berm encloses a depressed central lagoon composed of dense hurricane mud, aragonite (Craighead 1969). Summer rains cause salinities in the lagoon to vary and mat-like beds of periphyton grow amidst sparse stands of *A. germinans*. Pigeons nest in the *R. mangle* and *A. germinans* fringe, the hammock/strand community, and in the *A. germinans* of the central lagoons.

White-crowned Pigeons fly daily to the well-developed tropical hardwood hammocks of the larger keys to feed. We conducted flowering and fruiting phenology surveys at three locations on the mainline Keys, representative of the habitats available to foraging pigeons. Lignumvitae Key (Fig. 2), a state botanical preserve, contains a mature, uncut hammock similar to the hardwood forests of the larger keys prior to human development (Siemon 1985). Hammocks on Plantation Key and northern Key Largo are young second growth forest and represent suburban and forest

edge habitats respectively. These keys lie 5-20 km southeast and east of the breeding keys used in our study and well within the foraging radius of breeding pigeons (pers. obs.).

The Upper Keys are composed of Key Largo limestone which is fossilized pleistocene coral reef (Schomer and Drew 1982). Maximum elevation of the Upper Keys is around 5-6 m. The development of hardwood forests on the mainline Keys varies with the elevation and with the rainfall. Annual rainfall is higher in North Key Largo than it is on Long Key. Species diversity of woody plants is high in these forests. More than 90 woody species have been recorded in North Key Largo and roughly 70% of these produce fleshy fruit (Tomlinson 1980).

METHODS

PHENOLOGY OF FLOWERING AND FRUITING

In December 1986, we began semi-monthly censuses of flowers and fruits on selected trees at Lignumvitae Key. In January 1987, we added census routes on Plantation Key and in northern Key Largo. At least 10 individuals of the major food species were censused (cf. Fournier and Charpentier 1975, Frankie *et al.* 1974), however, some less important species had fewer censused individuals. In August 1987, we added *G. discolor* and some additional individuals of the other species to the Plantation Key and Key Largo surveys. Surveys were conducted at two-week intervals until November 1989 when we switched to monthly surveys. When survey trees were removed by the power company or by individual landowners, we replaced them with trees of similar flowering and fruiting stages.

At each tree, we used binoculars to record the intensity of flowering and fruiting following Wheelwright's (1985) technique (0%, 1%, 2-25%, 26-75%, 76-100% of canopy area bearing flowers or fruit). We used this same scale of intensity to measure the percentage of the canopy that was foliated. The proportion of open flowers and the developmental stage of the most advanced fruit were recorded. At times, the categorizing of fruiting as stage 4 (ripe) for the tree as a whole was based on the observation of only one ripe fruit. This technique is repeatable and provides an unambiguous estimate of phenological state (Wheelwright 1985). This method also allows direct comparisons of the phenological peaks between trees of different sizes and in different habitats.

To provide a measure of fruit availability to frugivores, we calculated a competitive index for each plant species (Wheelwright 1985). The proportion of individuals during each month that had ripe fruit was multiplied by the mean intensity of fruiting to determine the fruiting competitive index. For example, in census 1, 70% of *M. toxiferum* had ripe fruit with a mean intensity of 1.14. The competitive index, the product of these two variables, was therefore 0.80. A value of 2.0 or greater indicates that much ripe fruit was available for consumption, while a value of less than 1.0 indicates that very little ripe fruit was available.

During 1987, we were unclear on what criteria to use to consider a *B. simaruba* fruit ripe. Some fruits develop a reddish "blush" quite early, but this coloration is not indicative of a ripe fruit. The presence of ripe fruit in the June through October period of 1987 is, therefore, erroneous (Fig. 7b). As *B. simaruba* fruits ripen, the endocarp becomes bright red. The fruit coat gradually dries and splits into three sections, exposing the red endocarp. Starting in 1988, we began using the presence of these "exposed" seeds to determine fruit ripeness.

Our assessment of fruit abundance was based on fruit crops observed in 1987, the first year of our phenology studies. Thus, for *M. toxiferum* in particular, a crop considered abundant in 1987 would, in all likelihood, have been rated lower had we begun the study in a year such as 1988. Therefore, the overall competitive indices for *M. toxiferum* reflect somewhat higher ratings in 1987 than they should. We have not attempted to adjust these values.

PIGEON ABUNDANCE

During the first hour after sunrise large flocks of pigeons leave the breeding keys and fly to the larger keys to forage. By counting departing birds from 1/2 h before sunrise to 1 h after, we obtained a relative index of population size. Semi-monthly counts from April to September, when pigeons were most abundant, and monthly counts from October to March, were made from a boat anchored 1/4 mile off the key and between it and the mainline Keys. During the periods of greatest pigeon abundance, one observer was placed on each side of the boat. Cowpens Key, located adjacent to Plantation Key (Fig. 2), is excellent for these counts because it lies close to the larger keys and is regularly used as a roost and for breeding. For comparative purposes we also performed counts at Middle Butternut Key, primarily a breeding key.

Road counts similar to those run for the U.S. Fish and Wildlife Breeding Bird Survey program provided a population index of pigeons foraging in the hardwood hammocks. We used two routes, one running south for 9 miles from Plantation Key and one running north for 11 miles from the intersection of US Highway 1 and Florida State Road 905 on Key Largo (Fig. 2). Counts were made semi-monthly from April to September and monthly from October to March. Stops were made at half-mile intervals and all birds seen or heard in a 3 minute period were recorded. For months in which more than one survey was performed on a route, we averaged the counts and present the results as a monthly estimate.

NESTING DISTRIBUTION

We conducted surveys for White-crowned Pigeons from early July through late August, typically the period of peak nesting activity. Most of the surveys were completed from 1987-1989; a few initial surveys were done in 1986. Surveys were conducted from sunrise to approximately 1300. We followed the methodology outlined in Florida's Breeding Bird Atlas Handbook (Noss *et al.* 1985) to determine nesting status for each area searched. We walked through all suitable habitat when searching small keys; for larger keys, we set a pre-determined search time (generally 30 to 50 min) and covered as much of the key as possible during that period. For each area searched, we recorded the status and number of active nests, number of old nests, and collective search time. In addition to recording White-crowned Pigeon nests, we noted the presence or sign of all potential nest predators.

We determined nest abundance (nest encounter rate) by adding the number of old and new nests found in the area and dividing by the total time spent searching the area. A frequency distribution of nest encounter rates revealed a natural break at 0.08 nests/min. We used this value to distinguish between areas of high (> 0.08 nests/min) and low (≤ 0.08 nests/min) nest abundances.

REPRODUCTIVE SUCCESS

To study nesting and reproductive success, we set up two transects on Middle Butternut Key in 1985. In July 1986, we also started two transects on Bottle Key and attempted to search all of West Butternut Key. The transects surveyed areas of the hammock/strand berm and areas of the

central lagoon. At Middle Butternut Key, we attempted to monitor nests located in the higher *R. mangle* trees growing over the deeper parts of the central lagoon. Some of these nests, however, were inaccessible and not surveyed.

The west transect on Middle Butternut Key was expanded slightly in 1986 when Bowman began on the project. Only nesting success and growth of young were studied on the Middle Butternut Key transects. Some experimental manipulation of nests to examine hatching asynchrony were done on West Butternut and Bottle keys. Experimental nests are excluded from any analyses of nesting success.

Once established, transects were walked three times weekly and all new nests were marked with numbered surveyor's tape. Beginning in 1986, we recorded nest height, species of plant supporting the nest, and whether the nest was over dry ground or water. Nest contents and the presence or absence of the adult was recorded at each nest visit. Eggs were individually marked with a permanent felt-tipped marker. Nestlings were banded with USFWS aluminum bands at 12 days of age. Nestlings usually left the nest by day 16 and we recorded their presence near the nest whenever subsequently observed.

White-crowned Pigeons begin incubation with the laying of the first egg. According to Wiley and Wiley (1979) the incubation period is 14 days and chicks hatch on successive days. We back-dated 14 days from the hatching dates of first eggs to determine the date the first egg was laid for nests found after laying was completed. When nests failed during incubation we determined the laying date by assuming the second egg was laid 1 day before the nest was first located. When nestlings were found in new nests, we estimated their age from growth data of known-age nestlings, then back-dated from the estimated hatch date.

We determined the fate of each egg laid. We considered eggs or young that were cold and wet, moribund, or dead to have been abandoned. Disappearance of all eggs or healthy young from a nest was recorded as predation. We considered loss of single eggs or apparently healthy young from nests with other eggs or young remaining as having been depredated. Single eggs rolled out of the nest by departing adults were invariably found beneath the nest. If the bird flushed as a result of researcher activity and the egg was deemed viable, we placed it back into the nest. Loss of individual young was recorded as starvation if it was found dead in the nest or had not been growing normally prior to its loss. Unless the exact date was known, mortality was assumed to have occurred at the mid-date between the last visit and the date the final fate was determined.

We calculated reproductive success by the Mayfield Method. This method (Mayfield 1961, 1975; Hensler and Nichols 1981; Hensler 1985) prorates survival of known, repeatedly visited nests for the entire reproductive cycle. The Mayfield Method, however, assumes that nests fail at a constant rate throughout the nesting period. Murton (1958) found that mortality of nestling Wood Pigeons (*Columba palumbus*) was much lower than that of eggs and Harris *et al.* (1963) reported similar results for Mourning Doves (*Zenaida macroura*). In 1986, we found mortality rates of White-crowned Pigeon eggs to be higher than that of nestlings on two keys, but obtained the opposite result on the third key (Bancroft and Bowman 1987). Separate estimates can be made for periods within the cycle that differ, regardless of how they differ (Hensler 1985), hence, we calculated estimates of survivorship during the incubation and nestling period separately. Overall success estimates were derived by combining the separate incubation and nestling period estimates (Hensler 1985). Refinements to Mayfield's method (Hensler and Nichols 1981; Hensler 1985) allow rigorous statistical comparisons. Tests of significance between two groups were performed using the standard normal test. A z-value greater than 1.65 is significant at the 0.05 level (Steel and Torrie 1960). Simultaneous comparisons between more than two groups were accomplished using the Bonferroni Multiple Comparisons Test (Neter and Wasserman 1974). All notations and formulae used to calculate Mayfield success estimates are found in Appendix 1. The Mayfield calculations are presented in Appendices 2-4.

EGG SIZE

Egg length and width were measured to the nearest 0.1 mm with dial or vernier calipers. Individual eggs found within 24 h of laying were marked as to sequence and weighed to the nearest 0.1 g with a 50 g Pesola scale. We returned to sequence and weigh the second egg within 24 h whenever possible. We determined laying sequence for some eggs by assuming the first egg pipped or hatched was the first egg laid.

GROWTH

Nestlings were weighed to the nearest 0.1 or 1.0 g depending on whether a 50 or 300 g Pesola scale was used. Six morphological variables were measured to the nearest 0.1 mm: culmen, manus, tarsus, seventh primary, and central rectrix lengths and gape width. We noted whether nestlings crops were full, partially full, or empty.

To describe the general growth patterns of young, we calculated mean size of known-age young. To examine yearly, seasonal, and hatching order effects on growth, we calculated day 8 weight. We used linear regression analysis to estimate weight at day 8 for young that were measured on at least 5 days in the nestling period. To be included, at least one measurement had to be taken before the young was 4 days old and at least one when it was 10 days old or older. This provided a sample of 298 young.

FOOD HABITS

We investigated White-crowned Pigeon food habits through crop samples non-destructively collected from squabs. Crop samples were taken on West Butternut and Bottle keys only. Crop samples were obtained by gently massaging the crop and throat of the squab. To minimize the influence on nestling survival, individual squabs were sampled only once. In 1986, survival of nestlings on West Butternut and Bottle keys was higher than that on Middle Butternut Key (Bancroft and Bowman 1987), suggesting that our crop sampling did not negatively influence survival. We detected no fruit when massaging the expanded crops of young less than 3 days old and, therefore, did not collect any samples from nestlings less than 3 days old.

Crop samples were frozen and later sorted by food species, individual items were counted and weighed, and relative volume determined by displacement. Individual food items were then dried over concentrated sulfuric acid under a vacuum at room temperature. Dry weight was recorded and water content calculated by subtraction. Samples were stored for later nutritional analyses.

We examined the crops and digestive tracts of all dead White-crowned Pigeons found or delivered to us in Florida for fruits or seeds. In addition, we collected feces from nesting areas in Florida Bay. Mary Carrington (pers. comm.) identified all fruits and seeds from these samples.

NUTRITIONAL AND ENERGETIC VALUE OF FRUIT

Samples of ripe fruit were collected from trees throughout the year. Whole fruits were weighed, dried for 48 h in a vacuum desiccator over concentrated sulfuric acid, and reweighed. Water content was calculated by subtraction. For most species, pulp was separated from seeds and both weighed, dried, and reweighed. For the five most common fruits in the White-crowned Pigeon

diet, we measured fruit length, width, and weight. Whole fruits were separated into pulp and seeds and the number of seeds per fruit recorded. Both pulp and seeds were dried then the pulp/seed ratio calculated from dried weights. Individual fruit volumes were calculated from crop sample data by dividing the volume of each species in a crop by the number of individual fruit in the sample.

Each dried sample was homogenized in a Wiley mill. Protein was extracted in 5 ml 1N NaOH and assayed colorimetrically using the technique described by Bradford (1972) as modified by Appenroth and Augsten (1987). Total lipid was measured gravimetrically by the hot chloroform-methanol method (Freeman *et al.* 1957). Soluble carbohydrates, including starch, were extracted in hot trichloroacetic acid and measured colorimetrically using the method described by Dubois *et al.* (1956). Insoluble carbohydrates were calculated by subtraction. Ash content was measured gravimetrically after incineration in a muffle furnace at 500° C for 4 h (Paine 1971). Total energy was calculated by multiplying the protein, lipid, and soluble carbohydrate content (g) by the following energetic constants: 23.9 Kj/g protein, 39.8 Kj/g lipid, and 17.2 Kj/g soluble carbohydrates (Lawrence and Schreiber 1974). TCA-insoluble carbohydrates are presumably comprised largely of indigestible compounds such as cellulose and lignin (Foster 1977) and were excluded from the total energy content.

We compared nutritional content between fruit species by one-way ANOVA and compared individual differences using the Fisher LSD analysis. A two-way ANOVA was used to compare temporal differences in nutritional content. Results of this analysis suggested that inter-year variation was not significant so data from 1988 and 1989 were pooled to examine seasonal variations. Differences in the nutritional and energetic content of pulp and seed for individual fruit species were analyzed using the Mann-Whitney U Test.

RESULTS

PHENOLOGY OF FLOWERING AND FRUITING

We surveyed 165 individually-marked trees of ten species from December 1986 through December 1989. We have pooled the data from our three sites to present a more uniform assessment of phenologies for the three years. Both *M. toxiferum* and *Bursera simaruba* are dioecious. We have not separated out the male trees in our analyses and, therefore, the percent of

trees with fruit, as well as the competitive index, are uniformly suppressed for these two species. Individual male trees of both species occasionally produce a few fruits, however, they do not persist through maturation (pers. obs.).

Breeding Season Fruits

Guapira discolor -- In August 1987, we added 10 trees to the North Key Largo survey and 15 trees to the suburban survey which effectively tripled our sample size from the original 10 on Lignumvitae Key. The phenologies of *G. discolor* showed a distinct seasonal pattern. Flowering began in May and continued into October (Fig. 3a). In 1988, flowering continued into November. Peak flowering occurred in June. In 1987, the peak included all survey trees, but in 1988 and 1989, the peak included slightly less than 100% of all trees. In 1989, flowering continued to drop off after the June peak except for a short plateau in September and October.

Ripe fruit was available for 5 months in 1987 and for 8 and 7 months, respectively, in 1988 and 1989 (Fig. 3b). In 1987, fruit production peaked in September when 80% of the survey trees contained ripe fruit. In 1988, although the fruiting season was longer by 3 months, the percent of trees with ripe fruit never exceeded 43%. In 1989, the percent of trees with ripe fruit peaked at 61% in July, however, the percentage with ripe fruit usually centered around 40%.

The competitive indices were approximately twice as high in 1987 as in 1988, but of shorter duration (Fig. 3c). The 1989 competitive index peaked in July before gradually decreasing through the fall.

Metopium toxiferum -- Flowering in *M. toxiferum* was highly seasonal. It began in February and peaked in April and May (Fig. 4a). Flowering declined rapidly in June and, only in 1988, did it extend into July. In 1989, flowering peaked in April and declined rapidly thereafter. This deviation from 1987 and 1988 flowering patterns probably was a result of the drought in south Florida in 1989.

M. toxiferum began setting new fruit in March and April (Fig. 4b). By June, ripe fruit began to appear and by July nearly all trees had some ripe fruit. *M. toxiferum* ripened fruit over a long period of time and, hence, ripe fruit was present nearly every month of the three-year survey period. The highest percentage of trees with fruit occurred in June each year. By July, a portion of these

trees (maximum: 10% in 1988) had aborted their fruit before ripening. Several of our trees were males and set no fruit or small numbers of ephemeral fruit. The percent of trees with ripe fruit did not exceed 80% because of these trees. The percentage of trees with ripe fruit remained between 60% and 70% through January of each year and then declined rapidly. Several trees each year did not lose their last ripe fruits until well into the flowering period. New fruit was already developing shortly after the last of the previous year's fruit was dropped.

The competitive index showed a rapid increase in June of each year with a gradual decrease to the nadir in May (Fig. 4c). The rate of decrease of the competitive indices was faster in both 1988 and 1989 than in 1987. Although the peak competitive index was sustained from July through September in 1987 and 1988, it declined rapidly in 1989 after a peak in July.

Ficus aurea -- The flowers of *Ficus* spp. are produced inside of a bud which later develops into a fruit (Tomlinson 1980). We, therefore, only present the fruiting phenology and competitive indices for these species. *Ficus* trees are distinctly asynchronous in their fruiting patterns between individual trees (Tomlinson 1980). Therefore, there was nearly always some ripe fruit present during all months of the year (Fig. 5a). Only in December 1986 was no fruit present. In that month, however, our sample consisted of only two trees. Within any year, however, there were distinct periods when fruit abundance increased in *F. aurea*. In 1987 and 1988, fruit abundance peaked during June, July, and August, while in 1989, ripe fruit abundance peaked in May and June and again in August and September. Late in each year a secondary peak occurred in November or December. The December 1987 peak included the largest percentage of trees with ripe fruit of any survey (95.0%).

The competitive indices for *F. aurea* peaked during the summer for all three years, however, the peaks were all of different duration. In 1987, the competitive index peaked during June, July and August, while in 1988, only June showed a competitive index above 2. The competitive index showed a bimodal peak in 1989, one in May-June and a second in August. The late fall values were much higher in 1987 than 1988, while the competitive indices dropped sharply in 1989.

Ficus citrifolia -- Fruit production in *F. citrifolia* usually peaked in June and/or July (Fig. 6a). In 1987, a secondary peak occurred during the September through November period. The

September peak included a higher percentage of trees with ripe fruit than any other survey during the entire 3-year period. In 1988 and 1989, the percentage of trees with ripe fruit never exceeded the peak values of 1987. The percentages of ripe fruit for both 1988 and 1989 were considerably less than the percentages in 1987 for nearly every month. Individual trees of *F. citrifolia* produce crops of ripe fruit less consistently than *F. aurea* (unpubl. data) and this may be the reason for the overall lower percentage of trees with ripe fruit on each survey.

The competitive indices for *F. citrifolia* only exceeded 1.5 in June-July of 1987 (Fig. 6b). The peak competitive indices of 1988 and 1989 did not exceed even the second peak of the September through November period in 1987. The lowest competitive index for both *Ficus* spp., 0.08, occurred in February of 1989. Overall, the peak competitive indices for *F. citrifolia* were always less than those for *F. aurea*.

Non-Breeding Season Fruits

Bursera simaruba -- *B. simaruba* is dioecious and flowering of female trees is highly seasonal (Fig. 7a). The primary flowering period usually began in April and continued into June. Sporadic flowering occurred during all months of the year, but normally only involved male trees. Peak flowering occurred in May of 1987 and 1988 and in both April and May of 1989 and included 100% of the survey trees in each year. A secondary peak also occurred in each year but timing varied between years. In 1987, a second peak occurred in September, while in 1988, it occurred in August and in 1989 in October. These flowering bouts and the low level of flowering during the winter of 1988-1989, only involved male trees (pers. obs.). Most often, these flowering bouts only involved one or two individual trees.

For these analyses, we have not separated the male and female trees. The percent of trees with ripe fruit, as well as the competitive index for this species is, therefore, somewhat suppressed. The percent of trees with ripe fruit never exceeds 62% for this reason. Some male trees set a few fruit, but they were always aborted long before ripening (pers. obs.). The first ripe fruits began appearing in November of each year. *B. simaruba* had an extended fruiting period with ripe fruits appearing asynchronously from November through April. Usually the last of the previous year's fruits abort just prior to new flower set. In the weeks preceding flower set, the entire canopy is usually lost making the remaining fruit quite visible to birds and mammals.

The competitive indices for this species never exceeded 1.5, partially the result of including male trees in the analyses (Fig. 7c). The November peak in 1987 is the result of calling fruit ripe too early in its cycle (see **METHODS**). The competitive indices peaked in March of 1987 and 1988, and in December of 1988. Although the percent of trees with ripe fruit increased during the December through March period, the competitive indices gradually decreased. This indicates that the abundance of fruit present on individual trees was continuously decreasing during an earlier time period in 1989 than in either 1987 or 1988.

Thrinax radiata -- Flowering in *T. radiata* was seasonal, however, this species reflowered when fruit set did not occur or was very poor (Fig. 8a). In 1987, flowering peaked in June and July, but fruit set was poor and a second flowering occurred in September. These flowering periods only involved 30% and 50% of the survey trees, respectively. In 1988, flowering peaked in June and included 100% of all survey trees. Fruit set was also very synchronous and a large crop was set. No second flowering occurred in this year. Flowering in 1989 peaked in August but, as in 1987, fruit set was poor and a second flowering occurred in November. Both flowerings involved less than 55% of the survey trees.

Fruit set occurred during and shortly after the brief flowering period (Fig. 8b). Green fruit persisted for approximately three months before the first ripe fruits appeared. Ripening proceeded rapidly thereafter, and ripe fruits persisted on individual trees for up to eight months. Ripe fruit was present from December 1986 (the beginning of the study) through May of 1987, October of 1987 through May of 1988, and September 1988 through April of 1989. In the fall of 1989, only small numbers of ripe fruit were produced and the fruit did not persist past December. The percent of trees with ripe fruit was only 40% and 54% in 1986-87 and 1987-88, respectively. In 1988-89, however, 100% of survey trees produced abundant fruit crops. In the fall of 1989, no more than 32% of the survey trees produced ripe fruit.

The competitive indices exceeded 1.5 only in October 1988 (Fig. 8c). The competitive indices rose each year from 1986-1988, but declined to 0.39 in the fall of 1989.

Bourreria ovata -- *B. ovata* had an extended flowering period (Fig. 9a). There was considerable variation during the three-year survey period. Flowering occurred from May 1987

through April 1988. No flowering was recorded in May 1988 but 75% of survey trees flowered again in June. Flowering continued until December 1988. No flowering was observed during the first three months of 1989, but it increased rapidly from April through June and peaked during the period July through September. Flowers were present through the end of the year. In 1989, although flowering peaked during the summer months, the average flowering intensity was not as high as the previous two years (unpubl. data).

Fruiting in *B. ovata* also occurred over several months duration (Fig. 9b). In 1987 through 1989, ripe fruit was present over a 9-month period with peak fruit production occurring from November through March. In 1988 through 1989, ripe fruit was present over 8 months but peak fruiting only occurred in October and November. Fruit production in 1989 was more sporadic with ripe fruit never present on more than 90% of the survey trees, whereas ripe fruit was often present on 100% of the survey trees in 1987 and 1988. The peak of 88.9% only occurred during October.

The competitive indices for *B. ovata* are shown in Figure 9c. In 1987 through 1988, the competitive index peaked at 2.0 from November through January. The peak during the 1988 through 1989 season was also 2.0 but only occurred in October. The peak in the fall of 1989 occurred in October also, but was less than first two years and dropped more rapidly than the previous years.

Mastichodendron foetidissimum -- Although this species occurs in many hammocks throughout the Upper Keys, it is rare in both our suburban and roadside North Key Largo sites. Therefore, we only surveyed *M. foetidissimum* on Lignumvitae Key. *M. foetidissimum* is distinctly seasonal in flowering (Fig. 10a), but flowering periods varied from year to year. The flowering period in 1987 was the longest of the 3-year survey period. Flowers were present from June through November. Peak flowering occurred from July through October. Peak flowering also occurred during June-July of 1988 and July-September of 1989. A second flowering during November and December was also observed but involved only about 70% of the trees.

M. foetidissimum fruit had a long ripening period. In 1987-1988, green fruit was present for 5 months before the first ripe fruit began to appear in the sixth month. In that year, ripe fruit was present for 7 months, from December through the following June. Ripe fruit was present for at least 6 months during 1986-1987. Since the 1987-1988 season, virtually no ripe fruit has been produced

on any of our survey trees. The ripe fruit indicated in March of 1989 involved only one fruit on one tree. Although fruit was set, it was aborted long before ripening.

The competitive index peaked at 1.0 in March of 1987 and only 0.73 in February 1988 indicating that not much ripe fruit was present at any given time (Fig. 10c). There was nearly complete failure to produce any ripe fruit in 1989.

Solanum erianthum -- Individuals of *S. erianthum* flowered irregularly throughout the year (Fig. 11a), however, there were nearly always some flowers present during any given month in this species. Fruiting was also irregular in this species (Fig. 11b). Although our sample size was small, peak fruiting occurred in mid-winter and early summer of 1987, early fall in 1988, and February and August of 1989, suggesting no regular fruiting season. The competitive indices also showed much fluctuation (Fig. 11c) reflecting the irregular fruiting patterns. In August of 1987, we lost all our survey trees to roadside pruning and they were not replaced until May 1988.

Nectandra coriacea -- We only surveyed *N. coriacea* in North Key Largo. Our original sample of 3 trees were cut down by road crews in July of 1987. They were replaced with 5 trees in May of 1988. Flowering of *N. coriacea* peaked in April and May in 1987, June of 1988 and May of 1989 (Fig. 12a). Only in 1988 did flowering occur on 100% of all survey trees. In 1987, 100% of the survey trees had ripe fruit in January and February (Fig. 12b). In 1988, although all survey trees had unripe fruit for three months, no more than 60% of the trees held fruit through ripening. Ripe fruit was present for a four-month period. During the drought year of 1989, very little fruit was produced and most of that fruit was aborted before ripening. One tree produced a small amount of ripe fruit in July of that year.

The competitive indices varied considerably between years (Fig. 12c). The highest competitive index, 1.62, occurred at the beginning of the surveys in 1987 and indicated the presence of abundant ripe fruit at the start of that year. The competitive index peaked at only 0.80 in October of 1988 and never exceeded 0.40 in 1989. Fruit production was minimal in both of these years.

PIGEON ABUNDANCE

We conducted boat counts of White-crowned Pigeons flying from Cowpens Key to the mainline Keys and from Middle Butternut Key to the mainline Keys from May 1986 through December 1989. We conducted road counts from Tavernier through Islamorada and in North Key Largo from July 1986 through December 1989. Cowpens Key lies only a short distance off Plantation Key and many birds, in addition to those that nest there, roost there at night. Middle Butternut Key is a major nesting key and birds on this count are presumably breeding or courting. The Islamorada road count runs through suburban neighborhoods where numerous isolated fragments of forest still remain. The North Key Largo count runs through an area that has extensive second growth tropical forest. Only a small amount of the area along the North Key Largo route has been developed.

To illustrate the seasonal occurrence of White-crowned Pigeons in the Florida Keys, we summed the monthly estimates from each of the four counts (Fig. 13). Cowpens is relatively close to the northern end of the Islamorada road count and it is possible that a few birds counted at Cowpens could also have been counted on the Islamorada count but we do not think the number is great.

Pigeon numbers in the keys increased in April and reached an initial breeding season peak in early June (Fig. 13). This peak was caused by large numbers of pigeons roosting at Cowpens Key. These pigeons presumably dispersed to nesting keys by July. A second and generally larger peak was reached in September. At this time large numbers of juvenile birds were often seen. In 1989, the late summer peak came in August rather than September. In 1989, nesting was not very successful and large numbers of juveniles were not present in the Upper Keys. The largest counts came in September 1988 immediately following an extremely successful nesting year. During this month, we counted almost 2,000 pigeons on the four surveys. Between September and October of each year, most pigeons left the Upper Keys. A small population wintered in the keys each year.

Numbers of White-crowned Pigeons on the Islamorada survey varied from none in 3 months to 69 in one month (Fig. 14). Annual peak counts occurred in August 1989, September 1986 and 1988, and October 1987. Immediately after the annual peak the number counted decreased to wintering levels. Wintering numbers (November-March) averaged 11 pigeons per survey, which was significantly fewer than the 35 pigeons averaged during the summer surveys (May-September; K-W

$\chi^2 = 16.1$, $P < 0.0001$). During the winter, average numbers varied significantly between years (K-W $\chi^2 = 8.36$, $P < 0.039$). Mean numbers in winter ranged from 4 in 1987-88, 7 in 1986-87, 12 in 1988-89, to 23 in 1989-90. During the summer, average numbers did not vary significantly between years (K-W $\chi^2 = 99.0$, $P = 0.8027$). May through September numbers averaged 35 birds and varied from 41 per survey in 1988 to 31 per survey in 1986 and 1989.

Numbers of White-crowned Pigeons on the North Key Largo survey varied from 2 to 700 birds (Fig. 15). More than 100 pigeons were counted during 4 surveys. Major peaks occurred in September 1986 and 1988, February 1989. More than 200 pigeons were still present in October 1988. No peaks were evident in early fall of 1987 or 1989. Mean number of pigeons per survey in North Key Largo did not vary significantly between summer and winter (K-W $\chi^2 = 1.42$, $P = 0.2337$). Number of pigeons per survey averaged 84 birds in summer and 32 in winter. During both winter (K-W $\chi^2 = 7.09$, $P = 0.0691$) and summer (K-W $\chi^2 = 4.65$, $P = 0.1991$), mean numbers did not vary significantly between years. Numbers of White-crowned Pigeons on the Cowpens boat count showed a bimodal peak during each year (Fig. 16). The first peak occurred during June of each year and the second peak in September except in 1989 when it occurred in August. Numbers of pigeons decreased during the intervening months. Mean number of pigeons per count for the five summer months (May - September) averaged 385 birds for the four years. During summer, the mean number between years did not vary significantly (K-W $\chi^2 = 2.99$, $P = 0.39$). Relatively few birds used Cowpens as a roost during the winter months. Only 6 of 17 surveys recorded any pigeons during the 5 winter months (November - March). As a result, significantly more pigeons used Cowpens during the summer than the winter (K-W $\chi^2 = 27.38$, $P < 0.0001$).

Numbers of White-crowned Pigeons on the Middle Butternut Key boat count varied from no pigeons during all the winter surveys to more than 200 pigeons during two counts (Fig. 17). Peak annual counts varied by a factor of 4 from 59 in August 1987 to 235 in September 1988. In 1989, the annual peak occurred in June when 120 pigeons were counted. Numbers in August 1989 were lower than the June count. Mean number of pigeons on summer counts (K-W $\chi^2 = 6.70$, $P = 0.08$) did not vary significantly between years. The mean number ranged from 33 in 1987, to 69 in 1989, to 107 in 1986, to 120 in 1988 and showed considerable variance within years.

Site Variation

During the summer, significantly more pigeons were counted on Cowpens boat counts than on Middle Butternut Key counts (Paired T -test = 5.08, df = 19, P < 0.001). Similarly, significantly more pigeons were counted at Cowpens in the winter than at Middle Butternut Key (Paired T -test = 2.39, df = 16, P = 0.030).

The number of pigeons per survey during the summer did not vary significantly between Islamorada and North Key Largo road counts (Paired T -test = 1.27, df = 17, P = 0.220) but significantly more pigeons wintered on the North Key Largo route than on the Islamorada route (Paired T -test = 3.04, df = 15, P = 0.008).

NESTING DISTRIBUTION

White-crowned Pigeon Nesting Distribution

We searched 169 keys in Florida Bay, Card Sound and Barnes Sound. A total of 384 nests were found in 204.1 h of survey work (Appendix 5). Number of nests found per key ranged from one on many keys to 22 on West Key. We found no nests on the mainland or in Whitewater Bay in 23.7 h of censuses. One nest was observed in 1990 in a development at the north end of Key Largo. No additional nests were found in 11.0 h of surveys on the mainline Keys from northern Key Largo north to Elliott Key. Development in this area is sparse and a significant percentage of land is within Biscayne National Park, Crocodile Lake National Wildlife Refuge or Key Largo Hammocks State Botanical Site. Extensive field work conducted by National Audubon Society personnel, including breeding bird surveys, in the tropical hardwood forests from north Key Largo to Long Key has not detected any additional nesting activity.

White-crowned Pigeon nests were found on 88 of the 169 keys surveyed (52%). Keys with nesting pigeons were widely distributed across Florida Bay (Fig. 18). Over an east-west gradient, White-crowned Pigeon nesting keys spanned the entire bay with the exception of two keys in the extreme western bay. Except for nesting in three disjunct areas, the main nesting distribution in the central bay was much farther from the mainland than in either the extreme eastern or western portions. In general, keys closest to the mainland did not support nesting pigeons, whereas keys closest to the mainline Keys often did.

Nest abundances ranged from 0.01 to 0.71 nests/min. Although keys with similar nest abundances indicate similar nest encounter rates, differences in sizes of keys do not allow a direct comparison of absolute population sizes. The area of highest nest abundance was located in the central portion of the bay with the distribution constricted away from both the mainland and the mainline Keys. Although several outlying keys did support high nest abundances, the extremities of the range usually had decreased nest abundances.

Two keys on the Florida Straits side of the mainline Keys had low densities of nesting White-crowned Pigeons (Fig. 18). Also two keys in Card Sound supported nesting White-crowned Pigeons (Fig. 19). The nesting location in Barnes Sound was the closest (0.3 km) to the mainland that we encountered. White-crowned Pigeons were nesting in isolated clumps of red mangroves on a spoil bank adjacent to Card Sound Road, separated from the mainland by a canal.

Distribution of Nest Predators

Both avian and mammalian nest predators were recorded during our surveys. Potential avian nest predators were Red-winged Blackbirds (*Agelaius phoeniceus*), Laughing Gulls (*Larus atricilla*), and American Crows (*Corvus brachyrhynchos*). Red-winged Blackbirds were abundant throughout Florida Bay where they occurred on 100 of 169 keys surveyed. Laughing Gulls were also common and could be seen from the periphery of most keys. However, we found only three small nesting colonies during our surveys. We recorded American Crows on three keys in Florida Bay. They are common on the mainland, but are rarely observed on the mainline Keys.

We recorded the presence of four potential mammalian predators during the nesting surveys. Few were seen; most were identified by tracks or scat. The opossum (*Didelphis virginiana*) and bobcat (*Lynx rufus*), were found only on the mainland, the mainline Keys and one key each within Florida Bay. We recorded rats (*Rattus rattus*, and *Rattus* sp.) on eight keys, widely dispersed throughout Florida Bay. Several keys harboring rats were not directly connected to the mainland or the mainline Keys by banks.

Raccoons (*Procyon lotor*) were present and often common on the mainland and mainline Keys (Appendix 5). We found evidence of raccoons on 33 keys (Figs. 18 and 19). The most widespread populations occurred in the north central and northwestern portions of the bay. In the northwestern bay, raccoons were found on seven keys. These keys, although widely separated, are connected by extensive mudflats and seagrass beds (primarily *Thalassia testudinum*, Fig. 1) that are

exposed at low tides. In the north central bay, raccoons were located on 21 keys. All keys in this area are connected to each other and the mainland by banks (Fig. 1). In Figure 18, we depict the distribution as being continuous throughout this area. However, evidence of raccoon presence was found on only 21 of 32 (including the southernmost) keys within this chain. We feel raccoons must at least use the remaining keys in this range as travel lanes and are present on all of them for some portion of the year. Two keys adjacent to the mainline Keys have raccoon populations (Fig. 18).

Degree of Overlap Between Potential Nest Predators and Nesting Locations

Red-winged Blackbirds had the highest proportion of overlap with nesting White-crowned Pigeons. They occurred on 59 of 88 (67%) keys with nesting pigeons. This occurrence rate was actually higher than we found on non-nesting keys ($G = 4.43$, $P < 0.05$).

The three keys on which we recorded nesting Laughing Gulls all had nesting White-crowned Pigeons. We were mobbed by Laughing Gulls on an additional seven keys, all of which supported nesting White-crowned Pigeons. Two of the three keys on which we recorded American Crows had nesting White-crowned Pigeons. All three of the keys with crows also had wading bird or Brown Pelican (*Pelecanus occidentalis*) and Double-crested Cormorant (*Phalacrocorax auritus*) colonies.

Of the eight keys that supported rats, five had nesting White-crowned Pigeons. Three of these keys had high pigeon nest abundances. Neither of the keys on which opossums or bobcats occurred had nesting pigeons. Of the 33 keys that supported raccoons, only six (18%) had nesting White-crowned Pigeons. The proportion is similar (9 of 44 keys, 20%) if the entire chain of keys in the central bay is considered to be occupied by raccoons. All of the keys that supported both raccoons and pigeons had low nest abundances (range = 0.01 to 0.08 nests/min).

The proportion of nesting keys with raccoons is significantly different than the proportion of non-nesting keys with raccoons ($G = 19.97$, $P < 0.005$). The maximum number of nests found on keys containing raccoons was seven. Three keys had four to seven nests; however, these were small keys and the total number of nests found probably represents most of the nesting population.

CHRONOLOGY OF BREEDING

We followed nesting chronology of White-crowned Pigeons on three keys in eastern Florida Bay. Complete nesting cycles were followed during five years on Middle Butternut Key (1985-1989),

three years on Bottle Key (1987-1989) and two years on West Butternut Key (1987-1988). Transects were started on Bottle Key and West Butternut Key half way through the 1986 season and those data are not included in the chronology analyses.

We followed a total of 987 nests during these study years. New clutches were laid from the second week of May through the second week of September (Fig. 20). A small peak in the number of new clutch starts occurred during late May and early June before rising to the large peak during the last week of July. July had more nest starts than any other month (45.1%). August was second (30.2%) and June was third (16.7%). Relatively few nests were started in May (7.1%) or September (1.0%).

Overall, the total number of active nests (nests with eggs or young less than 17 days old) increased throughout the nesting season to a peak in late July and August (Fig. 20). More than 350 nests were active during the fourth week of July and the first three weeks of August. Only about 140 nests were active during the plateau of activity in June. From the peak in August the number of active nests decreased rapidly during late August and September. The latest nest fledged young during the first week of October.

Middle Butternut Key

At Middle Butternut Key, we monitored 430 nests from 1985-1989. White-crowned Pigeons had active nests from early May into late September (Fig. 21). New clutches were started over a 120 day span (Table 1). The earliest clutch was started on 12 May (1989). The latest clutch could have been started as late as 8 September. This clutch was found on 9 September with two eggs. It failed on 19 September so, to estimate laying date, we back-dated from the date it was found. A clutch started on 2 September was the latest clutch that was successful.

The number of new clutches per week showed a bimodal pattern (Fig. 21). One peak occurred in early to mid June and a second larger peak occurred in late July and early August. A distinct decrease in the number of new clutches occurred during late June. The first peak of nesting occurred from the fourth week of May through the third week of June when 104 new clutches were started, 24.2% of the total. The second peak of nest starts occurred from mid-July through mid-August when 182 new nests were started. This represented 42.3% of all starts. Of the 430 clutches, 8.4% were laid in May, 22.8% in June, 39.1% in July, 29.1% in August, and 0.7% in August.

Total active nests (nests with eggs or young) increased from early May to a small peak during the third week of June when 91 nests were active (Fig. 21). A small dip in activity occurred during late June and early July before rising to the major peak of activity during the second week of August when 160 nests were active. The number of active nests decreased rapidly from the third week of August through September as many nests fledged young and the number of new starts decreased.

Yearly Variation. We monitored 59 clutches in 1985, 73 in 1986, 87 in 1987, 121 in 1988, and 90 in 1989 (Table 1). Search effort and area covered increased some in 1986 when Bowman began working on the project. Search effort was similar between 1986 through 1989, so the differences in number of nests found reflects differences in the nesting activity of pigeons. Clearly, many more pigeon nests were started in the same area during 1988 than during the other years of the study.

The onset of nesting varied between the years from 12 May in 1989 to 23 May in 1986 (Table 1). The date the last clutch was laid varied from 21 August in 1989 to 8 September in 1988. The range of laying dates in a given year varied from 101 days in 1986 to 111 days in 1988. The mean date of nest initiation varied from 4 July to 22 July (Table 1).

Clutches started before 9 July generally fledged young before much ripe *M. toxiferum* became available to feed those young. We divided nesting activity into two periods (before 9 July and after 8 July) to look at differences in nesting activity between years relative to the availability of *M. toxiferum* (Table 2). The number of clutches started on Middle Butternut Key before 9 July varied relatively little between years from 24 in 1989 to 38 in 1988. The number started after 8 July, however, varied substantially. In 1985, only 29 were started, whereas 83 were started in 1988. The relative proportion of clutches started during each period varied significantly between years ($G = 15.3$, $df = 4$, $P < 0.005$).

