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# ECOLOGY AND BEHAVIOR OF THE ZENAIDA DOVE

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*Resumen.* Ecología y comportamiento de la Tórtola Cardosantera. Se resumen datos de un estudio de 10 años sobre la Tórtola Cardosantera (*Zenaida aurita*) en Puerto Rico y sus islas adyacentes. La tórtola exhibe un diformismo sexual en tomaño, con los machos generalmente mayores que las hembras. La mayoría de las actividades (alimentación, cortejo, agresiones) ocurrieron por las mañanas y tardes, mientras que el reposo y actividades de mantenimiento fueron más prevalentes al mediodía. Registré 77 especies de plantas usadas como alimento por la Tórtola Cardosantera en Puerto Rico. Las principales expecies usadas como alimento incluyeron *Scleria lithosperma*, *Argemone mexicana*, *Croton rigidus*, *Phyllanthus amarus*, *Cordia angustifolia*, *Zanthoxylum martinicense*, *Euphorbia heterophylla*, y diversa especies de leguminosas. Las Tórtolas Cardosanteras tienen dos vocalizaciones principales: el "*Kuu*", o Llamada de Anuncio, dada en contextos asertivos y sexuales, y la Llamada de Nido, mayormente usada en o cerca del nido. Las tórtola anidaron en una amplia variedad de hábitats, incluyendo el borde de bosques, manglares, matorral seco y áreas mixtas agrícola-urbanas. Los nidos generalmente fueron colocados en árboles, pero las tórtolas anidaron en el suelo en aquellos lugares donde ciertos predadores terrestres estuvieron ausentes. Nidos se encontraron en todos los meses del año, aunque una mayor frecuencia de nidificación ocurrió de marzo hasta mayo o julio. Las tórtolas repusieron nidadas cuando los nidos fueron destruidos, y repitieron el ciclo hasta cuatro veces en una temporada. Los machos eligieron la ubicación del nido y comenzaron su construcción. Los huevos (2) fueron puestos en días alternos, empezando alrededor de dos días después de haberse completado el nido. La incubación y el período en el que el pichón permaneció en el nido duraron un promedio de 13.9 ± 0.5 días y 14.3 ± 0.6 días, respectivamente. El macho atendió el nido desde la media mañana ($\bar{x}$ = 08:59 hr) hasta la media tarde ($\bar{x}$ = 16:53), para ser entonces relevado por la hembra en las tareas de incubar y empollar durante la noche. Los nidos fueron continuamente atendidos desde la puesta del primer huevo hasta el séptimo día, cuando aun los pichones continuaban en el nido. Después de eso, el atendimiento por parte de los adultos cayó sostenidamente hasta el día 14, cuando estos llegaban al nido sólo para alimentar a los pichones. Los pichones (0 a 15 días) mostraron una ganancia de peso diaria en un promedio de 18.3% y al llegar a la etapa de volantones llegaron a pesar unos 120g (81% del peso adulto). El crecimiento diario promedio (culmen, tarsometatarso, ulna) fue de 6.8% (rango: 4.0—9.8 diariamente). La productividad de las tórtolas varió entre y dentro de las áreas de estudio a través de los 10 años. El número promedio de pichones por nido que contenía huevos varió entre 0.3 y 1.6 en tres áreas de estudio. El número promedio de pichones volantones por nido varió entre 0.3 y 1.4. La productividad fue más baja en la área de estudio en el seco suroeste de Puerto Rico (bosques de Susúa y Guánica; $\bar{x}$ = 0.7 pichones volantones por nido) y fue más alta en la área mixta agrícola-urbana de baja montaña (Cidra; 1.2). Poblaciones anidando en matorrales y manglares (Base Naval Roosevelt Roads) tuvieron un promedio de 0.9 pichones volantones por nido. El éxito de la nidada siguió un patrón geográfico similar: suroeste de Puerto Rico — 40% de los nidos con huevos tuvieron éxito, Cidra — 62.6%, y Roosevelt Roads — 52.0%. La más importantes causas de pérdida de huevos y pichones lo fueron el Zorzal Pardo (*Margarops fuscatus* — 49% de las pérdidas) y las ratas (*Rattus rattus* — 16%).

*Abstract.* Data are summarized from a 10 year study of the Zenaida Dove (*Zenaida aurita*) in Puerto Rico and its offshore islands. The dove displays sexual size dimorphism, with males generally larger than females. Most

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activities (feeding, courtship, fighting) occurred in mornings and afternoons, whereas loafing and maintenance activities were more prevalent at mid-day. I recorded 77 plant species used as food by Zenaida Doves in Puerto Rico. Major food species included *Scleria lithosperma*, *Argemone mexicana*, *Croton rigidus*, *Phyllanthus amarus*, *Cordia angustifolia*, *Zanthoxylum martinicense*, *Euphorbia heterophylla*, and several species of legumes. Zenaida Doves have two major vocalizations: the "*Coo*", or Advertisement Call, given in assertive and sexual contexts, and the Nest Call, primarily used at or near the nest. Doves nested in a wide variety of habitats, including forest edge, mangrove forest, dry scrub, and mixed agriculture-urban areas. Nests were generally placed in trees, but doves nested on the ground where certain terrestrial predators were absent. Nests were found in all months of the year, although a breeding peak occurred from March through May or July. Doves replaced clutches when nests were destroyed, and recycled up to four times in a season. Males selected nest sites and initiated building. Eggs (2) were laid on alternate days, beginning about two days after the nest was completed. Incubation and nestling stages averaged 13.9 ± 0.5 [SE] and 14.3 ± 0.6 days. The male attended the nest from mid-morning ($\bar{x}$ = 08:59 hr) through mid-afternoon ($\bar{x}$ = 16:53), then the female took over incubation and brooding duties for the night. Nests were continuously covered from the laying of the first egg through day seven of the nestling stage. Thereafter, adult attendance dropped steadily until day 14, when they came to the nest only for chick feedings. Chicks (days 0—15) showed a mean daily weight gain of 18.3% and attained a fledging weight of about 120 g (81% of adult weight). The mean daily growth (culmen, tarsometatarsus, ulna) was 6.8% (range = 4.0—9.8% daily). Dove productivity varied among and within study areas over the 10 years. Mean number of chicks hatched per nest that held eggs ranged from 0.3 to 1.6 for 3 study areas. Mean number fledged per nest ranged from 0.3 to 1.4. Productivity was lowest in the dry southwestern Puerto Rico study area (Susua and Guánica forests; $\bar{x}$ = 0.7 chicks fledged per nest) and was highest for the lower montane mixed agriculture/urban area (Cidra; 1.2). Populations nesting in scrub and mangrove forests (Roosevelt Roads Naval Station) fledged an average of 0.9 chicks/nest. Nest success followed a similar geographic pattern: southwestern Puerto Rico — 40.9% of nests with eggs were successful, Cidra — 62.6%, and Roosevelt Roads — 52.0%. The most important sources of dove egg and chick loss were Pearly-eyed Thrashers (*Margarops fuscatus* — 49% of losses) and roof rats (*Rattus rattus* — 16%). *Accepted 12 August 1991.*

*Key words: Columbid behavior, breeding, diet, ecology, habitat, productivity, Puerto Rico, Zenaida Dove*, Zenaida aurita.

## INTRODUCTION

The Zenaida Dove (*Zenaida aurita*; Fig. 1) is common throughout most of the Caribbean Region, including the Bahama Islands, most of the West Indies, and the coast of the Yucatán Peninsula and its adjacent islands (Goodwin 1970). Formerly, the Zenaida Dove was found in southern Florida (Audubon 1840) and still makes an occasional appearance there (Allen 1950, Langridge *et al.* 1982). Throughout its range, the Zenaida Dove is in great demand for its edible flesh and because it is still abundant enough to provide sport in countries where game bird populations have become limited in numbers. In fact, the Zenaida Dove is one of only a few native species that have increased in number and range as a result of man's agricultural practices in the West Indies (Wiley 1985). Although Zenaida Dove populations are heavily harvested, biological data on which to base a sound management program for this species are lacking.