The proportion of total yearly initiations occurring in the second half of the season increased substantially in 1988 and 1989. In 1988, a large increase occurred during the second half of the year, apparently related to the increased availability of *M. toxiferum*. In 1989, fewer clutches than average were initiated during the first half of the season when availability of *Ficus* and *G. discolor* fruit appeared lower than in previous years.

In 1985, White-crowned Pigeons showed two distinctive peaks in the initiation of new clutches (Fig. 22). The first peak occurred during the first three weeks of June when 26 clutches (44.1%) were laid. No clutches were started during the fourth week of June or the first week of July. The second major peak occurred during the fourth week of July when 17 clutches (28.8%) were started. Slightly more than half (50.8%) were laid before 8 July. Total number of active nests showed a distinctive bimodal pattern. The largest peak occurring during the third week of June when 27 nests were active. The number of active nests dropped steadily to the third week of July when only 7 nests were active before rising to a second peak during the first week of August when 22 nests were active. The number of active nests decreased from this peak through the second week of September. No nests contained eggs or young less than 17 days old during the second half of September.

In 1986, clutch initiation showed considerable variation between weeks (Fig. 23). A small peak occurred in June and a larger peak occurred during the first half of August. A definite lull in initiations occurred during the second week of July when only one clutch was started. Slightly less than half the clutches (49.3%) were laid before 9 July. The total number of active nests increased to 20 during the second half of June, decreased slightly in July before increasing to a second peak during the third week of August when 29 nests were active. The number of active nests decreased rapidly from the peak through the third week of September.

In 1987, two distinctive waves of nesting by White-crowned Pigeons occurred (Fig. 24). The first major wave occurred during the first three weeks of June when 22 clutches were laid. A lull in starts occurred from the latter part of June through mid July. The second major wave occurred from 15 July through the third week of August when 51 clutches were started. By 8 July only 35.6% of the clutches had been laid. Total number of active nests per week increased to a plateau of 18 nests during late June and early July before increasing to the peak during the first three weeks of August when 35 nests were active. The number of active nests decreased rapidly during late August and September. The last nest fledged during the third week of September.

In 1988, the distribution of nest initiations suggests three waves of nesting (Fig. 25). The first wave occurred during May and the first week of June, the second extended from the fourth week of June through July, and the third wave included the last 3 weeks of August. Sixteen clutches were laid during the first wave, 52 in the second, and 54 in the third. Total number of

clutches started by 8 July was similar to previous years with 38 starts. Total number of active nests increased from mid-May to a plateau during June of 18-19 active nests before increasing through July to a major peak during August when more than 50 nests were active. Activity was still high during the first half of September when more than 30 nests remained active. In none of the previous three years were more than 11 nests active in a week during September. The last nest fledged young during the last week of September.

In 1989, White-crowned Pigeon nest starts showed two disjunct waves (Fig. 26). The first occurred from early May through the second week of June when 17 clutches were completed. The second wave occurred from first week of July through the third week of August when 73 clutches were laid. No clutches were started during the second half of June. By 8 July, only 24 (26.7%) clutches had been laid. Total number of active nests showed a bimodal pattern. The first and smaller peak occurred during late May and early June when 12 nests were active. Activity decreased to late June when only two nests were active. The second peak occurred in early August when 37 nests were active. The number of active nests decreased through the remainder of August. Only six nests were active during September. The last nest fledged young during the second week of September.

Bottle Key

At Bottle Key, White-crowned Pigeons laid new clutches from 15 May (1989) through 14 September (1988) (Table 1). The 14 September clutch was not successful. It was found with two eggs on 15 September. By 21 September, this clutch had been abandoned. The latest clutch that produced young was laid on 7 September. The laying season extended over a 122-day period.

We followed a total of 473 clutches during three nesting seasons on Bottle Key (1987-1989). The number clutches started per week increased to a small peak in late May before decreasing during June (Fig. 27). From the low in June, the number of clutches initiated per week increased to a peak during the fourth week of July when 81 (17.1%) clutches were started. About half of the peak number were started during each of the first three weeks of August.

The number of active nests per week paralleled the number of new clutches (Fig. 27). They increased to a plateau during June of less than 50 active nests before rising to the overall peak of 200 active nests during the fourth week of July. The number of active nests decreased rapidly from mid-August to the end of September.

Yearly Variation. At Bottle Key, we studied nesting chronology during 1987, 1988, and 1989. We followed 112 clutches in 1987, 209 in 1988, and 152 in 1989. Part of the increase in 1988 is a result of increasing the lengths of the transects. However, some of the increase does reflect an extremely good nesting year. Our search effort in 1989 was similar to 1988 and we found only three-quarters the number of nests.

In 1987, two distinctive peaks in the number of nest initiations occurred (Fig. 28). The first nesting wave occurred from the fourth week of May through the end of June when 22 clutches were started. The second and major nesting effort began in the second half of July and extended through the third week of August. The last clutch was laid on 27 August.

Total number of active nests increased to a plateau during June and early July before increasing to the seasonal high in mid-August. Nesting extended through mid-September.

In 1988, pigeons had a small wave of clutch starts during late May and early June before tapering down to only two new nests per week during mid-June (Fig. 29). The second major nesting wave began during the third week of June and extended through the third week of August. Except for one week in July, 18 to 33 clutches were started each week. The number of active nests per week increased to the seasonal high during the third week of August when more than 80 nests were active. Nesting extended into early October. The last nest fledged young on 3 October.

In 1989, two distinctive and separate waves of nesting occurred at Bottle Key (Fig. 30). The first began during the second week of May and lasted through the first week of June. Twenty-two clutches were started during this period. The second wave began during the last week of June and extended through August. Most of the new clutches (107 of 130) were laid during July. The number of active nests per week showed two distinctive peaks, the first during early June and the second during late July. During the second peak, the number of active nests was more than three times higher than the first. Nesting extended into mid-September.

West Butternut Key

On West Butternut Key, we followed nesting throughout the season in 1987 and 1988. In 1989 few pigeons attempted to nest on this key and we stopped thorough searches of the island mid-way through the season. During the two years we found 84 nests. The laying season extended from 29 May through 27 August, a span of 90 days (Table 1). Based on the combined

sample, clutch initiations showed a small wave in late May and early June, a lull in late June, and a second major wave encompassing July and August (Fig. 31). A decrease in the number of new clutches occurred in early August with a final peak during the third week of August. This latter peak included a number of nests that were abandoned during incubation. Some of those could have been started during the week before. The number of active nests increased throughout the season to a high from late July through August. From the peak in late August the number of active nests dropped rapidly in September as many nests failed.

CLUTCH SIZE

Of the 1,076 clutches we followed on the three keys during this study, 88.1% had two eggs (Table 3). We found 121 clutches in which we never saw more than one egg. Some no doubt represent true one egg clutches, but many probably had two eggs laid and one was depredated. We found seven nests that contained three eggs. In several of these nests one egg was a slightly different shade of white or substantially different in size. This suggests that these eggs may have been dumped in these nests by a second female. For some of the clutches, however, all eggs were essentially identical. These may have been true 3-egg clutches.

Over the entire study, clutch size average 1.89 eggs ($n = 1076$). Between years and keys, clutch size varied relative little (Table 3). Only at West Butternut Key in 1988 was the mean size substantially below the other means. During 1988, predation was high on West Butternut Key and the relatively large number of single egg clutches probably reflects many partial losses.

REPRODUCTIVE SUCCESS

Middle Butternut Key

Based on 429 nests located and followed during the 1985 through 1989 nesting seasons on Middle Butternut Key, overall nest success averaged 32.3% (Table 4). Overall nesting success varied between the years (Table 4). Success in 1988 (51.6%) was significantly higher than success in other years (all $z > 7.601$, $P < 0.05$). Nesting success in 1985 (30.1%) and 1986 (33.2%) did not differ significantly ($z = 1.154$, $P > 0.05$) but were significantly higher than success in either 1987 (21.0%) or 1989 (20.4%)(all $z > 3.664$, $P < 0.05$).

Incubation period success averaged 58.3% and ranged from 43.6% in 1989 to 71.3% in 1986 (Table 4). Success in 1986 and 1988 was significantly higher than success in 1985 and 1987 which were significantly higher than in 1989 (all $z > 1.65$). Nestling period success averaged 55.3% (Table 4). Nestling period success varied from 41.4% in 1987 to 75.6% in 1988. Success in 1988 was significantly higher than success in the other years (all $z > 1.65$). Success in 1987 was significantly lower than all other years (all $z > 1.65$). Success in 1985, 1986, 1989 was intermediate and did not differ significantly between them (all $z < 1.65$).

Based on the five years combined, nesting success was significantly higher during the incubation period than during the nestling period (Table 4, $z = 2.357$, $P < 0.05$). In 1985 ($z = 1.274$, $P > 0.05$) and 1989 ($z = 0.933$, $P > 0.05$) nesting success did not vary significantly between the incubation and nestling periods. In 1986 ($z = 8.104$, $P < 0.05$) and 1987 ($z = 2.738$, $P < 0.05$) incubation period success was significantly higher than nestling period success, whereas in 1988 the reverse was true ($z = 3.590$, $P < 0.05$).

Seasonal Variation. We examined seasonal variation in nesting success by dividing the season into early and late periods. Early nests were those in which the first egg was laid before 9 July; in late nests the first egg was laid after 8 July. These dates correspond to periods when *M. toxiferum* dominates the diet of nestlings (late) or other fruit species are most important (early).

Based on the five years of data, overall nesting success between early (29.8%) and late (33.8%) in the season varied significantly (Table 4; $z = 2.56$, $P < 0.01$). Between years, however, considerable seasonal variation occurred in nesting success (Table 4). In 1985 ($z = 5.836$, $P < 0.05$) and 1989 ($z = 4.729$, $P < 0.05$), early nests had a significantly higher probability of fledging young than later nests. In 1986 ($z = 6.881$, $P < 0.05$) and 1988 ($z = 7.773$, $P < 0.05$), late hatching nests had higher success. In 1987 nesting success did not vary seasonally ($z = 0.179$, $P > 0.05$).

Between the years, early season nesting success varied significantly, ranging from 41.0% in 1985 to 20.5% in 1987 (Table 4). Early success in 1985 did not differ significantly from success in 1988 ($z = 1.568$) but was significantly higher than the other years (all $z > 1.673$). Early season success in 1988 and 1989 did not differ significantly nor did early season success in 1986 and 1987 ($z = 0.160$). Early season success in 1988 and 1989 were, however, significantly higher than in either 1986 or 1987 (all $z > 2.844$).

Between the years late season nesting success also varied significantly, ranging from 59.7% in 1988 to 15.3% in 1989 (Table 4). Late season nesting success in 1988 was significantly higher than success in 1986 ($z = 4.281$) which was significantly higher than success in 1987 ($z = 7.713$). Late season success in 1987 did not differ significantly from success in 1985 ($z = 0.833$) but was significantly higher than success in 1989 ($z = 2.265$). Late season success in 1985 did not differ significantly from late season success in 1989 ($z = 0.951$).

Early season incubation period success was 57.9% which was not significantly different from the late season value of 58.6% ($z = 0.412$). Between the years early season incubation period success varied significantly from 47.4% in 1989 to 67.7% in 1986 and late season incubation period success varied significantly from 42.3% in 1989 to 76.3% in 1988 (Table 4). In 1986 ($z = 1.552$) and 1989 ($z = 0.978$), incubation period success did not vary seasonally. In 1985 ($z = 3.449$) and 1987 ($z = 1.709$) early period incubation period success was significantly higher than late period success, whereas in 1988 ($z = 6.546$) late period incubation success was significantly higher.

Based on the five years combined, nestling period success during the early season was 51.5% which was significantly lower than nestling period success of 57.6% during the late season ($z = 3.05$). Between the years, early season nestling period success varied significantly from 31.1% in 1986 to 70.6% in 1989 whereas late season success varied from 36.3% in 1989 to 78.2% in 1988 (Table 4). In 1987, nestling period success did not vary seasonally ($z = 1.437$). In 1985 ($z = 4.386$) and 1989 ($z = 7.820$), success during the nestling period was significantly higher during the early season than during the late season, whereas in 1986 ($z = 7.126$) and 1988 ($z = 3.292$), the reverse was true.

Bottle Key

We followed 458 nests over 3.5 nesting seasons on Bottle Key. Based on the combined sample overall nesting success was 25.4% but varied significantly between the years (Table 5). For the three years with complete coverage, nesting success was significantly higher in 1988 than it was in 1987 ($z = 1.928$) and success in 1987 was significantly higher than it was in 1989 ($z = 8.692$).

On Bottle Key, incubation period success averaged 42.8% and nestling period success averaged 59.5%. Between the years with complete coverage, both incubation period and nestling period success varied significantly. All yearly comparisons were significantly different.

Combined nesting success was significantly higher during the nestling period than during the incubation period ($z = 12.413$). In 1987 ($z = 0.370$) and 1989 ($z = 1.170$), incubation and nestling period survival did not vary significantly. In 1986 ($z = 2.003$) and 1988 ($z = 20.940$), nestling period survival was significantly higher than incubation period survival.

Seasonal Variation. Based on the four years of data, overall nesting success was significantly higher during the second part of the season (Table 5; $z = 3.287$). In 1988, nesting success did not vary significantly between the two parts of the season ($z = 0.794$). In 1987, early season success was significantly higher than late season success ($z = 5.875$), whereas in 1989, late season success was significantly higher than early season ($z = 3.287$). Comparing success between years showed that all three early season nesting success values were significantly different. Late season nesting success in 1988 was significantly higher than all other years. Late season success in 1986 and 1987 did not differ significantly nor did success in 1987 and 1989, however late season nesting success between 1986 and 1989 were significantly different.

Early season incubation period success was 40.2% which was not significantly different from late season incubation period success of 43.5% ($z = 1.342$). Early season incubation period success varied from 21.9% in 1989 to 62.8% in 1987. Late season incubation period success varied from 38.2% in 1988 to 50.8% in 1987. Early season incubation period success was significantly higher in 1987 ($z = 2.620$) and 1988 ($z = 3.063$) than late season success, whereas in 1989, late season success was higher ($z = 5.685$).

Nestling period success during the early part of the season was 53.5% which was significantly lower than late season success of 61.6% ($z = 3.622$). Early season nestling period success varied from 14.1% in 1989 to 73.2% in 1987. Late season nestling period success varied from 43.2% in 1989 to 86.3% in 1988. In 1987, early season nestling period success was significantly higher than late season success ($z = 6.747$), whereas in 1988 and 1989, late season nestling period success was higher ($z = 5.794$ and $z = 6.060$, respectively).

West Butternut Key

Based on 104 nests followed through the nesting cycle at West Butternut Key, overall nesting success averaged 21.2% (Table 6). Between the years overall success varied from 5.0% in

1988 to 25.9% in 1987. Incubation period success averaged 45.6% and varied significantly between 1987 and 1988 ($z = 9.682$). Nestling period survival averaged 45.6% and did not vary significantly between 1987 and 1988 ($z = 0.388$). Based on the combined sample, nesting success did not vary significantly between the incubation period and the nestling period ($z = 0.289$). In 1987, however, incubation period survival was significantly greater than nestling period survival ($z = 5.826$), whereas in 1986 and 1988, nestling period survival was significantly greater ($z = 2.148$, $z = 3.153$, respectively).

Seasonal Variation. Based on the three years of data, overall nesting success during the early part of the season did not differ significantly from success during the later part (Table 6; $z = 1.041$). However, both incubation period ($z = 3.514$) and nestling period ($z = 4.159$) success did vary significantly seasonally although in opposite directions. Incubation period success was higher during the early part of the season, whereas nestling period success was higher during the late part of the season. In 1987, overall nesting success was significantly higher during the second part of the season ($z = 2.385$), whereas in 1988 overall nesting success did not vary significantly over the season ($z = 1.603$).

SOURCES OF MORTALITY

Middle Butternut Key

Of the 829 eggs laid in clutches at Middle Butternut Key during the five years, 265 (32.0%) produced fledglings and 564 (68.0%) were lost. Predation was the single greatest source of mortality accounting for 76.8% of the losses (Table 7). Egg predation accounted for 35.3% and young predation accounted for 41.5% of the total. Starvation of young and abandonment of eggs or nestlings were the next greatest source of mortality. Of the 586 eggs that reached hatching age, 4.4% failed to hatch either because the eggs addled during development or because they were infertile.

The fate of eggs laid at Middle Butternut Key varied significantly with year (Table 8; $G = 49.88$, $P < 0.05$). The percentage lost to predation varied between the years from only 10.5% in 1986 to 36.5% in 1989. The depredation rate in 1986 and 1988 was lower than in the other years. Other egg mortality factors did not vary substantially between years. The percentage of eggs that hatched varied from 58.2% in 1989 to 76.9%.

The fate of nestlings at Middle Butternut Key varied significantly with year (Table 9; $G = 58.99$, $P < 0.05$). The percentage lost to predation varied from only 26.0% in 1988 to 58.6% in 1989. The percentage of nestlings starving also varied between years from 4.0% in 1989 to 17.1% in 1985. The percentage of nestlings fledging ranged from 35.4% in 1989 to 66.7% in 1988.

Bottle Key

Of the 855 eggs laid at Bottle Key during our study period of mid July 1986 through 1989, 466 hatched and 247 produced fledglings. Predation was the single greatest source of failure, accounting for 79.8% of all the losses (Table 10). Egg predation represented 50.5% of the mortality and young predation 29.3%. Abandonment of eggs and nestlings and starvation of young were the next most important sources of mortality. Of the 499 eggs that reached hatching age, 33 or 6.6% failed to hatch either because they were infertile or had addled.

The fate of eggs laid at Bottle Key varied significantly among years (Table 11; $G = 16.1845$, $df = 6$, $P < 0.02$). In 1986 and 1987, slightly more than 60% of the eggs hatched, whereas in 1988 and 1989 only about 50% hatched. Predation was the primary cause of egg loss and the differences between years in survival during incubation were a result of differences in predation rates.

The fate of nestlings at Bottle Key varied significantly between years (Table 12; $G = 61.5854$, $df = 9$, $P < 0.01$). The proportion of nestlings fledging varied from 34.7% in 1989 to 73.0% in 1988. Variation between years in the predation rate accounted for most of the variation. The proportion lost to predators was lowest in 1988 and highest in 1989. The proportion classified as starving varied little between years.

West Butternut Key

Of the 189 eggs laid in clutches at West Butternut Key during the 2.5 years of study, 117 (61.9%) hatched and 52 (27.5%) produced fledglings. Predation was the single greatest source of mortality, accounting for 64.9% of the losses (Table 13). Egg predation represented 27.7% of the mortality and nestling predation represented 37.2%. Hatching failure was high at West Butternut Key. Of the 134 eggs that survived to hatching age, 12.7% were infertile or addled during development.

The fate of eggs at West Butternut Key varied significantly between years (Table 14; $G = 26.92$, $df = 4$, $P < 0.01$). The proportion hatching in 1988 was extremely low compared with the other years, primarily because the predation rate was extremely high. The high predation rate coupled with the low total number of nests probably were driving forces in the abandonment of this key as a nesting site.

The fate of nestlings at West Butternut Key did not vary significantly between years (Table 15; $G = 11.09$, $df = 6$, $P > 0.05$). Predation was the largest source of mortality in all years. Because few eggs hatched in 1988, sample sizes for that year were small.

EGG SIZE

White-crowned Pigeon eggs are pure white with no markings on the shell. The mean weight of eggs the day they were laid was 13.1 g (Table 16). The mean body weight of 23 female pigeons during the breeding season was 232 g (s.d. = 15). Thus egg weight represents 5.6% of female body weight. Female pigeons generally lay two eggs in a complete clutch, so the mean weight of the complete clutch represents 11.3% of female weight.

A much larger sample of eggs were measured for their length and width (Table 16). Pigeon eggs averaged 35.2 mm in length and 26.0 mm in width. The length (L) and width (W) can be used to predict the volume of eggs with an equation from Hoyt (1979):

$$V = 0.51 * L * W^2$$

We were able to calculate the volume of eggs for 1802 eggs. Egg volume is highly correlated with egg weight ($r = 0.8592$, $P < 0.01$, $df = 465$) and, therefore, a good measure of a female's energetic investment in eggs. We will use volume for all comparisons of egg size. Eggs averaged 12.1 cc in volume and ranged from 8.6 cc to 16.8 cc.

The egg-width distributions did not fit a normal distribution (Fig. 32, Kolmogorov-Smirnov Z statistic = 1.634, $P < 0.01$). Egg-length distributions (Fig. 33; K-S $Z = 1.304$, $P = 0.067$), egg-weight distributions (Fig. 34; K-S $Z = 1.294$, $P = 0.07$), and egg-volume distributions (Fig. 35; K-S $Z = 1.350$, $P = 0.052$) were not significantly different from normal distributions. The egg width distribution was skewed slightly to larger eggs. The egg width distribution was also slightly platykurtic, indicating that the distribution was flatten slightly.

The elongation index of bird's eggs is the length divided by the width and gives an indication of the shape of the egg (Table 16; see Preston 1969). The length and width of eggs are significantly correlated ($r = 0.4331$, $P < 0.01$), but the correlation only accounts for 18.8% of the variation. The mean elongation index for 4 columbid species was 1.35 with a high of 1.36 and a low of 1.33. Thus White-crowned Pigeon eggs are similar in shape to other columbid eggs.

Rahn, Paganelli, and Ar (1975) provided a series of allometric equations that predict egg weight (EW) from female body weight (B) for different taxa of birds. The equation for Columbidae was

$$EW = 0.21 * B^{0.76}.$$

Based on a 232 g female, this formula predicts an egg weight of 13.2 g for White-crowned Pigeons. Rahn and Ar (1974) provide an allometric equation that predicts the incubation period (I) of an egg based on its weight:

$$I = 12.03 * EW^{0.217}$$

The predicted incubation period for a 13.1 g egg would be 21 days. The observed incubation period of 14 days is shorter than expected based on egg weight.

Site Variation

The mean volume of eggs varied significantly between the nesting keys ($F = 13.895$, $df = 2, 1799$, $P < 0.001$). Eggs on Middle Butternut Key averaged 12.3 cc which was significantly bigger than the 12.0 cc average volume for eggs on both Bottle Key and West Butternut Key (Table 17). During each year eggs on Bottle and West Butternut keys were smaller than eggs on Middle Butternut Key.

Seasonal and Yearly Variation

We used egg volume data from Middle Butternut Key to examine yearly and monthly variation in egg volume because for this site we had complete data sets for five years. Egg volume varied significantly with year and with month (Tables 18, 19, 20). In the ANOVA, the interaction of year and month was not significant (Table 18). Monthly means for each year are plotted in Figure 36 and show the general pattern of egg volume increasing with month during each year.

Comparing the change in weight through the months with all the years of data pooled showed that

mean volume in July and August was significantly greater than mean volume in May and June (Duncans Multiple Range Test). Because of small sample size we excluded September. Pooling months and looking at differences between years showed that mean volume in 1988 was significantly larger than the mean volume in 1987 but that all other pairwise comparisons were not significant (Duncans Multiple Range Test).

GROWTH

At hatching, squabs have pink skin and are covered with a fine down. The skin gradually darkens and by 4 days, the skin is dark brown-black. Primary 7 first emerged on 3-day squabs and all squabs had measurable primaries by 5 days (Table 21, Fig. 37). At day 16, primary 7 had attained 64% of the length of a 1-2 month old juvenile (123.2 mm). Primary 7 showed linear growth from emergence through day 16. By day 17-20, primaries 1-3 were approaching full length with the sheaths almost gone. The central rectrices were first measurable on 3-day young and all day-7 young had measurable central rectrices (Table 22, Fig. 38). By day 16, the central rectrices averaged 41% of the length of a 1-2 month old juvenile (112.1 mm). By day 20, the juvenal plumage is almost completed, although young still have growing pin feathers on the head when 30 days old.

Young will often leave the nest when disturbed at age 16-20 days. At this point they can fly short distances. Undisturbed young generally do not fledge until around day 20 although they may move out of the nest.

At hatching, culmen length averaged 47% of adult length ($\bar{x} = 27.4 \pm 1.8$ mm, $N = 36$). Culmen length increased rapidly through day 6 at which point the growth rate began to decline (Table 23, Fig. 39). By day 12, culmen length of young did not differ significantly from that of adults.

Gape width at hatching averaged about 75% (Table 24, Fig. 40) of adult width ($\bar{x} = 8.5 \pm 1.0$ mm, $N = 35$). Width increased through day 10, after which no significant growth occurred. From day 3 through the nestling period, gape width averaged larger than adult size primarily because of flanges that form on the lateral sides of the culmen. The size of these flanges begin to decrease around day 15 and a 1-2 month old juvenile had a gape width and shape similar to that of adults. These flanges presumably function in the efficient transfer of food from adults to young.

At hatching, the manus averaged 22% (Table 25, Fig. 41) of adult length ($\bar{x} = 54.0 \pm 3.6$, $N = 4$). Manus growth was approximately linear through day 7 at which time growth rates began to decrease. By day 14, manus lengths of young were within the range of adults.

At hatching, tarsal length averaged 39% (Table 26, Fig. 42) of adult length ($\bar{x} = 27.0 \pm 1.7$ mm, $N = 35$). Growth showed a sigmoid pattern with the rate of increase decreasing after day 5 (Fig. 42). By day 12, tarsal lengths of young were not significantly different from those of adults. By day 15 in the nestling period, young are capable of jumping from the nest and running across the ground.

At hatching, squabs averaged 5.4% (Table 27, Fig. 43) of adult weight ($\bar{x} = 245 \pm 26$ g, $N = 40$). Mean weight of young increased rapidly through day 12 after which weight gain decreased. The decrease in weight from day 15 to day 16, we feel, is not real (Fig. 43) but reflects small sample size for that period. Also, well developed young will often leave the nest at day 15 or 16, which biases the sample to less-developed young. By day 14, young averaged 63% of adult weight and some young weighed more than 200 g. A 1-2 month old juvenile weighed 171 g, which suggested that weight gain to adult size may not occur until sometime after fledging. Mean weight through the latter part of the nestling period was quite variable because of variation in the contents of squabs' crops. Young at the time of weighing had crops that ranged from empty to being stuffed. Crop samples taken from 207 squabs with food averaged 12.1 g (s.d. = 5.5) and ranged from 2.2 g to 40.0 g.

Asynchronous Hatching In Growth

Most 2-egg clutches of White-crowned Pigeons hatch over a half day to full day period. The first-hatched young, therefore, has from several hours to a day to grow before the second young hatches. A size hierarchy normally results between the young. As a result, the weight of second-hatched young at day 8 in the nestling period is significantly less than that of the first-hatched young ($F = 42.96$, $df = 1,296$, $P < 0.0001$). First-hatched young averaged 107.9 g (s.d. = 16.1, $N = 196$) at day 8 whereas second-hatched young averaged 94.9 g (s.d. = 16.6, $N = 102$).

The general growth curves begin to diverge substantially at day 3 in the nestling period (Fig. 44). By day 3, second-hatched young average significantly lighter than first-hatched young. The curve for second-hatched young is shifted half-a-day to the right to reflect the spread in hatching times.

Yearly and Seasonal Variation in Growth

We performed a two-way ANOVA on the estimated weights at day 8 to examine yearly and seasonal variation (Table 28). Weight at day 8 varied significantly both seasonally and yearly. The non-significant interaction indicates that seasonal effects were not different between years.

Mean weight at day 8 varied from 92.8 g in 1985 to 108.2 g in 1986 (Table 29). Mean weight in 1985 was significantly lower than mean weight in 1986, 1987, and 1988 (Tukey test). No other comparisons were significantly different. Mean weight at day 8 was significantly lower during the period before *M. toxiferum* was available than it was when *M. toxiferum* was available (Table 30). Pigeons gained an additional 10 g by day 8 if *M. toxiferum* was available.

FOOD HABITS

From 1986 through 1989, we collected 207 crop samples from pigeon nestlings. Most samples were collected on West Butternut and Bottle keys but a few samples were collected from fledging age young on Middle Butternut Key. These included 51 in 1986, 53 in 1987, 68 in 1988, and 35 in 1989. Samples were collected from 3- to 15-day-old nestlings (Fig. 45). For each day of age from day 4 to 14, at least 10 samples were collected. Nestlings older than 13 days would often jump from the nest so we did not try to attain large sample sizes from older young. Nestlings younger than 4 days old rarely contained fruit and we did not collect many samples. All nestlings that we checked less than 3 days old with full crops appeared to have only crop milk. In all years we attempted to obtain a few samples from all age classes.

White-crowned Pigeons, like other columbids, produce crop milk which supplements the nestling diet. Crop milk was present in 206 of the 207 samples (Table 31). Based on aggregate percent weight and volume, crop milk accounted for more than 52% of the nestlings diet. We found flowers of one species, *A. germinans* and fruit of 12 species (2 native *Ficus*) in the crop samples. We found fruits or seeds from 32 species of trees in the combined sample from young and adult pigeons and from analysis of seeds from fecal samples (Table 32). This included trees or shrubs from 22 families of plants.

Fruits of 5 species (2 *Ficus*) accounted for over 97% by weight and volume of the fruit found in the crop samples from nestlings. *M. toxiferum* was the most important, occurring in 78% of the samples and representing 61% of the fruit diet based on aggregate percent weight and volume

(Table 31). *G. discolor* was the second most important fruit, occurring in 46% of the samples and representing 19% of the diet based on volume and weight. Fruit of *F. aurea* and *F. citrifolia* were found in almost 17% of the samples. We could not separate the fruit of these two species and therefore present the data with these two species pooled. We know they regularly eat the fruit of both species (pers. obs.). *Ficus* fruit represented slightly less than 10% of the fruit diet by weight. *E. fruticosa* was found in 26% of the samples and represented about 6% by weight of the diet. *E. fruticosa* is a common shrub on the nesting keys where we collected most of the samples and it fruited sporadically throughout the nesting season. Flowers of *A. germinans* were found in 11 samples and represented about 1% of the non-crop milk diet. The other fruit species represented less than 1% of the diet and were found only in a few samples.

Adult White-crowned Pigeons gradually shifted the diet of nestlings from all crop milk at ages zero through 2 days old to one containing more than 50% fruit by volume at day 9 (Fig. 46). At day 3, more than 80% of the diet consisted of crop milk. The proportion of crop milk decreased significantly through the nestling period ($r = -0.5855$, $P < 0.01$, $n = 206$, arcsin transformed). Mean crop volume did not vary significantly with age (Fig. 47, $F = 1.5075$, $P = 0.1240$, $df = 12,193$), although mean volume showed a slight trend to increase with age ($r = 0.1916$, $F = 7.748$, $P = 0.0059$). The mean weight of crop milk in the samples changed significant with age ($F = 1.9192$, $P = 0.0342$, $df = 12,193$) and showed a significantly decrease with age ($r = -0.2810$). This suggests a gradual replacement of crop milk by fruit as the nestlings grow rather than simply an increase in the quantity of fruit.

Nestling diet showed some distinctive seasonal shifts in the type of fruit consumed (Fig. 48). *Ficus* was most important during June and early July. *Ficus* comprised as much as 50% of the fruit diet during late June and early July but decreased to an extremely small amount during the rest of the summer. *G. discolor* was consumed throughout the season, however, its importance was variable. The presence of *G. discolor* varied from over 30% of the fruit diet in early June to only 2% of it in early July. *E. fruticosa* occurred in small amounts throughout the season. It was most important during early July before *M. toxiferum* became readily available and when *G. discolor* was not abundant. Flowers of *A. germinans* appeared in the diet only during June and early July.

Yearly Variation

The mean weight of crop samples collected between years did not vary significantly ($F = 1.41$, $df = 3,203$, $P = 0.239$). 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 substantially between years. Crop milk represented 53.4 % of the total weight in 1986, 53.7% in 1987, 49.3 % in 1988, and 45.6% in 1989. The relative contribution of various fruit species however did vary between years. In all years *M. toxiferum* was the most important species. Of the fruit part of the samples, the aggregate percent weight of *M. toxiferum* varied from 44.8% in 1989, 47.7% in 1987, to 69.7% in 1986 and 74.2% in 1988. The proportion of samples containing *M. toxiferum* did not vary significantly between years. *G. discolor* was the second most important fruit in all years. It was less important in years that *M. toxiferum* was more important. The aggregate percent weight 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 also varied significantly between years ($G = 14.27$, $P < 0.01$). In 1986 and 1988 less than half the samples contained *G. discolor* whereas in 1987 and 1988 more than half contained it. The relative importance of *Ficus* fruit varied substantially between years. In 1986, it was practically nonexistent in the diet. However, in 1986 we did not begin to collect samples until late July and by that time *M. toxiferum* had become ripe. Had we collected samples in June, *Ficus* would have been substantially more important (pers. obs.). In 1987 (16.5%) and 1989 (15.7%), the aggregate percent weight was almost twice what it was in 1988 (7.1%). Between 1987, 1988, and 1989, the proportion of samples containing *Ficus* did not vary significantly ($G = 4.76$, $P > 0.05$, $df = 2$). The importance of *E. fruticosa* also varied between the years. The aggregate percent weight 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 between the years ($G = 0.85$, $P > 0.05$).

FRUIT CHARACTERISTICS, NUTRITIONAL AND ENERGETIC VALUES

Whole *M. toxiferum* fruit contained more energy per gram of dried material than any other fruit consumed by White-crowned Pigeons (Table 33). When compared with the other four common fruits consumed during the breeding season: *E. fruticosa*, *F. aurea*, *F. citrifolia*, and *G. discolor*, *M. toxiferum* had significantly more ($F = 40.6$, $P < 0.05$) energy per dried gram of whole fruit. *E.*

fruticosa had significantly more energy than either of the *Ficus* species or *G. discolor*. It also had a significantly lower ($P < 0.01$) insoluble carbohydrate content than all other fruits. Several winter fruits also had high energetic contents (*N. coriacea* and *Bumelia salicifolia*; Table 33), but most fruit energy contents ranged from 6.2 - 8.2 KJ/g of dried whole fruit.

Of the 5 common breeding season fruits, *M. toxiferum* had significantly less soluble carbohydrates ($F = 61.5$, $P < 0.01$) but was similar to the winter fruit, *N. coriacea*. *M. toxiferum*, however, had significantly greater ($F = 469.65$, $P < 0.001$) amounts of lipids than all fruits except *N. coriacea*. Lipids are more energetically valuable than carbohydrates (39.8 KJ/g lipid vs. 17.2 KJ/g carbohydrates), contributing to the overall higher energy level in *M. toxiferum*. *M. toxiferum* also had significantly less ($F = 231.31$, $P < 0.001$) water content than other common fruits consumed during the breeding season. Several of the fruits available during the non-breeding season had similarly low water contents, but in general most fruits ranged from 60 - 70% water. Except for *M. toxiferum* and *N. coriacea*, the distribution of proximate constituents in other fruit food sources was similar. They tended to be high in soluble carbohydrates (24.5 - 38.3%) and low in lipids (4 - 7.6%). There were few differences in the levels of insoluble carbohydrates.

A. germinans flowers, consumed only during the early part of the breeding season when pigeons are feeding on relatively energy-poor *Ficus* fruit, had high levels of protein and lipids (Table 33). They had a relatively high energy content (10.2 KJ/g), however *A. germinans* flowers are very small and a large number of them would need to be consumed by a foraging pigeon to be comparable to the amount of energy obtained by consuming relatively few *M. toxiferum* fruit. *A. germinans* was found in only 11 of 207 (5.3%) crops sampled from 1986 to 1989.

Crop milk was present in 99.5% of all crop samples and is fed to nestlings throughout the breeding season. It was the single greatest source of energy fed to nestlings (Table 33). Crop milk is proliferative epithelial tissue produced by the inner lining of the adult pigeon's crop. It was very high in protein (25.9%) and lipids (52.9%) and virtually absent of soluble carbohydrates (0.5%). As a consequence of the high protein and, especially, lipid levels, crop milk was significantly higher energy content than any whole fruit consumed by White-crowned Pigeons.

We compared seasonal variations in the nutritional and energetic content of *M. toxiferum*, *F. aurea*, *F. citrifolia*, and *G. discolor* from May to December during both 1988 and 1989 (Fig. 49). For all four species, protein levels remained relatively constant throughout the sampling period.

Soluble carbohydrates peaked in June and then declined thereafter in *M. toxiferum* (Fig 49). *G. discolor* had a similar pattern but the carbohydrates peaked in July (Fig 49). Both *Ficus* species, however, showed variable levels of carbohydrates with no particular seasonal trends except that highest levels occurred in both species during the fall (Fig 49). In all fruits, energy content varied significantly with time. Except for *M. toxiferum*, changes in energy content coincided with fluctuating carbohydrate levels. Lipid levels were low and relatively constant throughout the sampling period. In *M. toxiferum*, however, lipids varied significantly over time ($F = 214.16$, $P < 0.001$). Lipids increased during June and July, when most *M. toxiferum* fruit is ripening, then peaked in August and gradually declined throughout the fall. Energy content also peaked in August. The lowest levels of energy occurred in all four fruits during the winter.

We also compared the nutritional and energetic values of pulp and seeds for eight species of fruit, four consumed during the breeding season and present in nestling crop samples, and four consumed by pigeons outside the breeding season. In both *M. toxiferum* and *G. discolor*, and for all fruits consumed by adults during the nonbreeding season, pulp contained significantly more energy than did seeds, ranging from 1.8 to 2.5 times the Kj per gram dry weight (Table 34 and 35). *G. discolor* pulp had only 1.1 times the energy of seeds but the value was still significantly different. Energy content in pulp and seeds for both *Ficus* species did not differ. *M. toxiferum* pulp had the highest amount of energy per gram dry weight. Pulp energy ranged from 4.0 Kj/g for *G. discolor* to 16.5 Kj/g for *M. toxiferum*. Seed energy content ranged from 2.9 Kj/g (*T. radiata*) to 8.9 Kj/g (*F. citrifolia*).

In most fruits, pulp had significantly higher levels of soluble carbohydrates than seeds, however, *M. toxiferum* pulp and seeds did not differ (Table 34). Correspondingly, seeds had significantly more insoluble carbohydrates, probably in the form of cellulose and lignin, than did pulp for all fruits except *F. aurea*. Protein levels were not significantly different between pulp and seeds. Again, for most species except *M. toxiferum*, pulp contained higher amounts of ash than did seeds. *M. toxiferum* pulp also had significantly more lipid than did seeds. For all species, pulp contained more water than did seeds.

By determining the mean wet weight of each fruit species in all crops sampled during the study, we can estimate the average energetic contribution for each fruit in the average nestling crop. Since we could not distinguish the two *Ficus* fruits from crop samples for this analysis, we pooled

their energetic levels (Kj/g) and percent water content. In both cases the values were not significantly different. *M. toxiferum* had the highest mean wet weight in all crop samples (Table 36). By subtracting the percent water, and multiplying the mean dry weight by the Kj/g, we calculated the mean energetic contribution of each fruit. *M. toxiferum* contributes significantly more ($\chi^2 = 47.4$, $P < 0.01$, $df = 2$) energy than either *Ficus* spp. or *G. discolor* per average crop delivered by an adult to a nestling White-crowned Pigeon.

The five fruits most commonly consumed during the breeding season and fed to nestlings also varied in several characteristics. *Ficus* fruit tend to be large and heavy (Table 37), perhaps because of their high water content. *F. citrifolia* fruits were significantly larger and heavier than other fruits and both *G. discolor* and *E. fruticosa* were significantly smaller ($\chi^2 = 17.2$, $P < 0.05$, $df = 4$). The number of seeds per fruit ranged from 0.8 - 84 (Table 37), but only *M. toxiferum* had a significantly different ($\chi^2 = 38.4$, $P < 0.001$, $df = 4$) pulp/seed ratio. *M. toxiferum* averaged < 1 seed per fruit, supporting our hypothesis that some ripe *M. toxiferum* fruits reabsorb their seeds during the mid-summer. Reabsorption of seeds might explain the high pulp/seed ration found in *M. toxiferum*.

DISCUSSION

PIGEON ABUNDANCE

White-crowned Pigeons are extremely seasonal in their occurrence in the keys. They are most abundant during the months of May through September and much less abundant from October through April. The average abundance each month is correlated ($r = 0.6580$, $t = 2.763$, $P < 0.05$) with the cumulative CI of the four most common food species in the pigeons' diet during the nesting season (Fig. 50). As the availability of those fruits increase in April and May many pigeons return to the keys and they leave in the fall as the availability of these fruits decrease.

All four surveys showed significant seasonal variation in pigeon abundance. More were present in the summer than the winter. Virtually no pigeons roosted on the two mangrove islands in Florida Bay during the winter. The double summer peak at Cowpens Key appears to result from large increases in the number of birds roosting on the key. Apparently in June these are prebreeding birds that then disperse to other nesting keys during the wave of nesting that begins in late June or early July. The September peak includes many flying juveniles as well as post-

breeding adults. The decrease in October corresponds with the exodus of most of the pigeon population from the keys. Several mangrove keys (potential roost sites) are situated between Middle Butternut Key and the mainline Keys. We, therefore suspect that all the adults we record on this boat survey are actively nesting or courting.

The North Key Largo survey had four months with more than 100 pigeons recorded. Three of these large counts occurred in the fall when many pigeons moved into the large contiguous forests of North Key Largo. They appeared to be exploiting an abundant supply of *M. toxiferum* fruit. In February 1989, a large number of pigeons moved into North Key Largo for a few weeks. We counted more than 150 pigeons on our survey and found a roost of over 1000 birds. We have no evidence that these birds were wintering in Florida before moving to North Key Largo and suspect this represented a large influx from the Florida mainland or the Bahamas. These birds were absent by the March survey and we received no reports of unusual numbers of pigeons from elsewhere in Florida during March.