In late 1973, I began a study of the Zenaida Dove in Puerto Rico. Here, I present general ecology and behavior data from 10 years (1973—1983) of studies of the Zenaida Dove in Puerto Rico and its offshore islands. Also, I present general management recommendations based on these data.

## STUDY AREAS

Most field work was conducted at two study areas: Roosevelt Roads Naval Station (Ceiba) in easternmost Puerto Rico, and Cidra in east-central Puerto Rico (Fig. 2). Shorter-term studies were made at Guánica and Susua Commonwealth Forests in southwestern Puerto Rico, Ramey Air Force Base (Aquadilla) on the northwestern coast, and the offshore islands of Mona and Culebra (Fig. 2).

The Roosevelt Roads Naval Station (3.260 ha) study area is within the subtropical dry forest zone (Ewel & Whitmore 1973) and is characterized by pannes and mangrove (*Avicennia germinans*, *Rhizophora mangle*, *Laguncularia racemosa*, *Conocarpus erectus*) forests in the lowlands and exotic leadtree-(*Leucaena leucocephala*) dominated scrub in the drier areas (Wiley & Wiley 1979). I visited this study area every two or three days during the breeding season and at one to two week intervals during the non-breeding season (August—February; see Table 9c).

FIG. 1. Adult male Zenaida Dove on nest with two squabs, black mangrove forest, Roosevelt Roads Naval Station, Puerto Rico.

The Cidra study area is altered subtropical moist forest (Ewel & Whitmore 1973) in the lower montane zone. Man has completely replaced the original forest with farmland, pastureland, as well as urban and industrial developments. Small second growth woodlots in ravines and surrounding abandoned pasturelands are characterized by *Cecropia peltata*, *Didymopanax morototoni*, *Bambusa vulgaris*, *Eugenia jambos*, and *Zanthoxylum martinicense*. I visited the Cidra study area at least twice weekly from November 1973 to December 1975, at least every other week from January 1977 to December 1978, and in alternate weeks for most months from February 1980 to December 1982 (Table 9a).

I visited the two study areas in southwestern Puerto Rico at least twice weekly from October 1973 to December 1975 (Table 9b). Susua Forest (1.355 ha) is in the subtropical moist forest zone, whereas Guánica Forest (4.006 ha) is a subtropical dry forest. Both forests are characterized by *Bursera simaruba*, *Exostema caribaeum*, *Linociera axilliflora*, *Coccoloba microstachya*, and *Neolaugeria resinosa*.

I studied Zenaida Dove behavior on the golf course of Ramey Air Force Base (Ramey AFB, now deactivated) near Aguadilla in northwestern Puerto Rico (within the subtropical moist forest zone) at irregular intervals from December 1973 to April 1975. The open golf course allowed unobstructed observations of dove activity and made it possible to follow individuals for long periods. Zenaida Doves used the scattered coconut palms (*Cocos nucifera*) for roosting and nesting, and fed on weed seeds in unmowed patches along the greens and on fruits and seeds of exotic shrubs surrounding the course.

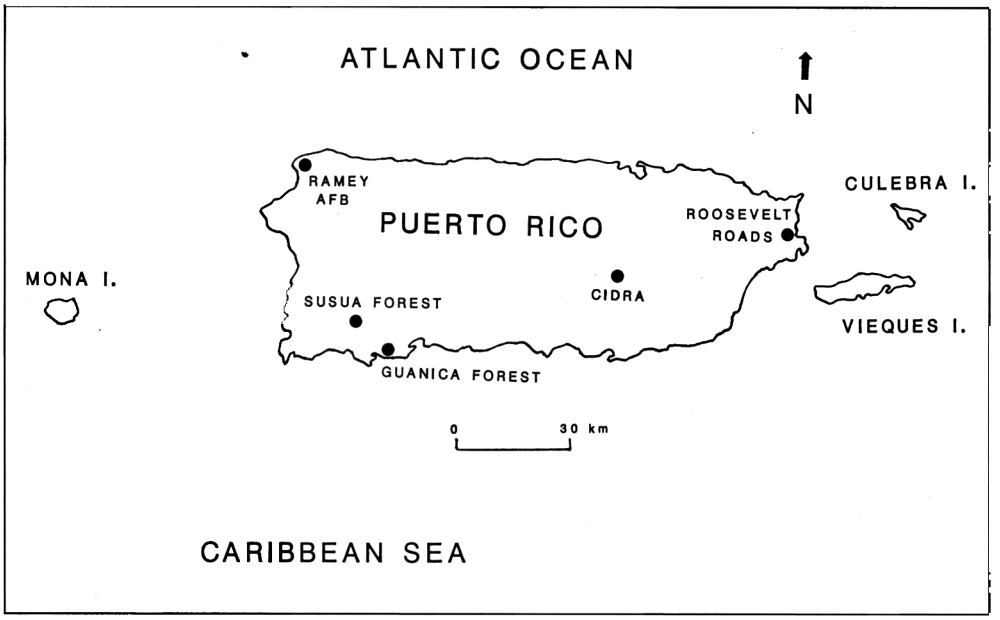


FIG. 2. Puerto Rico and its offshore islands, showing study areas and localities mentioned in text.

The dry, 5.530 ha Mona Island is midway between Puerto Rico and Hispaniola in the Mona Channel. Characteristic vegetation includes *Metopium toxiferum, Ficus citrifolia, Bursera simaruba, Swietenia mahagoni, Cephalocereus royenii*, and *Opuntia rubescens* (Woodbury *et al.* 1977, Wiley & Wiley 1979). I made observations on Mona as follows: 11—15 May 1974, 26 June—14 August 1974, 10—15 September 1974, 27—29 December 1974, 9—11 March 1975, 22—24 May 1975, 20—24 August 1975, 2 November 1977, 11—15 January 1978, and 26 May 1978.

Culebra Island (2.730 ha) is 37 km northeast of Puerto Rico, and 25 km west of St. Thomas, U.S. Virgin Islands. The natural vegetation is subtropical dry forest (Ewel & Whitmore 1973). Little remains of this once extensive forest vegetation (Kepler & Kepler 1977). I visited the Culebra archipelago as follows: 30 October—1 November 1974, 19—21 February 1975, 22—23 April 1975, 8—9 November 1977, 18—19 July 1978, 31 July—1 August 1978, and 20—23 June 1980.

## METHODS

I studied daily activity of doves in December 1973, and March, June, and October 1974. One-zero sampled observations of focal animals (Slater 1978) were taken during full-day observation periods; individuals were kept under continuous observation until they moved out of sight. Activities were divided into five discrete categories: resting, feeding, maintenance, courtship, and agonistic behavior. Each activity was scored at 15 s intervals on standardized data sheets.

Dove nesting habitat was sampled using a modified version of James and Shugart's (1970) technique. Habitat analyses were performed immediately after squabs fledged or the nest failed. Plant names follow the National List of Scientific Plant Names (U.S. Department of Agriculture 1982).

I inspected nests at two- (usually) or three-day intervals. Where possible, nests were checked from a distance with binoculars to avoid inadvertent disclosure of their locations to predators. To view the contents of some inaccessible nests it

was necessary to use a mirror at the end of a pole. Nests where chick growth information was regularly taken were not included in the calculations of productivity and nest success, as my extensive activities at those nests probably placed them at above-normal risk to predators. I considered a nest successful if it fledged at least one chick. Chicks that attained an age of 14 days were considered to have fledged, even if they were not observed leaving the nest nor subsequently seen in the nest area.

Chicks were measured and weighed at the selected nests every two to three days. Until they were old enough for banding, individuals were marked on an inconspicuous part of the body (e.g., belly or under leg) with blue or green food color or color flow pen. I took measurements (following Baldwin *et al.* 1931) to the nearest 0.1 mm with dial or vernier calipers. Weights were taken to the nearest gram with spring scales. I used Brody's (1945) "instantaneous percentage rate of growth" to characterize the mean daily weight increase of chicks. I noted characteristics of chick development at each visit.

Nearly all chicks and some adult doves were fitted with unique color combinations of three celluloid leg bands. I also marked some chicks with U.S. Fish and Wildlife Service metal leg bands.

I monitored adult and chick behavior from blinds in trees, 3 to 6 m from the nest. Observations were made with 7×35 and 10×40 binoculars and a 15—60× spotting scope. I used a narrative note style to record behavior at nests. Only full-day observations were used during incubation and nestling periods for the behavioral analyses in this report; i.e., the observer entered the blind before dawn and left after dark. Observation days when there was an apparent disturbance to adults that affected nest attendance were eliminated from the analyses.

I recorded vocalizations on a Uher 4000 Report IC tape recorded at 19 cm per s. Analyses were made with a model 4500 Kay Electric Sound Uniscan Spectrum Analyzer and Digital Sona-graph 7800 on the wide band, 18.8—1200 Hz setting.

I collected digestive tracts from hunter- and road-killed doves from central and southwestern Puerto Rico. The digestive tracts were fixed in 10% formalin and later rinsed with water and preserved in 40% isopropyl alcohol. I sorted food items for each tract and counted materials in the lowest identifiable taxonomic category (numerical analysis). I also determined the frequency of occurrence and the volumetric displacement (a measure of biomass) for each food category.

Statistical procedures follow Zar (1975) and Sokal & Rohlf (1981). Significance level is set at 0.05. Standard errors are presented as the measure of variability about the mean, unless otherwise stated.

## RESULTS AND DISCUSSION

### Physical characteristics of the Zenaida Dove

*Zenaida aurita* is a member of a seven species assemblage that includes the closely related *Zenaida macroura*, *Z. auriculata*, *Z. galapagoensis*, *Z. asiatica*, *Z. melpoda*, and the extinct *Ectopistes migratorius* (Goodwin 1970). The Zenaida Dove differs from the other species in the group in having 12 rather than 14 retrices. It averages 28—30.5 cm in length and is similar to the Mourning Dove's (*Zenaida macroura*) medium size and general build, but it lacks the long, pointed tail. Zenaidas are brown above and vinaceous below, with cinnamon on the head and neck. There are black spots on the upper wing coverts. The tips of the outer secondaries and tail feathers are white. Dark violet-blue streaks that appear black from a distance are above and below the ear coverts. Males are more vividly colored than females and have a metallic violet wash on the sides of the neck.

Adult female Zenaida Doves ($\bar{x}$ = 132.55 ± 1.51 g, range = 120—145 g, n = 20) weighed less than adult males ($\bar{x}$ = 163.19 ± 1.78 g, range = 149—180 g, n = 27; $t$ = 12.541, $P < 0.001$). Adult doves weighed more than first year birds ($\bar{x}$ = 133.6 ± 2.11 g, range = 110—160 g, n = 35; $t$ = 6.534, $P < 0.001$). Acosta & Berovides (1982) reported mean weights of Zenaida Doves from western Cuba as 147.5 ± 2.3 g for females (n = 8) and 167.4 ± 5.2 g for males (n = 9; $P < 0.001$).

I found significant size differences between the sexes, with males averaging larger than females in all body parts examined, except halux length (Table 1).

TABLE Measurements (mm) and weights (g) of male and female Zenaida Doves from Puerto Rico.

| Statistic | Weight | | Culmen | | Tarsometatarsus | | Ulna | |
|---|---|---|---|---|---|---|---|---|
| | Female | Male | Female | Male | Female | Male | Female | Male |
| | 20 | 27 | 20 | 27 | 20 | 27 | 20 | 27 |
| | 132.55 | 163.19 | 8.62 | 9.54 | 22.33 | 23.75 | 44.09 | 47.39 |
| | 1.51 | 1.78 | 0.06 | 0.06 | 0.06 | 0.09 | 0.11 | 0.16 |
| | 120-145 | 149-180 | 8.0-8.9 | 8.8-9.9 | 22.0-22.9 | 22.8-24.3 | 43.1-45.3 | 45.9-49.0 |
| | $P < 0.001$ | | $P < 0.001$ | | $P < 0.001$ | | $P < 0.001$ | |
| | $t = 12.541$ | | $t = 10.957$ | | $t = 12.838$ | | $t = 15.729$ | |

| Span[1] | | Halux | | Middle Toe | | 10th primary | | Tail[2] | |
|---|---|---|---|---|---|---|---|---|---|
| Female | Male | Female | Male | Female | Male | Female | Male | Female | Male |
| 20 | 27 | 20 | 27 | 20 | 26 | 92 | 129 | 92 | 124 |
| 41.00 | 42.31 | 12.14 | 12.10 | 22.07 | 22.50 | 100.77 | 103.48 | 83.18 | 88.19 |
| 0.13 | 0.08 | 0.08 | 0.07 | 0.05 | 0.07 | 0.50 | 0.35 | 0.59 | 0.41 |
| 39.8-41.9 | 41.7-43.2 | 11.5-12.7 | 11.5-12.9 | 21.7-22.5 | 21.8-23.0 | 84-114 | 88-112 | 60-98 | 77-99 |
| $P < 0.001$ | | $P > 0.05$ | | $P < 0.001$ | | $P < 0.001$ | | $P < 0.001$ | |
| $t = 9.497$ | | $t = 0.379$ | | $t = 4.972$ | | $t = 4.654$ | | $t = 7.096$ | |

Span = expanded foot from halux to middle toe. 2 Tail = outer retrices.

General ecology

The Zenaida Dove favors clearings and forest edge habitat. It is characteristic of lower slopes and the coastal plain, where it inhabits savannas, mangrove swamps, open woodlands and second growth forests, and edges of cultivated fields. It is less common in higher elevations where the hills, denuded by agriculture, are in various stages of reforestation.

Like most other *Zenaida* species (Goodwin 1970), the Zenaida Dove is arboreal for the most part; it usually feeds (fruits and seeds), nests, and roosts in trees. However, it also courts, gleans food (particularly grass seed and spilled grain), and drinks on the ground.

Zenaida Doves form flocks in fall and may aggregate at seasonal food concentrations, but generally they are solitary, traveling singly or in pairs, and associating in small family groups. Nests are generally dispersed. It usually feeds alone or in small flocks, but may mix with foraging flocks of other columbids, especially Mourning Doves, White-winged Doves (*Zenaida asiatica*), Plain Pigeons (*Columba inornata*), White-crowned Pigeons (*C. leucocephala*), and Common Ground-Doves (*Columbina passerina*).

General behavior

*Comfort movements.* — Zenaida Doves displayed a characteristic columbid stretch sequence: the bird fanned its tail, stretched one of its wings, extended the leg on the same side as the outstretched wing, stood up tall on the opposite leg, stretched the wing out farther, drew the tail feathers together, pulled the leg and wing into the body, then stretched both wings halfway out over the back, and assumed a relaxed perching posture.

During loafing periods, Zenaida Doves perched in a shady tree, often resting their belly against the tree branch.

The Zenaida Dove exhibited characteristic movements when landing and walking. In contrast to many species of columbids, the Zenaida Dove did not throw up its tail after landing on the ground. Characteristically, when walking, it would intermittently "flip" its tail up at an angle slightly above normal ($\bar{x} = 22.4° \pm 1.27°$, r = 10—50°, n = 85); i.e., every few steps, the dove would hesitate, pumps its tail up, then quickly back down to the normal position (in line with the axis of the body), and resume walking. The tail flip was not displayed during feeding or supplantations.