NESTING DISTRIBUTION

White-crowned Pigeon nests are relatively easy to locate. Adults remain on nests until an intruder approaches closely and then they flush with loud wing claps. Thus, we feel that we have accurately described the current nesting distribution of White-crowned Pigeons in Florida Bay and Card and Barnes Sounds. White-crowned Pigeons also nest south of Long Key on offshore islands along the mainline Keys, but the current nesting distribution and population status in this area is unknown (T. Wilmers, pers. comm.).

Although Figures 18 and 19 represent the current breeding distribution of White-crowned Pigeons, temporal shifts in distribution may occur even in high density nest areas. West Butternut Key experienced a reduction in nesting pigeons from 1987-1989 (with 68 nests in 1987, 15 nests in 1988 and only one nest in 1989), whereas Middle Butternut Key, located 0.5 km away, supported more than 100 nests throughout this period. Although we have no explanation for this decrease, the high predation rate probably played a role.

In Florida Bay, pigeon nesting occurs in a broad, v-shaped band that diverges from the mainland in the central portion of the bay. Low nesting abundances or the absence of pigeons on keys with a high incidence of raccoons suggests that raccoons at least limit the distribution of high

density nesting areas. The distribution of raccoons is nearly parapatric with that of pigeons. The only overlap occurred at the outer edges of the nesting range on six keys with low nest abundances. Four of these keys had nest abundances less than 0.04 nests/min and two keys had only one old nest. We found no evidence of nesting by White-crowned Pigeons on the mainland or most of the mainline Keys. We feel that this is a response to high densities of mammalian predators. Wiley (1979), however, reported six nesting locations on Puerto Rico, suggesting that in other localities, mammalian predators may not exert such an influence.

The presence of sympatric raccoons and nesting pigeons may indicate recent raccoon colonization of a particular key. We have no indication of how effective raccoons are as predators on White-crowned Pigeon nests. They have been cited as nest predators on a variety of both ground- and tree-nesting species (Allen 1942, Lopinot 1951, Rearden 1951, Kilham 1986, Frederick and Collopy 1989, Post 1990). Wilcove (1985) felt that nest predation by mammals was less significant at nests greater than 1 m above ground level. White-crowned Pigeons frequently nest 1-2 m above ground, therefore, colonization of a nesting key by raccoons may not immediately eliminate the pigeon population. Raccoon scats found in Florida Bay contained primarily fish, crab, and shellfish fragments. Consequently, the two species may temporarily coexist on a key.

The current raccoon distribution reflects the unique arrangement of shallow mud banks in Florida Bay. Over the past 50 years, raccoons have been observed on additional keys within Florida Bay (Allen 1942; R. Paul, W. Robertson, pers. comm.) indicating that populations may be fairly mobile. Most raccoons probably reached bay keys from the mainland by following these banks and swimming across deeper channels. Raccoons on the keys in the southern and eastern portions of the bay most likely colonized from the mainline Keys. Although the intracoastal waterway separates the mainline Keys from keys within Florida Bay, mud banks still allow access to these keys with minimal swimming.

Allen (1942) felt raccoon distribution and abundance in Florida Bay was correlated with the occurrence of hurricanes. Moderate to large hurricanes occur in Florida Bay at approximately 25 year intervals. These events most certainly decimate the raccoon population on many keys in the bay and may periodically push the raccoon range back to the mainland, allowing the central bay to remain raccoon-free.

The influence of other potential predators seems to be minimal. Red-winged Blackbirds can be effective nest predators at unattended nests (Blankinship 1977, Sprunt 1977, pers. obs.). In Florida Bay, the absence of human disturbance on nesting keys probably diminishes the effect of blackbird predation. However, blackbird predation may be a factor in areas where human disturbance is unregulated, such as keys in the Florida Straits and in Card and Barnes Sounds. The high degree of overlap between Red-winged Blackbirds and pigeons suggests that blackbirds may select keys with nesting pigeons. However, like pigeons, they may also avoid keys with raccoons.

All 10 keys on which we recorded Laughing Gull nesting or mobbing activity supported nesting pigeons. Frohring and Kushlan (1986) listed Laughing Gull nesting colonies on 26 keys in Florida Bay. We found White-crowned Pigeons nesting on 24 of those keys and gulls and pigeons on two additional keys that were not documented as nesting sites for gulls by Frohring and Kushlan. Therefore, we do not suspect that gulls play a major role in limiting pigeon nesting distribution. Crows (*Corvus* spp.) have been cited as nest predators in a number of other studies (Burger and Hahn 1977, Verbeek 1982, Shields and Parnell 1986), however, in Florida Bay, their distribution seems to coincide with wading bird, pelican, and cormorant colonies. White-crowned Pigeons did not nest on two keys with major wading bird colonies in Florida Bay, but were found in high densities in a wading bird colony in the northeastern bay. Of the three keys on which we recorded crows, one had high pigeon nest abundances, one had a single nest and the other had no nesting. Therefore, their influence is difficult to evaluate.

We found evidence of rats on eight keys, including keys with both high and low pigeon nest abundances. Although rats have been cited in the reduction or elimination of several ground or burrow-nesting island birds (Austin 1948, Kepler 1967, Berger 1972:86, Cruz and Cruz 1987), their presence on keys does not seem to preclude nesting by White-crowned Pigeons. Wiley and Wiley (1979) reported *R. rattus* depredation on White-crowned Pigeon nests in Puerto Rico when lowered water levels permitted easier access to nest trees. Given the wide (but patchy) distribution of rats and their secretive and nocturnal behavior, they may be more common than we observed during the nesting surveys. As with raccoons, rat populations may be regulated by hurricanes.

PHENOLOGY/FRUIT PRODUCTION

Tropical hardwood hammock trees have a year-round growing season. Therefore, trees may flower and produce fruit throughout the year. Individual species, however, have developed several different strategies which optimize the results of their annual production of fruit. The two native figs, *F. aurea* and *F. citrifolia* are asynchronous in their production of fruit. An individual tree may produce fruit at any time of the year. To maintain populations of their host-specific pollinators, some *Ficus* individuals of both species must be in fruit during all months of the year (Bronstein 1989). Therefore, during all months of the year, there is some *Ficus* spp. fruit available. As a result, *Ficus* fruit is available to a variety of birds and mammals throughout the year. During a year, however, there are periods (summer and late fall) when production of fruit is maximized on a larger percentage of trees. Birds and mammals appear to take advantage of these boom crops.

A second strategy is to produce fruit only during certain seasons of the year. Trees using this strategy may produce fruit over a relatively short period of time or fruit may ripen over a span of many months and thereby be available for a relatively long time period. In the first group are tree species such as *G. discolor* and *E. paniculata*. *G. discolor* is available only during the summer and early fall when individual trees produce several fruit crops. *E. paniculata* flowers and fruits during late spring. In the second group is *M. toxiferum*. This species flowers in mid-spring, but the first ripe fruit does not appear until July and thereafter some fruit ripens continuously throughout the fall and winter.

Fruit production varies between years. A major determinant of this variability appears to be rainfall. Seasonality in the tropical hammocks is one of dry vs. wet season rainfall and adequately timed rains of sufficient quantity are necessary for fruit set and development. Long- and short-term drought conditions have occurred in south Florida during our study and seem to have affected flower and fruit production. In 1987, the summer rains did not start until August while a major south Florida drought began in the fall of 1988 and continued until summer of 1990. In 1987, when the onset of summer rains was delayed, much of the early *M. toxiferum* and *G. discolor* crops were delayed in ripening or aborted. In *G. discolor*, the drought in early summer appeared to be the cause of the bimodal peak in flowering. When rains returned in August, there was a second small flush of flowering before dropping off for the season. In 1988, summer rains began in late May and continued through the summer. As a result, large crops of both *M. toxiferum* and *G. discolor* fruits

were produced. Fruit of *M. toxiferum* ripened earlier in 1988 than in 1987 or 1989. In 1989, south Florida was in the middle of a two-year drought. Crops of both *M. toxiferum* and *G. discolor*, as well as the early season crop of *Ficus* was substantially reduced. In *M. toxiferum*, there was a substantial abortion of fruit in the July through September period.

In *Ficus* spp., abundant rainfall seems responsible for increases in fruit production, while a lack of rain can drastically cut fruit production. The December 1987 peak, containing the largest number of *F. aurea* trees with ripe fruit of any survey, occurred after a very wet late summer and fall. Likewise, during the drought in 1989, the sharp drop in the competitive indices is probably associated with lack of rainfall. *F. citrifolia* shows similar responses to rainfall patterns.

The drought of 1989 also affected several other tree species. *B. simaruba* develops ripe fruit during the winter months and its competitive indices usually peak in March. During the winter of 1988-1989, the competitive index peaked in December and, although the percent of trees with ripe fruit increased through March, the amount of fruit present decreased faster than in the previous two years. Since the fall and winter were unusually dry, this loss of fruit appeared to have been drought related.

Flowering in *B. ovata* appears closely tied to the summer-fall rainy season. Peak flowering was delayed until August in 1987, approximately the time when summer rains began during that year. However, a wet fall in that year may be the reason for the extended peak which lasted through March 1988. Summer rains started "on time" in June of 1988 and flowering also rapidly increased. Rains diminished by September, however, and flowering rapidly decreased. This period coincides with the beginning of the extended drought.

Fall/winter fruiting species such as *T. radiata* and *M. foetidissimum* have also shown flowering/fruiting responses which were associated with drought or abundant rainfall. In *T. radiata*, the best flowering/fruiting year occurred in 1988, when abundant rains coincided with the flowering/fruiting period. During drought years, fruiting has generally been poor. The best fruiting year in *M. foetidissimum* during our surveys occurred in 1987 during a wet fall and winter. Both of these species also seem to reflower as a result of poor fruit set. This has been most noticeable during drought conditions.

The location of survey areas also played a role in our estimates of overall fruit production. The trees in our suburban phenology site seem to be least affected by lack of rainfall. Presumably,

the effects of drought are mitigated by extraneous water sources such as lawn watering and septic system outflow. The trees in our sites on Lignumvitae Key and in North Key Largo, however, produce crops which vary considerably from year to year and may reflect differences in amounts of rainfall.

The pooling of data from our three sites tends to "smooth out" the yearly variation observed at individual sites and also eliminates site variation. For *M. toxiferum*, the combining of data appears to be problematic in that both the percent of trees with ripe fruit and the competitive indices indicate that *M. toxiferum* was similarly abundant in 1987 and 1988. However, when individual site data are examined, variation did exist between sites which may have had important effects on foraging pigeons. Only *M. toxiferum* trees at the Lignumvitae site had higher competitive indices in 1987 than 1988 for the period June through September (Table 38). The competitive indices from the North Key Largo site were virtually the same in 1987 and 1988. However, the competitive indices in 1988 at the suburban site were substantially higher than in 1987. The 1988 values were also higher than those in 1989. The 1989 values, however, were not as low as one might expect considering the severity of the drought. Again, extraneous water sources in our suburban site may help to alleviate the effects of drought. The foraging habitat of our suburban site is perhaps more representative of the type of fragmented forest currently available to breeding pigeons than is either the North Key Largo or Lignumvitae site. Telemetry data indicate that neither of the latter two sites were used extensively by pigeons nesting on our study keys in northeastern Florida Bay (unpubl. data). If breeding pigeons are preferentially using proximate feeding areas, then the fragmented forests and suburban areas of the mainline Keys from Plantation Key to the southern half of Key Largo may be chosen if preferred food crops such as *M. toxiferum* are particularly abundant. During boat counts at Middle Butternut Key in 1988, large flight lines were observed from Bottle and Middle Butternut keys heading toward Key Largo during the second half of the breeding season (unpubl. data). These large flight lines toward the mainline Keys were not observed in either 1987 or 1989, but there is evidence indicating that large numbers of birds were flying north to the mainland in 1989 (unpubl. data).

Although we feel that the fruit crop of *M. toxiferum* was more abundant in 1988, the data we present do not support this claim. Our categories may be too broad to adequately demonstrate yearly variation at the upper levels of fruiting intensity.

Throughout the year, a wide variety of fruits are eaten by pigeons (Fig. 51, Table 32). The largest variety of fruits are available during mid-fall to early winter (N=27), while the smallest variety are available during late spring through early summer (N=18). Many of the tree species produce fruit at times of the year that make fruits unavailable to nesting pigeons. Others are available during all or part of the pigeon nesting season but are not used to any great extent by nesting pigeons (unpubl. data). Trees such as *N. coriacea*, *T. radiata*, *B. simaruba*, *Chiococca* spp., *Eugenia* spp., *B. ovata*, *Guettarda* spp., and *Coccoloba* spp. produce fruit that is mostly available after the nesting season. These fruits seem to be particularly important to juveniles and to wintering adults. In spring, *B. simaruba* and *Coccoloba diversifolia* are used heavily by pigeons returning to the keys in April (pers. obs.; unpubl. data, Carrington *et al.*). Other species such as *S. erianthum*, *Krugiodendron ferreum*, *Ilex cassine*, and *B. salicifolia* are generally available during the nesting season, but their use seems to be sporadic and dependent upon availability of more preferred fruits (unpubl. data).

NESTING SEASON

White-crowned Pigeons started new clutches over a 125 day span during this study. The earliest clutch was started on 12 May and the latest on 14 September. The onset of nesting varied by 11 days between the years, but the termination of nesting varied by more than 2 weeks. The onset of nesting is probably determined by the ability of birds to reach reproductive condition which is probably related to food availability. Our phenology data is not on a fine enough scale to elucidate the reasons for the differences. The termination of nesting appears also to be related to food availability. In 1988 new clutches were started into mid-September and a substantially larger number of nests were active during September than in any other year. Of the three years of phenology data, 1987 and 1988 had the most abundant supply of *M. toxiferum* fruit. In 1989, the supply was substantially less and few nests remained active into September.

Food supply also appeared to influence the total number of pigeons attempting to nest. In all years except 1985, more nests were started after *M. toxiferum* fruit became available. In 1988, almost 33-50% more nests were started on Middle Butternut Key than in any other year. These additional nests were initiated in the second half of the season when *M. toxiferum* fruit was ripe. Also in 1988, the second wave of nesting began earlier in the summer than in the other years and

this appeared to be correlated with *M. toxiferum* beginning to ripen two weeks earlier than it did in the other years. We suspect that the lull in new nest starts that occurs between the first nesting wave and the second nesting wave is a result of pigeons waiting for *M. toxiferum* fruit to ripen.

The onset of nesting at Bottle Key was always a few days to a week later than the onset at Middle Butternut Key. Bottle Key is 3-4 km farther from the mainline Keys than Middle Butternut Key. The first birds to attain reproductive condition may settle on keys closer to the foraging areas. Birds nesting on keys closer to the foraging areas would need to expend less energy on flight than those from farther keys. We know from banding returns that some birds do nest on the same key on which they hatched. We also know from telemetry data that adults do occasionally shift nesting keys during the breeding season. We suspect that flight distance to foraging grounds may play an important role in breeding ecology but much work still needs to be done. In 1988, large flight lines from both Bottle Key and Middle Butternut Key were headed toward the mainline Keys (pers. obs.). In 1989, when *M. toxiferum* fruit was scarce, flight lines from Bottle Key were headed primarily to the southern tip of mainland Florida. *M. toxiferum* fruit appeared more abundant in some of the wetlands on the mainland (Strong, Sawicki and Bancroft, unpubl. data) but the flight distances to these areas were 20 km longer. We suspect this added flight distance and time may have contributed to the lower nesting success in 1989 versus 1988.

Variation in the timing and duration of the breeding season in other Columbids also have been attributed to food availability. The nesting season of Wood Pigeons in Europe varies with the availability of mast crops (Cramp 1972). In Puerto Rico, White-crowned Pigeons breeding lasted only 92 days at a site characterized by seasonality of resources, but lasted 192 days in an area where food was available year-round (Wiley and Wiley 1979). In Puerto Rico, White-crowned Pigeons have bred outside the normal nesting season when an unseasonal abundance of fruits was occurring (Faaborg, in Wiley and Wiley 1979).

NESTING SUCCESS/PHENOLOGY

The nesting success of White-crowned Pigeons is closely tied to the fruiting abundance of four species: *M. toxiferum*, *G. discolor*, *F. aurea*, and *F. citrifolia*. All four of these species show the greatest increase in fruit production during the summer nesting period. Fruit of *F. aurea* and *F. citrifolia* are available all year, however, during the period June through August fruit production

increases and a large percentage of trees are producing fruit. The fruits of *M. toxiferum* do not begin to ripen until July, but are then available for the remainder of the pigeon nesting season. The period of peak fruit abundance occurs during August, also the period of highest pigeon nesting activity. *G. discolor* produces fruit throughout the summer and into the fall. Although the period of peak fruit production (June - September) overlaps the nesting season of White-crowned Pigeons, within this period are continuous cycles of fruit production. Since the period from flowering to ripe fruit is approximately two weeks, there are several periods throughout the summer when *G. discolor* is abundant. Since *G. discolor* produces successive crops of fruit throughout the summer, it is particularly dependent on rainfall to sustain the flowering/fruiting cycle.

The nesting season of White-crowned Pigeons closely overlaps the period of peak fruit abundance of these four tree species (Fig. 52). Within this period, however, there are clearly preferences for particular types of fruit at different points in the nesting season. During the first wave of nesting in June and early July, the two *Ficus* spp. occupy a much larger segment of the fruit diet (up to 50%) of nestling White-crowned Pigeons than any other fruit (Fig. 48). Presumably, this choice is based on availability of *Ficus* fruit more than any other factor. *G. discolor* is second in importance in the diet during this period and reflects the initial flush of new ripe fruit. Omitting crop milk, the rest of the diet consists of miscellaneous species. During the second, and larger, wave of nesting that occurs in July and August there is distinct switch from *Ficus* spp. to *M. toxiferum*. This switch occurs during the period when *M. toxiferum* fruit is beginning to ripen and continues through peak fruit availability. *M. toxiferum* is clearly a preferred fruit to feed to nestlings. Indeed, the fruit content of crop samples taken from nestlings at this time contain over 60% *M. toxiferum* fruit (Fig. 48). During this same period, *Ficus* has nearly dropped out of the nestling diet although it is still available. The remainder of the fruit content of the nestling crop samples consists of a large percentage of *G. discolor* and smaller percentages of miscellaneous fruits.

Although *M. toxiferum* visually appears ripe in June (Fig. 4b), we did not find it in crop samples until July, suggesting that pigeons are using something other than visual cues to determine a "ripe" fruit. Foraging observations have demonstrated that pigeons spend much time searching while foraging in *M. toxiferum* (unpubl. data), often ignoring fruits which visually appear ripe, and sometimes even tugging on fruits to find ripe ones (unpubl data ,pers. comm. - M. Carrington). In 1990, pigeons were observed in *M. toxiferum* up to two weeks before the fruit began to appear in

crop samples. Presumably, these birds were "sampling" the fruit crop during the early stages of ripening (unpubl. data). The actual ripening period of *M. toxiferum* probably varies somewhat from year to year. In 1988 the competitive index was nearly as high in June as in July (Fig. 4c). Crop samples in that year contained *M. toxiferum* fruit earlier than any other year of the study.

Comparing the nesting success during the period 1987 through 1989 demonstrates the importance of *M. toxiferum*. In 1987, the fruit crop of *G. discolor* was good, but somewhat late because of a delay in the onset of the rainy season. The ripening of the *M. toxiferum* crop was also delayed and some fruit abortion near the time of ripening resulted in a moderate fruit crop that summer. Overall nesting success was only slightly better in 1987 than in 1989. In 1988 the rainy season started on time and rains were ample. Summer fruit crops, particularly *M. toxiferum* and *G. discolor* were good to abundant. Overall nesting success was slightly over 50%. In 1989, south Florida was in the middle of a protracted drought. Production of fruit by all species decreased and availability of *M. toxiferum* was particularly low in the keys' hammocks. Overall nesting success was less that year than any other study year, even the last drought year, 1985.

Although some year-to-year variation occurs, nesting success is generally higher in the second half of the season than in the first half. Nestling survival also shows a similar trend for most years of the study. On Middle Butternut Key in the drought years of 1985 and 1989, the reverse was true, early season success was higher than late season. Availability of ripe *M. toxiferum* fruit is directly correlated with increased nesting success. Therefore, during drought years such as 1989 (and presumably 1985, although phenology studies were not being done at that time), lack of sufficient ripe *M. toxiferum* fruit, and perhaps a lower nutritional content of the fruit itself, was responsible for lower nesting success later in the season. On Bottle Key in 1989, however, late season nesting success was significantly higher than early season. Predation by Red-winged Blackbirds was extremely high early in the season. Much of this predation seems to have occurred as a result of disturbance to nesting adults during our nest-check procedure. Several adult Red-winged Blackbirds apparently learned to follow the biologists along the transects. The drought of 1989 may have exacerbated the situation making the blackbirds more opportunistic than usual.

The length of the nesting season also varies between years. Although nest initiations were always later on Bottle Key than Middle Butternut Key, yearly variations also occurred which probably were related to fruit availability. Between years, the earliest nests were found up to nine days apart,

on Middle Butternut Key, and 12 days apart on Bottle Key. Variability in *Ficus* spp. production probably determines when the earliest nests are initiated. Nest initiations generally started earlier during drought years (1985, 1989) than non-drought years. In 1987, nest initiations started only slightly later and again may be related to the drought which lasted until July in the keys. The May competitive index for *F. aurea* was much higher in 1989 than in either 1987 or 1988 and may be the reason for the earlier nest initiations observed in 1989. Although phenology surveys were not yet being performed, the similar starting date in 1985 on Middle Butternut Key suggests an earlier abundance of *Ficus* spp. in that year also. Late in the nesting season, however, there is even greater variation between years. The nesting period extended approximately two weeks longer in 1988 than in either 1987 or 1989 on both Middle Butternut and Bottle keys. At this point in the nesting season, *M. toxiferum* is the most important component of the fruit diet of nestlings. The availability of this fruit apparently contributed, not only to increased nesting success in 1988, but also permitted the nesting season to extend well into September. Overall, the nesting season on both Middle Butternut and Bottle keys was longer in 1988 than any other year of the study.

Further evidence pointing towards the importance of *M. toxiferum* in the diet of nestling White-crowned Pigeons is the high energy content of this fruit. *M. toxiferum* fruit contained more energy per gram of dry weight than any other fruit found in crop samples. Much of the difference is in the lipid content of these fruits. Of the fruit species which we analyzed, *M. toxiferum* had the highest levels of lipids of all fruits except for *N. coriacea*. The fruit of *N. coriacea*, however, generally does not ripen and become available until after the nesting season and is more important to fledged young and "wintering" White-crowned Pigeons. Of the energetic components of fruit (carbohydrates, proteins, and lipids), lipids are by far the most energetically valuable. They contain twice the stored energy per gram of carbohydrates. The high level of lipids in *M. toxiferum* relative to the other three important summer crops makes this fruit an important component of the nestling's diet.

Each parent only makes one trip per day to a foraging site (unpubl. data), so it is important to have a high energy food source. An additional energetic consideration is the ratio of pulp to seed(s) in an individual fruit. If nestling pigeons are digesting seeds along with pulp, as appears to be occurring in *G. discolor* and *M. toxiferum*, then a certain amount of energy is also being derived from these seeds. In *M. toxiferum*, energetic content of seeds may be an additional factor in its

overall nutritional value. The seeds of *Ficus* spp. are not digested (unpubl. data) and, therefore, the energy content is not available to nestlings. Indeed, more than 1/2 of the energy content in *F. aurea* and *F. citrifolia* is found in the seeds. *G. discolor* also is used more heavily than *Ficus* when available. Pigeons can consume two to three times more *G. discolor* fruit than *Ficus* fruit in a single foraging bout (unpubl. data). When the energetic content of the seed is added to *G. discolor* and subtracted from *Ficus*, *G. discolor* provides more energy per payload delivered to nestlings.

Seasonal variation in energetic content of these fruits also demonstrates the value of *M. toxiferum*. Protein levels remained fairly constant throughout the May through December sampling period. Soluble carbohydrates were the highest in June in *M. toxiferum*. This time period pre-dates ripening of this fruit, and, therefore comes at a time when pigeons are not utilizing this fruit. In *G. discolor* soluble carbohydrates peak in July and may explain why this fruit is particularly important before *M. toxiferum* fruit is available. In the *Ficus* spp., carbohydrate levels were variable throughout the nesting period. Lipid levels in all fruits, except for *M. toxiferum*, remained low throughout the nesting period. In *M. toxiferum*, however, lipid levels increased in June and July, during the fruit ripening stage, and peaked in August.

In summary, early in the nesting season, none of the consumed fruits are high in lipids or protein and most energy must be derived from carbohydrates. *Ficus* spp. may be chosen largely on the basis of availability. Likewise, *G. discolor*, which is also available in varying amounts throughout the nesting season, may be chosen because of general abundance throughout many hammock and suburban foraging areas. When *M. toxiferum* is most available, *i.e.* ripe, it also contains the highest levels of lipids (August). The availability of this fruit and the marked shift to it in the diet of nestlings during the peak nesting period, is strongly indicative of the importance of this high energy fruit to the development of nestlings.

NUTRITIONAL CONSIDERATIONS

Willson (1986) found that bird-dispersed fruits in Illinois varied greatly in nutrient and energetic content. Our results are within ranges reported by Johnson *et al.* (1985) for protein, lipids, and soluble carbohydrates. Consistent with our findings, Willson (1986) reported higher energetic content in the pulp than the seed of bird-dispersed fruits.

Many of the biological patterns we have observed have a common temporal pattern. The peak in nest initiations, shift in diet, and increase in nestling survival, all coincide with the ripening of *M. toxiferum* fruit. Our nutritional analyses not only indicate that *M. toxiferum* has the highest energy content of all fruits consumed by White-crowned Pigeons during the breeding season, but that they reach a seasonal peak in lipids and energy content when they ripen in late July and August. This parallels the second and major peak in pigeon breeding activity. Snow (1971) suggested that the nutritional features of bird dispersed fruits vary seasonally to match the seasonal demands of the main dispersers. In the Mediterranean, fruits ripening during the dry summer have the highest water content when water demands of avian dispersers are high (Herrera 1982). During the rainy winter, when birds have peak energy demands, fruits have the highest lipid content. Willson (1986), however, found no seasonal trends in nutrient content in bird-dispersed fruits in Illinois. Except for *M. toxiferum*, none of the major fruits used during the nesting season had seasonal trends that appeared related to the needs of avian dispersers. However, the fall peak in carbohydrates and energy in *Ficus* may be timed to coincide with the needs of wintering migrants.

Willson (1986) also reported that feeding preferences of birds in coniferous forest in Washington indicated that birds forage preferentially on fruits with large amounts of pulp; fruit nutrients had no detectable effect on choice. *M. toxiferum*, thus has 2 characters that might make it a preferential foraging item; it has high lipid and energy content that coincides with the peak demands of White-crowned Pigeons and the fruit is largely pulp.

Based on the analysis of crop samples, *M. toxiferum* and *G. discolor* seem preferred to both *Ficus* species. Sorenson (1981) concluded that factors other than nutritional quality, such as palatability, may be important in determining the feeding preferences of different species of frugivorous birds. In addition, brightly colored fruits may serve as attractants to foraging birds (Willson and Thompson 1982). *G. discolor* is bright red. It may be especially attractive and palatable to pigeons without being energetically rewarding. The consumption of either *Ficus* species or *G. discolor* alone may impose constraints on efficient energy utilization. *Ficus* fruit has 3 times the volume of *M. toxiferum* but only about half the energy. Nestlings may not be able to process the bulk of fruit needed to satisfy energy demands on a *Ficus* diet. *G. discolor* is only half the size and energy of *M. toxiferum*. Adult pigeons would need to consume large amounts of this fruit to obtain a comparable amount of energy. In a heavily laden *G. discolor*, they can consume large

numbers of fruit in a relatively short time (Sawicki and Strong, unpubl. data), whereas in *M. toxiferum* trees they spend a great deal of time searching for a ripe fruit before they attempt to eat one. Long-tailed manakins (*Chiroxiphia linearis*) feeding on lower-quality fruit experience a 5.8-fold increase in the time needed to feed themselves, influencing their ability to feed young and possibly influencing fledging success (Foster 1977).

Herrera (1982) supported the hypothesis that fruit features have evolved to meet dispersers' demands. *M. toxiferum* and *G. discolor* produce a relatively soft seed that pigeons generally digest. Pigeons do occasionally drop the fruit of these species especially when transferring the fruit to young. Nesting adults and young, therefore, represent poor dispersers of the seeds of these two plant species. For the other food species, pigeons either pass the seeds or regurgitate them. Seeds of a number of these species have successfully germinated after passing through a pigeon's digestive system (M. Carrington, pers. comm.). Feeding *M. toxiferum* and *G. discolor* fruit to young represents a significant energy savings to adults because more of the bulk of food is digestible by the young.

Whether the ecological correlates between White-crowned Pigeon reproduction and *M. toxiferum* is the result of diffuse coevolution or the result of complementarity between bird and plant requirements for energy, water, and nutrients (Janzen 1980) cannot be answered. However, the data clearly suggest that *M. toxiferum* is the single most important fruit available to White-crowned Pigeons during the breeding season.

MORTALITY SOURCE

Those factors that reduce the production of young most are the ones that place the greatest selective pressures for modification of breeding (Ricklefs 1973). Predation was by far the greatest source of mortality of eggs and nestlings. Predation accounted for over 75% of the losses on Middle Butternut Key, 80% on Bottle Key, and 65% on West Butternut Key. Our classification of abandonment and starvation were distant second and third affects. Red-winged Blackbirds are common breeding birds on the keys. Blackbirds have been observed poking holes in eggs at unattended nests and eating the contents. On Bottle Key, they represented a serious nest predator in some years because some individuals learned to follow us. Red-winged Blackbirds occasionally chase adult pigeons from the nest (pers. obs., Blankinship 1977), but they are probably not a

significant predator of medium-sized or larger young. Rats were common on Middle Butternut Key and we suspect also on West Butternut and Bottle keys. These could represent a significant nest predator. We did find nests in which the egg shells were broken in hundreds of small pieces suggesting mammalian rather than avian predation. In some years many medium to large size young disappeared from nests and we characterized the loss as predation. These couldn't have been taken by Red-winged Blackbirds and we rarely found pieces of carcasses. American Crows were not on these three nesting keys during this study although they did appear on Bottle and Middle Butternut keys in 1990. Great White Herons (*Ardea herodias occidentalis*) may also represent a potential nest predator. Land crabs (*Cardiosoma guanhum*) and hermit crabs (*Coenobita clypeatus*) are common on these three keys and we suspect they will scavenge dead birds but we doubt they represent a significant predator. We suspect predation rate on nest contents is controlled by the nest attendance behavior of the parents.

Predation rates between the years on Middle Butternut Key were correlated with general availability of fruit. The predation rate on both eggs and nestlings tended to be higher in years that food was less available. In 1989, egg predation accounted for 36% of all eggs and nestling predation accounted for 59% of all nestlings, whereas in 1988 only 18% of the eggs were lost to predators and only 26% of the nestlings. We suspect that nest attendance may decrease during poor fruiting years and this exposes eggs or young to increased predation risk. We also suspect that abandonment rates are higher in poor fruiting years and because nest contents disappear so quickly we record them as predation. Based on our telemetry work we know that females incubate eggs and brood young during the night and that males incubate and brood during the day (Strong, Sawicki, Bancroft, unpubl. data). When young are 5-7 days old, males decrease their brooding time, only returning to the key long enough to feed young but females continue to brood through the night until the young are much older. We have had an adult male pigeon skip a day of feeding young and we have had one abandon a young that was still in the nest. If a female does not return to the nest for the night this will expose the young to possible rat predation and may account for some of the losses of medium to large young during poor fruiting years.

RECOMMENDATIONS

White-crowned Pigeons are currently listed as a threatened species in Florida (Kale 1978, Wood 1990). We agree with the FGFWFC that they should remain listed as threatened (Milsap *et al.* 1990). Their small population size and nesting and feeding habitat requirements contribute to their vulnerable status.

We suspect the breeding population in Florida is relatively small. Reeves (1977) gave an estimate of 10,000 breeding individuals, however, this value was extrapolated from only a few nesting keys (R. Paul, pers. comm.). During the 1991 breeding season, we plan to do some field work that will provide a better estimate of the actual breeding population in Florida Bay. The techniques we refine during 1991 may also be useful in the Lower Keys to provide a total estimate for Florida. The relatively small population size places the species at risk in Florida.

White-crowned Pigeon nesting areas are primarily on mangrove islands that are protected in Everglades National Park or in Federal Refuges in the Lower Keys. These should continue to provide safe nesting habitats from human disturbance and development. Raccoon expansion on to more of the nesting keys may represent a serious threat in some areas. In addition the gradual expansion of American Crows on to more islands in Florida Bay and into the Florida Keys may represent a future threat. Currently, in Florida Bay crows are found only on islands with heron, pelican or cormorant colonies.

Destruction of suitable foraging habitat on the mainline Keys represents the most serious threat to White-crowned Pigeons. Our data suggest that suitable foraging habitat on the mainline Keys are critical for successful nesting by White-crowned Pigeons. Although adults are capable of flying the long distances to foraging areas on the mainland, these areas do not appear to provide sufficient food for high nesting success. The overall diversity of fruiting species used by pigeons is lower on the mainland than on the mainline Keys (Snyder *et al.* 1990: appendix, Bancroft *et al.*, unpubl. data). In the years when major flight lines went to the mainland, nesting success was relatively low, whereas in the years with the best nesting success, *M. toxiferum* fruit production on the mainline Keys was high. In addition, when young pigeons first disperse from the nesting keys, most fly to the mainline Keys rather than to the mainland (Strong and Sawicki, unpubl. data). This happened in both 1989 and 1990 when feeding conditions were relatively poor on the mainline Keys. We suspect that suitable feeding areas for young pigeons in the mainline Keys may be

critical for increasing the probability that they survive while they are learning how to feed on their own.

Much of North Key Largo (areas north of junction of US 1 and SR 905) are in state or federal ownership and are currently protected as natural areas. However, we do not feel that these areas substitute for suitable feeding areas farther south on Key Largo or on other mainline Keys. Most of North Key Largo is as far from nesting keys as mainland Everglades National Park and may place the same constraints on nesting birds as flying to the mainland. In addition, these areas are too far from nesting keys to represent suitable landing sites for the first flights of young birds. If young birds fly to the mainline Keys, they will land in developed areas of Plantation Key and Key Largo. We, therefore, feel that protecting suitable habitat throughout the mainline Keys will be critical for maintaining a healthy population of White-crowned Pigeons.

Abundant *M. toxiferum* fruit appears critical for large numbers of breeding pigeons to successfully produce young. When *M. toxiferum* fruit is abundant more pigeons nest, more are successful, more young survive, and young grow faster. *M. toxiferum* produces a toxin that creates a severe skin rash on most humans. As a result *M. toxiferum* trees are generally removed from developed areas. This procedure will continue to decrease the volume of fruit available to breeding pigeons. Where possible, maximum protection of *M. toxiferum* trees in the Florida Keys should be pursued. Where they cannot be protected, we recommend that the Florida Game and Freshwater Fish Commission develop a series of recommendations for planting trees that will provide alternative food for pigeons during the breeding season. Monroe County currently requires the planting of native trees or bushes under certain conditions before a person can receive their occupational certificate to move into a new house. Trees that provide fruit should be encouraged to be planted under this plan and under other replanting plans.

We recommend the planting of *G. discolor* and *B. ovata* as suitable breeding season foods for pigeons. *G. discolor* regularly fruits throughout the nesting season. In suburban areas where they receive supplemental water from septic systems, *B. ovata* appears to fruit regularly during the nesting season. Both these trees grow to attractive medium-size trees. We do not recommend the planting of *Ficus* species primarily because they grow to extremely large size and their roots create problems for septic tanks, driveways, and foundations. We feel that the planting of *Ficus* would be difficult to justify considering these problems. We, however, do not encourage the removal of *Ficus*

trees. Most of the other species recorded as food of pigeons either do not fruit during the nesting season or generally do not produce large fruit crops.

LITERATURE CITED

- Allen, R.P. 1942. The Roseate Spoonbill. Dover Publications, Inc., New York, New York.
- American Ornithologists' Union. 1983. Check-list of North American Birds. 6th Edition. A.O.U., Washington, D.C.
- Appenroth, K.J. and H. Augsten. 1987. An improvement of the protein determination in plant tissues with the dye-binding method according to Bradford. *Biochem. Physiol. Pflanzen* 182:85-89.
- Austin, O.L. 1948. Predation by the common rat (Rattus norvegicus) in the Cape Cod colonies of nesting terns. *Bird-Banding* 19:60-65.
- Bancroft, G.T. and R. Bowman. 1987. Relationship between the reproductive ecology of the White-crowned Pigeon and the fruiting phenology of tropical hardwood hammock trees. Annual Report to the Florida Game and Fresh Water Fish Commission, Tallahassee, Fl. 68 pp.
- Bent, A.C. 1932. Life histories of North American gallinaceous birds. U.S. Nat. Mus. Bull. 162.
- Berger, A.J. 1972. P. 86 in *Hawaiian Birdlife*. The Univ. Press of Hawaii, Honolulu, Hawaii.
- Biegii, V. 1970. *Las aves de Puerto Rico*. Univ. of Puerto Rico. Barcelona, Spain. 371 pp.
- Blankinship, D.R. 1977. Studies of White-crowned Pigeon populations, natural history and hunting in the Bahamas. Pp. 36-39 in *Proceedings of the International White-crowned Pigeon Conference*. Bahamas National Trust, Nassau, Bahamas.
- Bradford, M.M. 1972. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Anal. Biochem.* 72:248-254.
- Bronstein, J.L. 1989. A mutualism at the edge of its range. *Experientia* 45:622-637.
- Burger, J. and C. Hahn. 1977. Crow predation on Black-crowned Night Heron eggs. *Wilson Bull.* 89:350-351.
- Craighead, F.C. Sr. 1969. Vegetation and recent sedimentation in the Everglades National Park. *Florida Natur.* 42:62-69.

- Craighead, F.C. Sr. 1971. The trees of South Florida: Vol. 1, The natural environment and their succession. Univ. Miami Press, Miami, Florida. 212 pp.
- Cramp, S. 1972. The breeding of urban woodpigeons. *Ibis* 114:163-171.
- Cruz, F. and J.B. Cruz. 1987. Control of Black Rats (Rattus rattus) and its effect on nesting Dark-rumped Petrels in the Galapagos Islands. *Vida Sylvestre Neotropical* 2:3-13.
- Dubois, M., K.A. Gilles, J.K. Hamilton, P.A. Rebers and R. Smith. 1956. Colorimetric method of determination of sugars and related substances. *Anal. Chem.* 28:350-356.
- Foster, M.S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58:73-85.
- Fourneir, L.A. and C. Charpentier. 1975. El tamano de la muestra y la frecuencia de las observaciones en el estudio de las características fenologicas de los arboles tropicales. *Turrialba* 25:269-287.
- Frankie, G.W., H.G. Baker and P.A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecology* 62:881-919.
- Frederick, P.C. and M.W. Collopy. 1989. The role of predation in determining reproductive success of colonially nesting wading birds in the Florida Everglades. *Condor* 91:860-867.
- Freeman, N., F.T. Lindgren, Y.C. Ng and A.V. Nichols. 1957. Serum lipid analysis by chromatography and infrared spectrophotometry. *J. Biol. Chem.* 227:449-464.
- Frohring, P.C. and J.A. Kushlan. 1986. Nesting status and colony site variability of Laughing Gulls in southern Florida. *Fla. Field Nat.* 14:1-17.
- Goodwin, D. 1967. Pigeons and Doves of the World. Trustees of the British Museum (Nat. Hist.), London, U.K.
- Harris, S.W., M.A. Morse and W.H. Longley. 1963. Nesting and production of the mourning dove in Minnesota. *Amer. Midl. Nat.* 69:150-172.
- Hensler, G.L. 1985. Estimation and comparison of functions of daily nest survival probabilities using the Mayfield method. pp 289-301 *In*: Morgan, B.J.T. and P.M. North, (eds.). *Statistics in Ornithology*. Springer-Verlag, New York, New York. 418 pp.
- Hensler, G.L. and J.D. Nichols. 1981. The Mayfield method of estimating nest success: A model, estimators, and simulation results. *Wilson Bull.* 93:42-53.

- Herrera, C.M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* 63:773-785.
- Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of birds' eggs. *Auk* 96:73-77.
- Janzen, D.H. 1980. When is it coevolution? *Evolution* 34:611-612.
- Johnson, R.A., M.F. Willson, J.N. Thompson and R.L. Bertin. 1985. Nutritional values of wild fruit and consumption by migrant frugivorous birds. *Ecology* 66:819-827.
- Kale, H.W. II (Ed.). 1978. Birds, Vol. 2, Rare and endangered biota of Florida. Univ. Presses of Florida. 121 pp.
- Kepler, C.B. 1967. Polynesian rat predation on nesting Laysan Albatrosses and other Pacific seabirds. *Auk* 84:426-430.
- Kilham, L. 1986. Renesting of American Crows in Florida and predation by raccoons. *Fla. Field Nat.* 14:21-23.
- Lawrence, J.M. and R.W. Schreiber. 1974. Organic material and calories in the egg of the Brown Pelican, *Pelecanus occidentalis*. *Comp. Biochem. Physiol.* 47:435-440.
- Lopinot, A.C. 1951. Raccoon predation on the Great Blue Heron, *Ardea herodias*. *Auk* 68:235.
- Mayfield, H.F. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73:255-261.
- Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87:456-466.
- Milsap, B.A., J.A. Gore, D.E. Runde and S.I. Cerulean. 1990. Setting priorities for the conservation of fish and wildlife species in Florida. *Wild. Monogr.* 111. 57 pp.
- Murton, R.K. 1958. The breeding of woodpigeon populations. *Bird Study* 5:157-183.
- Neter, J. and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc. Homewood, Illinois. 327 pp.
- Noss, R.F., H.W. Kale, II and C.W. Biggs. 1985. Florida Breeding Bird Atlas 1986-1990 - Handbook for Cooperators. Florida Audubon Society, Maitland, Florida.
- Owre, O.T. 1978. White-crowned Pigeon. Pp. 43-45 in Rare and Endangered Biota of Florida - Birds. Vol. II. (H.W. Kale II, ed.). Univ. Presses of Florida, Gainesville, Florida.
- Paine, R.T. 1971. The measurement and application of the calorie to ecological problems. *Ann. Rev. Ecol. Syst.* 2:145-164.

- Post, W. 1990. Nest survival in a large ibis-heron colony during a three-year decline to extinction. *Colonial Waterbirds* 13:50-61.
- Powell, G.V.N. 1987. Habitat use by wading birds in a subtropical estuary: implications of hydrography. *Auk* 104:740-749.
- Preston, R.W. 1969. Shapes of birds' eggs: extant North American families. *Auk* 86:246-264.
- Rahn, H. and A. Ar. 1974. The avian egg: incubation time and water loss. *Condor* 76:147-152.
- Rahn, H., C.V. Paganelli and A. Ar. 1975. Relation of avian egg weight to body weight. *Auk* 92:750-765.
- Rearden, J.D. 1951. Identification of waterfowl nest predators. *Jour. Wildl. Manage.* 15:386-395.
- Reeves, H.M. 1977. White-crowned Pigeons in the United States. Pg. 10 *in* Proceedings of the International White-crowned Pigeon Conference. Bahamas National Trust, Nassau, Bahamas.
- Ricklefs, R.E. 1973. Fecundity, mortality, and avian demography. Pp. 366-435 *in* D.S. Farner (ed.). *Breeding biology of birds*. Nat. Acad. of Science, Washington, D.C.
- Schomer, N.S. and R.D. Drew. 1982. An ecological characterization of the Lower Everglades, Florida Bay, and the Florida Keys. U.S. Fish Wildl. Serv., Off. Biol. Serv. FWS/OBS-82/58.
- Shields, M.A. and J.F. Parnell. 1986. Fish Crow predation on eggs of the White Ibis at Battery Island, North Carolina. *The Auk* 103:531-539.
- Siemon, C.L. 1985. Florida Keys Growth Management Plan: Background data elements. Monroe County Commission.
- Snow, D.W. 1971. Evolutionary aspects of fruit-eating in birds. *Ibis* 113:194-202.
- Snyder, J. R., A. Herndon, and W. B. Robertson, Jr. 1990. South Florida Rockland. Pp. 230-277 *in* *Ecosystems of Florida* (R. L. Myers and J. J. Ewel, eds.). Univ. of Central Florida Press, Orlando, Florida.
- Sorensen, A.E. 1981. Interactions between birds and fruit in a temperate woodlot. *Oecologia* 50:242-249.
- Sprunt IV, A. 1977. Notes on the breeding biology of the White-crowned Pigeon in Florida Bay. Pp. 40-42 *in* Proceedings of the International White-crowned Pigeon Conference. Bahamas National Trust, Nassau, Bahamas.

- Tomlinson, P.B. 1980. The Biology of Trees Native to Tropical Florida. Harvard Univ. Printing Office. Allston, Massachusetts.
- Verbeek, N.A.M. 1982. Egg predation by Northwestern Crows: its association with human and Bald Eagle activity. *Auk* 99:347-352.
- Wetmore, A. 1931. The birds of Haiti and the Dominican Republic. U.S. Natl. Mus. Bull. 155. 483 pp.
- Wheelwright, N.T. 1985. Competition for dispersers, and timing of flowering and fruiting in a guild of tropical trees. *Oikos* 44:465-477.
- Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
- Wiley, J.W. 1979. The white-crowned pigeon in Puerto Rico: status, distribution and movements. *J. Wildl. Manage.* 43:402-413.
- _____ and B.N. Wiley. 1979. The Biology of the White-crowned Pigeon. *Wildl. Monogr.* 64. 54 pp.
- Willson, M.F. 1986. Avian frugivory and seed dispersal in Eastern North America. *Current Ornithology* 3:223-279.
- Willson, M.F. and J.N. Thompson. 1982. Phenology and ecology of color in bird dispersed fruits, or why some fruits are red when they are "green". *Can. J. Botany* 60:701-713.
- Wood, D.A. 1990. Official lists of endangered and potentially endangered fauna and flora in Florida. 1 August 1990. Fla. Game and Fresh Water Fish Comm., 23 pp.

Table 1. Laying dates of White-crowned Pigeons nesting in Florida Bay.

Location	Year	# clutches	Dates of Clutches			Range (days)
			first	last	mean	
Middle Butternut	1985	59	13 May	29 Aug	4 July	108
	1986	73	23 May	1 Sep	11 July	101
	1987	87	16 May	26 Aug	14 July	102
	1988	121	21 May	9 Sep	22 July	111
	1989	90	12 May	21 Aug	13 July	101
	combined	430	12 May	9 Sep	14 July	120
Bottle	1987	112	26 May	27 Aug	23 July	93
	1988	209	27 May	14 Sep	25 July	110
	1989	152	15 May	29 Aug	12 July	106
	combined	473	15 May	14 Sep	25 July	122
West Butternut	1987	66	29 May	27 Aug	23 July	90
	1988	18	30 May	24 Aug	10 July	86
	combined	84	29 May	27 Aug	20 July	90

Table 2. The number of clutches started in each year at Middle Butternut Key before and after poisonwood became available.

	Before poisonwood	After poisonwood
1985	30	29
1986	36	37
1987	31	56
1988	38	83
1989	24	66

Table 3. Clutch size relative to location and year for White-crowned Pigeons in south Florida.

Location	Year	Clutch size			Total	Mean	s.d.
		1	2	3			
Middle Butternut	1985	6	53		59	1.90	0.30
	1986	4	68	1	73	1.96	0.26
	1987	7	80		87	1.92	0.27
	1988	7	112	2	121	1.96	0.27
	1989	9	79	1	89	1.90	0.34
	combined	34	392	4	429	1.93	0.29
Bottle	1986	7	46		53	1.87	0.34
	1987	12	99	1	112	1.90	0.33
	1988	29	178	2	209	1.87	0.36
	1989	20	132		152	1.87	0.34
	combined	68	455	3	526	1.88	0.35
West Butternut	1986	4	32		36	1.89	0.32
	1987	6	60		66	1.91	0.29
	1988	9	9		18	1.50	0.51
	combined	19	101		120	1.84	0.37

Table 4. Reproductive success of White-crowned Pigeons nesting at Middle Butternut Key during 1985 through 1989.

Year	Period	# of clutches	Survival Probability (s.d.)					
			Incubation		Nestling		Overall	
1985	early	30	0.653	(0.030)	0.629	(0.032)	0.410	(0.028)
	late	29	0.486	(0.038)	0.376	(0.048)	0.183	(0.027)
	combined	59	0.573	(0.024)	0.526	(0.028)	0.301	(0.020)
1986	early	36	0.677	(0.032)	0.311	(0.035)	0.211	(0.026)
	late	37	0.741	(0.026)	0.626	(0.027)	0.464	(0.026)
	combined	73	0.713	(0.020)	0.466	(0.023)	0.332	(0.019)
1987	early	31	0.558	(0.036)	0.367	(0.042)	0.205	(0.027)
	late	56	0.479	(0.029)	0.442	(0.031)	0.211	(0.020)
	combined	87	0.507	(0.023)	0.414	(0.025)	0.210	(0.016)
1988	early	38	0.520	(0.033)	0.673	(0.030)	0.349	(0.027)
	late	83	0.763	(0.017)	0.782	(0.014)	0.597	(0.017)
	combined	121	0.682	(0.016)	0.756	(0.013)	0.516	(0.015)
1989	early	25	0.474	(0.044)	0.706	(0.032)	0.335	(0.035)
	late	64	0.423	(0.028)	0.363	(0.030)	0.153	(0.016)
	combined	89	0.436	(0.024)	0.467	(0.023)	0.204	(0.015)
Total	early	161	0.579	(0.015)	0.515	(0.016)	0.298	(0.012)
	late	269	0.586	(0.012)	0.576	(0.012)	0.338	(0.010)
	combined	430	0.583	(0.009)	0.553	(0.009)	0.323	(0.008)

Table 5. Reproductive success of White-crowned Pigeons nesting at Bottle Key during 1986 through 1989.

Year	Period	# of clutches	Survival Probability (s.d.)					
			Incubation		Nestling		Overall	
1986	late	53	0.445	(0.033)	0.533	(0.029)	0.238	(0.021)
1987	early	25	0.628	(0.039)	0.732	(0.029)	0.460	(0.034)
	late	67	0.508	(0.024)	0.460	(0.028)	0.234	(0.018)
	combined	92	0.536	(0.021)	0.547	(0.021)	0.293	(0.016)
1988	early	43	0.504	(0.035)	0.707	(0.025)	0.356	(0.028)
	late	136	0.382	(0.019)	0.863	(0.010)	0.330	(0.017)
	combined	179	0.407	(0.017)	0.820	(0.010)	0.334	(0.014)
1989	early	44	0.219	(0.035)	0.141	(0.041)	0.031	(0.010)
	late	90	0.454	(0.022)	0.432	(0.025)	0.196	(0.015)
	combined	134	0.377	(0.019)	0.343	(0.022)	0.129	(0.010)
Total	early	116	0.402	(0.022)	0.535	(0.020)	0.215	(0.014)
	late	342	0.435	(0.011)	0.616	(0.010)	0.268	(0.008)
	combined	458	0.428	(0.010)	0.595	(0.009)	0.254	(0.007)

Table 6. Reproductive success of White-crowned Pigeons nesting at West Butternut Key during 1986 through 1988.

Year	Period	# of clutches	Survival Probability (s.d.)					
			Incubation		Nestling		Overall	
1986	late	36	0.440	(0.039)	0.544	(0.036)	0.239	(0.026)
1987	early	15	0.889	(0.029)	0.208	(0.051)	0.185	(0.046)
	late	35	0.564	(0.031)	0.552	(0.036)	0.311	(0.026)
	combined	50	0.638	(0.025)	0.406	(0.031)	0.259	(0.022)
1988	early	7	0.221	(0.080)	0.491	(0.121)	0.108	(0.048)
	late	11	0.056	(0.055)	0.390	(0.142)	0.022	(0.024)
	combined	18	0.114	(0.048)	0.444	(0.093)	0.050	(0.024)
Total	early	26	0.602	(0.042)	0.318	(0.043)	0.192	(0.029)
	late	78	0.432	(0.024)	0.527	(0.026)	0.227	(0.017)
	combined	104	0.465	(0.021)	0.456	(0.023)	0.212	(0.014)

Table 7. Sources of mortality in White-crowned Pigeon eggs and nestlings at Middle Butternut Key during the 1985-1989 seasons.

Source	Eggs				Nestlings			
	#	%	% mort	% eggs	#	%	% mort	% nest.
Unhatched	26	9.7	4.7	3.1	-	-	-	-
Abandoned	36	13.4	6.4	4.3	6	2.0	1.1	1.1
Nest fell	4	1.5	0.7	0.5	4	1.4	0.7	0.7
Depredated	199	74.0	35.3	24.0	234	79.3	41.5	41.8
Starved	-	-	-	-	45	15.3	8.0	8.0
Rolled	3	1.1	0.5	0.4	2	0.7	0.4	0.4
Other	1	0.4	0.2	0.1	4	1.4	0.7	0.7
Total	269	100.0	47.7	32.4	295	100.0	52.3	52.7

Table 8. Yearly variation in the fate of eggs laid at Middle Butternut Key.

	Number (percent)				
	1985	1986	1987	1988	1989
Hatched	70 (62.5)	110 (76.9)	104 (62.3)	177 (74.7)	99 (58.2)
Unhatched	4 (3.6)	7 (5.0)	4 (2.4)	5 (2.1)	6 (3.5)
Depredated	28 (25.0)	15 (10.5)	52 (31.1)	42 (17.7)	62 (36.5)
Abandoned	10 (8.9)	9 (6.3)	4 (2.4)	11 (4.6)	2 (1.2)
Other	0	2 (1.4)	3 (1.8)	2 (0.8)	1 (0.6)
Total	112	143	167	237	170

Table 9. Yearly variation in the fate of nestlings at Middle Butternut Key.

	Number (percent)				
	1985	1986	1987	1988	1989
Fledged	28 (40.0)	46 (41.8)	38 (36.5)	118 (66.7)	35 (35.4)
Starved	12 (17.1)	6 (5.5)	11 (10.6)	12 (6.8)	4 (4.0)
Depredated	28 (40.0)	51 (46.4)	51 (49.0)	46 (26.0)	58 (58.6)
Other	2 (2.9)	7 (6.4)	4 (3.8)	1 (0.6)	2 (2.0)
Total	70	110	104	177	99

Table 10. Sources of mortality in White-crowned Pigeon eggs and nestlings at Bottle Key during the 1986-1989 seasons.

Source	Eggs				Nestlings			
	#	%	% mort	% eggs	#	%	% mort	% nest.
Unhatched	33	8.5	5.4	3.9	-	-	-	-
Abandoned	34	8.7	5.6	4.0	7	32.0	1.2	1.5
Nest fell	5	1.3	0.8	5.8	2	0.9	0.3	0.4
Depredated	307	78.9	50.5	35.9	178	81.3	29.3	38.2
Starved	-	-	-	-	26	11.9	4.3	5.6
Rolled	3	0.8	0.5	0.4	1	0.5	0.2	0.2
Broken	4	1.0	0.7	0.5	-	-	-	-
Killed	3	0.8	0.5	0.4	2	0.9	0.3	0.4
Other	-	-	-	-	3	1.4	0.5	0.6
TOTALS	389	100.0	64.0	45.5	219	100.0	36.0	47.0

Table 11. Yearly variation in the fate of eggs laid at Bottle Key.

	Number (percent)			
	1986	1987	1988	1989
Hatched	61 (61.6)	107 (60.8)	174 (52.4)	124 (50.0)
Unhatched	2 (2.0)	9 (5.1)	14 (4.2)	8 (3.2)
Depredated	34 (34.3)	49 (27.8)	123 (37.0)	101 (40.7)
Abandoned	2 (2.0)	8 (4.5)	9 (2.7)	15 (6.0)
Other	-	3 (1.7)	12 (3.6)	-
Total	99	176	332	248

Table 12. Yearly variation in the fate of nestlings at Bottle Key.

	Number (percent)			
	1986	1987	1988	1989
Fledged	31 (50.8)	46 (43.0)	127 (73.0)	43 (34.7)
Abandoned	3 (4.9)	4 (3.7)	-	-
Depredated	21 (34.4)	50 (46.7)	35 (20.1)	72 (58.1)
Starved	5 (8.2)	5 (4.7)	10 (5.7)	6 (4.8)
Other	1 (1.6)	2 (1.9)	2 (1.1)	3 (2.4)
Total	61	107	174	124

Table 13. Sources of mortality in White-crowned Pigeon eggs and nestlings at West Butternut Key during the 1986-1988 seasons.

Source	Eggs				Nestlings			
	#	%	% mort	% eggs	#	%	% mort	% nest.
Unhatched	17	23.6	12.4	9.0	-	-	-	-
Abandoned	13	18.1	9.5	6.9	7	10.8	3.1	6.0
Nest fell	4	5.6	2.9	2.1	-	-	-	-
Depredated	38	52.8	27.7	20.1	51	78.5	37.2	43.6
Starved	-	-	-	-	7	10.8	5.1	6.0
Total	72	100.0	52.6	38.1	65	100.0	45.4	55.6

Table 14. Yearly variation in the fate of eggs laid at West Butternut Key.

	Number (percent)		
	1986	1987	1988
Hatched	41 (60.3)	69 (73.4)	7 (25.9)
Unhatched	13 (19.1)	4 (4.3)	0
Depredated	10 (14.7)	13 (13.8)	15 (55.6)
Abandoned	4 (5.9)	6 (6.4)	3 (11.1)
Other	-	2 (2.1)	2 (7.4)
Total	68	94	27

Table 15. Yearly variation in the fate of nestlings at West Butternut Key.

	Number (percent)		
	1986	1987	1988
Fledged	23 (56.1)	26 (37.7)	3 (42.9)
Abandoned	1 (2.4)	4 (5.8)	2 (28.6)
Depredated	13 (31.7)	36 (52.2)	2 (28.6)
Starved	4 (9.8)	3 (4.3)	0
Total	41	69	7

Table 16. Weight (g), volume (cc) and linear measurements (mm) of White-crowned Pigeon eggs in south Florida.

	N	Mean	S.D.	Minimum	Maximum
Fresh egg weight	465	13.1	1.3	9.4	17.4
Length	1802	35.2	1.5	30.7	40.6
Width	1802	26.0	0.9	23.0	29.5
Volume	1802	12.1	1.2	8.6	16.8
Length/width ratio	1802	1.35	0.06	1.13	1.61

Table 16. Weight (g), volume (cc) and linear measurements (mm) of White-crowned Pigeon eggs in south Florida.

	N	Mean	S.D.	Minimum	Maximum
Fresh egg weight	465	13.1	1.3	9.4	17.4
Length	1802	35.2	1.5	30.7	40.6
Width	1802	26.0	0.9	23.0	29.5
Volume	1802	12.1	1.2	8.6	16.8
Length/width ratio	1802	1.35	0.06	1.13	1.61

Table 17. Mean volume of White-crowned Pigeon eggs relative to nesting key.

Key	N	Mean	S.D.
Middle Butternut	739	12.3	1.2
Bottle Key	876	12.0	1.2
West Butternut	187	12.0	0.9

Table 18. Two-way analysis of variance of year and month for egg volume at Middle Butternut Key.

Source of variation	Sum of squares	DF	Mean square	F	P
Year	14.155	4	3.539	2.555	0.038
Month	40.574	3	13.525	9.767	0.000
Interaction	23.010	12	1.917	1.385	0.168
Error	987.332	713	1.385		
Total	1063.896	732	1.453		

Table 19. Mean volume of White-crowned Pigeon eggs on Middle Butternut Key relative to year.

Year	N	Mean	S.D.
1985	103	12.3	1.1
1986	118	12.4	1.2
1987	149	12.1	1.0
1988	211	12.4	1.3
1989	158	12.2	1.2

Table 20. Mean volume of White-crowned Pigeon eggs on Middle Butternut Key relative to month of laying.

Month	N	Mean	S.D.
May	51	11.9	1.3
June	176	12.0	1.1
July	286	12.4	1.2
August	220	12.6	1.2
September	6	11.5	0.7

Table 21. Growth of primary 7 (mm) in nestling White-crowned Pigeons.

Age	N	Mean	SD	Minimum	Maximum
0	127	0.0	0.0	0.0	0.0
1	134	0.0	0.0	0.0	0.5
2	133	0.1	0.6	0.0	6.0
3	140	1.2	1.7	0.0	9.5
4	160	5.9	3.3	0.0	22.6
5	130	11.3	3.6	2.0	21.0
6	136	17.6	4.6	1.0	28.5
7	136	24.1	4.4	13.5	38.2
8	136	30.9	5.4	13.3	42.9
9	132	37.9	6.0	6.4	64.1
10	160	44.4	6.4	15.1	65.0
11	146	52.3	7.2	27.8	75.1
12	138	58.0	6.3	35.1	75.2
13	119	64.8	7.5	34.7	81.4
14	79	70.1	5.9	57.8	84.0
15	66	73.7	7.3	43.2	87.5
16	41	78.5	7.1	59.4	92.9

Table 22. Growth of the central rectrices (mm) in nestling White-crowned Pigeons.

Age	N	Mean	SD	Minimum	Maximum
0	127	0.0	0.0	0.0	0.0
1	134	0.0	0.0	0.0	0.0
2	133	0.0	0.0	0.0	0.0
3	140	0.1	0.8	0.0	9.0
4	160	0.2	0.9	0.0	9.3
5	130	1.6	1.6	0.0	7.4
6	136	4.6	2.3	0.0	10.0
7	136	7.9	3.1	1.0	17.5
8	136	11.5	4.0	0.0	25.5
9	132	15.6	4.4	0.0	28.1
10	159	20.2	6.2	0.0	39.0
11	146	26.0	7.4	5.3	48.5
12	138	30.4	6.9	10.3	47.0
13	119	35.6	8.8	6.7	50.8
14	79	40.7	7.9	20.0	58.9
15	66	43.2	9.6	6.8	63.0
16	41	45.6	10.2	21.1	64.3

Table 23. Growth of the culmen (mm) in nestling White-crowned Pigeons.

Age	N	Mean	SD	Minimum	Maximum
0	127	12.9	0.9	10.9	16.2
1	134	15.0	1.2	10.4	18.0
2	133	17.3	1.1	13.9	20.1
3	139	19.2	1.1	15.8	22.7
4	160	20.6	1.3	11.2	23.5
5	130	21.8	1.1	19.3	24.3
6	136	22.8	1.1	19.3	24.9
7	136	23.3	1.1	19.1	25.7
8	136	23.7	1.2	20.2	27.0
9	132	24.2	1.0	21.3	26.3
10	160	24.4	1.1	21.3	27.3
11	146	24.7	1.1	22.1	27.2
12	138	24.8	1.0	21.9	27.2
13	119	25.1	1.1	21.2	28.4
14	79	25.3	1.2	21.6	28.3
15	66	25.2	1.1	22.5	27.5
16	41	25.2	0.8	23.4	27.5

Table 24. Growth of the gape (mm) in nestling White-crowned Pigeons.

Age	N	Mean	SD	Minimum	Maximum
0	127	6.4	1.3	4.6	16.6
1	134	7.4	1.2	5.4	17.4
2	133	8.4	0.9	6.2	10.7
3	140	9.5	1.0	6.7	11.9
4	160	10.5	1.4	7.2	21.3
5	130	11.3	1.2	4.8	14.6
6	136	11.7	1.2	8.6	14.3
7	136	12.2	1.3	9.1	15.2
8	136	12.5	1.7	3.7	19.5
9	132	12.9	1.4	10.2	16.0
10	159	13.1	1.5	10.3	16.9
11	146	13.3	1.5	10.4	16.5
12	138	13.2	1.4	10.6	17.0
13	119	13.3	1.5	10.6	16.9
14	79	13.2	1.5	10.7	16.4
15	66	13.4	1.4	10.3	16.3
16	41	13.4	1.3	10.8	16.3

Table 25. Growth of the manus (mm) in nestling White-crowned Pigeons.

Age	N	Mean	SD	Minimum	Maximum
0	127	11.8	1.6	7.2	16.2
1	134	14.2	1.8	6.4	19.0
2	132	17.9	2.5	8.8	25.4
3	140	21.4	2.8	12.9	27.4
4	160	25.6	3.6	16.6	35.2
5	130	29.4	4.0	18.2	40.0
6	136	32.8	5.0	16.4	44.3
7	136	36.3	5.0	23.1	44.6
8	136	38.8	5.3	24.8	49.1
9	132	42.1	5.8	26.5	50.1
10	160	43.8	5.9	24.4	52.8
11	146	46.0	6.4	25.9	55.2
12	138	48.1	5.6	26.4	55.3
13	119	47.7	7.1	25.4	58.7
14	79	49.2	5.7	35.3	56.9
15	66	49.7	6.3	27.1	57.5
16	41	50.6	4.8	37.1	58.4

Table 26. Growth of the tarsus (mm) in nestling White-crowned Pigeons.

Age	N	Mean	SD	Minimum	Maximum
0	127	10.3	0.8	8.8	13.0
1	134	11.9	1.0	7.5	14.7
2	133	14.0	1.1	11.3	17.2
3	139	16.1	1.2	12.8	19.3
4	160	17.9	1.6	13.7	25.4
5	130	19.6	1.4	16.1	24.0
6	136	21.2	1.5	15.4	25.1
7	136	22.2	1.5	18.2	28.6
8	136	23.1	1.3	17.8	26.2
9	132	23.9	1.5	18.7	29.1
10	159	24.5	1.4	19.2	28.7
11	146	25.0	1.5	18.7	28.7
12	138	25.5	1.1	21.4	28.4
13	119	25.5	1.4	20.4	28.4
14	79	26.0	1.2	22.0	28.7
15	66	25.9	1.2	21.3	28.3
16	41	25.9	1.2	24.1	28.7

Table 27. Weight (g) in nestling White-crowned Pigeons.

Age	N	Mean	SD	Minimum	Maximum
0	126	13.2	2.8	7.9	25.2
1	134	20.7	4.2	10.9	41.5
2	132	32.7	6.9	18.6	51.0
3	140	45.4	10.1	16.5	80.0
4	160	59.3	12.8	20.4	102.0
5	129	74.4	14.4	42.0	117.0
6	133	85.9	19.2	34.0	131.0
7	135	99.1	18.5	48.0	147.0
8	135	107.8	22.1	39.1	163.0
9	132	118.0	23.4	50.0	175.0
10	157	128.7	24.7	50.0	177.0
11	144	134.0	25.6	40.0	198.0
12	137	145.1	23.1	72.0	192.0
13	119	149.7	28.5	51.0	219.0
14	78	154.8	24.7	83.0	204.0
15	66	156.3	27.0	72.0	213.0
16	41	147.7	26.0	87.0	195.0

Table 28. Analysis of variance of the effects of year and *Metopium toxiferum* availability on Day 8 weight in White-crowned Pigeons.

Source	df	Mean square	F	P
Year	4	1076.5	4.031	0.003
<i>M. toxiferum</i>	1	4159.6	15.575	0.001
2-way interaction	4	421.0	1.577	0.181
Residual	288	267.061		

Table 29. Mean weight of 8-day old White-crowned Pigeons relative to study year.

Year	N	Mean	s.d.
1985	36	92.8	20.9
1986	43	108.2	17.8
1987	59	106.5	13.7
1988	92	105.8	14.7
1989	68	100.2	18.8

Table 30. Mean weight of 8-day old White-crowned Pigeons relative to the availability of *M. toxiferum* fruit.

Availability	N	Mean	s.d.
Unavailable	92	96.4	19.6
Available	206	106.6	15.3

Table 31. Analysis of food items from 207 crop samples taken from nestling White-crowned Pigeons in Florida Bay during 1986-1989.

Food Species	# samples	%	# items	%	Total weight (g)	Aggregate % weight		Total volume (cc)	Aggregate % volume	
						with milk	no milk		with milk	no milk
Crop milk	206	99.5	-	-	1262.97	52.55	-	1201.9	52.93	-
<u>Metopium toxiferum</u>	162	77.9	2420	40.05	749.89	28.70	61.30	689.9	28.03	60.76
<u>Guapira discolor</u>	95	45.7	2189	36.23	240.60	9.57	19.01	221.2	9.50	19.14
<u>Ficus sp.</u>	35	16.8	316	5.23	150.17	5.48	9.41	149.4	5.57	9.58
<u>Erithalis fruticosa</u>	54	26.0	816	13.51	58.82	2.52	6.31	63.0	2.82	7.22
<u>Avicennia germinans</u>	11	5.3	93	1.54	5.13	0.20	0.70	6.9	0.31	1.12
<u>Bumelia salicifolia</u>	2	1.0	5	0.08	0.91	0.05	0.10	1.3	0.07	0.16
<u>Krugiodendron ferreum</u>	2	1.0	2	0.03	0.95	0.03	0.04	0.9	0.03	0.04
<u>Simarouba glauca</u>	1	0.5	2	0.03	3.47	0.09	0.12	4.2	0.12	0.18
<u>Chrysobalanus icaco</u>	1	0.5	1	0.02	1.79	0.07	0.10	1.8	0.08	0.10
<u>Cocoloba diversifolia</u>	1	0.5	1	0.02	0.92	0.08	0.10	1.0	0.09	0.11
<u>Bourreria ovata</u>	1	0.5	1	0.02	0.69	0.02	0.02	0.6	0.02	0.02
<u>Trema spp.</u>	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		6042		2486.26			2352.2		

Table 32. Fruits consumed by White-crowned Pigeons during this study (some data courtesy of M. Carrington).

Family Species	Common Name
Anacardiaceae	
<i>Metopium toxiferum</i>	Poisonwood
<i>Schinus terebinthifolia</i>	Florida Holly
Aquifoliaceae	
<i>Ilex cassine</i>	Dahoon Holly
Arecaceae	
<i>Thrinax morrisii</i>	Key Thatch Palm
<i>Thrinax radiata</i>	Florida Thatch Palm
Boraginaceae	
<i>Bourreria ovata</i>	Strongbark
Burseraceae	
<i>Bursera simaruba</i>	Gumbo-limbo
Canellaceae	
<i>Canella winterana</i>	Cinnamon Bark
Chrysobalanaceae	
<i>Chrysobalanus icaco</i>	Coco-plum
Euphorbiaceae	
<i>Drypetes lateriflora</i>	Guiana Plum
Fabaceae	
<i>Pithecellobium</i> spp.	Catclaw
Lauraceae	
<i>Nectandra coriacea</i>	Lancewood
Moraceae	
<i>Ficus aurea</i>	Stranger Fig
<i>Ficus citrifolia</i>	Short-leaf Fig
<i>Ficus microcarpa</i>	Exotic Fig
Myrtaceae	
<i>Calyptanthus</i> sp.	Spicewood
<i>Eugenia foetida</i>	Spanish Stopper
Nyctaginaceae	
<i>Guapira discolor</i>	Bolly
Polygonaceae	
<i>Coccoloba diversifolia</i>	Pigeon Plum
<i>Coccoloba uvifera</i>	Sea-grape
Rhamnaceae	
<i>Krugiodendron ferreum</i>	Black Ironwood
Rubiaceae	
<i>Chiococca alba</i>	Snowberry
<i>Erithalis fracticosa</i>	Black Torch
<i>Randia aculeata</i>	Randia
Sapindaceae	
<i>Exothea paniculata</i>	Inkwood
Sapotaceae	
<i>Bumelia salicifolia</i>	Willow Busic
<i>Chrysophyllum oliviforme</i>	Satin Leaf
<i>Mastichodendron foetidissimum</i>	Mastic
Simaroubaceae	
<i>Simarouba glauca</i>	Paradise Tree
Solanaceae	
<i>Solanum erianthum</i>	Potato Tree
Surianaceae	
<i>Suriana maritima</i>	Bay Cedar
Ulmaceae	
<i>Trema</i> sp.	Trema

Table 33. Mean nutrient and energetic content (S.D.) of whole fruits consumed by White-crowned Pigeons during the breeding season.

Fruit	% water	Percent dry weight					Energy (kj/g)
		Protein	Soluble carbs.	Insoluble carbs.	Lipids	Ash	
<i>Metopium toxiferum</i> (N=79)	52.3(6.8)	3.0(1.3)	12.5(5.9)	59.8(7.5)	21.9(6.0)	4.0(0.8)	11.6(2.4)
<i>Ficus aurea</i> (N=75)	71.2(4.0)	2.8(0.9)	31.2(10.6)	58.0(9.8)	4.0(1.2)	6.0(0.7)	7.6(1.7)
<i>F. citrifolia</i> (N=73)	71.7(3.8)	2.9(1.0)	28.7(10.2)	59.5(10.3)	4.4(2.3)	6.3(0.4)	7.3(1.8)
<i>Guapira discolor</i> (N=49)	63.8(5.8)	5.1(1.9)	24.5(10.2)	62.7(8.8)	4.1(1.7)	4.9(0.6)	7.1(1.4)
<i>Nectandra coriacea</i> (N=5)	52.8(6.4)	2.3(1.0)	11.4(2.5)	63.7(2.9)	20.0(2.1)	5.7(1.0)	10.5(0.6)
<i>Bourreria ovata</i> (N=5)	70.9(1.7)	2.2(0.6)	32.4(4.5)	57.9(3.7)	5.2(3.5)	7.1(1.2)	8.2(1.1)
<i>Thrinax radiata</i> (N=5)	56.9(3.5)	4.0(2.4)	25.2(2.0)	65.3(3.2)	2.3(0.4)	4.7(0.5)	6.2(0.7)
<i>Bumelia salicifolia</i> (N=5)	51.9(2.8)	2.8(0.8)	32.9(9.4)	53.1(9.9)	7.6(1.1)	5.1(0.8)	9.4(1.4)
<i>Erithalis fruticosa</i> (N=5)	71.7(2.7)	6.9(3.1)	38.3(2.3)	43.6(2.7)	6.3(0.8)	4.5(1.0)	10.7(0.7)
<i>Avicennia</i> flower (N=5)	63.7(2.4)	10.6(0.6)	18.7(1.0)	55.0(2.2)	11.2(0.9)	5.0(0.1)	10.2(0.5)
Crop milk (N=30)	69.4(5.0)	25.7(4.1)	0.5(0.7)	21.1(1.1) ¹	52.9(6.2)	3.2(1.4)	27.3(3.2)

¹Percent of insoluble proteins

Table 34. Mean nutrient and energetic content (S.D.) of pulp and seeds of fruits consumed by White-crowned Pigeons during the breeding season.

Fruit	% water	Percent dry weight					Energy (kj/g)
		Protein	Soluble carbs.	Insoluble carbs.	Lipids	Ash	
<i>Metopium toxiferum</i>							
pulp only (N=15)	61.5(3.5)*	2.8(0.8)	12.1(3.3)	47.8(13.4)	37.1(7.6)*	2.6(0.8)	16.5(5.0)*
seed only (N=15)	55.6(3.2)	3.5(1.1)	11.1(4.2)	67.6(3.9)*	14.1(4.1)	3.7(1.0)*	8.4(1.3)
<i>Ficus aurea</i>							
pulp only (N=5)	74.9(3.1)**	1.3(0.3)	34.7(3.6)	59.5(4.2)	1.4(0.4)	3.2(0.6)	6.8(0.6)
seed only (N=5)	46.4(3.9)	1.9(0.7)	29.3(9.9)	59.7(9.1)	6.3(0.9)**	2.8(0.5)	8.0(1.5)
<i>F. citrifolia</i>							
pulp only (N=5)	72.8(4.6)**	5.1(0.9)	36.8(4.2)*	51.4(4.6)	2.0(0.1)	4.5(0.4)**	8.4(0.8)
seed only (N=5)	58.1(6.9)	4.6(0.7)	25.8(6.3)	58.0(2.7)*	8.3(4.1)*	3.2(0.3)	8.9(0.8)
<i>Guapira discolor</i>							
pulp only (N=15)	74.0(1.7)**	3.1(0.8)	14.4(1.5)**	76.2(3.3)	1.9(0.7)	6.7(0.9)*	4.0(0.4)*
seed only (N=15)	43.5(4.8)	4.5(0.7)	6.4(0.7)	83.4(2.3)**	3.4(1.7)*	3.4(0.9)	3.5(0.6)

* $P < 0.05$

** $P < 0.01$

Table 35. Nutrient and energetic content (S.D.) of pulp and seeds of fruits consumed by White-crowned Pigeons during the non-breeding season.

Fruit	% water	Percent dry weight					Energy (Kj/g)
		Protein	Soluble carbs.	Insoluble carbs.	Lipids	Ash	
<i>Bourreria ovata</i>							
pulp only (N=5)	83.0(1.5)*	7.1(1.3)**	53.1(8.9)**	35.5(7.5)	2.0(0.3)	2.4(0.5)**	11.6(1.2)*
seed only (N=5)	72.7(1.0)	2.5(0.4)	28.1(5.8)	66.8(5.6)**	1.9(0.4)	0.3(0.2)	6.2(0.7)
<i>Coccoloba diversifolia</i>							
pulp only (N=5)	73.5(1.9)*	7.0(2.9)	34.1(8.0)**	53.6(8.2)	1.9(0.6)	3.4(1.2)**	8.3(0.9)*
seed only (N=5)	50.8(2.3)	8.6(3.0)	8.1(1.8)	81.6(4.2)**	1.5(0.3)	0.2(0.2)	4.0(0.8)
<i>Bumelia salicifolia</i>							
pulp only (N=5)	72.7(2.1)*	8.4(1.1)*	26.7(6.7)**	53.9(7.7)	6.2(3.2)	4.8(0.9)*	9.1(1.8)*
seed only (N=5)	61.6(1.7)	5.9(1.2)	2.6(1.0)	83.4(2.1)**	6.9(0.8)	1.2(0.4)	4.6(0.9)
<i>Thrinax radiata</i>							
pulp only (N=5)	86.6(0.7)**	7.0(1.2)*	25.9(6.8)**	45.4(2.5)	2.8(0.7)	8.3(1.0)**	7.2(1.2)*
seed only (N=5)	55.5(1.6)	5.3(0.5)	5.1(2.1)	85.0(2.6)**	2.0(1.3)	2.6(0.4)	2.9(1.0)

* $P < 0.05$

** $P < 0.01$

Table 36. Energetic contributions of fruits consumed by White-crowned Pigeons on a per crop basis.

Parameter	<i>Metopium toxiferum</i> (N=80)	<i>Ficus</i> spp. (N=80)	<i>Guapira discolor</i> (N=80)
Kj/g	11.6(2.4)	7.45(1.75)	7.1(1.4)
% water	52.3(6.8)	71.4(3.9)	63.8(5.8)
$\bar{x}$ wet weight (g) of fruit in crops	5.3(3.8)	4.3(5.01)	2.4(2.4)
$\bar{x}$ dry weight (g) of fruit in crops	2.5	1.23	0.9
Kj available per crop	29.0**	9.16	6.4

* $P < 0.001$

Table 37. Characteristics of fruit consumed by White-crowned Pigeons during the breeding season (mean $\pm$ S.D.).

Fruit	Length (mm)	Width (mm)	Weight (g)	Volume (ml)	# of seeds per fruit	Pulp/seed ratio
<i>Metopium toxiferum</i>	11.2(1.9)	7.1(0.6)	0.23(0.06)	0.29(0.1)	0.83(0.04)	11.4 (4.9)**
<i>Ficus aurea</i>	8.0(0.9)	10.7(0.9)	0.57(0.2)	0.41(0.3)	66.9(30.3)**	1.6 (0.3)
<i>F. citrifolia</i>	11.3(2.0)	13.5(1.8)	0.91(0.3)	0.96(0.6)**	83.6(49.9)**	1.2 (0.3)
<i>Guapira discolor</i>	6.9(1.2)	5.6(0.8)	0.14(0.1)	0.11(0.03)*	1.0(0.0)	1.12(0.5)
<i>Erithalis fruticosa</i>	5.4(0.7)	6.9(0.9)	0.14(0.1)	0.09(0.07)*	8.4(1.8)	1.98(0.2)

* $P < 0.05$

** $P < 0.01$

Table 38. Competitive indices for *Metopium toxiferum* at individual sites from 1987-1989 during the breeding season.

		1987	1988	1989
Suburban	June	0.43	2.70	2.50
	July	2.29	2.70	2.50
	August	2.33	2.70	2.50
	September	2.42	1.80	2.20
Lignumvitae	June	0.00	1.00	0.20
	July	1.70	1.05	1.00
	August	1.60	0.90	0.70
	September	1.60	0.80	0.65
North Key Largo	June	0.80	0.86	0.00
	July	1.00	0.86	0.91
	August	0.73	0.73	0.64
	September	0.64	0.45	0.14

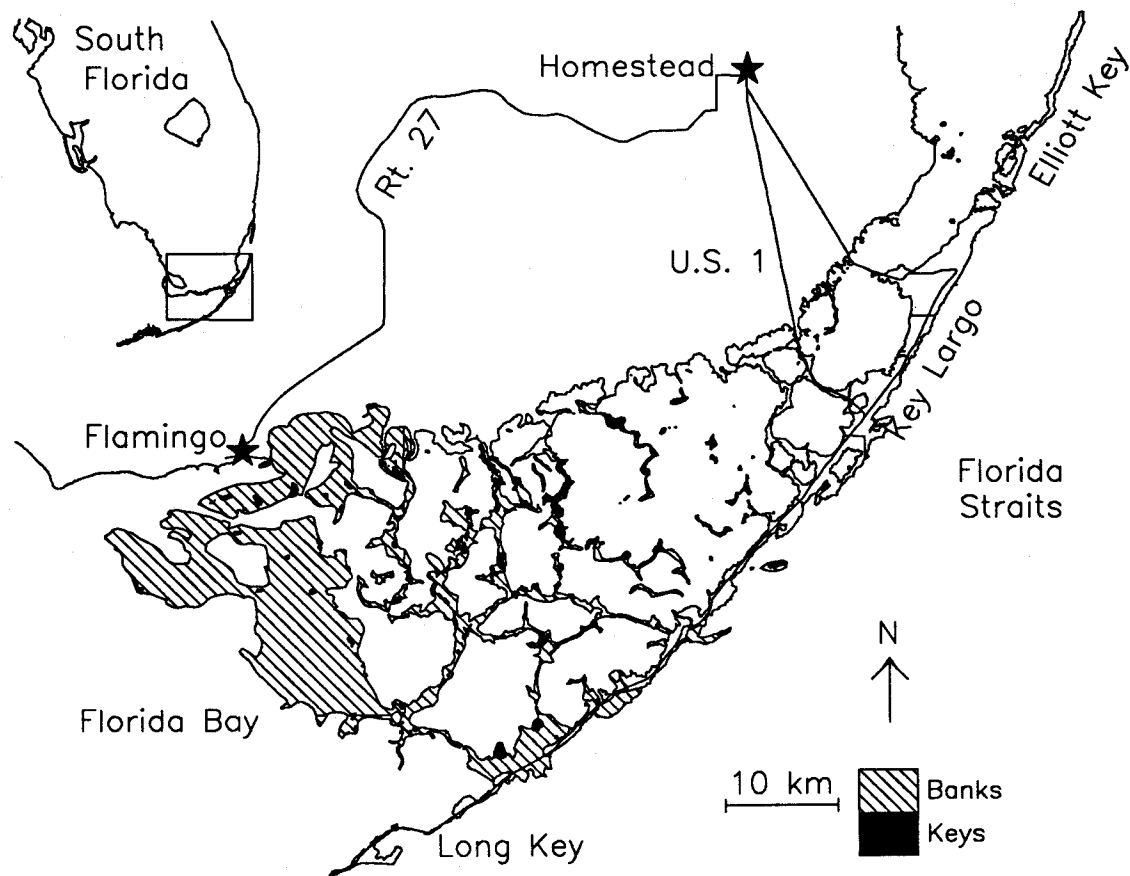


Figure 1. Southern Florida study area and the arrangement of banks and keys within Florida Bay.