*Bathing behavior.* — Zenaida Doves bathed in rain showers, in puddles of ground water, and such catchments as the base of bromeliad bracts. Bathing behavior was similar to that of other *Zenaida* species (Goodwin 1970). During light showers, Zenaida Doves walked back and forth

on a perch, holding up one wing, then the other, and at times stopping to roll to the side to wet feathers not previously exposed by lifting the wings. Once the bath was completed, the dove vigorously flapped its wings, then crouched with its abdomen resting on the perch and preened. Unattended nestlings were not seen to bathe in rain showers, but remained still and low in nests.

*Aggressive behavior.* — Zenaida Doves often battled over territories. The territory holder made silent, direct flights at an intruding dove, whereupon the invader retreated. However, some interactions escalated into confrontations and physical contact, with birds typically striking at one another with their wings. One wing was quickly flicked out at the other bird or, less commonly, both wings simultaneously so one wing made contact with the opponent as the birds confronted one another side by side. The wing struck the opponent with an audible "smack". After one bird had asserted its dominance over the other and the subordinate dove had flown away, the dominant bird strutted on its perch. The dominant dove often gave Advertisement Calls (see below) after aggressive encounters.

Intrapair aggression was also common. Males were usually the more aggressive of the pair members. When a male approached a prospective mate, she became alert, jumped back, raised the wing on the opposite side of her body from the male, showing the white trailing edge of the secondary feathers. If the male continued to move toward the displaying female, she sometimes struck at him with her near wing, but more often flew off. The male generally pursued the female and a series of supplantations would sometimes occur.

*Distraction display.* — Zenaida Dove parents performed a distraction display when a person approached a nest containing eggs or young chicks (days 0 to 7). To begin the display, incubating parents customarily walked from the nest, those with hatching eggs generally walked, but sometimes flew, whereas parents with chicks usually flew. If the nest was over land, the adult fluttered downward, then flapped along the ground giving a broken wing sham display. Sometimes moving in a semicircle around the nest tree, or moving a short distance away, it would beat its wings on the vegetation and ground, alternating fluttering with standing. If a nest was over water (e.g., mangrove forest), the adult flew to the shore and executed the broken wing act there. Burger *et al.* (1989a) noted that only Zenaida Doves with hatching eggs or chicks gave distraction displays.

## Daily activity pattern

The amount of time devoted to each category of activity varied with the time of day (Table 2).

TABLE 2. Summary of Zenaida Dove activity during 244 hrs of observation in December 1973 (65 hrs), March (69 hrs), June (54 hrs), and October (56 hrs) 1974; Ramey Air Force Base, northwestern Puerto Rico. Data have been adjusted for seasonal day-length differences. Data are from one-zero sampled observations of focal animals.

| Time (hour beginning) | Class of activity (% of observation time) | | | | |
|---|---|---|---|---|---|
| | Rest | Feed | Maintenance | Courtship | Agonistic |
| 06:00 | | 50.3 | 6.8 | 2.0 | 0.5 |
| 07:00 | | 75.3 | 5.0 | 7.5 | 1.3 |
| 08:00 | | 85.8 | 3.0 | 4.3 | 2.0 |
| 09:00 | | 79.3 | 6.3 | 6.0 | 0.8 |
| 10:00 | | 70.8 | 6.0 | 5.8 | 2.3 |
| 11:00 | | 77.0 | 6.8 | 1.3 | 1.8 |
| 12:00 | | 50.0 | 11.5 | 0 | 0.8 |
| 13:00 | | 36.0 | 12.8 | 0 | 0 |
| 14:00 | | 39.8 | 18.0 | 2.5 | 0.5 |
| 15:00 | | 65.5 | 8.3 | 2.8 | 2.3 |
| 16:00 | | 77.0 | 5.5 | 8.5 | 1.5 |
| 17:00 | | 53.3 | 8.8 | 5.0 | 1.3 |
| 18:00 | | 18.8 | 8.8 | 0 | |
| 19:00 | | 5.0 | 0 | 0 | 1.0 |
| Means | | 56.0 | 7.7 | 3.3 | 1.2 |

Mornings (06:00—12:00; times seasonally adjusted for time of sunrise) and late afternoons (15:00—18:00) were characterized by foraging. Early morning (> 07:00), midday, and evenings (> 17:00) were characterized by movements to and from roosts and loafing. Maintenance activities increased at mid-day and occurred more often in the afternoons than mornings. Courtship activities occurred most often from 07:00 to 11:00 and 14:00 to 18:00 hrs.

Doves spent the major part of the day feeding and resting during all periods I sampled; i.e., March (spring), June (summer), October (fall), December (winter; Table 2). The proportion of time spent in each activity varied among seasons, perhaps as a result of an increase in agonistic and courtship behaviors during breeding seasons: mean proportion of time individuals spent Feeding in breeding season = 52.2 ± 0.91% vs. non-breeding season = 59.9 ± 1.19% (1 factor

TABLE 3. Analyses of crop contents from 95 Zenaida Doves collected from lower montane second growth forest and pasture habitat, east-central, central, and southwestern Puerto Rico, 1974—1975.

| Food species | Numerical analysis | | Volumetric analysis | | Frequency of occurrence | |
|---|---|---|---|---|---|---|
| | Total no. items | % of total | Volume displaced (ml) | % of total | No. crops with species | % of total |
| *Scleria lithosperma** | 2254 | 44.4 | 58.3 | 49.8 | 10 | 10.6 |
| *Croton rigidus** | 541 | 10.7 | 5.5 | 4.7 | 11 | 11.6 |
| *Cordia angustifolia** | 421 | 8.3 | 11.5 | 9.8 | 19 | 20.0 |
| Fam. Leguminosae (11 spp.) | 409 | 8.1 | 9.5 | 8.1 | 38 | 40.0 |
| *Argemone mexicana* | 254 | 5.0 | 0.7 | 0.6 | 4 | 4.2 |
| *Phyllanthus amarus** | 175 | 3.4 | 0.6 | 0.5 | 2 | 2.1 |
| *Manisuris exaltata** | 103 | 2.0 | 2.3 | 2.0 | 1 | 1.1 |
| *Cardiospermum halicacabum** | 95 | 1.9 | 4.3 | 3.7 | 6 | 6.3 |
| *Euphorbia heterophylla* | 87 | 1.7 | 0.3 | 0.3 | 15 | 15.8 |
| *Scleria microcarpa** | 67 | 1.3 | 0.3 | 0.3 | 2 | 2.1 |
| *Croton lobatus** | 60 | 1.2 | 1.6 | 1.4 | 2 | 2.1 |
| *Sida acuta** | 51 | 1.0 | 0.2 | 0.2 | 3 | 3.2 |
| *Scleria secans** | 45 | 0.9 | 0.3 | 0.3 | 4 | 4.2 |
| *Sida acuta carpinifolia** | 27 | 0.5 | 0.1 | tr | 4 | 4.2 |
| *Cordia nitida* | 26 | 0.5 | 0.5 | 0.4 | 6 | 6.3 |
| *Oryza sativa* | 23 | 0.5 | 0.2 | 0.2 | 5 | 5.3 |
| *Triphasia trifolia** | 22 | 0.4 | 4.4 | 3.8 | | 1.1 |
| *Guapira* sp.* | 19 | 0.4 | 2.0 | 1.7 | 2 | 2.1 |
| *Cassia occidentalis** | 18 | 0.4 | 0.2 | 0.2 | 15 | 15.8 |
| *Miconia prasina* | 15 | 0.3 | 0.4 | 0.3 | 7 | 7.4 |
| *Solanum americanum* | 15 | 0.3 | 0.5 | 0.4 | 1 | 1.1 |
| *Polygonum* sp.* | 12 | 0.2 | 0.1 | tr | 3 | 3.2 |
| *Galactia striata** | 10 | 0.2 | 0.2 | 0.2 | 6 | 6.3 |
| *Clitoria ternatea** | 8 | 0.2 | 0.2 | 0.2 | 4 | 4.2 |
| *Manihot utilissima** | 7 | 0.1 | 0.3 | 0.3 | 1 | 1.1 |
| *Distictis lactiflora** | 4 | tr | 0.1 | tr | 4 | 4.2 |
| *Lasiacis sorghoidea** | 4 | tr | 0.1 | tr | 4 | 4.2 |
| *Casuarina equisetifolia** | 2 | tr | 0.1 | tr | 2 | 2.1 |
| *Roystonea borinquena* | 2 | tr | 0.4 | 0.3 | 1 | 1.1 |
| *Centrostachys indica** | 1 | tr | tr | tr | 2 | 2.1 |
| Fam. Loranthaceae | 1 | tr | tr | tr | 1 | 1.1 |
| *Miconia laevigata* | 1 | tr | 0.1 | tr | 2 | 2.1 |
| *Ricinus communis** | 1 | tr | 0.3 | 0.3 | 1 | 1.1 |
| *Bursera simaruba** | 1 | tr | 0.3 | 0.3 | 2 | 2.1 |
| unidentified plant material (14 spp.) | 279 | 5.5 | 7.4 | 6.3 | | |
| animal matter | 16 | 0.3 | 0.3 | 0.3 | 4 | 4.2 |
| rocks | 271 | | 3.4 | 2.9 | 26 | 27.4 |
| Totals | 5347 | 99.7 | | | | |