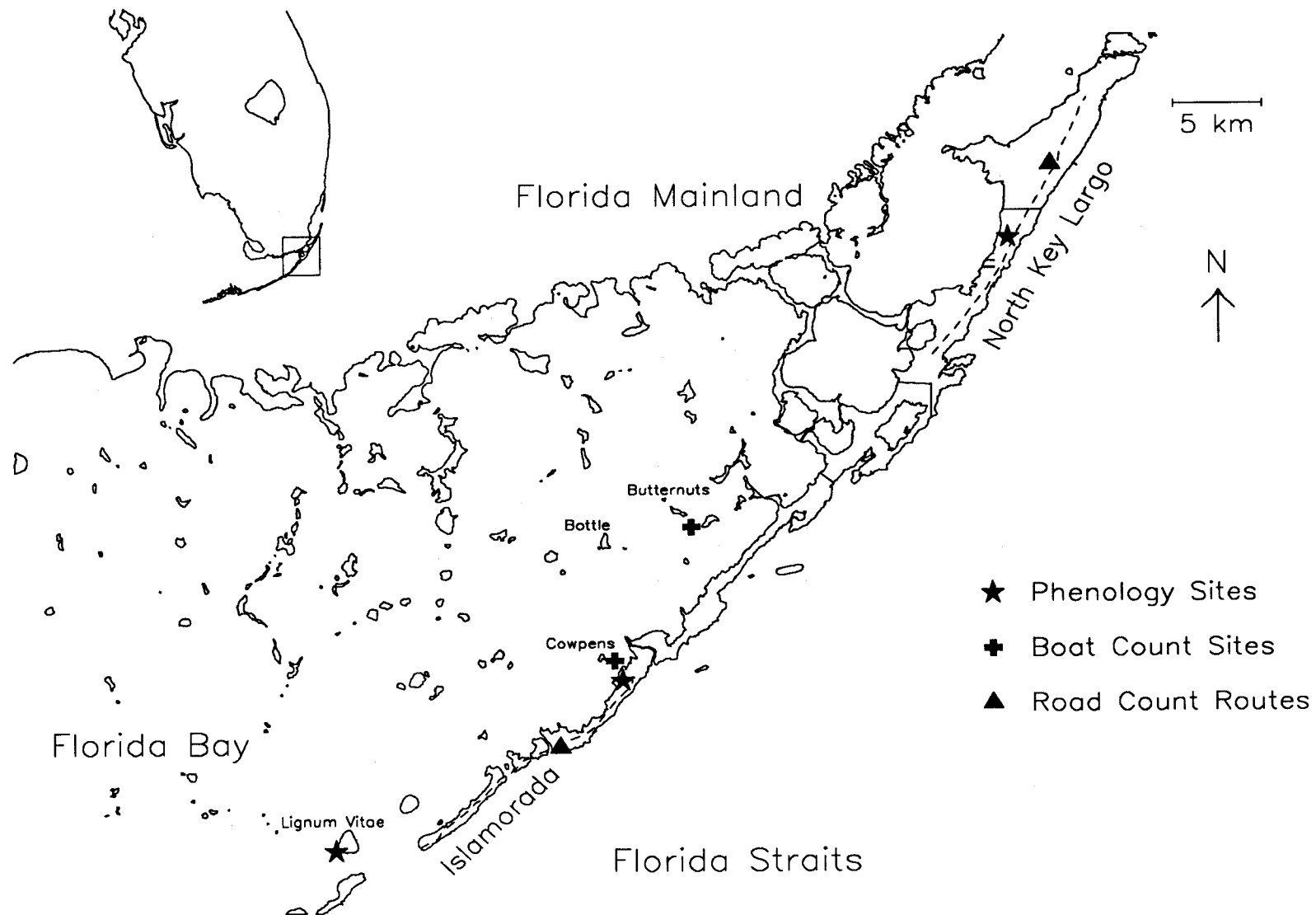
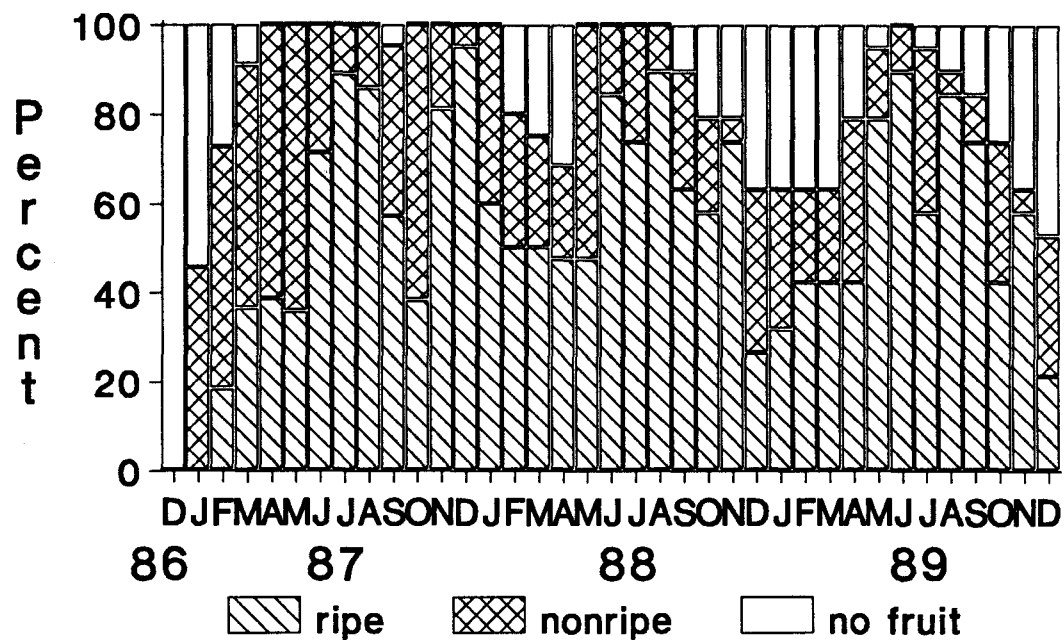


Figure 2. Locations of study keys, phenology study sites, boat count sites, and road count routes.

a.



b.

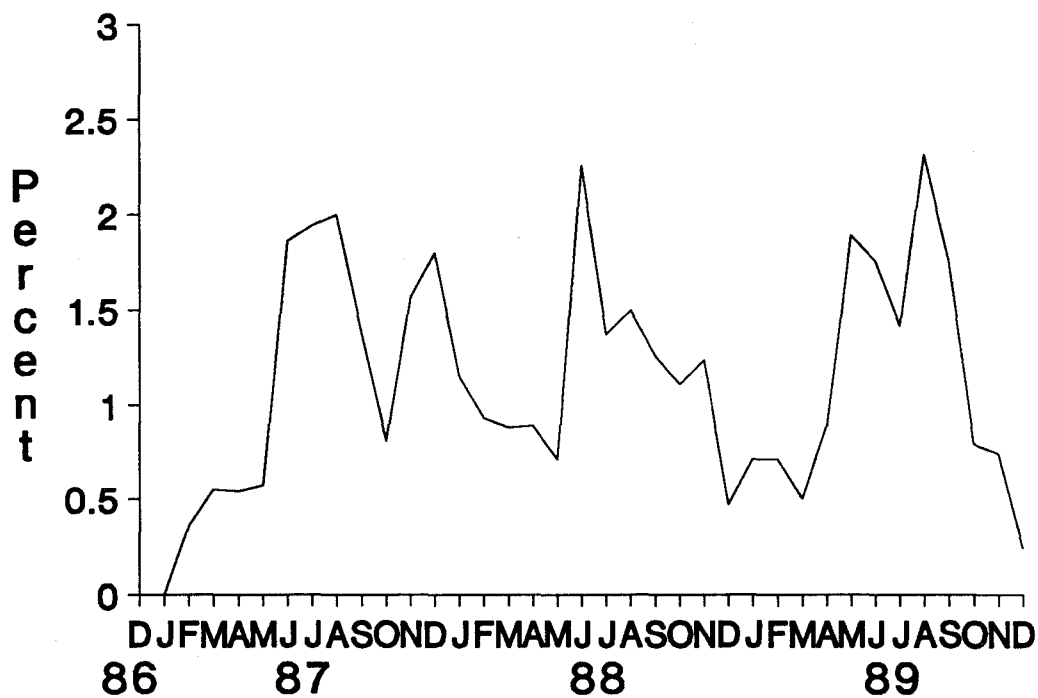
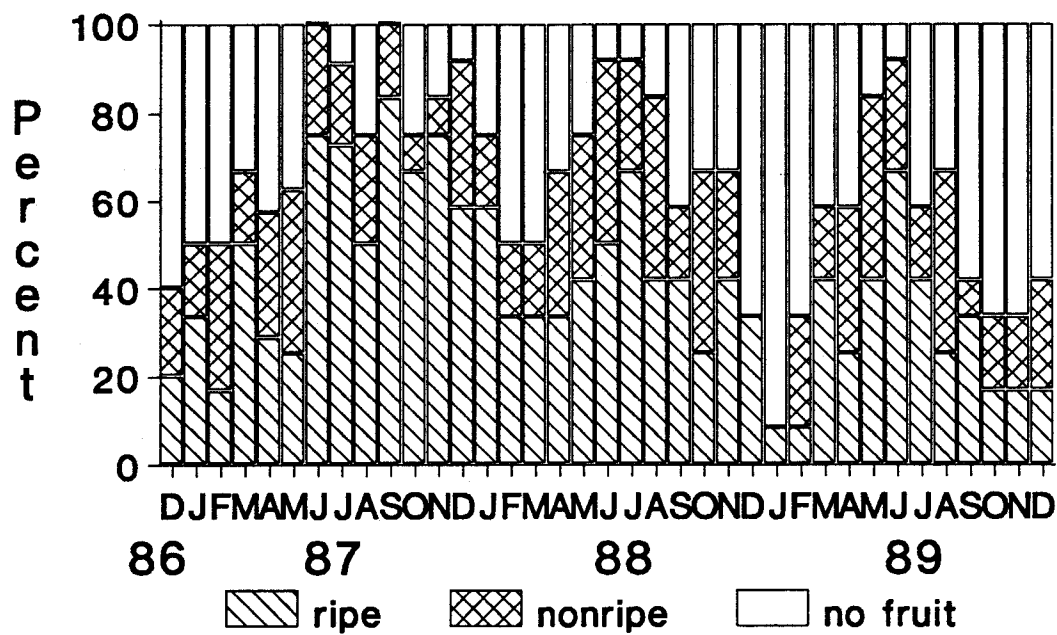


Figure 5. Percentage in fruit (a) and the competitive index (b) of *Ficus aurea* in each month.

a.



b.

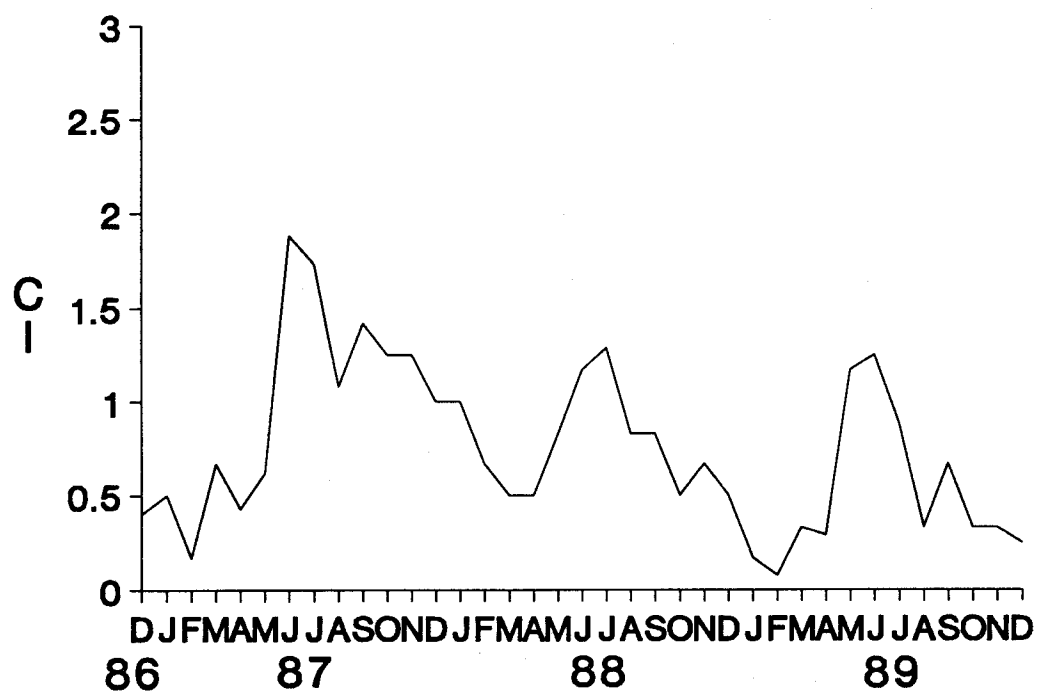


Figure 6. Percentage in fruit (a) and the competitive index (b) of *Ficus citrifolia* in each month.

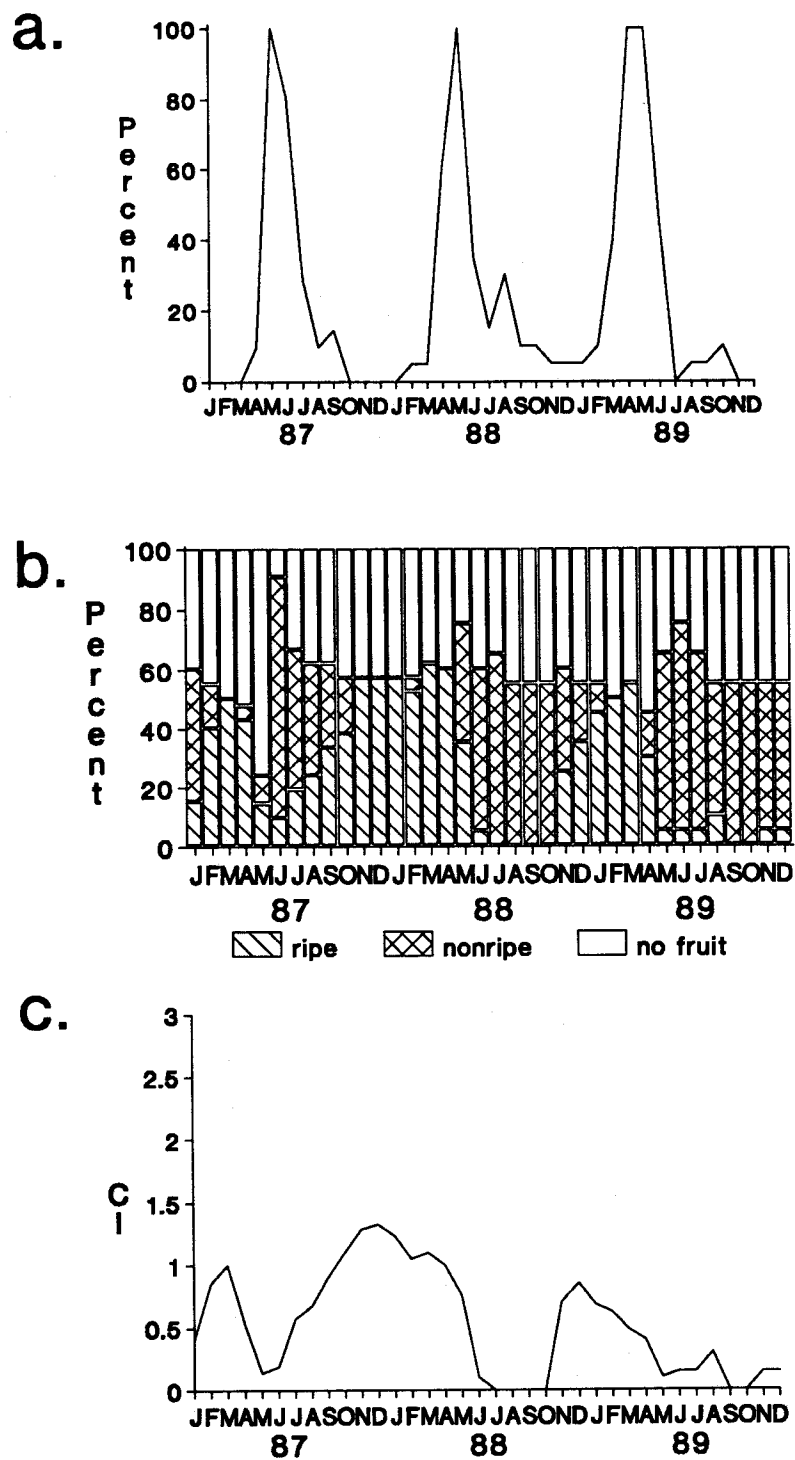


Figure 7. Percentage in flower (a) and fruit (b) and the competitive index (c) of *Bursera simaruba* in each month.

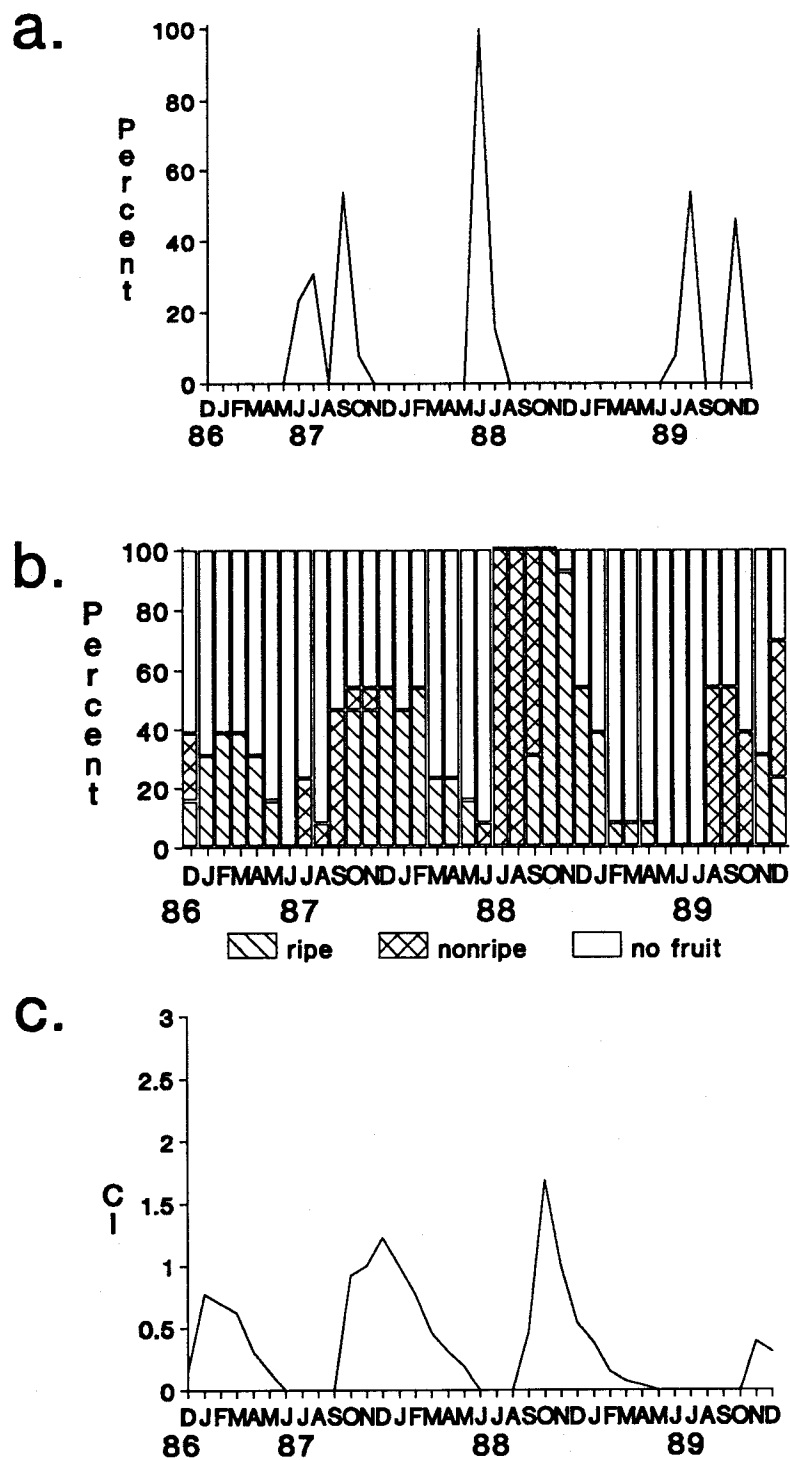


Figure 8. Percentage in flower (a) and fruit (b) and the competitive index (c) of *Thrinax radiata* in each month.

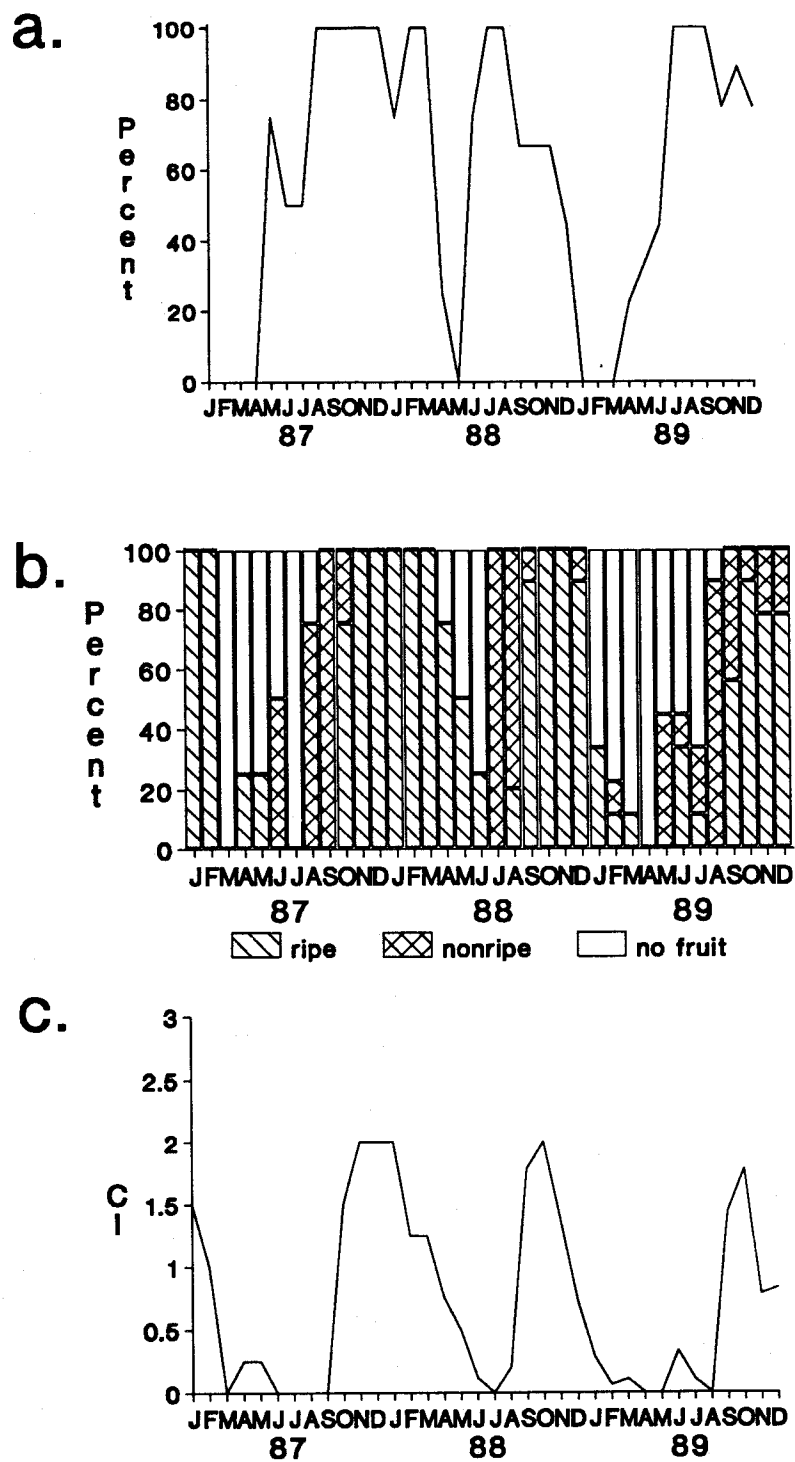


Figure 9. Percentage in flower (a) and fruit (b) and the competitive index (c) of *Bourreria ovata* in each month.

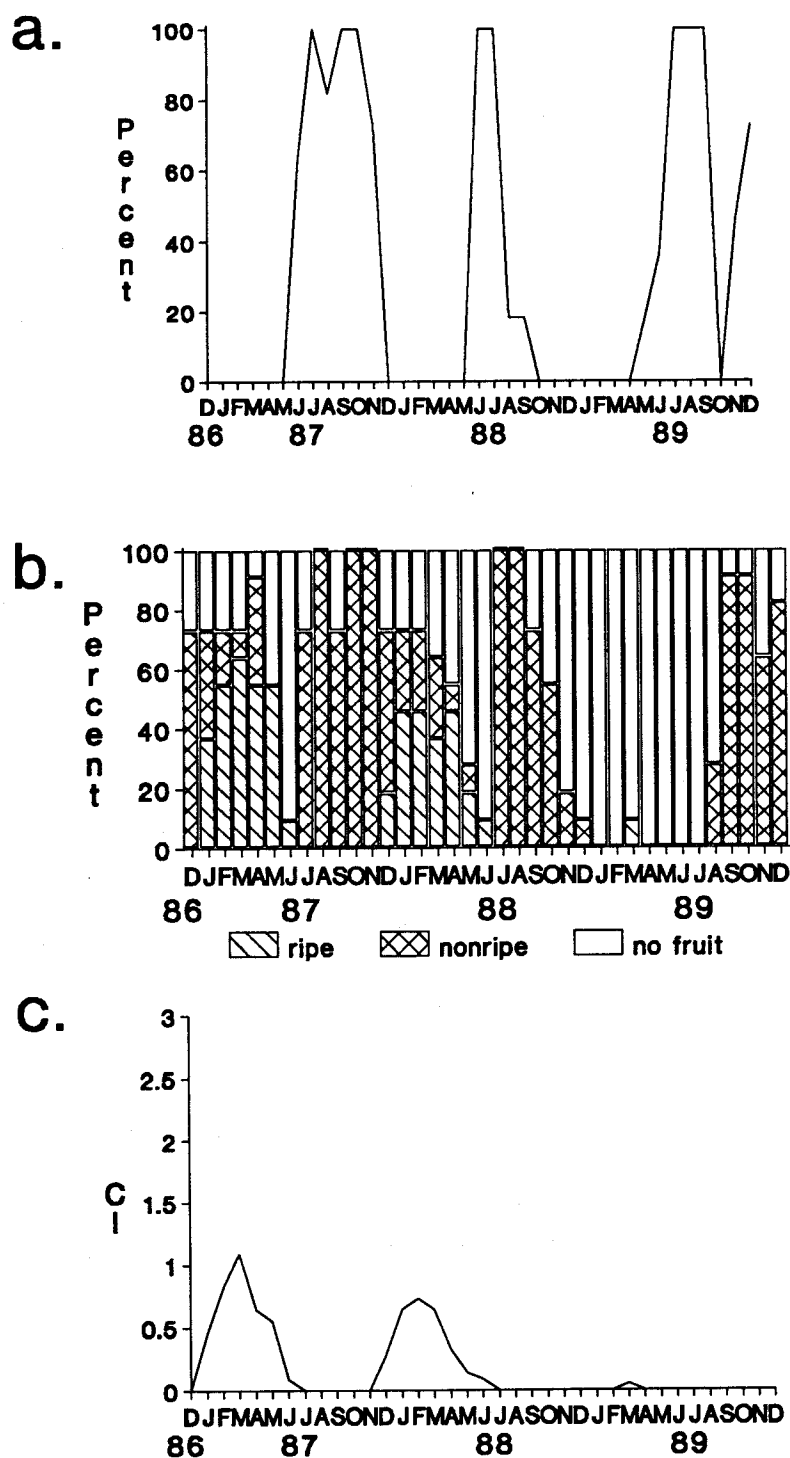


Figure 10. Percentage in flower (a) and fruit (b) and the competitive index (c) of *Mastichodendron foetidissimum* in each month.

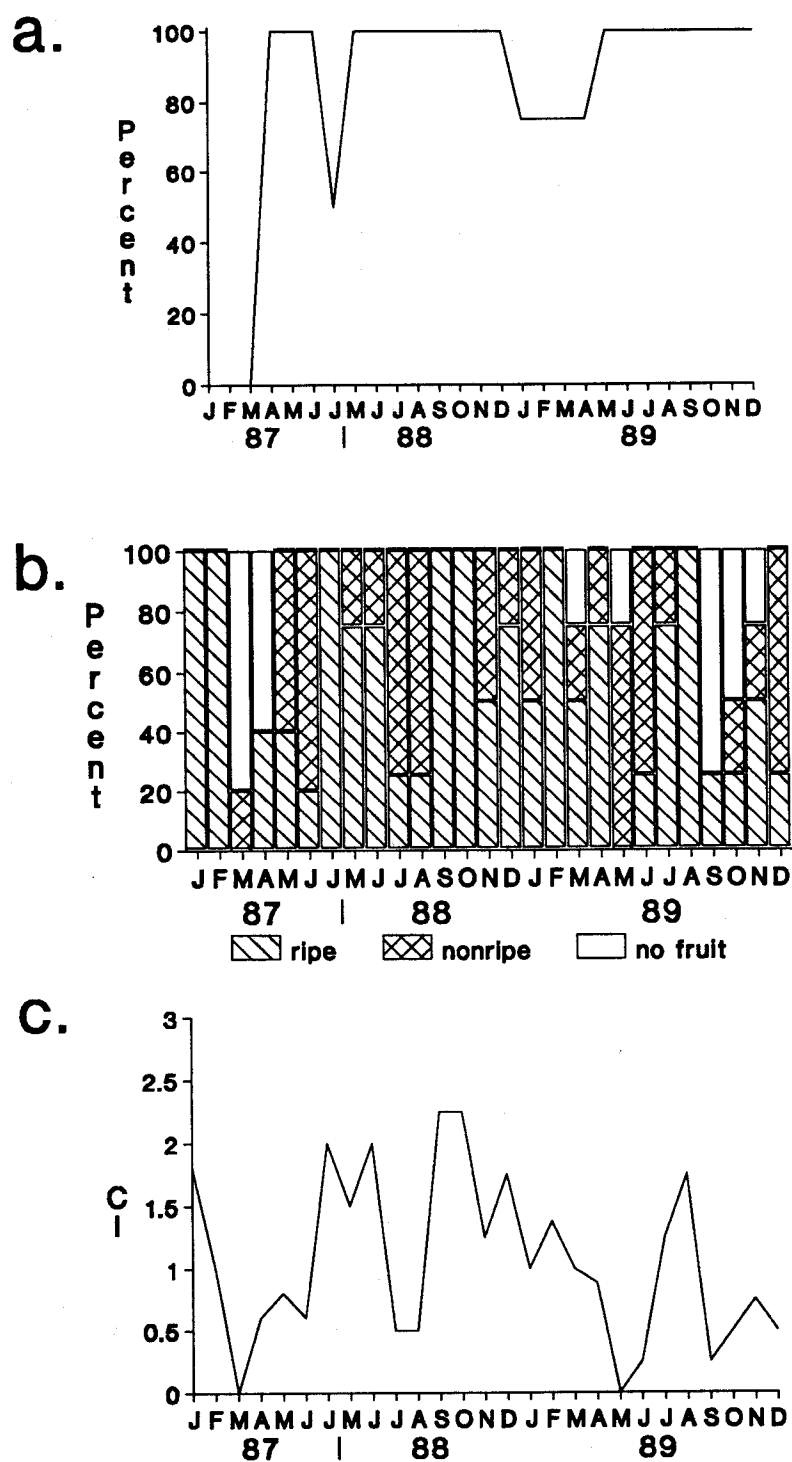


Figure 11. Percentage in flower (a) and fruit (b) and the competitive index (c) of *Solanum elaeagnifolium* in each month.

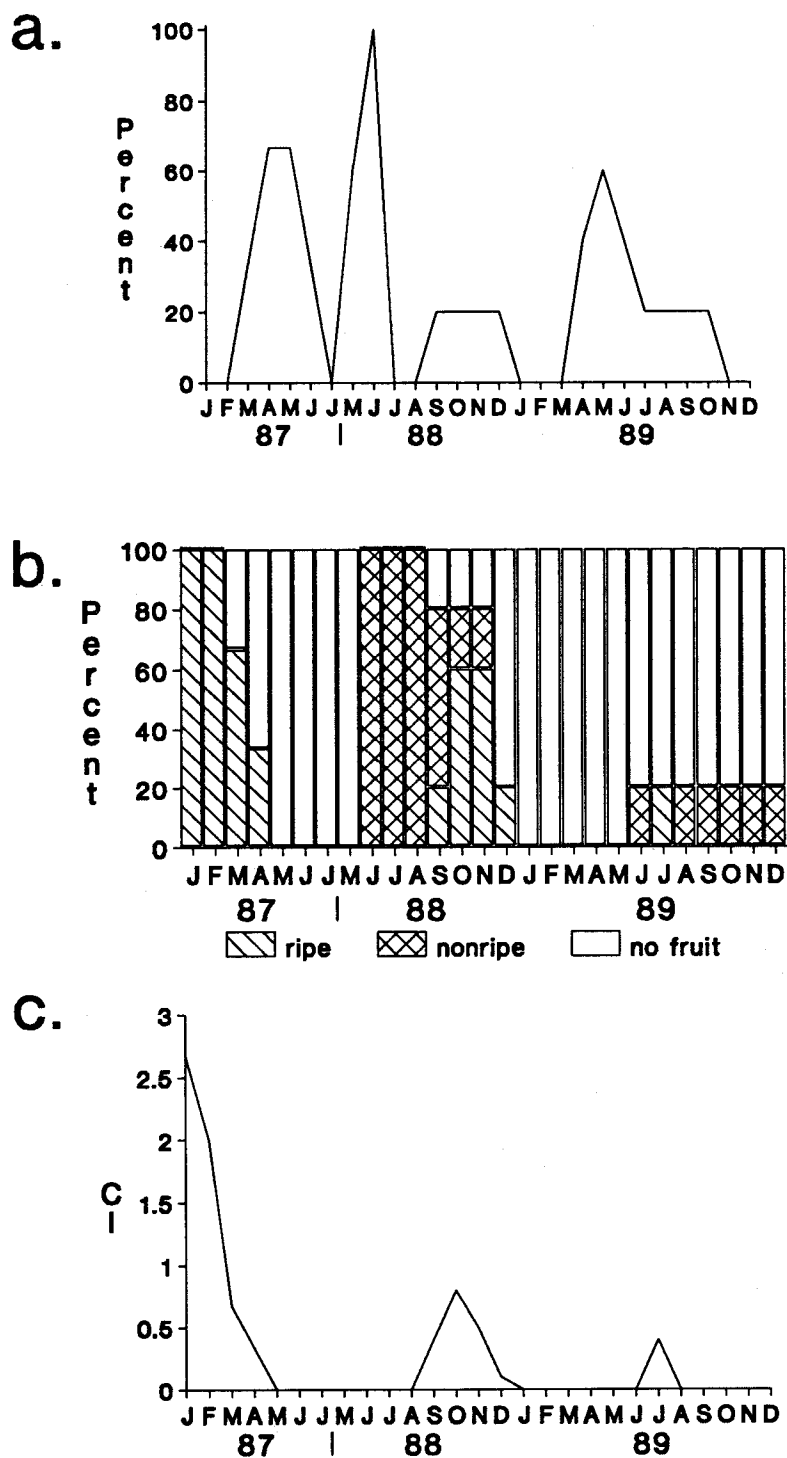


Figure 12. Percentage in flower (a) and fruit (b) and the competitive index (c) of *Nectandra coriacea* in each month.

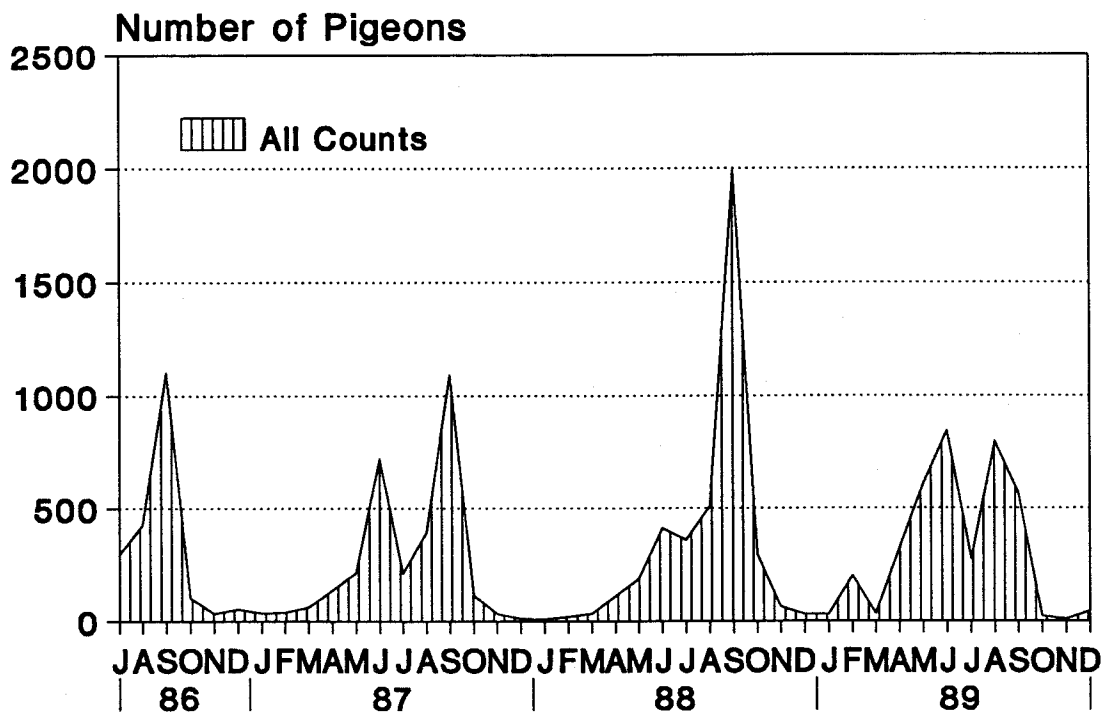


Figure 13. Total average monthly counts of White-crowned Pigeons for the Islamorada, North Key Largo, Cowpens, and Middle Butternut surveys from July 1986 through December 1989.

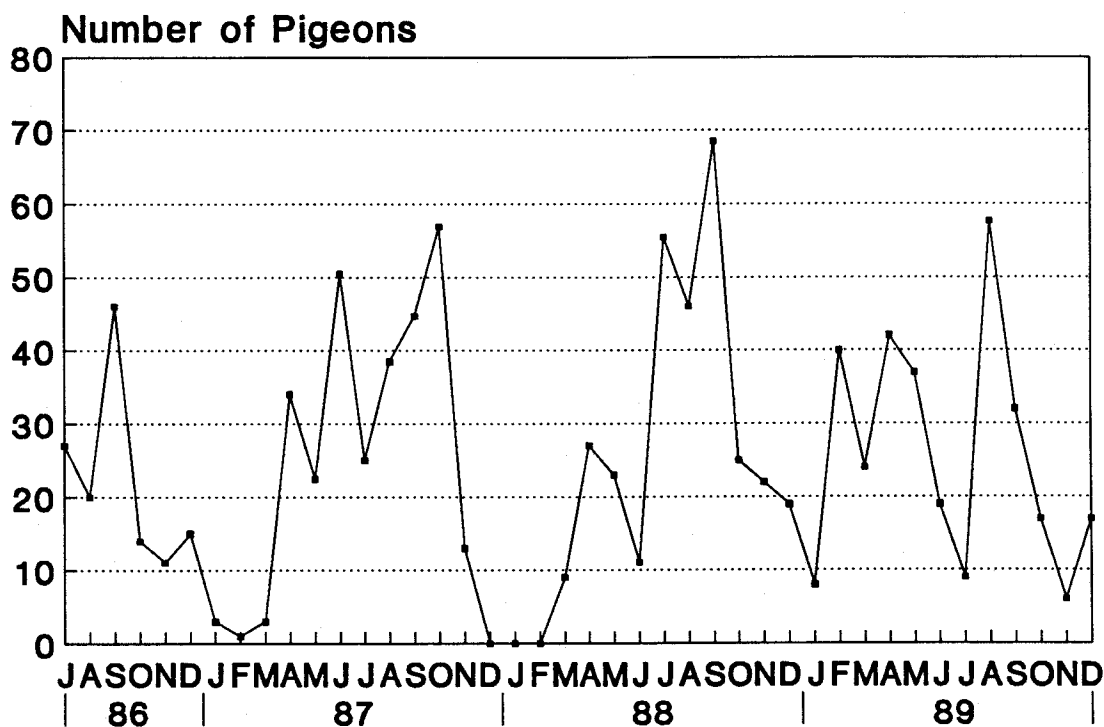


Figure 14. Average monthly counts of White-crowned Pigeons on the Islamorada Road Survey from July 1986 through December 1989.

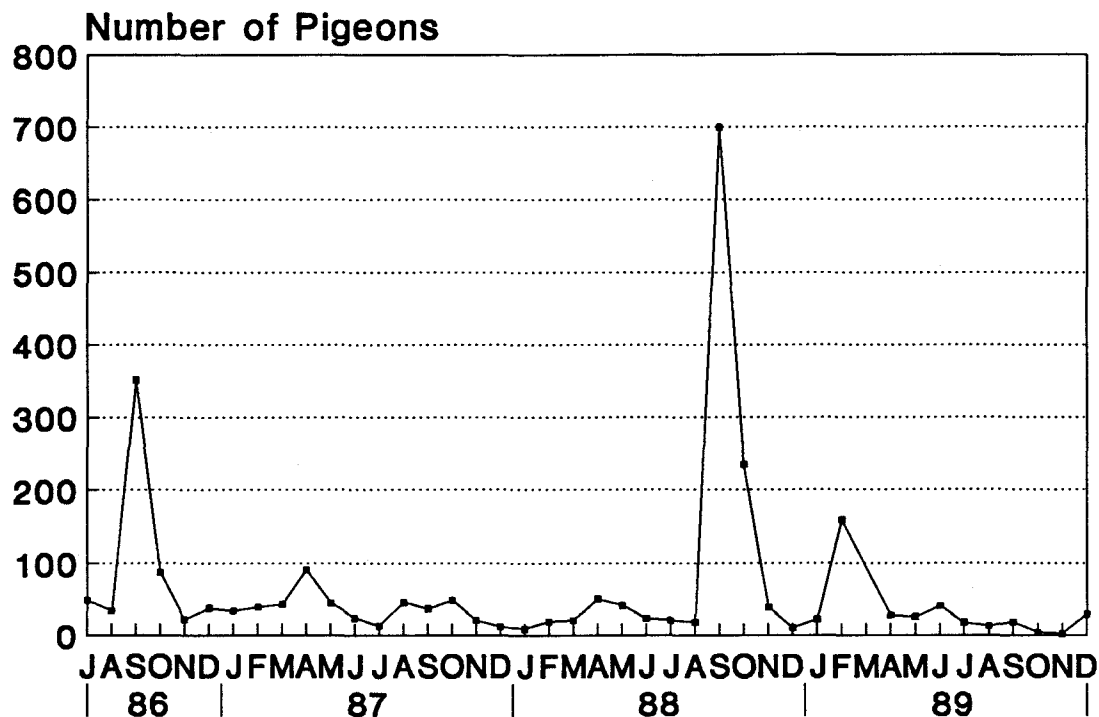


Figure 15. Average monthly counts of White-crowned Pigeons on the North Key Largo Road Survey from July 1986 through December 1989.

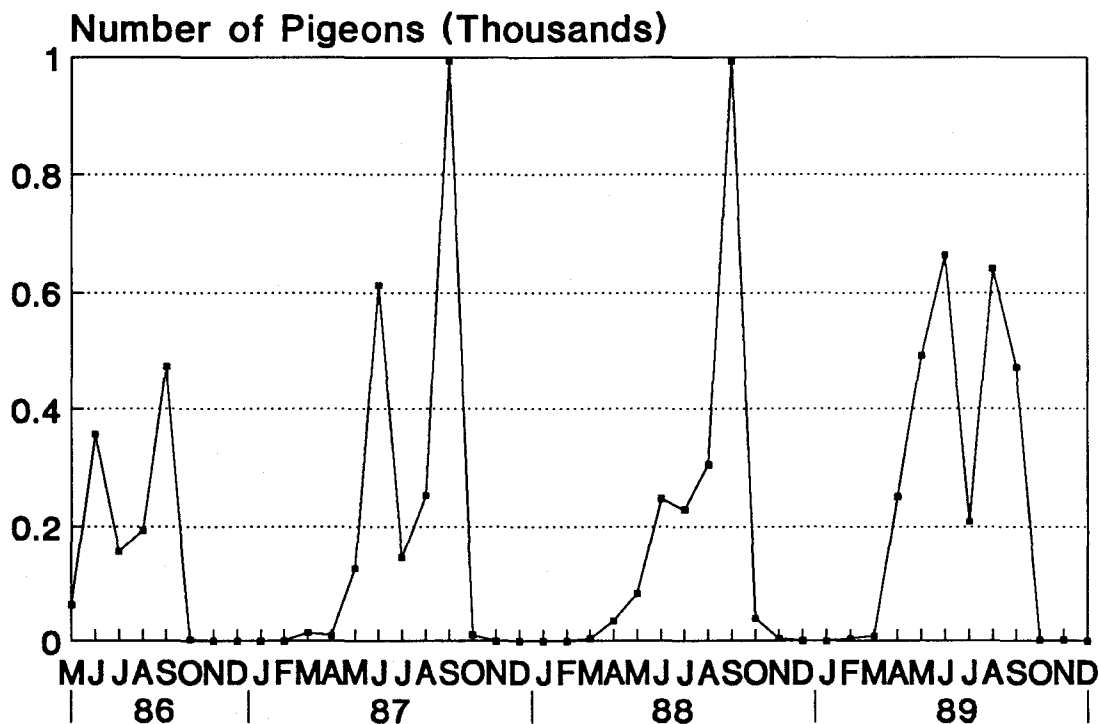


Figure 16. Average monthly counts of White-crowned Pigeons on the Cowpens Boat Survey from May 1986 through December 1989.

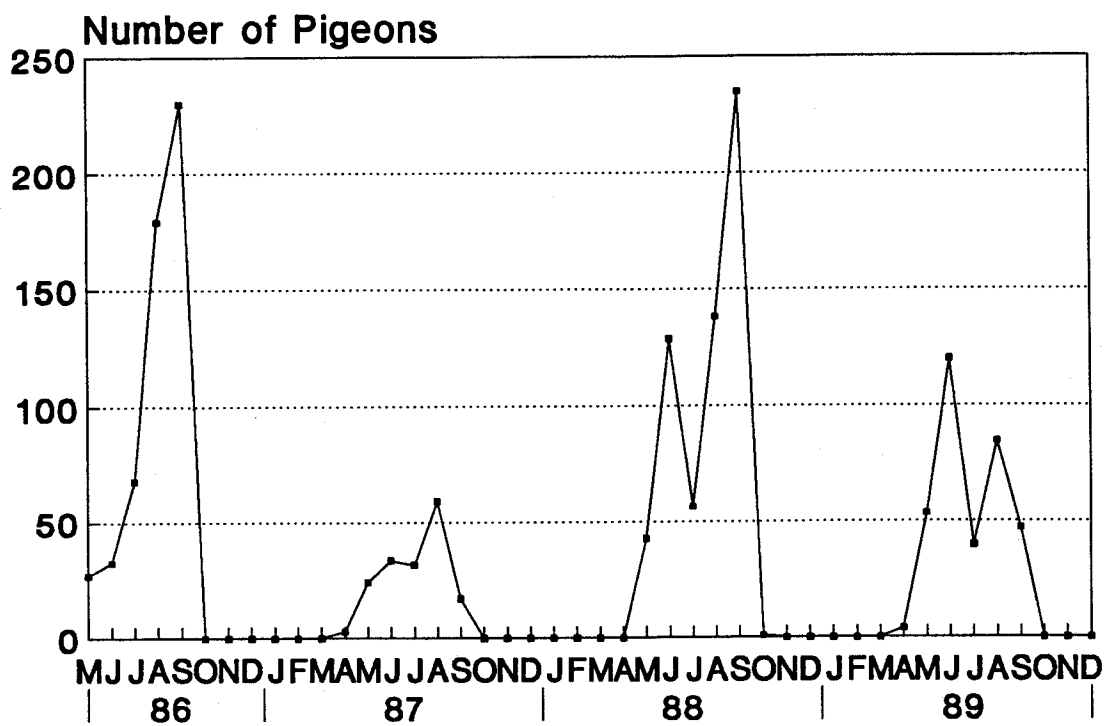


Figure 17. Average monthly counts of White-crowned Pigeons on the Middle Butternut Boat Survey from May 1986 through December 1989.

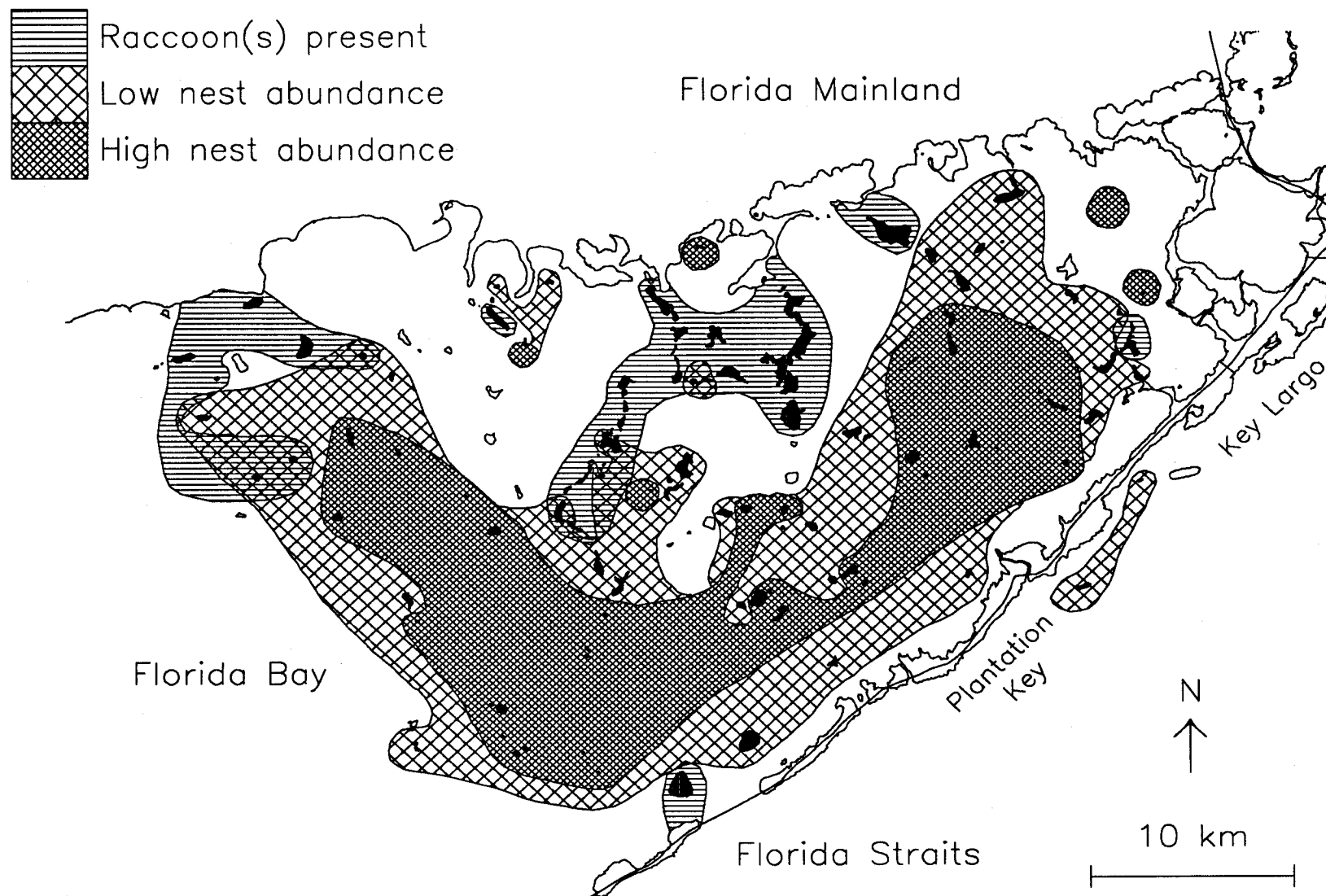


Figure 18. Distribution of raccoons and areas of high and low nest abundances of White-crowned Pigeons in Florida Bay.

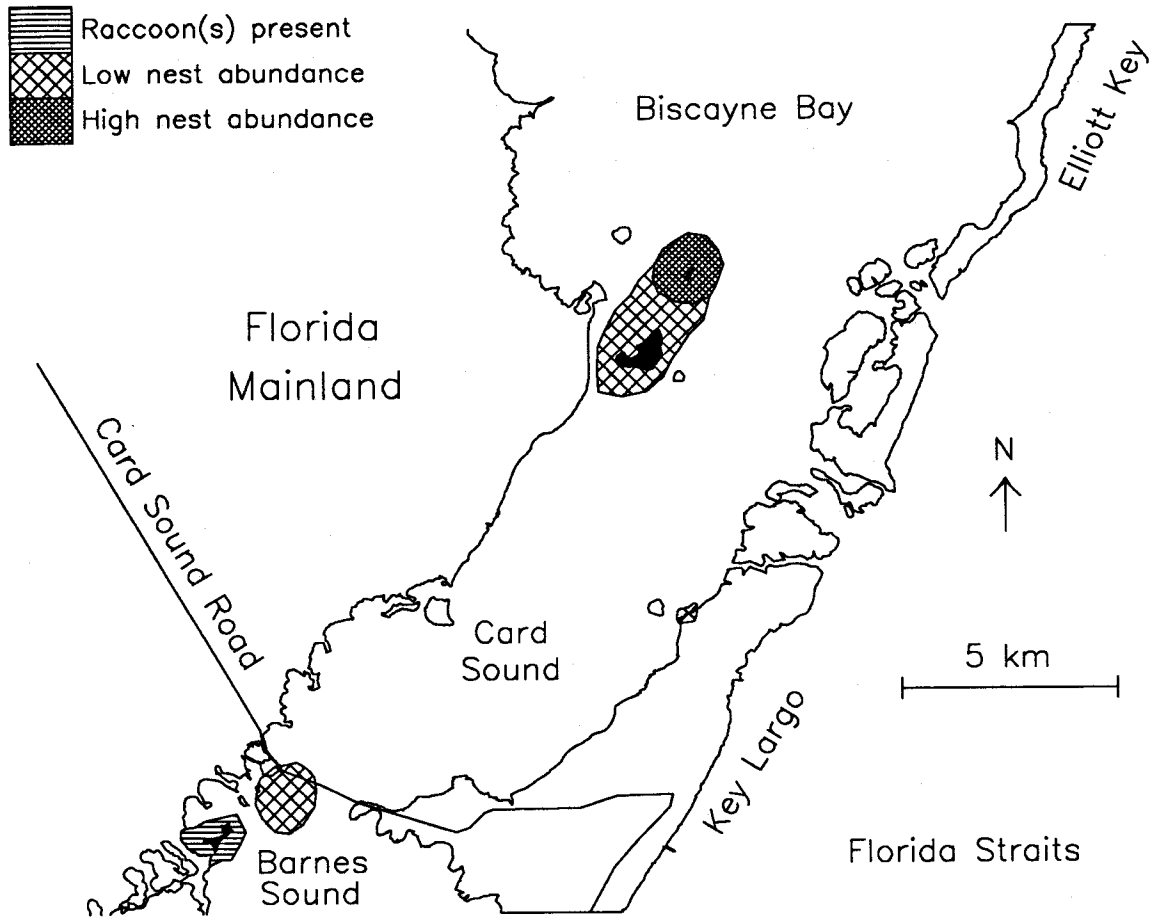


Figure 19. Distribution of raccoons and areas of high and low nest abundance of White-crowned Pigeons in Card and Barnes Sound.

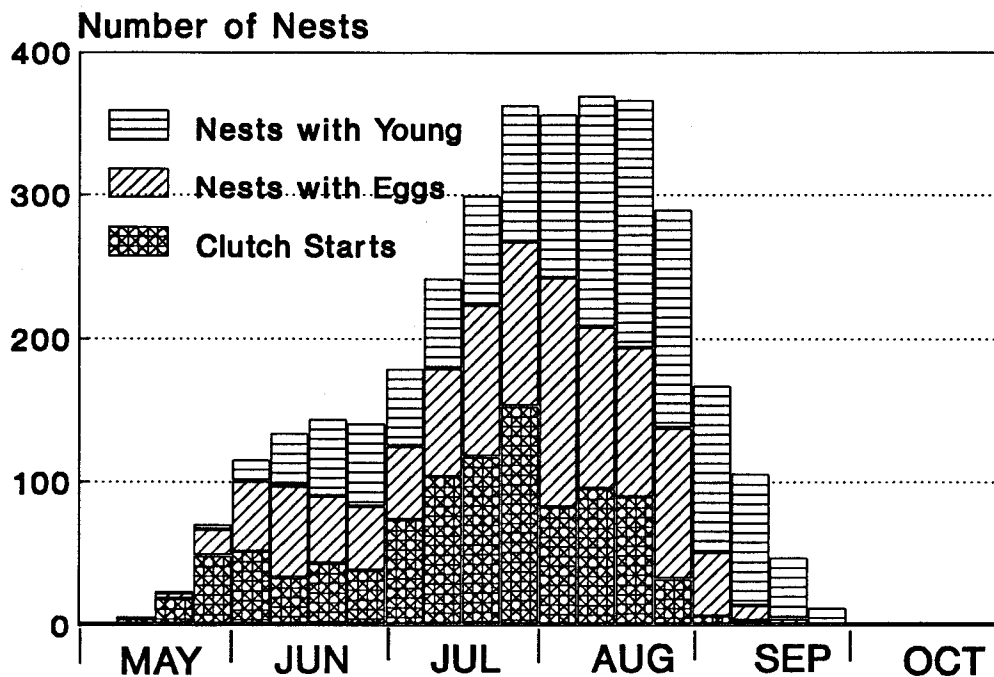


Figure 20. Breeding schedule of White-crowned Pigeons in Florida Bay during 1985-1989.

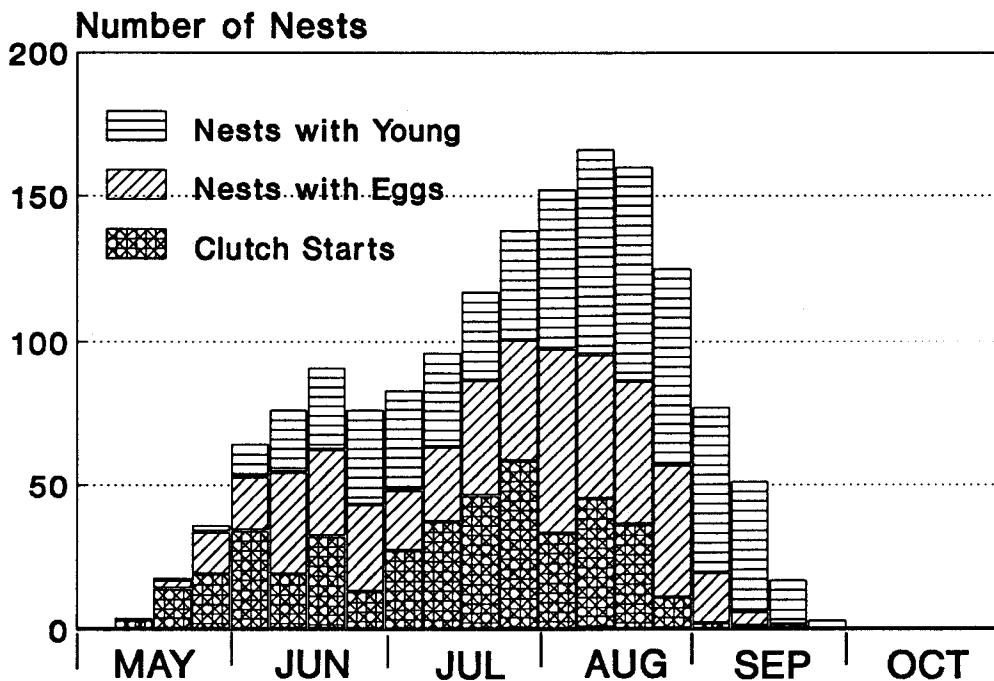


Figure 21. Breeding schedule of White-crowned Pigeons at Middle Butternut Key during 1985-1989.

The bars represent the total number of active nests, the cross-hatched area within the bars represents the number of new clutches, cross-hatched plus diagonal-hatched represents the number of nests with eggs, horizontal-hatched represents number of nests with young.

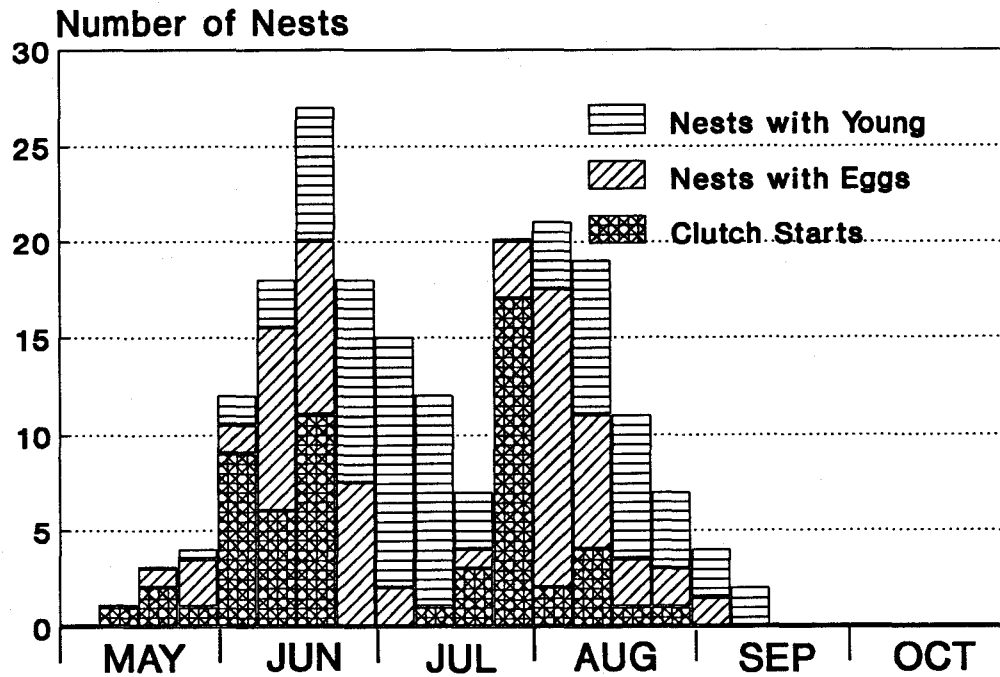


Figure 22. Breeding schedule of White-crowned Pigeons at Middle Butternut Key during 1985.

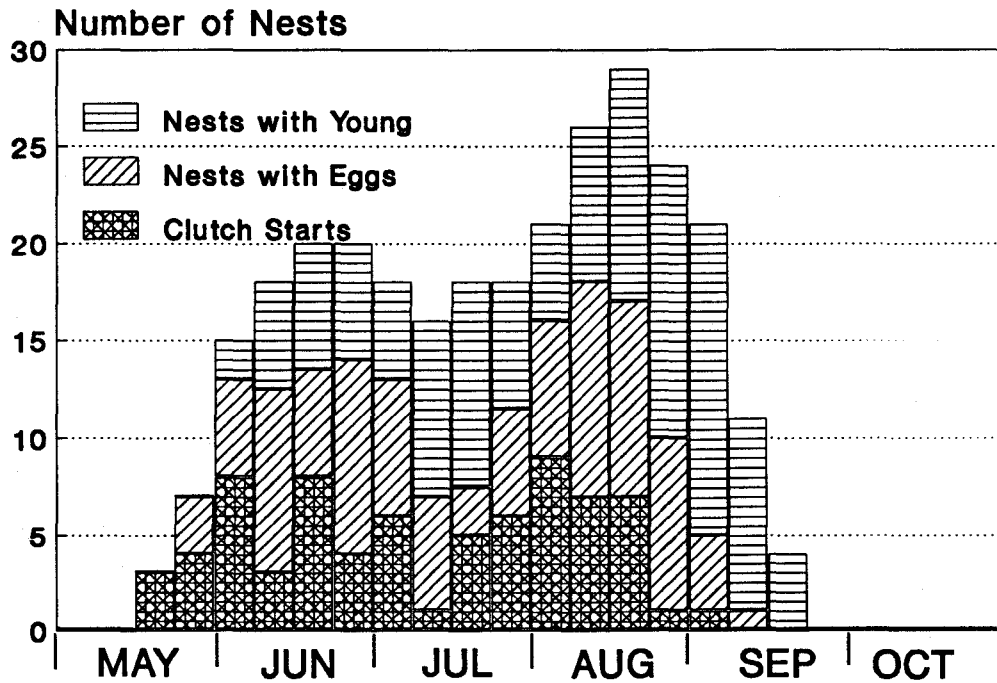


Figure 23. Breeding schedule of White-crowned Pigeons at Middle Butternut Key during 1986.

The bars represent the total number of active nests, the cross-hatched area within the bars represents the number of new clutches, cross-hatched plus diagonal-hatched represents the number of nests with eggs, horizontal-hatched represents number of nests with young.

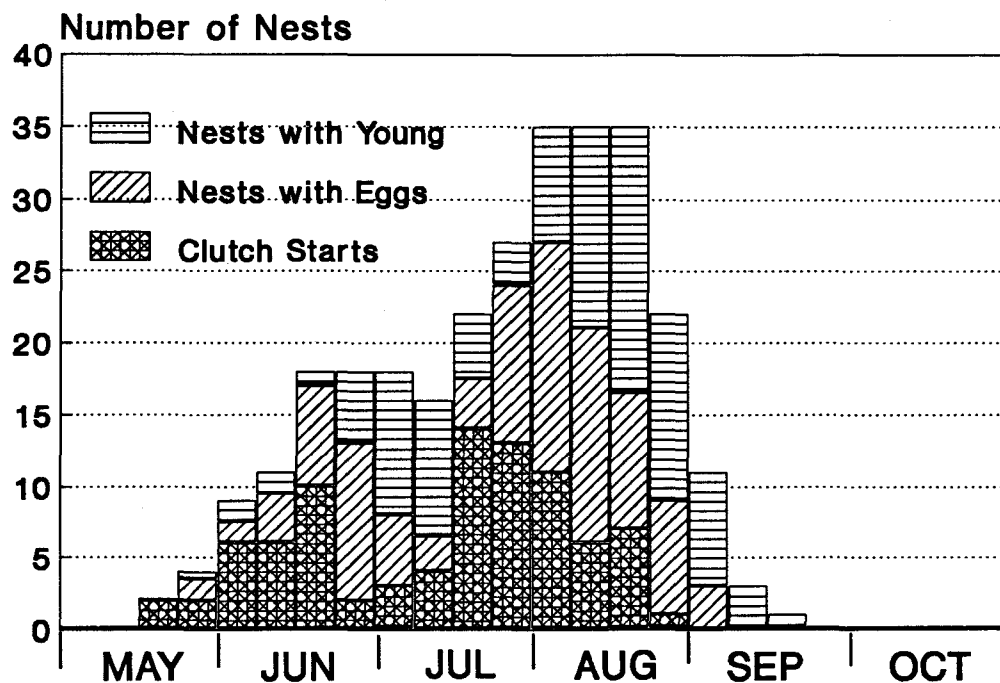


Figure 24. Breeding schedule of White-crowned Pigeons at Middle Butternut Key during 1987.

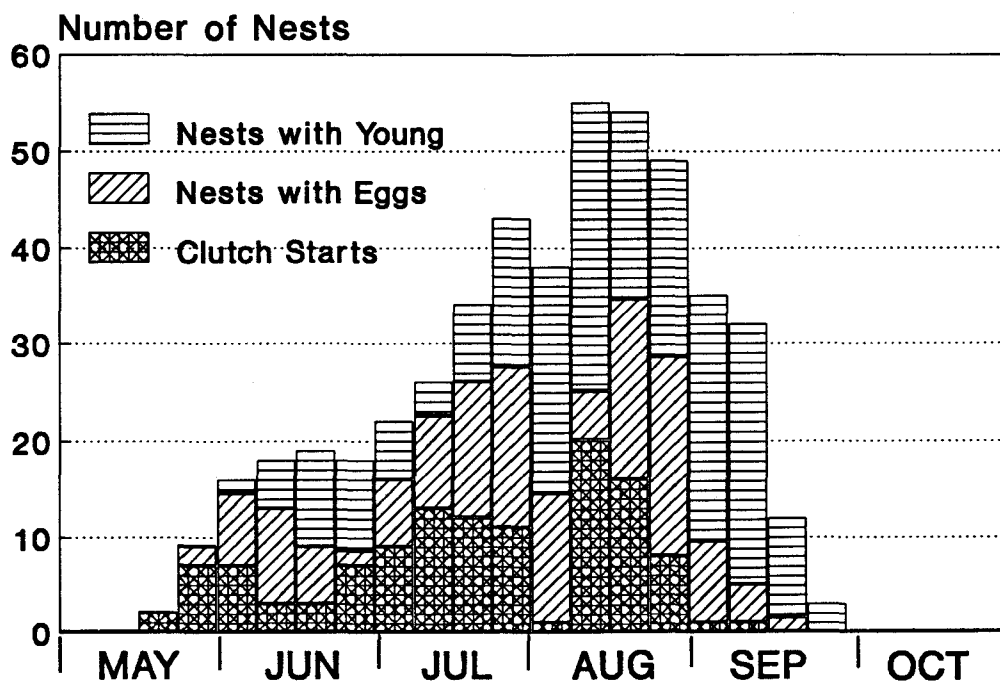


Figure 25. Breeding schedule of White-crowned Pigeons at Middle Butternut Key during 1988.

The bars represent the total number of active nests, the cross-hatched area within the bars represents the number of new clutches, cross-hatched plus diagonal-hatched represents the number of nests with eggs, horizontal-hatched represents number of nests with young.

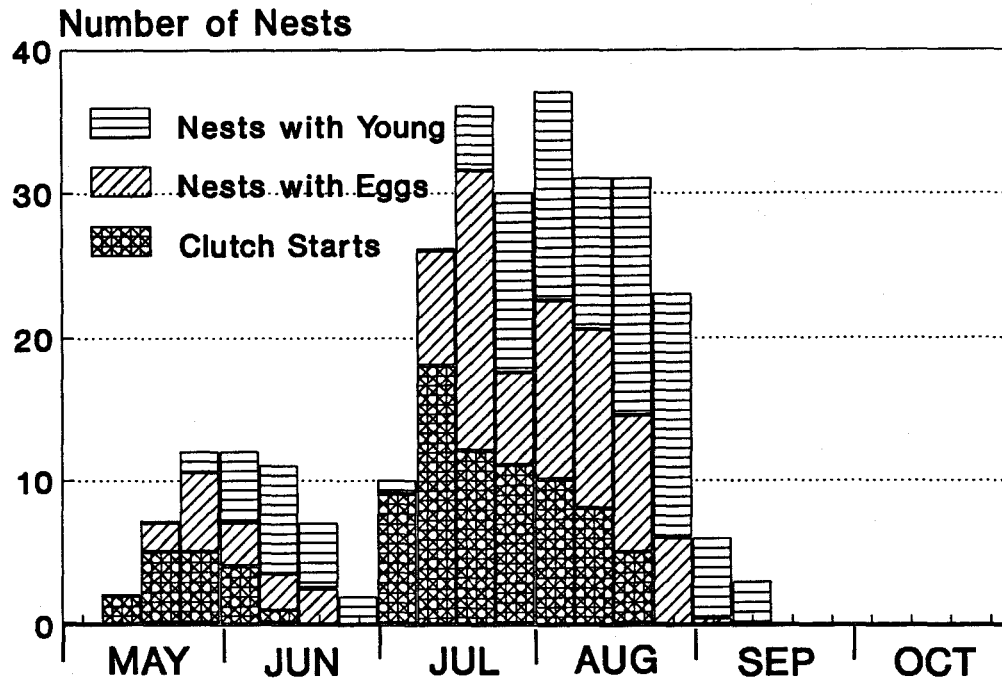


Figure 26. Breeding schedule of White-crowned Pigeons at Middle Butternut Key during 1989.

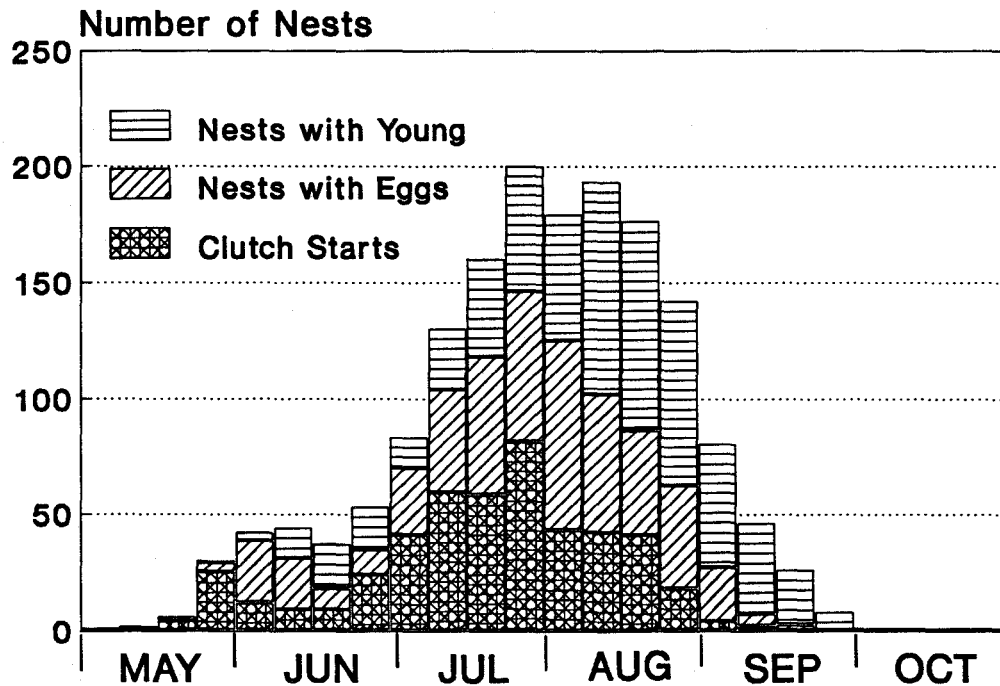


Figure 27. Breeding schedule of White-crowned Pigeons at Bottle Key during 1987-1989.

The bars represent the total number of active nests, the cross-hatched area within the bars represents the number of new clutches, cross-hatched plus diagonal-hatched represents the number of nests with eggs, horizontal-hatched represents number of nests with young.

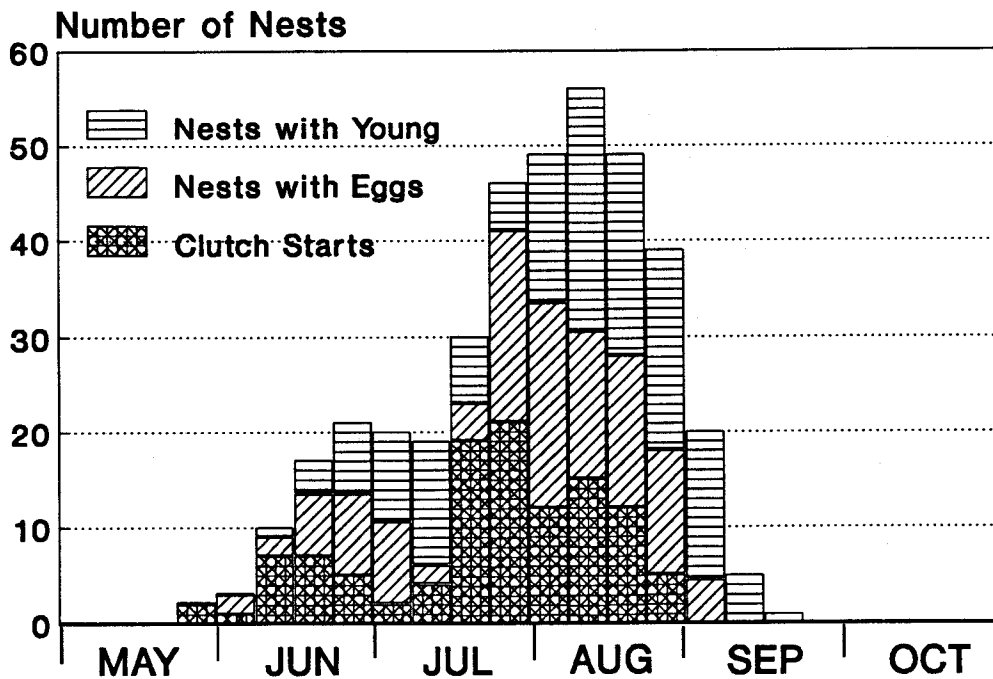


Figure 28. Breeding schedule of White-crowned Pigeons at Bottle Key during 1987.

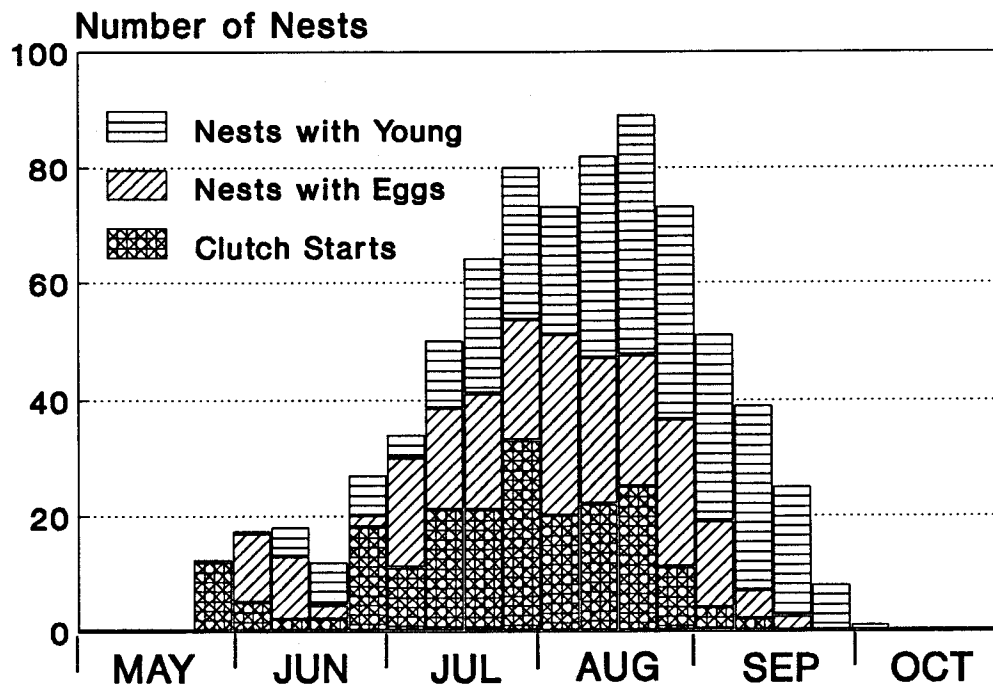


Figure 29. Breeding schedule of White-crowned Pigeons at Bottle Key during 1988.

The bars represent the total number of active nests, the cross-hatched area within the bars represents the number of new clutches, cross-hatched plus diagonal-hatched represents the number of nests with eggs, horizontal-hatched represents number of nests with young.