* Species not observed used by Zenaida Doves.

ANOVA, $F_{1, 10} = 26.441$, $P = 0.0004$); Resting — breeding season = 35.2 ± 1.46% vs. non-breeding season = 28.8 ± 1.05% ($F_{1, 10} = 12.653$, $P = 0.0052$); Maintenance — breeding season = 5.8 ± 0.18% vs. non-breeding season = 9.6 ± 0.28% ($F_{1, 10} = 130.776$, $P = 0.0001$); Courtship — breeding season = 4.9 ± 0.23% vs. non-breeding season = 2.1 ± 0.58% ($F_{1, 10} = 20.543$, $P = 0.0011$); and Agonistic behavior — breeding season = 1.7 ± 0.12% vs. non-breeding season = 0.6 ± 0.04% ($F_{1, 10} = 75.178$, $P = 0.0001$).

Food

Zenaida Doves feed on a variety of seeds and fruits. Audubon (1840) reported that Zenaida Doves in the Florida Keys fed on grass seeds, leaves of aromatic plants, and various kinds of berries. Gosse (1847) listed fruits and seeds (including those of pasture weeds) of several species of plants as dove food in Jamaica. Wetmore (1916, 1927) reported that the bulk of the dove's food in Puerto Rico consisted of seeds, including many wild legumes, euphorbias, mallows, knotweed, and pigweed; and also waste-grains and various small wild fruits in season. Barnés (1946) and Iñigo (1964) listed *Metopium toxiferum*, *Argemone mexicana*, *Elaphrium [Bursera] simaruba*, *Lantana involucrata*, *Plumeria alba*, *Bumelia obovata*, and seeds of leguminous plants from digestive tracts of Zenaida Doves taken on Mona Island. Iñigo (1964) also found *A. mexicana* and *Euphorbia heterophylla* in digestive tracts of doves from Puerto Rico. Danforth (1930) found seeds of several species, including *Cordia* sp. and perhaps *Crotolaria*, in the stomachs of doves from St. Croix. Zamore (1981) observed Zenaida Doves in Dominica (Lesser Antilles) feeding primarily on seeds, including *Tabebuia pallida* (August), *Crotalaria spectabilis* (March—June, December), *Gynandropsis [Habenaria] gynandra* (May, June, December, January), and the succulent berries of a species of the Myrtaceae family (July and November). Acosta & Berovides (1982) listed rice (*Oryza sativa*; 88.4% of contents) as the most common food found in digestive tracts of Zenaida Doves in western Cuba.

I recorded 58 species of plants in the digestive tracts of 95 doves collected from lower montane forests of Puerto Rico (Table 3). The most important food species were *Scleria lithosperma*, *Argemone mexicana*, *Croton rigidus*, *Cassia occidentalis*, *Cordia angustifolia*, *Euphorbia heterophylla*, and several species of legumes (f. Leguminosae). Rocks were found in 27% of the digestive tracts and were probably taken by doves incidental to collecting seeds from the ground or perhaps intentionally as grit. Animal matter formed only a small proportion (4.2%) of the crop contents in my samples. Wetmore (1916) reported 4 of 22 stomachs of doves collected in Puerto Rico contained animal matter (invertebrates). Zamore (1981) observed Zenaida Doves feeding on earthworms, ants, and flies.

I observed Zenaida Doves feeding on 28 plant species 5 or more times (Table 4). Nineteen of these species were not found in the dove digestive tracts, for a total of 77 food species I recorded for the Zenaida Dove in Puerto Rico. Wetmore (1916) listed 18 additional plant species found in crops of 22 doves he collected in Puerto Rico. Maldonado Colon and Pérez-Rivera (1977) listed 31 plants used as food by the Zenaida Dove in Puerto Rico, including 10 that I did not record: *Ipomoea tiliacea*, *Amaranthus dubius*, *Phytolacca rivinoides*, *Plantago major*, *Zea mays*, *Mangifera indica*, *Cordia sulcata*, *Gymnanthes lucida*, *Tabebuia haemantha*, and *Adenoropium [Jatropha] glossypiifolia*.

In summary, the Zenaida Dove is a generalist, feeding on a wide variety (105 species recorded for Puerto Rico) of suitably sized fruits and seeds as they are seasonably available.

Drinking and salt use

Zenaida Doves drank from ground sources of water, but also took water from arboreal water catchments, such as blossoms or bromeliad axils. Zamore (1981) also observed Zenaida Doves drinking from water collected in small air plants on Dominica. In Puerto Rico, doves made several visits to drinking sites from mid-morning to mid-afternoon. At Ramey AFB, I observed five individuals during dry full days. These birds made an average of 4.8 ± 0.23 trips to water per day to drink at an average of 54.0 ± 5.02 m from former locations.

Zenaida Doves ate salt from deposit-rich soils, and also from artificial sources such as livestock mineral blocks. Use of salt has been reported for several other species of columbids

TABLE 4. Food species observed used by Zenaida Doves in Puerto Rico, 1974—1983.

| Plant name | Month(s) | Observations No. | % |
|---|---|---|---|
| *Zanthoxylum martinicense** | | | |
| *Trema lamarckiana** | | | |
| *Miconia prasina* | | | |
| *Argemone mexicana* | | | |
| *Ficus citrifolia** | | | |
| *Pouteria multiflora** | | | |
| *Solanum americanum* | | | |
| *Metopium toxiferum** | | | |
| *Chrysobalanus icaco** | | | |
| *Ocotea leucoxylon** | | | |
| *Didymopanax morototoni** | | | |
| *Roystonea borinquena* | | | |
| *Euphorbia heterophylla* | | | |
| *Miconia laevigata* | | | |
| *Manilkara bidentata** | | | |
| *Lantana camara** | | | |
| *Chenopodium ambrosioides** | | | |
| *Aeschynomene americana** | | | |
| *Oryza sativa* | | | |
| *Solanum torvum** | | | |
| *Urena lobata** | | | |
| *Citrus sinensis** | | | |
| *Cordia nitida* | | | |
| *Alchornea altifolia** | | | |
| *Portulaca oleracea** | | | |
| *Tabebuia heterophylla** | | | |
| *Piper aduncum** | | | |
| *Chrysophyllum cynodendron** | | | |

Not recorded in the digestive tract samples.