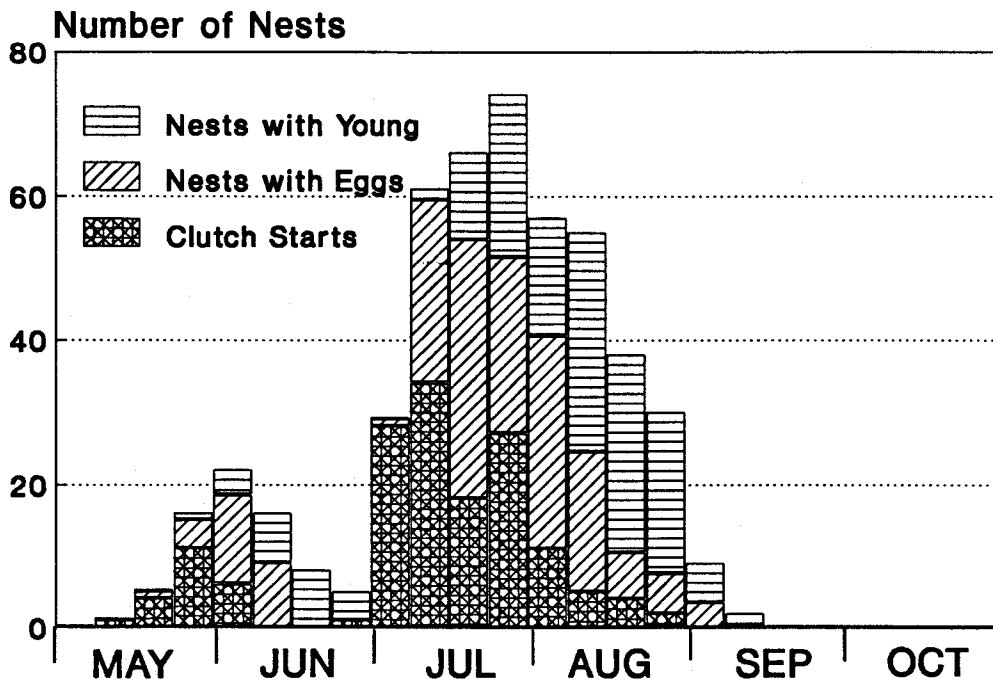
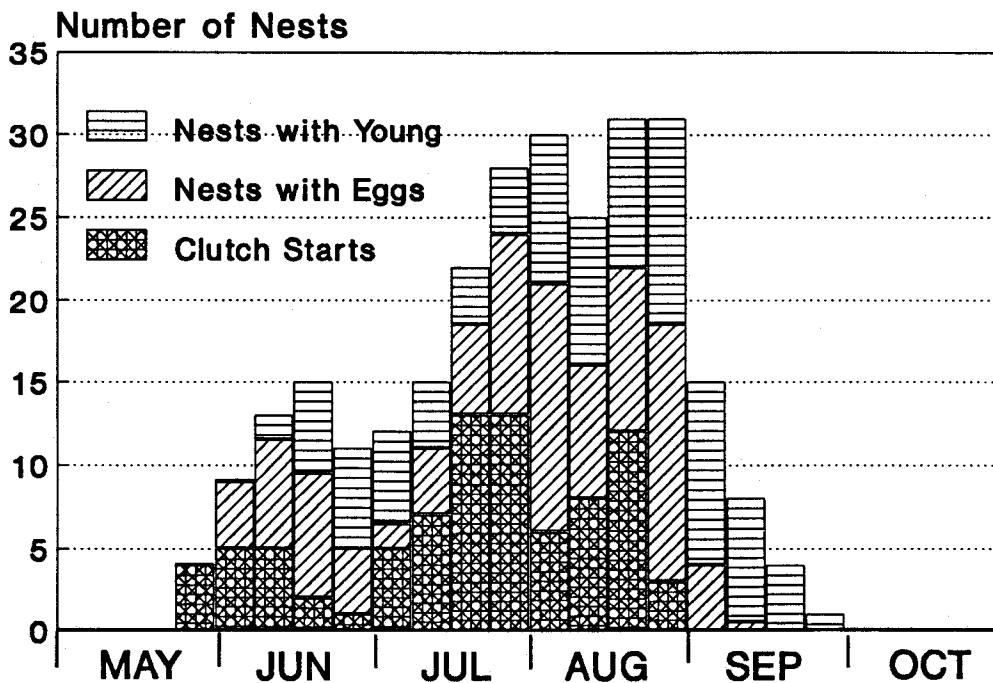


Figure 30. Breeding schedule of White-crowned Pigeons at Bottle Key during 1989.



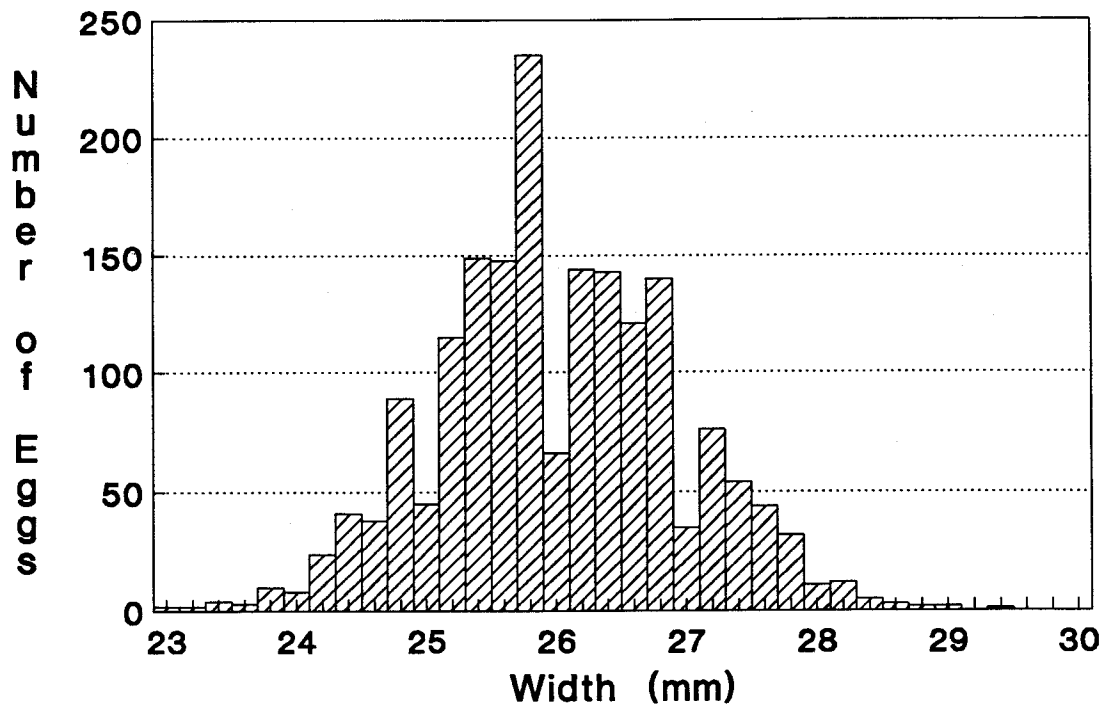


Figure 32. The frequency distribution of egg widths of White-crowned Pigeons.

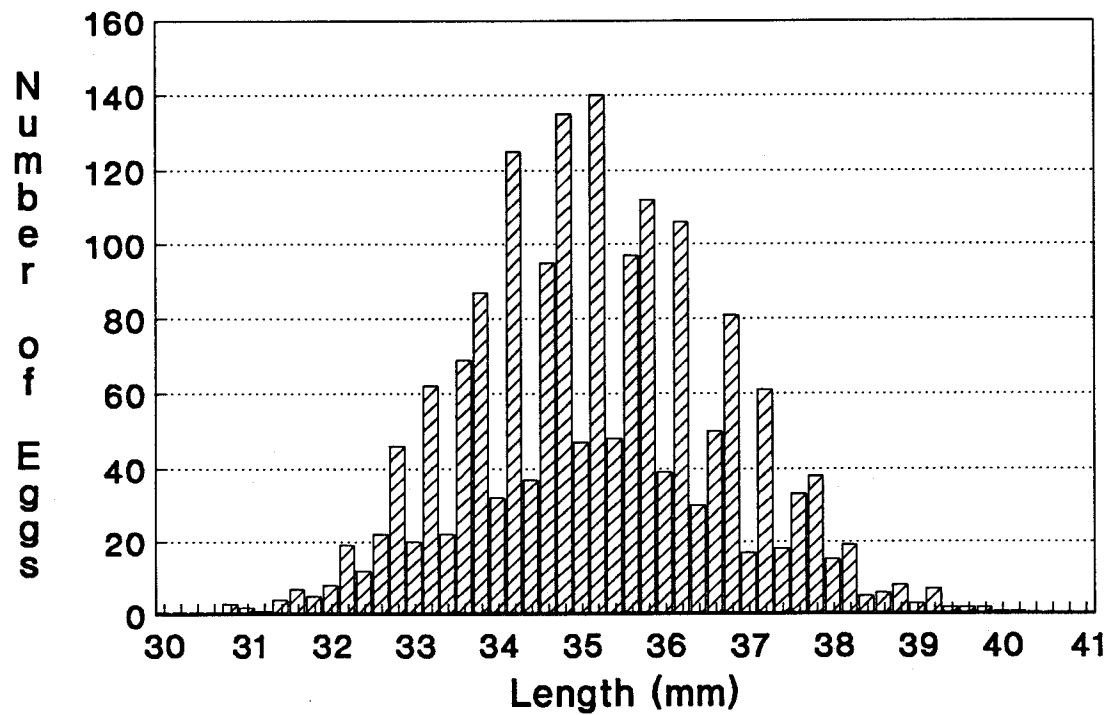


Figure 33. The frequency distribution of egg lengths of White-crowned Pigeons.

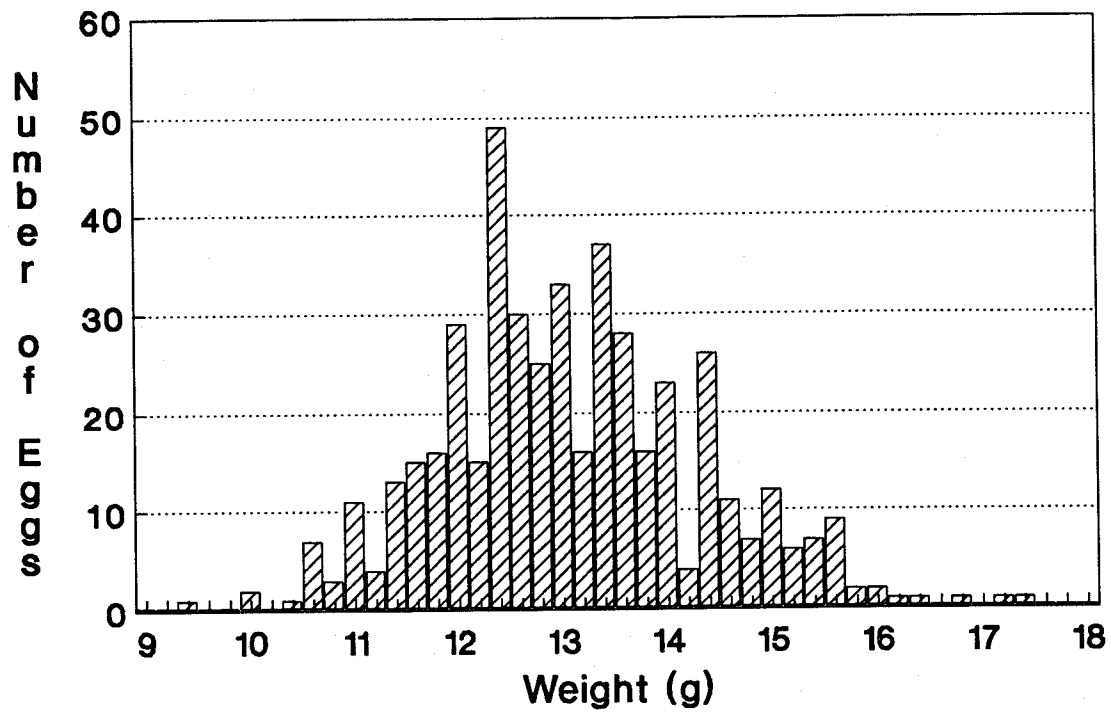


Figure 34. The frequency distribution of egg weights of White-crowned Pigeons.

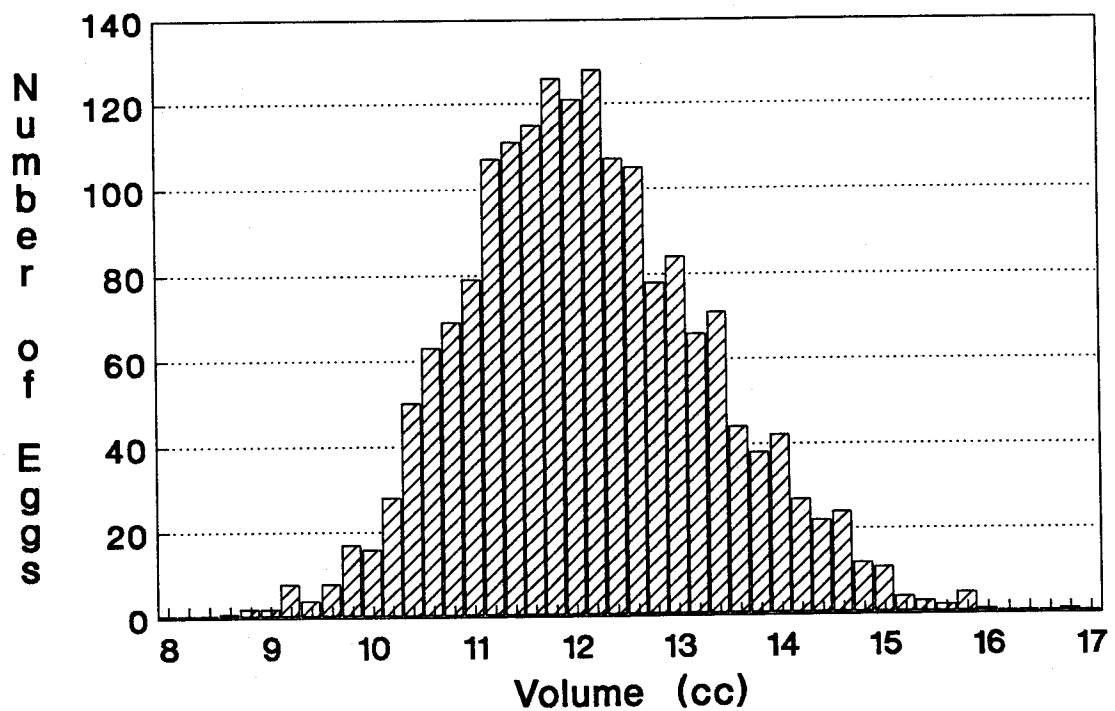


Figure 35. The frequency distribution of egg volumes of White-crowned Pigeons.

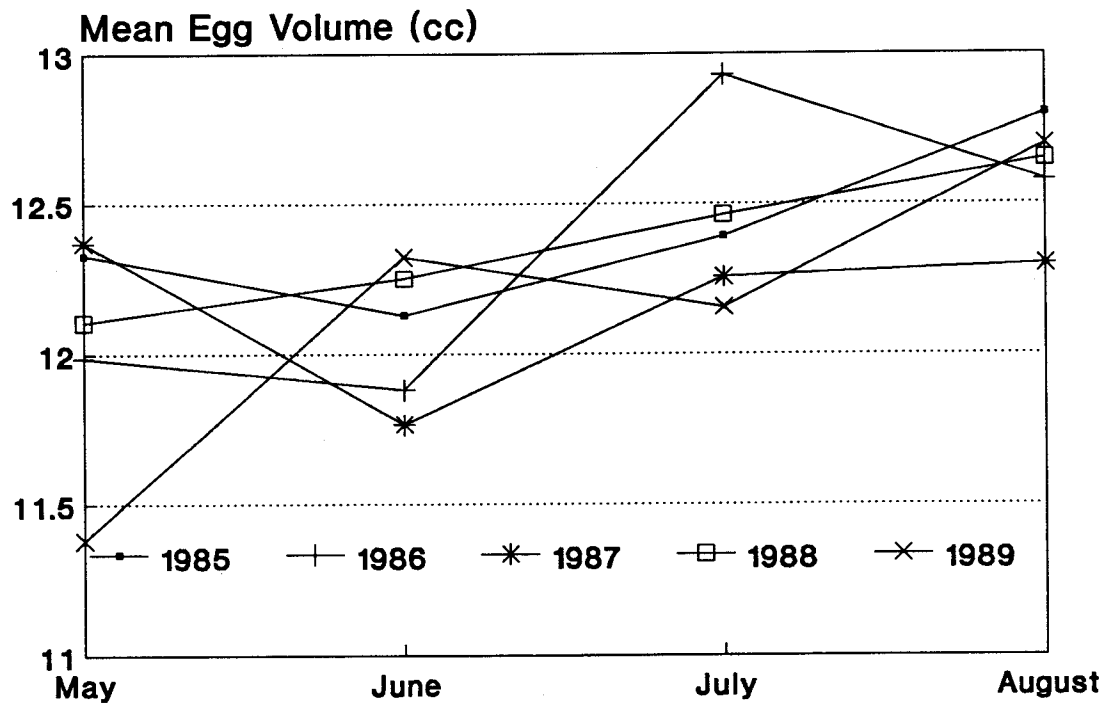


Figure 36. Mean egg volume relative to month and study year for White-crowned Pigeon eggs laid on Middle Butternut Key.

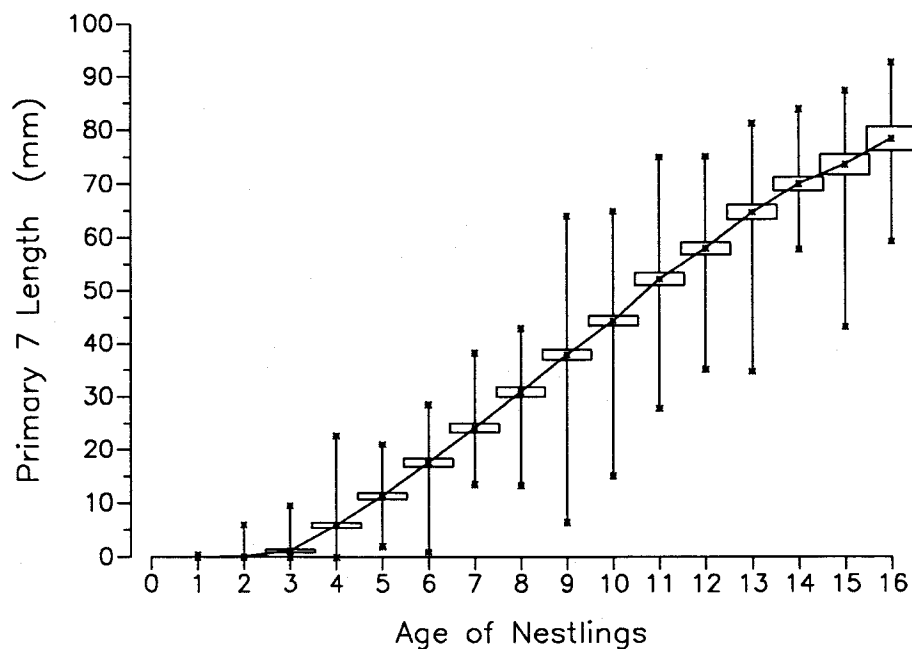


Figure 37. Growth of primary 7 relative to age for nestling White-crowned Pigeons. Mean length is shown by line, 95% confidence about mean by boxes, and range by vertical line.

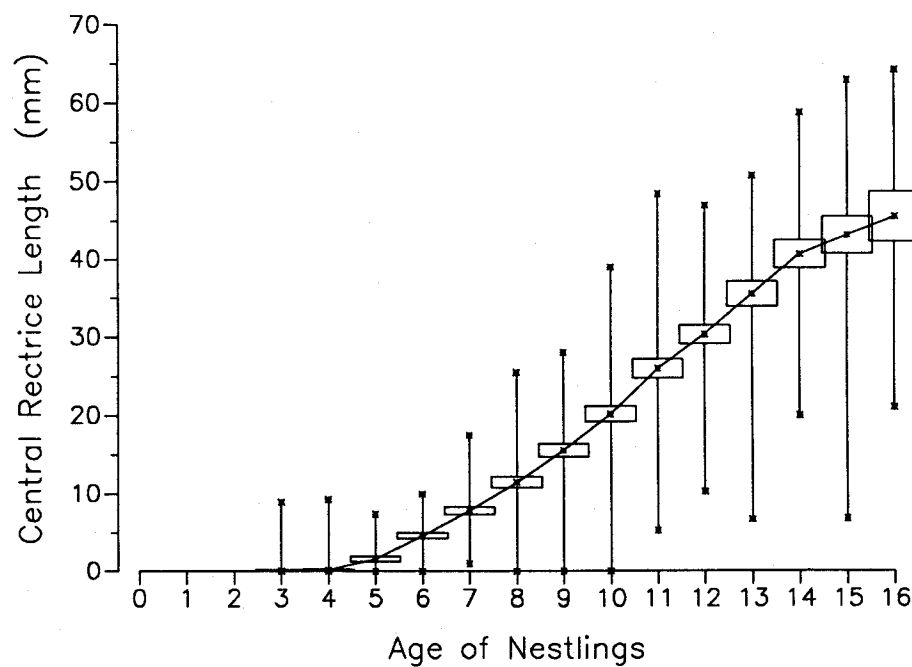


Figure 38. Growth of central rectrices relative to age for nestling White-crowned Pigeons. Mean length is shown by line, 95% confidence about mean by boxes, and range by vertical line.

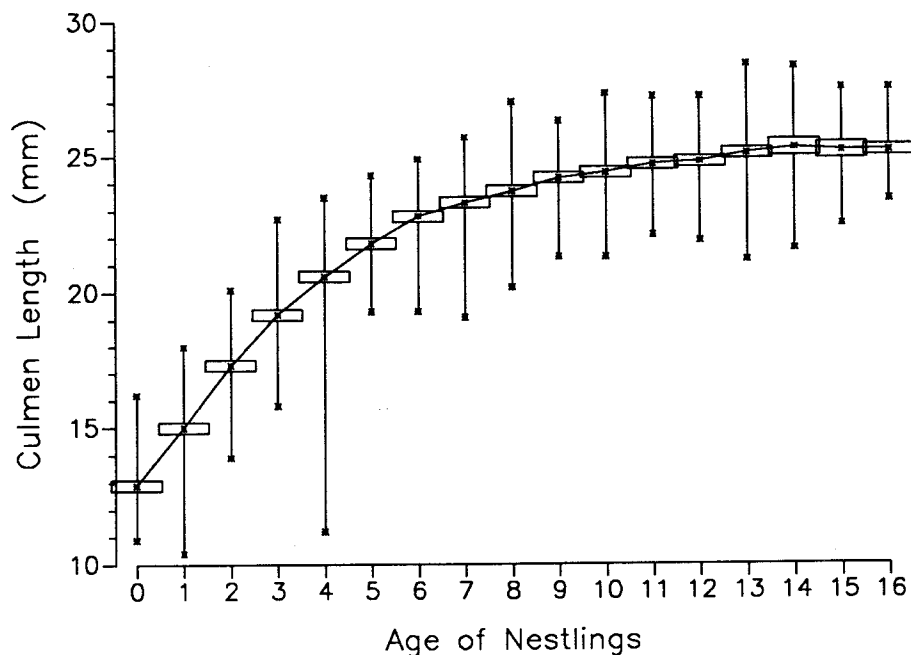


Figure 39. Growth of culmen relative to age for nestling White-crowned Pigeons. Mean length is shown by line, 95% confidence about mean by boxes, and range by vertical line.

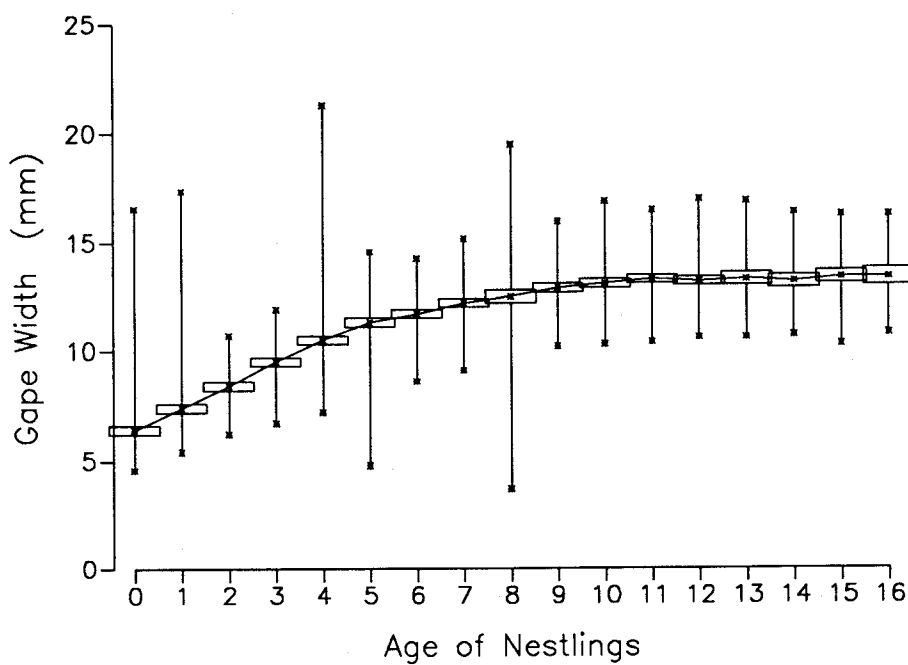


Figure 40. Growth of gape relative to age for nestling White-crowned Pigeons. Mean width is shown by line, 95% confidence about mean by boxes, and range by vertical line.

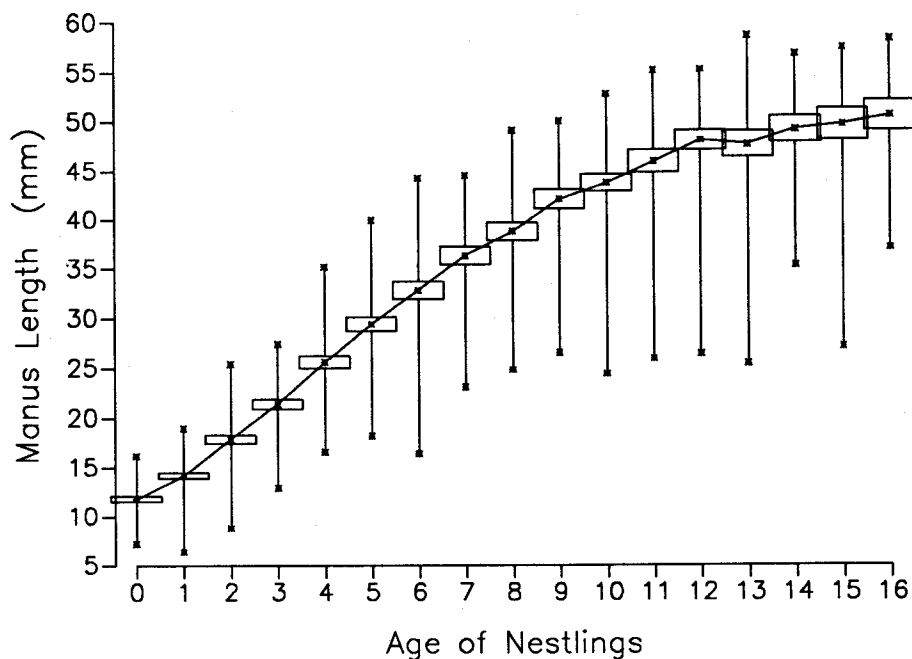


Figure 41. Growth of manus relative to age in nestling White-crowned Pigeons. Mean length is shown by line, 95% confidence about mean by boxes, and range by vertical line.

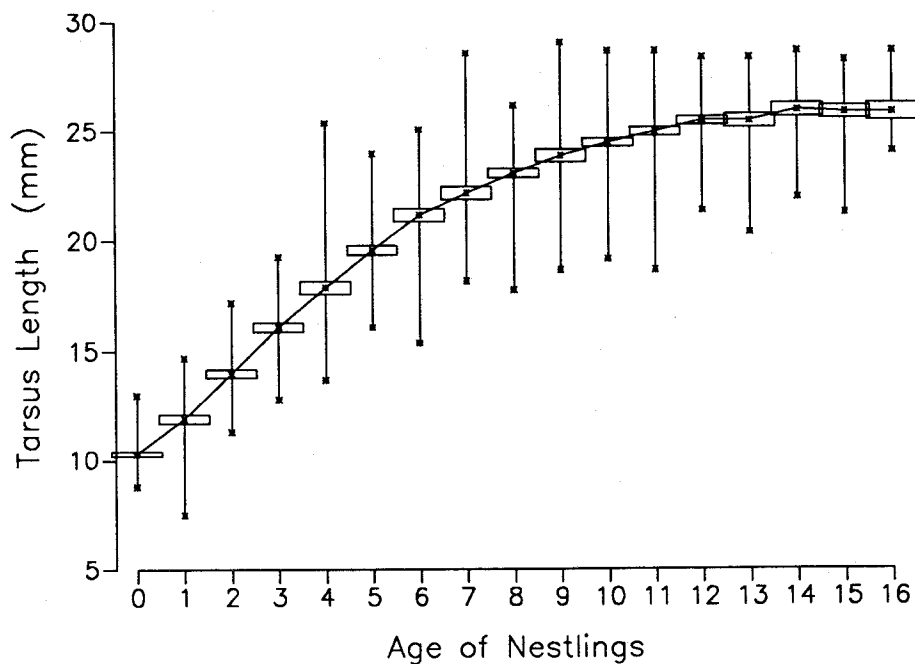


Figure 42. Growth of tarsus relative to age for nestling White-crowned Pigeons. Mean length is shown by line, 95% confidence about mean by boxes, and range by vertical line.

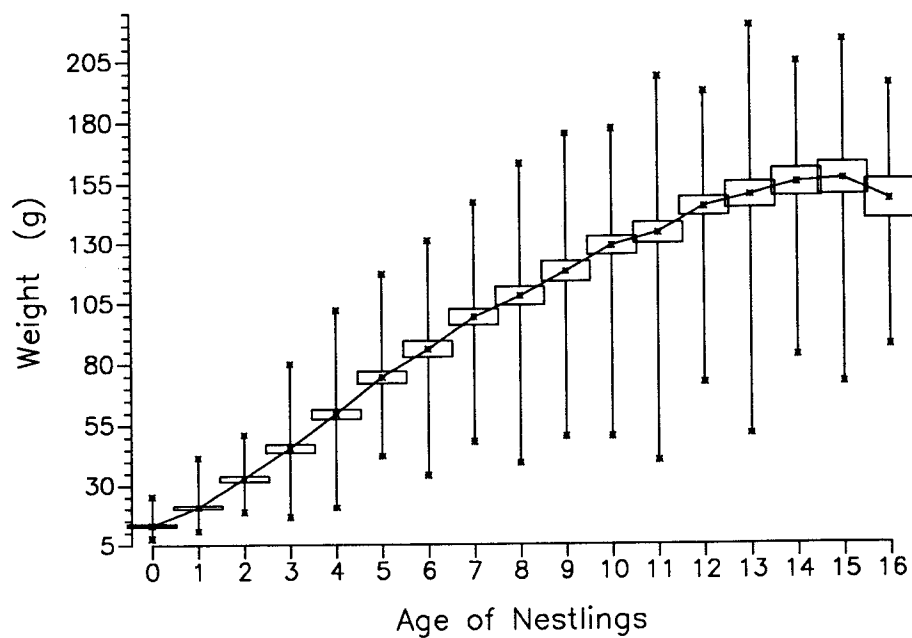


Figure 43. Weight of nestling White-crowned Pigeons relative to age. Mean weight is shown by line, 95% confidence about mean by boxes, and range by vertical line.

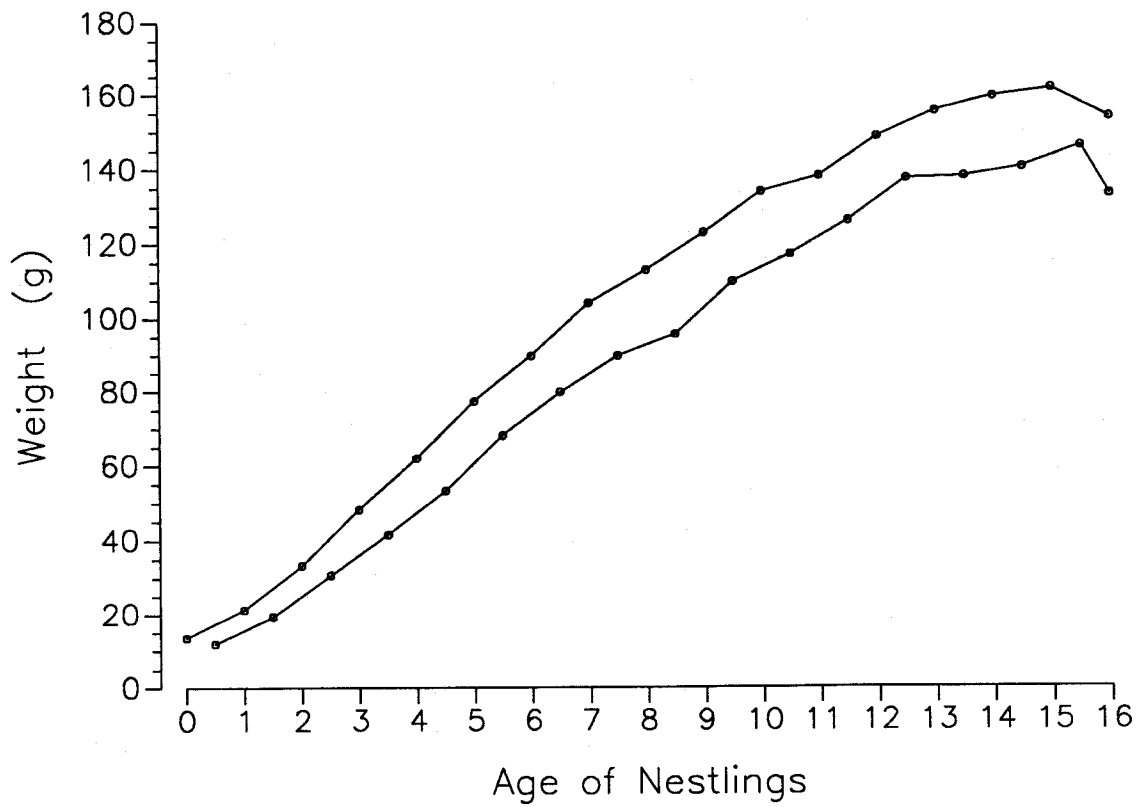


Figure 44. Asynchronous hatching and growth of nestling White-crowned Pigeons.

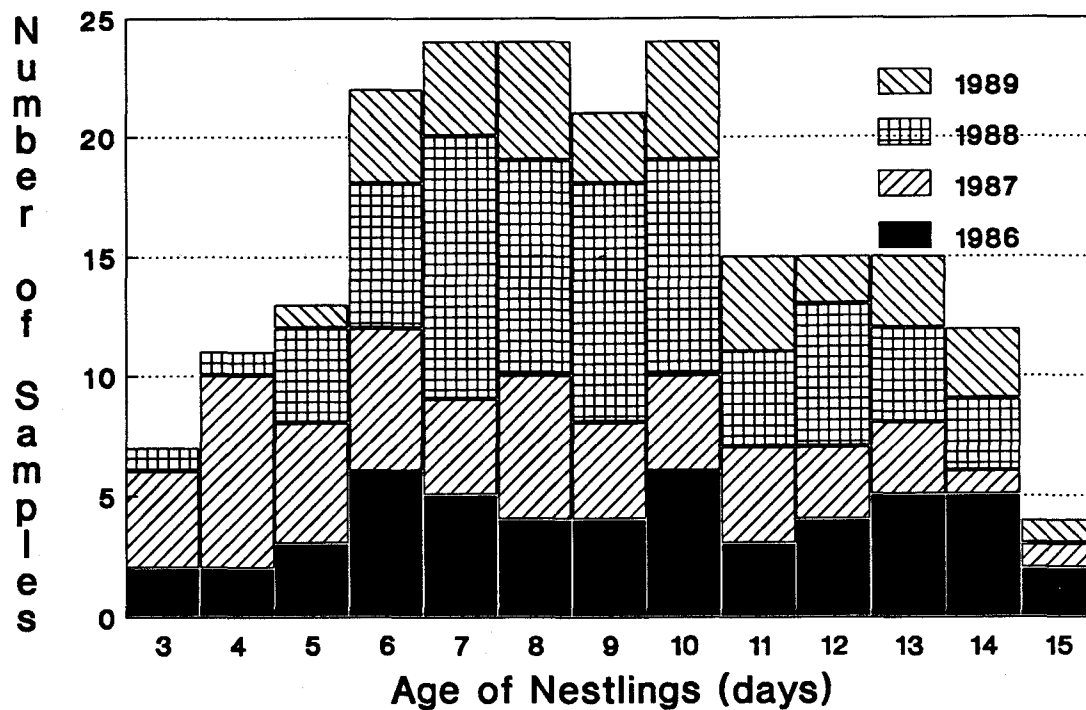


Figure 45. Number of crop samples collected from nestling White-crowned Pigeons relative to age.

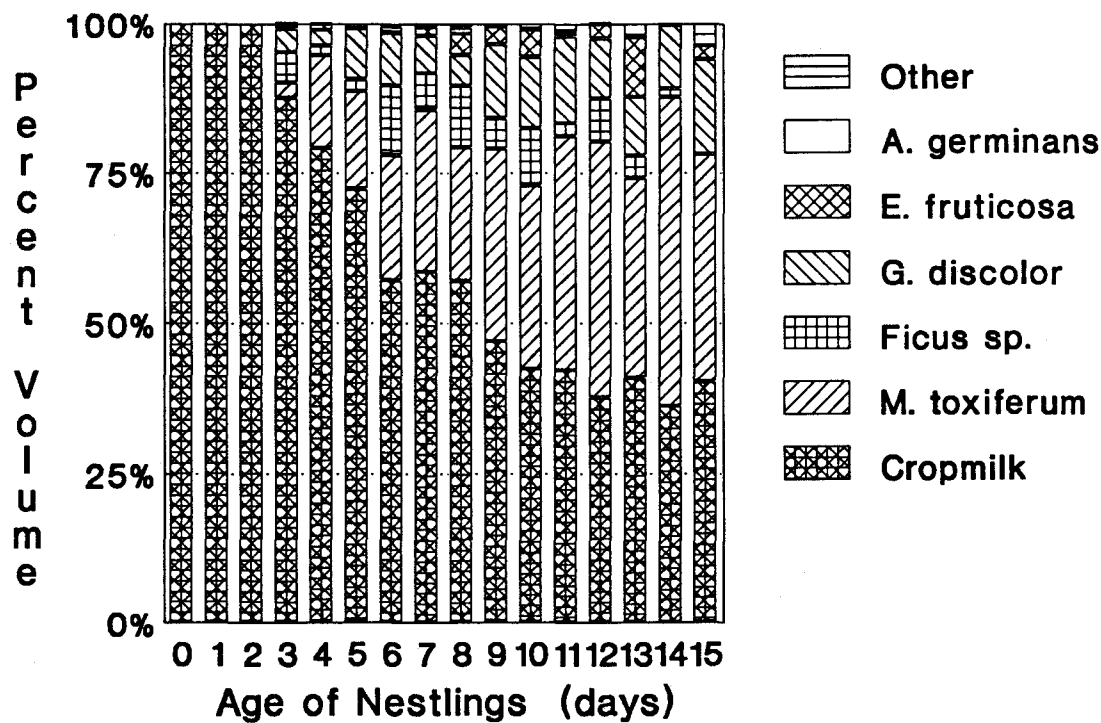


Figure 46. The percent volume of individual food items in crop samples of nestling White-crowned Pigeons relative to nestling age.

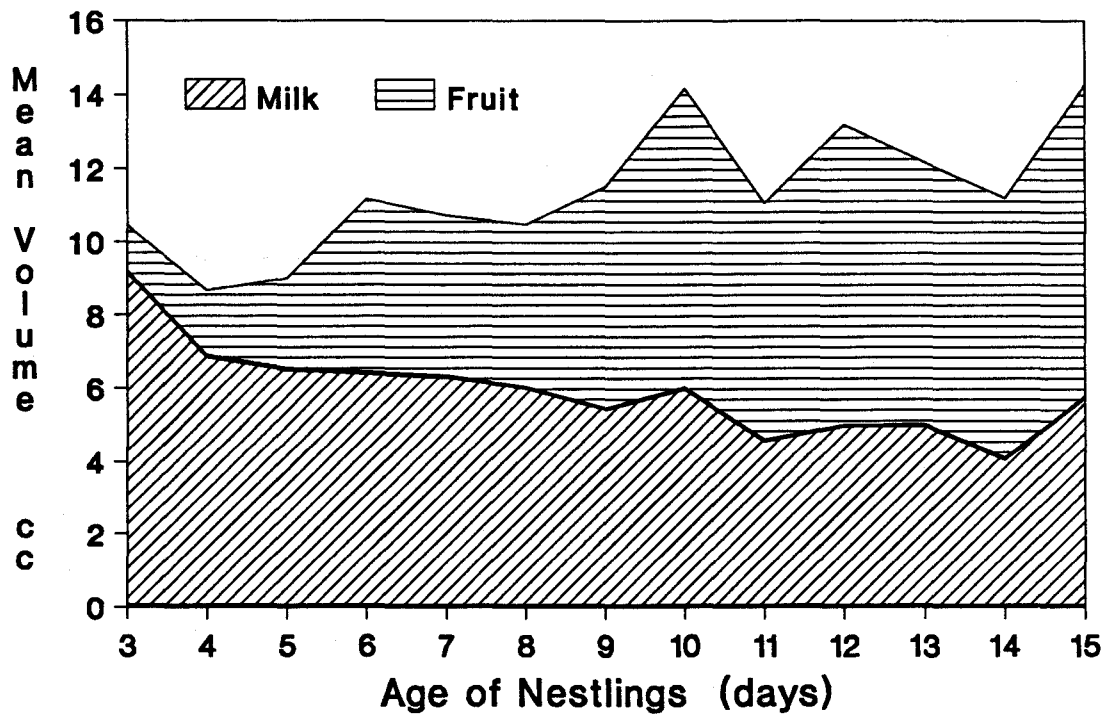


Figure 47. Mean volume of fruit and crop milk in samples from nestling White-crowned Pigeons relative to nestling age.

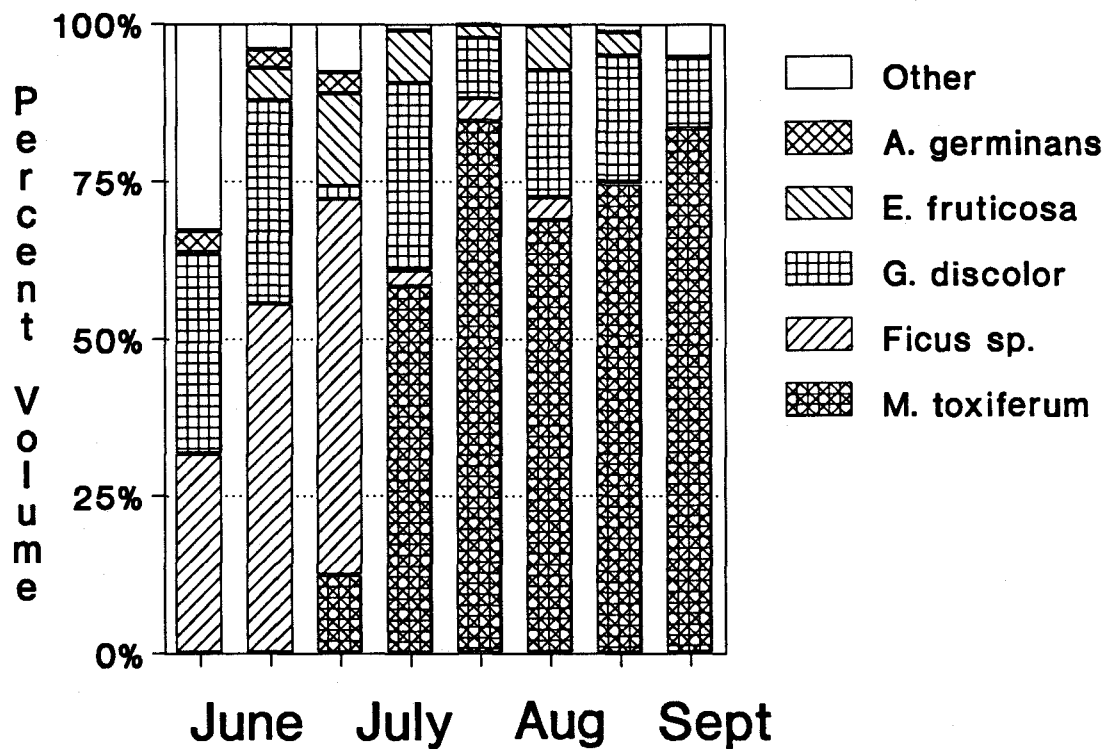


Figure 48. The percent volume of food items other than crop milk in samples from nestling White-crowned Pigeons relative to half-month periods.

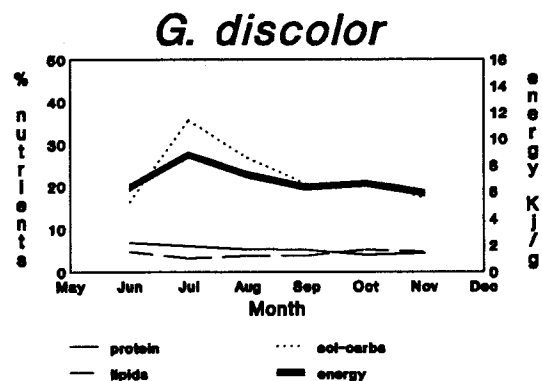
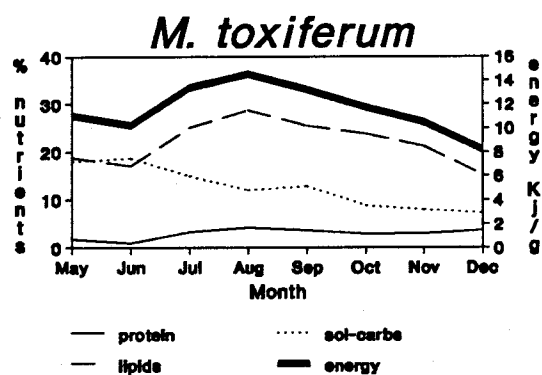
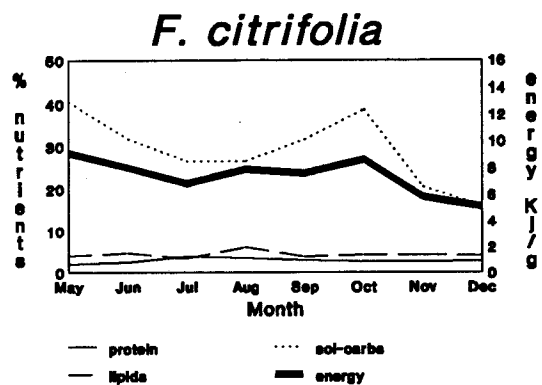
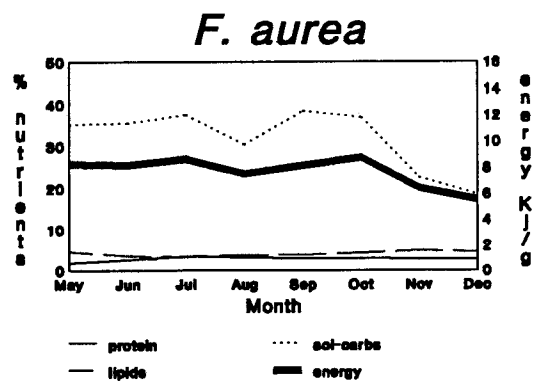


Figure 49. The percentage of nutrient and energy content in fruit relative to month for *Ficus aurea*, *F. citrifolia*, *Metopium toxiferum*, and *Guapira discolor*.

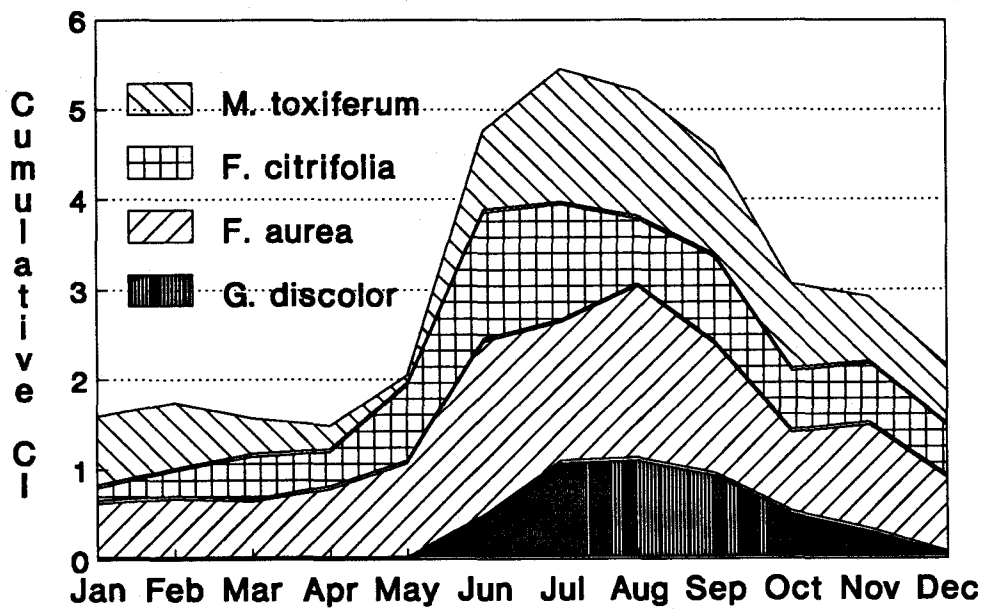
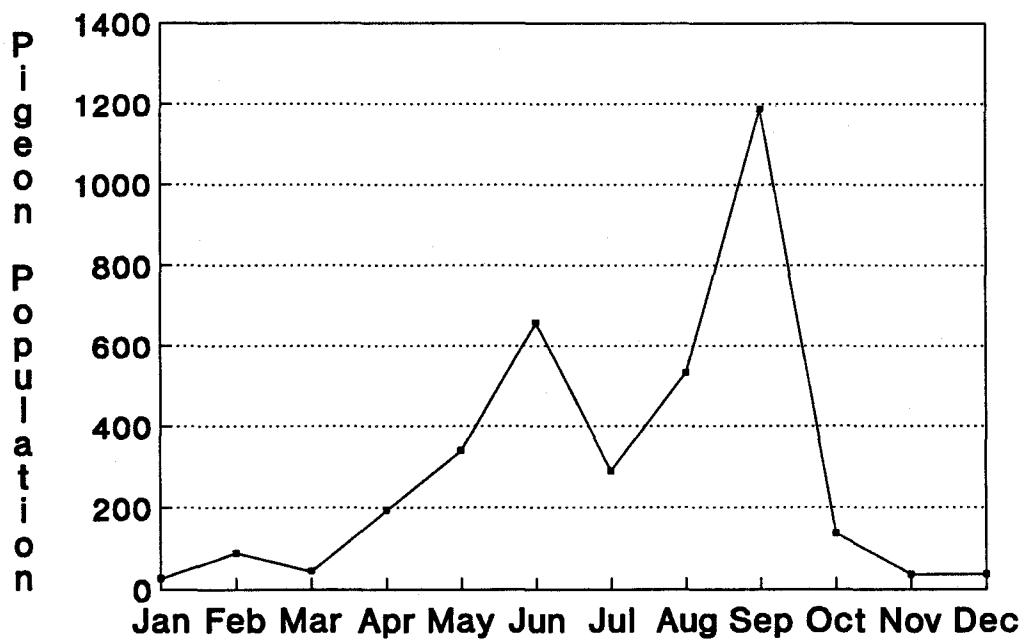


Figure 50. Mean number of White-crowned Pigeons seen on the four surveys relative to the cumulative competitive indices (CI) for the four most important food species.

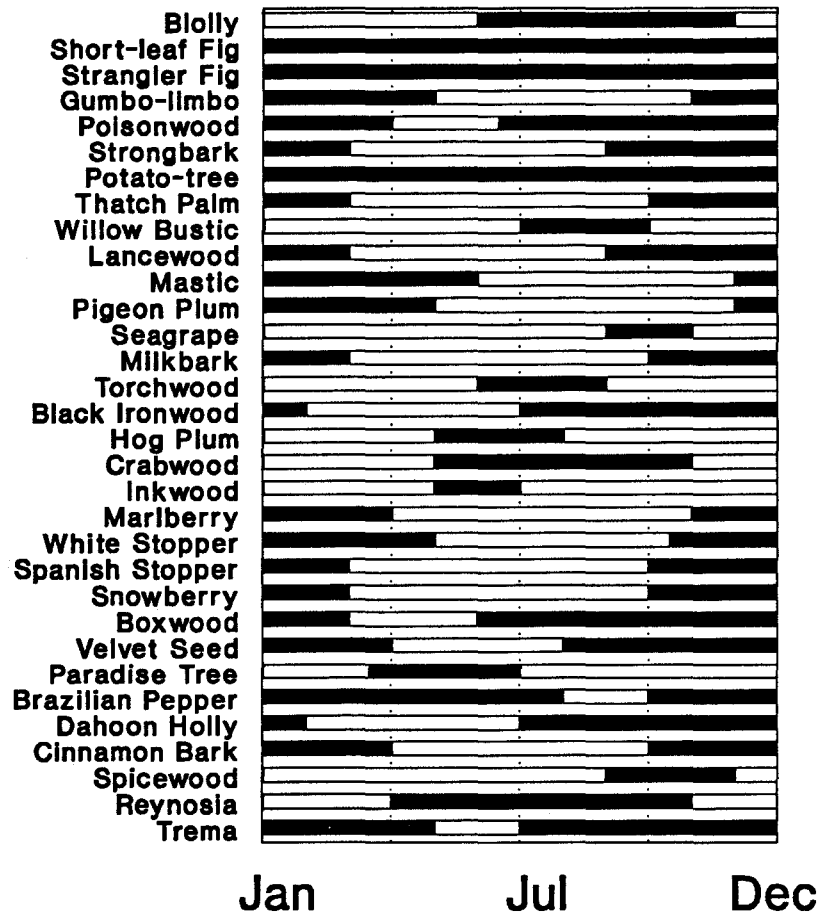


Figure 51. Seasonal ripe fruit availability of 32 select species used by White-crowned Pigeons.

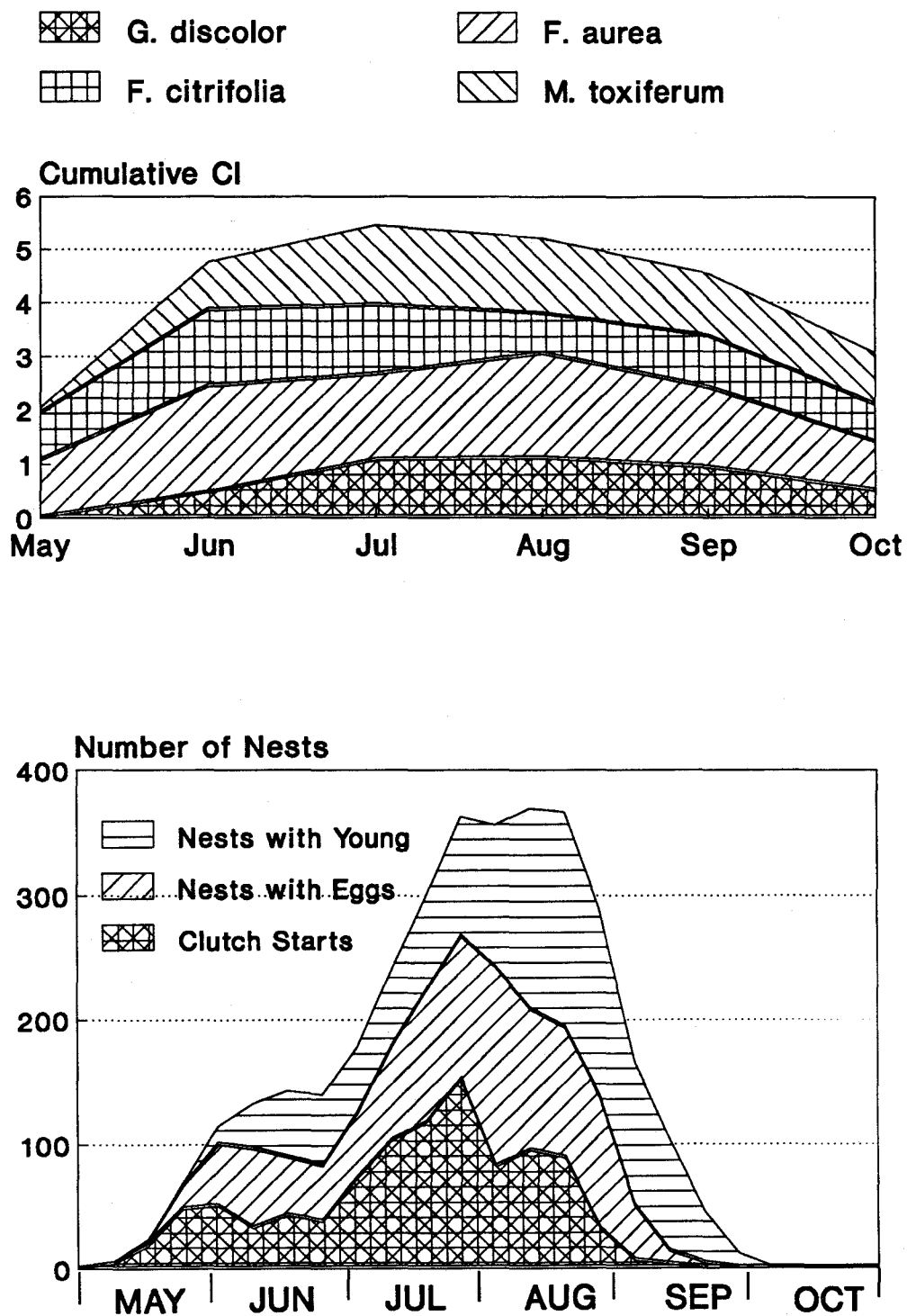


Figure 52. Upper graph shows cumulative competitive indices (CI) of four select species during the period May through October from 1987 through 1989. Lower graph shows chronology of nesting during the period 1985-1989 on all study keys.

Appendix 1. Formulae and definitions for calculating nesting success and daily survival probabilities using the Mayfield Method. Derivations for formulae have been modified from Hensler and Nichols (1981) and Hensler (1985).

j = the number of days in a given nesting period (e.g. incubation)

K = the number of nests observed

Y = a random variable taking the value of one if the K^{th} nest is successful

ΣY_k = the total number of successful nests for a given period

T = a random variable denoting the number of days the K^{th} nest was observed until it succeeded or failed

ΣT_k = the total number of exposure days for all nests within a given period

Daily survival rate (p):

$$p = 1 - \left(\frac{K - \Sigma Y_k}{\Sigma T_k} \right)$$

Variance of p (v):

$$v = \frac{p (1 - p)}{\Sigma T_k}$$

Survival for period (p_j):

$$p_j = (p)^j$$

Variance of p_j (v_j):

$$v_j = \frac{p (1 - p)}{\Sigma T_k} (jp^{j-1})^2$$

Overall nesting success for two periods (p):

$$p = (p_1)^{j_1} (p_2)^{j_2}$$

Overall variance of P for two periods (V_2):

$$V_2 = ((p_{j_1}^2 v_{j_2}) + (p_{j_2}^2 v_{j_1})) + (v_{j_1} v_{j_2})$$

Z statistic used to test for differences between nesting success estimates:

$$Z = \frac{P_1 - P_2}{\sqrt{V_1 + V_2}}$$

Appendix 2, Table 1. White-crowned Pigeon nesting success at Middle Butternut Key during the 1985 through 1989 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	151	111	
# of successful nest; Y_k	102	59	
Total nest days of observation; T_k	1280.0	1280.5	
Estimated daily survival; p	0.961	0.959	
Estimated standard deviation of p	0.005	0.005	
Estimated success probability for period; p^j	0.578	0.515	0.298
Estimated standard deviation of p^j	0.015	0.016	0.012
Late - after 8 July			
# of nests; K	250	187	
# of successful nest; Y_k	169	110	
Total nest days of observation; T_k	2163.5	2272.0	
Estimated daily survival; p	0.962	0.966	
Estimated standard deviation of p	0.004	0.003	
Estimated success probability for period; p^j	0.586	0.575	0.337
Estimated standard deviation of p^j	0.011	0.011	0.009
Total season			
# of nests; K	401	298	
# of successful nest; Y_k	271	169	
Total nest days of observation; T_k	3443.5	3552.5	
Estimated daily survival; p	0.962	0.963	
Estimated standard deviation of p	0.003	0.003	
Estimated success probability for period; p^j	0.583	0.553	0.332
Estimated standard deviation of p^j	0.009	0.009	0.007

Appendix 2, Table 2. White-crowned Pigeon nesting success at Middle Butternut Key during the 1985 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	29	21	
# of successful nest; Y_k	20	13	
Total nest days of observation; T_k	300.0	280.0	
Estimated daily survival; p	0.970	0.971	
Estimated standard deviation of p	0.009	0.009	
Estimated success probability for period; p^j	0.652	0.628	0.410
Estimated standard deviation of p^j	0.030	0.032	0.028
Late - after 8 July			
# of nests; K	26	16	
# of successful nest; Y_k	14	7	
Total nest days of observation; T_k	239.0	152.0	
Estimated daily survival; p	0.949	0.940	
Estimated standard deviation of p	0.014	0.019	
Estimated success probability for period; p^j	0.486	0.376	0.183
Estimated standard deviation of p^j	0.037	0.048	0.027
Total season			
# of nests; K	55	37	
# of successful nest; Y_k	34	20	
Total nest days of observation; T_k	539.0	432.0	
Estimated daily survival; p	0.961	0.960	
Estimated standard deviation of p	0.008	0.009	
Estimated success probability for period; p^j	0.573	0.526	0.301
Estimated standard deviation of p^j	0.024	0.027	0.020

Appendix 2, Table 3. White-crowned Pigeon nesting success at Middle Butternut Key during the 1986 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	31	30	
# of successful nest; Y_k	24	10	
Total nest days of observation; T_k	255.0	284.5	
Estimated daily survival; p	0.972	0.929	
Estimated standard deviation of p	0.010	0.015	
Estimated success probability for period; p^j	0.677	0.311	0.210
Estimated standard deviation of p^j	0.031	0.035	0.025
Late - after 8 July			
# of nests; K	34	30	
# of successful nest; Y_k	27	19	
Total nest days of observation; T_k	331.0	381.5	
Estimated daily survival; p	0.978	0.971	
Estimated standard deviation of p	0.007	0.008	
Estimated success probability for period; p^j	0.741	0.626	0.464
Estimated standard deviation of p^j	0.025	0.027	0.026
Total season			
# of nests; K	65	60	
# of successful nest; Y_k	51	29	
Total nest days of observation; T_k	586.0	666.0	
Estimated daily survival; p	0.976	0.953	
Estimated standard deviation of p	0.006	0.008	
Estimated success probability for period; p^j	0.712	0.466	0.332
Estimated standard deviation of p^j	0.020	0.022	0.018

Appendix 2, Table 4. White-crowned Pigeon nesting success at Middle Butternut Key during the 1987 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	30	21	
# of successful nest; Y_k	20	9	
Total nest days of observation; T_k	245.0	197.5	
Estimated daily survival; p	0.959	0.939	
Estimated standard deviation of p	0.012	0.016	
Estimated success probability for period; p^j	0.557	0.366	0.204
Estimated standard deviation of p^j	0.036	0.042	0.027
Late - after 8 July			
# of nests; K	50	35	
# of successful nest; Y_k	29	17	
Total nest days of observation; T_k	410.0	361.5	
Estimated daily survival; p	0.948	0.950	
Estimated standard deviation of p	0.010	0.011	
Estimated success probability for period; p^j	0.478	0.441	0.211
Estimated standard deviation of p^j	0.028	0.031	0.019
Total season			
# of nests; K	80	56	
# of successful nest; Y_k	49	26	
Total nest days of observation; T_k	655.0	559.0	
Estimated daily survival; p	0.952	0.946	
Estimated standard deviation of p	0.008	0.009	
Estimated success probability for period; p^j	0.507	0.413	0.209
Estimated standard deviation of p^j	0.022	0.025	0.015

Appendix 2, Table 5. White-crowned Pigeon nesting success at Middle Butternut Key during the 1988 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	36	23	
# of successful nest; Y_k	22	16	
Total nest days of observation; T_k	306.5	286.0	
Estimated daily survival; p	0.954	0.975	
Estimated standard deviation of p	0.011	0.009	
Estimated success probability for period; p^j	0.519	0.672	0.349
Estimated standard deviation of p^j	0.032	0.030	0.027
Late - after 8 July			
# of nests; K	79	69	
# of successful nest; Y_k	65	54	
Total nest days of observation; T_k	732.0	985.5	
Estimated daily survival; p	0.980	0.984	
Estimated standard deviation of p	0.005	0.003	
Estimated success probability for period; p^j	0.763	0.782	0.597
Estimated standard deviation of p^j	0.016	0.013	0.016
Total season			
# of nests; K	115	92	
# of successful nest; Y_k	87	70	
Total nest days of observation; T_k	1038.5	1271.5	
Estimated daily survival; p	0.973	0.982	
Estimated standard deviation of p	0.005	0.003	
Estimated success probability for period; p^j	0.682	0.756	0.515
Estimated standard deviation of p^j	0.015	0.012	0.014

Appendix 2, Table 6. White-crowned Pigeon nesting success at Middle Butternut Key during the 1989 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	25	16	
# of successful nest; Y_k	16	11	
Total nest days of observation; T_k	173.5	232.5	
Estimated daily survival; p	0.948	0.978	
Estimated standard deviation of p	0.016	0.009	
Estimated success probability for period; p^j	0.474	0.706	0.335
Estimated standard deviation of p^j	0.044	0.032	0.035
Late - after 8 July			
# of nests; K	61	37	
# of successful nest; Y_k	34	13	
Total nest days of observation; T_k	451.5	391.5	
Estimated daily survival; p	0.940	0.938	
Estimated standard deviation of p	0.011	0.012	
Estimated success probability for period; p^j	0.421	0.363	0.153
Estimated standard deviation of p^j	0.027	0.030	0.016
Total season			
# of nests; K	86	53	
# of successful nest; Y_k	50	24	
Total nest days of observation; T_k	625.0	624.0	
Estimated daily survival; p	0.942	0.953	
Estimated standard deviation of p	0.009	0.008	
Estimated success probability for period; p^j	0.435	0.467	0.203
Estimated standard deviation of p^j	0.023	0.023	0.015

Appendix 3, Table 1. White-crowned Pigeon nesting success at Bottle Key during the 1986 through 1989 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	96	73	
# of successful nest; Y_k	52	42	
Total nest days of observation; T_k	700.0	810.1	
Estimated daily survival; p	0.937	0.961	
Estimated standard deviation of p	0.009	0.006	
Estimated success probability for period; p^j	0.402	0.535	0.215
Estimated standard deviation of p^j	0.022	0.020	0.014
Late - after 8 July			
# of nests; K	321	199	
# of successful nest; Y_k	177	126	
Total nest days of observation; T_k	2499.5	2449.5	
Estimated daily survival; p	0.942	0.970	
Estimated standard deviation of p	0.004	0.003	
Estimated success probability for period; p^j	0.435	0.616	0.268
Estimated standard deviation of p^j	0.011	0.010	0.008
Total season (1986-1989)			
# of nests; K	417	272	
# of successful nest; Y_k	229	168	
Total nest days of observation; T_k	3199.5	3259.6	
Estimated daily survival; p	0.941	0.968	
Estimated standard deviation of p	0.004	0.003	
Estimated success probability for period; p^j	0.428	0.595	0.254
Estimated standard deviation of p^j	0.010	0.009	0.007

Appendix 3, Table 2. White-crowned Pigeon nesting success at Bottle Key during the 1986 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
# of nests; K	46	36	
# of successful nest; Y_k	28	21	
Total nest days of observation; T_k	321.0	390.0	
Estimated daily survival; p	0.943	0.961	
Estimated standard deviation of p	0.012	0.009	
Estimated success probability for period; p^j	0.445	0.533	0.238
Estimated standard deviation of p^j	0.033	0.029	0.021

Appendix 3, Table 3. White-crowned Pigeon nesting success at Bottle Key during the 1987 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	21	20	
# of successful nest; Y_k	15	15	
Total nest days of observation; T_k	184.0	259.6	
Estimated daily survival; p	0.967	0.980	
Estimated standard deviation of p	0.013	0.008	
Estimated success probability for period; p^j	0.628	0.732	0.460
Estimated standard deviation of p^j	0.039	0.029	0.034
Late - after 8 July			
# of nests; K	65	41	
# of successful nest; Y_k	39	20	
Total nest days of observation; T_k	551.5	444.0	
Estimated daily survival; p	0.952	0.952	
Estimated standard deviation of p	0.009	0.010	
Estimated success probability for period; p^j	0.508	0.460	0.234
Estimated standard deviation of p^j	0.024	0.028	0.018
Total season			
# of nests; K	86	61	
# of successful nest; Y_k	54	35	
Total nest days of observation; T_k	735.5	703.6	
Estimated daily survival; p	0.956	0.963	
Estimated standard deviation of p	0.007	0.007	
Estimated success probability for period; p^j	0.536	0.547	0.293
Estimated standard deviation of p^j	0.021	0.021	0.016

Appendix 3, Table 4. White-crowned Pigeon nesting success at Bottle Key during the 1988 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	35	30	
# of successful nest; Y_k	22	22	
Total nest days of observation; T_k	272.5	374.0	
Estimated daily survival; p	0.952	0.978	
Estimated standard deviation of p	0.012	0.007	
Estimated success probability for period; p^j	0.504	0.707	0.356
Estimated standard deviation of p^j	0.035	0.025	0.028
Late - after 8 July			
# of nests; K	127	74	
# of successful nest; Y_k	65	64	
Total nest days of observation; T_k	934.0	1095.0	
Estimated daily survival; p	0.933	0.990	
Estimated standard deviation of p	0.008	0.002	
Estimated success probability for period; p^j	0.382	0.863	0.330
Estimated standard deviation of p^j	0.019	0.010	0.017
Total season			
# of nests; K	162	104	
# of successful nest; Y_k	87	86	
Total nest days of observation; T_k	1206.5	1469.0	
Estimated daily survival; p	0.937	0.987	
Estimated standard deviation of p	0.006	0.002	
Estimated success probability for period; p^j	0.407	0.820	0.334
Estimated standard deviation of p^j	0.017	0.010	0.014

Appendix 3, Table 5. White-crowned Pigeon nesting success at Bottle Key during the 1989 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	40	19	
# of successful nest; Y_k	15	2	
Total nest days of observation; T_k	243.5	148.0	
Estimated daily survival; p	0.897	0.885	
Estimated standard deviation of p	0.019	0.026	
Estimated success probability for period; p^j	0.219	0.141	0.031
Estimated standard deviation of p^j	0.035	0.041	0.010
Late - after 8 July			
# of nests; K	83	52	
# of successful nest; Y_k	45	24	
Total nest days of observation; T_k	693.0	549.0	
Estimated daily survival; p	0.945	0.948	
Estimated standard deviation of p	0.008	0.009	
Estimated success probability for period; p^j	0.454	0.432	0.196
Estimated standard deviation of p^j	0.022	0.025	0.015
Total season			
# of nests; K	123	71	
# of successful nest; Y_k	60	26	
Total nest days of observation; T_k	936.5	697.0	
Estimated daily survival; p	0.932	0.935	
Estimated standard deviation of p	0.008	0.009	
Estimated success probability for period; p^j	0.377	0.343	0.129
Estimated standard deviation of p^j	0.019	0.022	0.010

Appendix 4, Table 1. White-crowned Pigeon nesting success at West Butternut Key during the 1986 through 1988 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	19	20	
# of successful nest; Y_k	13	7	
Total nest days of observation; T_k	169.0	188.5	
Estimated daily survival; p	0.964	0.931	
Estimated standard deviation of p	0.014	0.018	
Estimated success probability for period; p^j	0.602	0.318	0.192
Estimated standard deviation of p^j	0.042	0.043	0.029
Late - after 8 July			
# of nests; K	69	42	
# of successful nest; Y_k	34	24	
Total nest days of observation; T_k	601.5	459.0	
Estimated daily survival; p	0.941	0.960	
Estimated standard deviation of p	0.009	0.009	
Estimated success probability for period; p^j	0.432	0.527	0.227
Estimated standard deviation of p^j	0.024	0.026	0.017
Total season			
# of nests; K	88	62	
# of successful nest; Y_k	47	31	
Total nest days of observation; T_k	770.5	647.5	
Estimated daily survival; p	0.946	0.952	
Estimated standard deviation of p	0.008	0.008	
Estimated success probability for period; p^j	0.465	0.456	0.212
Estimated standard deviation of p^j	0.021	0.023	0.014

Appendix 4, Table 2. White-crowned Pigeon nesting success at West Butternut Key during the 1986 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
# of nests; K	24	23	
# of successful nest; Y_k	11	14	
Total nest days of observation; T_k	228.5	241.5	
Estimated daily survival; p	0.943	0.962	
Estimated standard deviation of p	0.015	0.012	
Estimated success probability for period; p^j	0.440	0.544	0.239
Estimated standard deviation of p^j	0.039	0.036	0.026

Appendix 4, Table 3. White-crowned Pigeon nesting success at West Butternut Key during the 1987 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	12	14	
# of successful nest; Y_k	11	3	
Total nest days of observation; T_k	120.0	118.0	
Estimated daily survival; p	0.991	0.906	
Estimated standard deviation of p	0.008	0.026	
Estimated success probability for period; p^j	0.889	0.208	0.185
Estimated standard deviation of p^j	0.029	0.051	0.046
Late - after 8 July			
# of nests; K	34	21	
# of successful nest; Y_k	21	12	
Total nest days of observation; T_k	324.5	247.5	
Estimated daily survival; p	0.959	0.963	
Estimated standard deviation of p	0.010	0.011	
Estimated success probability for period; p^j	0.564	0.552	0.311
Estimated standard deviation of p^j	0.031	0.036	0.026
Total season			
# of nests; K	46	35	
# of successful nest; Y_k	32	15	
Total nest days of observation; T_k	444.5	365.5	
Estimated daily survival; p	0.968	0.945	
Estimated standard deviation of p	0.008	0.011	
Estimated success probability for period; p^j	0.638	0.406	0.259
Estimated standard deviation of p^j	0.025	0.031	0.022

Appendix 4, Table 4. White-crowned Pigeon nesting success at West Butternut Key during the 1988 nesting season, as calculated by the Mayfield Method.

Parameter	Nesting Period		Overall Success
	Incubation	Nestling	
Expected # of days in period; J	14	16	
Early - before 9 July			
# of nests; K	7	2	
# of successful nest; Y_k	2	1	
Total nest days of observation; T_k	49.0	23.0	
Estimated daily survival; p	0.897	0.956	
Estimated standard deviation of p	0.043	0.042	
Estimated success probability for period; p^j	0.221	0.491	0.108
Estimated standard deviation of p^j	0.080	0.121	0.048
Late - after 8 July			
# of nests; K	11	2	
# of successful nest; Y_k	2	1	
Total nest days of observation; T_k	48.5	17.5	
Estimated daily survival; p	0.814	0.942	
Estimated standard deviation of p	0.055	0.055	
Estimated success probability for period; p^j	0.056	0.309	0.022
Estimated standard deviation of p^j	0.055	0.142	0.024
Total season			
# of nests; K	18	4	
# of successful nest; Y_k	4	2	
Total nest days of observation; T_k	97.5	40.5	
Estimated daily survival; p	0.856	0.950	
Estimated standard deviation of p	0.035	0.034	
Estimated success probability for period; p^j	0.114	0.444	0.050
Estimated standard deviation of p^j	0.048	0.093	0.024

Appendix 5. Location, search time, number of nests found, nest abundance, and predators on keys with nesting White-crowned Pigeons. Total search time is included for the mainland, the mainline Keys and keys without nesting White-crowned Pigeons.

Location	Latitude	Longitude	Search Time (min)	Number of Nests	Nest Abundance (nests/min)	Predators
Dead Terrapin	25° 2.47'	80° 48.17'	7	5	0.71	
South Peterson	24° 54.49'	80° 44.35'	14	8	0.57	
Big Bob	25° 6.35'	80° 35.11'	5	2	0.40	
Duck	25° 10.82'	80° 29.36'	10	4	0.40	
Southwest Calusa	25° 2.59'	80° 42.76'	44	17	0.39	
Fun	25° 3.77'	80° 50.15'	46	14	0.30	
South Rabbit	24° 58.87'	80° 49.61'	24	7	0.29	
Baby Bob	25° 6.10'	80° 35.46'	50	14	0.28	
South Twin	24° 57.83'	80° 44.67'	30	8	0.27	
Middle Buchanan	24° 55.18'	80° 46.47'	44	11	0.25	Am. Crow
North Crane	25° 0.31'	80° 36.88'	12	3	0.25	
North Peterson	24° 55.06'	80° 44.75'	28	6	0.21	
East	24° 59.96'	80° 36.53'	10	2	0.20	
South Park	25° 6.78'	80° 33.97'	5	1	0.20	
Little Middle Jimmie	25° 2.10'	80° 38.87'	5	1	0.20	
Squirt Buchanan	24° 55.23'	80° 45.91'	10	2	0.20	
Large Crab	24° 59.51'	80° 39.67'	10	2	0.20	
Main Arsenicker	25° 23.85'	80° 17.21'	26	5	0.19	
West	24° 59.15'	80° 38.95'	124	22	0.18	
Pigeon	25° 3.38'	80° 30.65'	108	19	0.18	Rattus sp.
North Twin	24° 58.06'	80° 44.64'	44	7	0.16	
South Pelican	25° 3.86'	80° 51.51'	109	16	0.15	
Sid	25° 1.45'	80° 47.37'	35	5	0.14	
West Buchanan	24° 55.04'	80° 46.73'	22	3	0.14	
North Gopher	24° 59.35'	80° 43.94'	30	4	0.13	
South Dump	25° 6.81'	80° 46.42'	25	3	0.12	
North Pelican	25° 4.33'	80° 51.51'	102	12	0.12	
South Gopher	24° 59.04'	80° 44.12'	32	4	0.12	
Porjoe	25° 8.31'	80° 28.38'	42	5	0.12	
Big Barnes	24° 56.34'	80° 47.18'	104	13	0.12	
Little Barnes	24° 56.44'	80° 47.48'	40	5	0.12	
East Bob Allen	25° 2.10'	80° 40.03'	100	11	0.11	
Green Mangrove	24° 55.53'	80° 47.11'	70	8	0.11	
North Park	25° 7.61'	80° 34.02'	20	2	0.10	Rattus sp.
Low	25° 3.05'	80° 34.76'	20	2	0.10	
West Butternut ^d	25° 5.45'	80° 31.36'	--	--	0.10	
Middle Butternut ^d	25° 5.06'	80° 30.90'	--	--	0.10	Rattus sp.
Middle Peterson	24° 54.75'	80° 44.63'	40	4	0.10	
Bottle ^d	25° 4.05'	80° 33.35'	--	--	0.10	
Cluett	25° 1.87'	80° 51.87'	68	6	0.09	
Madeira	25° 9.68'	80° 41.33'	54	5	0.09	
Stake	25° 3.58'	80° 35.16'	23	2	0.09	
Cormorant	25° 6.51'	80° 51.12'	78	6	0.08	Raccoon
South Jimmie	25° 1.54'	80° 38.93'	15	1	0.07	
Little Crab	24° 59.31'	80° 40.19'	59	4	0.07	
Southeast Calusa	25° 2.50'	80° 42.33'	124	9	0.07	
Northeast Calusa	25° 2.68'	80° 42.13'	76	5	0.07	
Dildo	25° 3.57'	80° 53.17'	102	7	0.07	Raccoon
Pass	25° 9.43'	80° 34.56'	34	2	0.06	Rattus sp.
Cotton	24° 57.62'	80° 37.39'	100	6	0.06	
South Crane	25° 0.02'	80° 37.47'	31	2	0.06	
Whaleback	25° 7.74'	80° 29.07'	41	2	0.05	
Northwest Calusa	25° 2.94'	80° 42.23'	92	5	0.05	
Deer	25° 11.10'	80° 32.32'	44	2	0.05	
South Nest	25° 8.23'	80° 30.41'	55	3	0.05	
East Manatee	25° 4.16'	80° 36.44'	20	1	0.05	

Appendix 5. (continued)

Location	Latitude	Longitude	Search Time (min)	Number of Nests	Nest Abundance (nests/min)	Predators
Lake	25° 8.63'	80° 33.68'	20	1	0.05	
Otter	25° 8.53'	80° 47.25'	48	2	0.04	
Johnson	25° 3.01'	80° 54.27'	104	4	0.04	Raccoon
Captain	25° 1.55'	80° 38.04'	25	1	0.04	
Cowpens	25° 0.20'	80° 33.48'	96	4	0.04	
Dove	25° 2.88'	80° 28.47'	82	3	0.04	
North Calusa	25° 3.31'	80° 41.84'	25	1	0.04	
Little Whipray #2	25° 3.44'	80° 44.49'	24	1	0.04	
East Lower Arsenicker	24° 55.12'	80° 49.57'	24	1	0.04	
South Upper Arsenicker	24° 55.73'	80° 49.78'	56	2	0.04	Am. Crow
Card Sound Bridge Mangroves	25° 17.52'	80° 22.88'	66	2	0.03	
Derelict	25° 8.65'	80° 45.69'	96	3	0.03	
Shell	24° 55.41'	80° 39.97'	196	5	0.03	
Tavernier	24° 59.81'	80° 30.13'	78	2	0.03	
Big Spy	25° 0.39'	80° 44.29'	63	2	0.03	
Panhandle	24° 59.87'	80° 43.66'	146	5	0.03	<i>Rattus</i> sp.
Middle Bob Allen	25° 1.94'	80° 40.68'	30	1	0.03	
Middle Swash	25° 5.90'	80° 28.56'	34	1	0.03	
Clive	25° 4.76'	80° 55.80'	130	3	0.02	
Big Buttonwood	25° 3.98'	80° 43.98'	105	2	0.02	Raccoon
West Swash (Shell)	25° 6.18'	80° 29.39'	41	1	0.02	
Tern	25° 9.65'	80° 33.12'	44	1	0.02	
South Coon	25° 3.02'	80° 44.25'	62	1	0.02	
West Lower Arsenicker	24° 55.07'	80° 50.01'	50	1	0.02	
East Butternut	25° 4.79'	80° 29.82'	112	2	0.02	
North Rabbit	24° 59.48'	80° 49.86'	62	1	0.02	
West Manatee	25° 4.31'	80° 36.90'	114	1	0.01	
East Brush	25° 5.82'	80° 41.24'	190	1	0.01	Raccoon
North Corrinne	25° 1.96'	80° 45.46'	85	1	0.01	
Curlew	25° 5.93'	80° 50.30'	72	1	0.01	
Long Arsenicker	25° 22.86'	80° 17.80'	138	1	0.01	
West Brush	25° 5.79'	80° 41.54'	110	1	0.01	Raccoon
Non-nesting Keys ^a			5176	0	0.00	Am. Crow Raccoon <i>Rattus</i> sp. Bobcat
Mainland ^b			1419	0	0.00	Raccoon <i>Rattus</i> sp. Bobcat
Mainline Keys ^c			661	0 ^d	0.00	Opossum Raccoon Opossum

^aComprised of 81 keys surveyed from 1986-1989 with no evidence of nesting by White-crowned Pigeons. Twenty-seven keys (33.3%) contained evidence of raccoon presence. Total survey time = 86.3 hours.

^bComprised of 23 surveys from 1987-89 to areas on mainland south Florida from western Florida Bay to Card Sound. Also includes a survey of the eastern portion of Whitewater Bay in Everglades National Park. Total survey time = 23.7 hours.

^cComprised of 17 visits to mainline Keys from Key Largo to Elliott Key during 1987-89. Total survey time = 11.0 hours.

^dStudy keys which were not surveyed separately. These keys have large numbers of nesting White-crowned Pigeons in most years.

^eOne nest located in 1990. See text.