(e.g., White-crowned Pigeon, Wiley & Wiley 1979; White-winged Dove, Neff 1947; Band-tailed Pigeon *Columba fasciata*, Packard 1946, Neff 1947; Passenger Pigeon *Ectopistes migratorius*, Lewis 1944, Neff 1947; Mourning Dove, Pierce 1921, Marshal 1940, Packard 1946, Neff 1947). Herson (1980) suggested that columbids, which normally have a low sodium diet (seeds and fruits), may feed on salt to meet the needs of egg formation and production of "pigeon milk" for chicks.

## Vocal behavior

*Calling activity.* — Zenaida Doves normally began calling about 33 ± 6.1 min before sunrise. Calling activity was greatest in the early morning and late afternoon (Fig. 3). Zamore (1981) reported a similar bimodal pattern of Zenaida Dove calling on Dominica, with the highest calling frequencies from 06:00—09:00 and 14:00—18:45. Zenaida Doves have two basic vocalizations: the "*Coo*", or Advertisement Call, and the Nest Call.

"*Coo*" *or Advertisement Call.* — The *Coo* is a musical "*Coo-oo Coo-oo Coo-oo*", similar to the Advertisement Call of the Mourning Dove (Baptista *et al.* 1983; Fig. 4). Gosse (1847) likened the *Coo* call to "Sary-coat-true-blue", all notes of which were the same tone, except the second which was short and elevated. The *Coo* is given in self-assertive contexts as well as during and after sexual displays. While calling, the bird postured with its throat feathers loosened, its neck arched down, and head pulled into the shoulders.

The *Coo* typically has four or five elements (Fig. 4), with a mean total duration of 3.32 ± 0.15 s (n = 13, range = 3.10—3.56 s; Table 5). The first element lasted an average of 0.88 ± 0.12 s (n = 9, range = 0.62—0.96 s) and had a

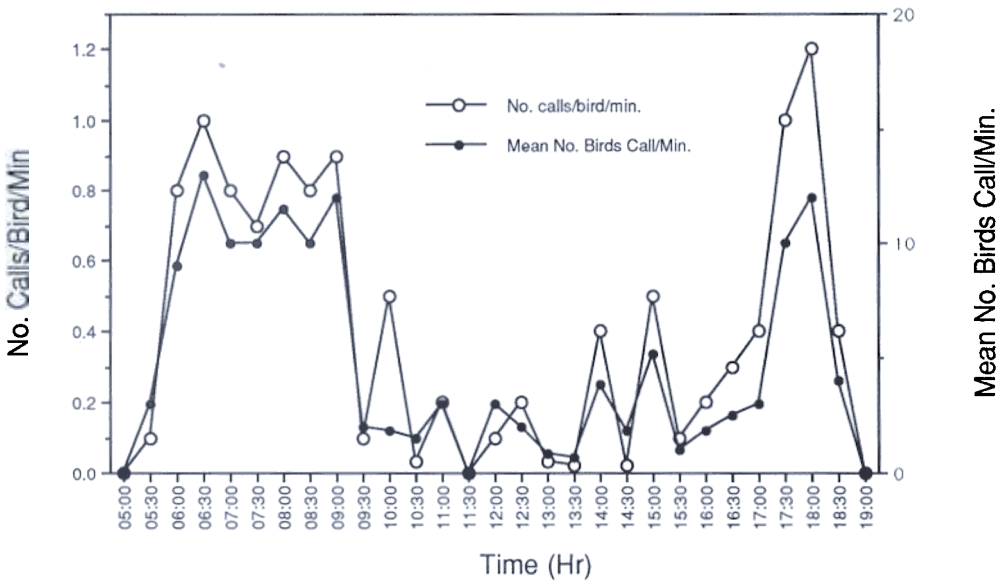


FIG. 3. Time of Zenaida Dove calling activity, Ramey Air Force Base (Aguadilla), Puerto Rico, April, 1975.

fundamental tone with occasionally 1 to 4 overtones (Table 5). The second element consisted of a fundamental tone and up to three overtones. The third and fourth elements had up to four overtones (typically 2) overlaying the fundamental tone.

*Nest Call.* — The Nest Call (Fig. 5) was typically given by birds at or near the nest. The female gave a softer, more subdued version of the call. Males characteristically gave this call on arriving in the nest tree and when moving onto the nest. When the attending adult gave the Nest Call, the other member of the pair often quickly returned to the nest. Zamore (1981) reported that the nest exchange was always accompanied by the incoming bird giving Nest Calls (*"oooa-oo-oo-oo"*), followed by Advertisement Calls. He reported that both sexes gave the call, but only the incoming bird produced it during nest exchanges.

The Nest Call typically consisted of 2 elements and had a mean duration of 1.54 ± 0.28 s (n = 9, range = 1.23—1.81 s; Table 6).

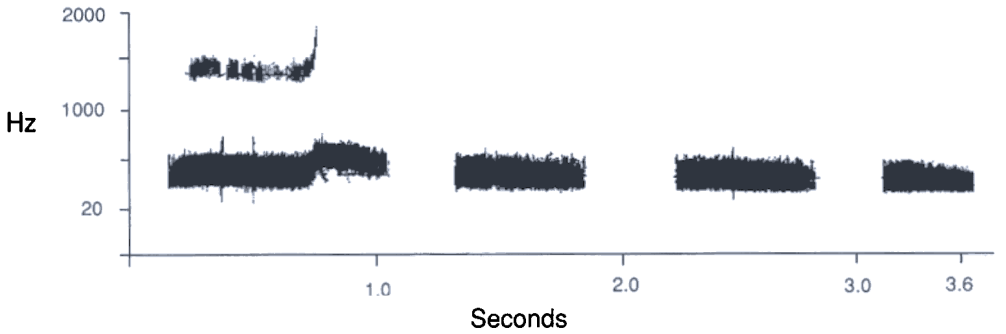


FIG. 4. Sonagraph of adult male Zenaida Dove Advertisement (*"Coo"*) Call, Cidra, east-central Puerto Rico, December 1975. Sonagraph produced on wide band setting, 18.8—1200 Hz.

TABLE 5. Characteristics of Zenaida Dove *Coo* vocalizations.

| Element number | Interval (s) between elements | Frequency mean ± SD Hz (Sample size, Range) | | | | | |
|---|---|---|---|---|---|---|---|
| | | Fundamental tone | Overtone 1 | Overtone 2 | Overtone 3 | Overtone 4 | Duration (s) |
| | | | 920 ± 76.59 (7, 840-1000) | 1460 ± 95.22 (4, 1320-1520) | 2070 ± 20.00 (4, 2040-2080) | 2580 ± 40.00 (4, 2520-2600) | |
| | 0.31 ± 0.03 (10, 0.29-0.37) | | | | | | |
| 2 | | 451.7 ± 36.64 (12, 400-520) | 895 ± 67.40 (8, 840-1000) | 1367 ± 119.78 (6, 1280-1520) | 1720 (2) | | 0.57 ± 0.03 (14, 0.53-0.60) |
| | 0.39 ± 0.02 (12, 0.36-0.44) | | | | | | |
| | | 438.3 ± 43.87 (12, 400-520) | 898 ± 60.37 (9, 840-1000) | 1353 ± 117.08 (6, 1240-1520) | | | 0.49 ± 0.08 (10, 0.41-0.60) |
| | 0.28 ± 0.02 (12, 0.24-0.33) | | | | | | |
| | | 431.7 ± 40.42 (12, 400-520) | 903 ± 72.51 (7, 840-1000) | 1367 ± 105.58 (6, 1280-1520) | | | 0.49 ± 0.08 (10, 0.34-0.55) |

"*Croo*". — Males sometimes gave a harsh, but low volume, "*Croo!*" as the female entered the nest area during nest exchanges. This response may have been a contact call to announce the male's presence and identity.

*Vocalizations of nestlings.* — Chicks gave a sibilant squeaking or "*Peeting*" call when disturbed or begging food from adults.

*Flight sounds.* — Zenaida Dove wings characteristically produced a whistle in flight, similar to that of the Mourning Dove and several other columbid species (Goodwin 1970). This sound was particularly noticeable during intraspecific chases. Doves produced a wing clapping sound on take-off during courtship flights.

Nesting habitat and nest spacing

Doves nested in habitats with broad differences in vegetative components (Table 7). The Roosevelt Roads leadtree-scrub forest was denser than any of the other sites sampled, with a mean of 421 trees per 0.04 ha sample. The Roosevelt Roads black mangrove forests (342 trees per 0.04 ha) and thick *Metopium* woodlands (247 trees) of Mona Island were denser than the dry mainland forests of Susua (14.7 trees) and Guánica (12.5 trees). Doves at Guánica and Susua appeared to concentrate nesting activity in the taller forests along intermittent waterways or moister ravines.

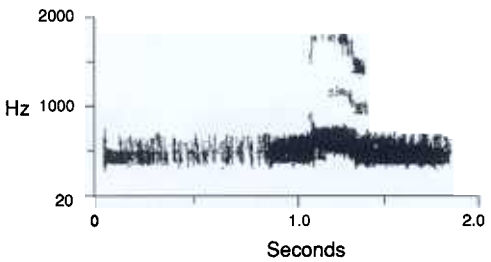


FIG. 5. Sonagraph of adult male Zenaida Dove Nest Call, Cidra, east-central Puerto Rico, May 1974. Sonagraph produced on wide band setting, 18.8—1200 Hz.

Shrub densities also varied considerably among study sites. Mona Island and the leadtree-scrub of Roosevelt Roads had the densest understory growth, whereas the other study areas had relatively open understories. The black mangrove forest of Roosevelt Roads is a near monoculture of even-aged trees, whereas the Guánica and Susua areas are generally sparsely vegetated over limestone plate.

Nests were placed lower in the vegetation of the dry study areas (Guánica, Susua, Mona Island) than in the more humid areas. The lower placement may have been related to the scarcity or absence of mammalian predators in dry study areas. The small Indian mongoose (*Herpestes auropunctatus*) is rare in the Guánica Forest and the roof rat (*Rattus rattus*) is scarce relative to other areas in Puerto Rico. The mongoose does not occur on Mona Island. Zenaida Doves will nest in grassy vegetation on the ground or in rocky crevices in areas that are free of most terrestrial predators (mongoose, cats, dogs). On the remote

TABLE 6. Characteristics of Zenaida Dove Nest Call vocalizations

| Element number | Interval (s) between elements | Frequency mean ± SD Hz (Sample size, Range) Fundamental tone | Overtone 1 | 2 | Duration (s) |
|---|---|---|---|---|---|
| 1 | | 436.7 ± 34.64 (9, 400-490) | 720 ± 69.28 (3, 680-800) | | |
| | 0.18 ± 0.13 (9, 0.041-0.38) | | | | |
| | | 613.9 ± 69.90 (9, 505-730) | 898 ± 275.24 (4, 720-1300) | 1750 (2) | 0.76 ± 0.20 (9, 0.51-0.94) |

cays off Culebra Island, I found doves commonly nesting among boulders as close as 10 m from the sea's edge. Zamore (1981) reported 14% of the Zenaida Dove nests (n = 37) he located in Dominica were on the ground. Danforth (1935) described nesting doves using tunnel-like excavations under matted grass on Little Saba Cay (Virgin Islands). Burger *et al.* (1989b) also reported on the ground nesting habit on the islands of the Culebra archipelago. However, Nellis *et al.* (1984) presented data that suggested there may be heavy predation by land crabs on eggs and chicks in such sites.

Some dove nests were placed next to the main trunk of the tree or shrub in all study areas, except the Susua Forest. Nests at Roosevelt Roads mangrove areas were placed farther from the tree center than at other sites.

Like many other columbid species that nest in trees or shrubs, Zenaida Doves chose nest sites which offered suitable horizontal support. Doves did not choose nest sites on the basis of tree species; i.e., use of nest tree was correlated with species' abundance in the area (Table 8). Doves in the Guánica and Susua study areas showed the strongest relationship between abundance of a tree species and use of those species for nesting: Guánica — $r$ [correlation coefficient] = 0.98 ($t$ = 2.012, $0.05 < P < 0.10$, n = 8 pairs, paired $t$-test), Susua — $r$ = 0.99 ($t$ = 2.598, $0.02 < P < 0.05$, n = 8), Cidra — $r$ = 0.53 ($t$ = 0.530, $P > 0.05$, n = 6; Table 8). Black mangrove made

TABLE 7. Mean values for selected parameters of nesting habitat of Zenaida Doves in 5 habitat types in Puerto Rico, 1974—1982. Ranges are given in parentheses.

| No. nests[1] | No. trees/ 0.04 ha sample | Tree height (m) | No. shrubs/ 0.04 ha sample | Shrub height (m) | % ground cover | % canopy cover | Nest tree Height (m) | Nest tree DBH (cm) | Nest Height (m) | Nest Distance from center (cm) |
|---|---|---|---|---|---|---|---|---|---|---|
| Mona Island — *Metopium*-dominated woodland | | | | | | | | | | |
| 19 | 246.8 (227-620) | 4.3 (3.14-5.01) | 835.6 (420-1400) | 0.9 (0.6-1.1) | 7.5 (5-35) | 39.5 (20-95) | 7.1 (2.8-10.5) | 7.6 (4.5-7.9) | 3.6 (0.9-7.7) | 1.5 (0-3.3) |
| Roosevelt Roads — black mangrove forest | | | | | | | | | | |
| 151 | 341.6 (20-800) | 5.1 (2.2-9.2) | 76.6 (0-200) | 0.6 (0.3-1.2) | 39.3 (0-95) | 38.8 (5-75) | 7.1 (3.9-12.3) | 11.6 (5.1-24.1) | 5.1 (2.2-9.3) | 112.5 (0-182.9) |
| Roosevelt Roads — leadtree-scrub forest | | | | | | | | | | |
| 78 | 421.3 (79-850) | 3.4 (2.1-5.5) | 496.6 (67-450) | 0.6 (0.3-1.2) | 87.3 (50-100) | 74.3 (20-95) | 5.9 (3.0-9.4) | 8.5 (4.3-15.3) | 3.7 (2.6-7.3) | 65.7 (0-21.8) |
| Guánica forest — Subtropical dry forest | | | | | | | | | | |
| 38 | 12.5 (6-31) | 6.9 (3.1-12.3) | 54.0 (20-85) | 1.3 (0.8-1.9) | 7.2 (5-10) | 26.1 (5-55) | 4.9 (2.2-10.8) | 15.1 (7.6-27.9) | 2.2 (1.7-3.7) | 21.7 (0-91.4) |
| Susua forest — subtropical moist forest | | | | | | | | | | |
| 32 | 14.7 (7-31) | 9.0 (4.6-12.3) | 45.6 (10-72) | 1.6 (0.9-3.1) | 6.8 (2-15) | 42.8 (5-75) | 8.0 (2.5-16.9) | 24.9 (3.8-40.6) | 3.6 (0.8-6.2) | 76.4 (12.7-183) |

[1] Each nest was center of habitat plot.

TABLE 8. Tree species used by nesting Zenaida Doves in 5 study areas, Puerto Rico, 1974—1982.

| Locality | Nest tree species | % nests | % of vegetative samples |
|---|---|---|---|
| Guánica forest | | | |
| (n = 38 nests) | *Swietenia mahagoni* | 31.6 | 12.8 |
| | *Cephalocereus royenii* | 26.3 | 13.4 |
| | *Bucida buceras* | 15.8 | 8.9 |
| | *Exostema caribaeum* | 10.5 | 7.3 |
| | *Comocladia glabra* | 5.3 | 5.1 |
| | *Amyris elemifera* | 5.3 | 4.7 |
| | *Opuntia rubescens* | 2.6 | 3.5 |
| | *Symplocos polyantha* | 2.6 | 3.1 |
| Susua forest | | | |
| (n = 32) | *Swietenia mahagoni* | 62.5 | 53.4 |
| | *Bursera simaruba* | 12.5 | 4.6 |
| | *Inga fagifolia* | 6.3 | 4.9 |
| | *Byrsonima spicata* | 6.3 | 6.6 |
| | *Casuarina equisetifolia* | 3.1 | 0.7 |
| | *Ocotea cuneata* | 3.1 | 2.0 |
| | *Tabebuia haemantha* | 3.1 | 1.2 |
| | *Machaonia portoricensis* | 3.1 | 1.5 |
| Roosevelt Roads — leadtree-scrub habitat | | | |
| (n = 78) | *Leucaena leucocephala* | 84.6 | 73.8 |
| | *Prosopis juliflora* | 15.4 | 8.2 |
| Roosevelt Roads — mangrove forest habitat | | | |
| (n = 151) | *Avicennia germinans* | 100.0 | 96.0 |
| Cidra | | | |
| (n = 56) | *Erythrina poeppigiana* | 28.6 | 20.3 |
| | *Eugenia jambos* | 17.9 | 33.3 |
| | *Cecropia peltata* | 17.9 | 13.5 |
| | *Bambusa vulgaris* | 25.0 | 10.8 |
| | *Roystonea borinquena* | 7.1 | 7.1 |
| | *Zanthoxylum martinicense* | 3.6 | 2.1 |

up all of the vegetation sampled in the Roosevelt Roads mangrove areas. The overall regression ($r$ = 0.97) for all study areas sampled (n = 5) was significant ($0.005 < P < 0.01$; $t$ = 3.073).

Maldonado Colon & Pérez-Rivera (1977) listed 20 species of trees used by nesting Zenaida Doves in Puerto Rico. Mango (*Mangifera indica*, 22.2% of all nests), royal palm (*Roystonea borinquena*, 14.5%), cactus (*Cephalocereus royenii*, 11.9%), and tall albizia (*Albizia procera*, 10.3%) were the most frequently used species (n = 117) in their study. Of the 37 nests studied by Zamore (1981) in Dominica, 57% were in *Haematoxylum campechianum*, the dominant tree in his study area.

Within woodlands, doves commonly nested on bromeliads attached to trees, a habit also reported by Barbour (1923) and Maldonado Colon & Pérez-Rivera (1977), who found 54% of Zenaida Dove nests (n = 37) were built on bromeliads (*Tillandsia* sp. and *Guzmania* sp.). Danforth (1925) found Zenaida Doves nesting on dense clumps of cattails (*Typha domingensis*) over water.

Normally, Zenaida Doves are not gregarious nesters, although Danforth (1935) described an "enormous breeding colony" of "thousands" of doves on Little Saba Cay, where the majority of nests were placed on the ground. Robertson (1962) also reported that Zenaida Doves bred in aggregations on the cays of the Virgin Islands. In my study areas, nesting Zenaida Doves were apparently more tolerant of other columbid species than they were of conspecifics nesting nearby ($P < 0.05$; Fisher-Behrens $t$-test, $t$ = -476, d.f. = 26). The distance between conspecific nests averaged 76.8 ± 15.4 m (range = 15—400 m, n = 23), whereas the mean distance between adjacent nests of Zenaida Doves and other columbids (White-winged Dove, Common Ground-Dove, Mourning Dove, White-crowned Pigeon) was 36.8 ± 4.9 m (range = 10—100 m, n = 25).

## Breeding biology

*Courtship displays.* — Males performed aerial displays over their territories. I observed most displays in the early morning (80% > 08:30; n = 151), although a lesser peak occurred in the late afternoon (13.3%). Aerial displays began with the male steeply climbing with rapid, deep wingbeats. Altitudes of up to about 60 m were attained in the climbing phase of the display, but the usual height was less than 25 m. A slapping sound was produced during the wing flapping-climbing part of the display. At the apogee, the dove set its wings and made a slow gliding turn of about 180 degrees as it descended to a perch. The bird tilted from side to side during the glide. The male sometimes repeated the display; at the perigee of the glide it flapped to regain altitude, and then descended in a second fixed wing, 180 degree turn. The white on the trailing edge of the dove's wing was particularly noticeable during the glide. In some flights as many as 3—360 degree spiralling descents on fixed wings were made before the male alighted on a perch. Occasionally, the displaying bird was joined in flight by a second dove that closely followed the male's path. Apparently, the resident male's display also stimulated displays by males on adja-

cent territories. The male characteristically *Coo*-called on landing (76% of observations, n = 151). The male alighted next to another bird in 45% of my observations and copulations were attempted on 12% of those occasions.

Zenaida Doves also displayed on the ground, with males "driving" (Goodwin 1970: 36) females. These activities began with the male pursuing the female in a moderate to rapid walk. Both birds moved in the same circular direction, but the male had to walk faster than the female, because he was on the outside, making larger circles (Fig. 6). The male jerked his head back and forth rapidly, or drew his neck into his shoulders and held his head slightly down as he walked. The female's neck was outstretched. As with the Mourning Dove and Eared Dove (*Zenaida auriculata*, Goodwin 1970), males did not perform bowing displays. The male typically ended his driving with a quick tail spread that flashed the white tips of the retrices. Whereas the driving display could end in allopreening (17% of observations; female-initiated in 65% of observations) and copulation (17% of observations),

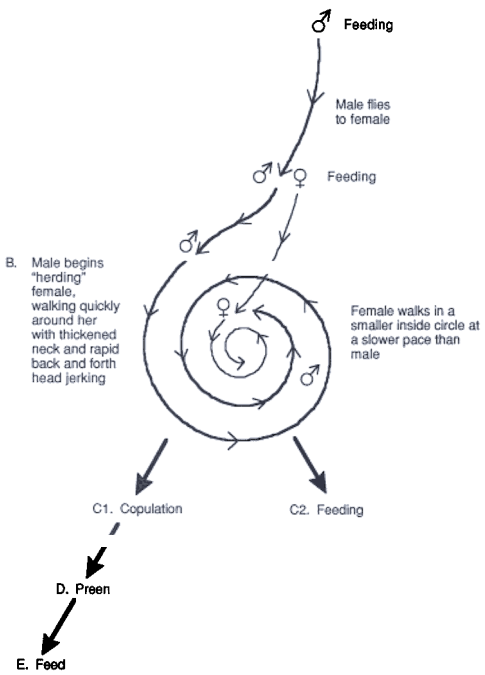


FIG. 6. Diagram of Zenaida Dove courtship behavior

most driving activity terminated in the female flying off, with the male in pursuit. Most (76%; n = 255) driving display activity was performed before 11:00 hr.

In the pursuits, the female usually changed perches several times, with the male following her in each of her flights. Once the female tolerated him within about 0.3 m, the male squatted low next to her and began twitching his wing(s) up and down. The female normally wing twitched, too. Both autopreened for 10 to 290 sec before allopreening began. Females initiated allopreening bouts in 77% of observed cases (n = 49). Females usually concentrated on preening the mate's neck, head, and breast. Allopreening was occasionally interrupted by one or both doves pacing. Finally, the female crouched, twitched the wing on the same side as the male, or both wings. Zamore (1981) also observed Zenaida Doves allopreening about the neck and wing-twitching in pre-copulatory displays. Females solicited copulation in 78% of my observations where the full display sequence could be seen (n = 13). The male mounted the female and balanced with partially outspread wings during copulation. At cloacal contact, the male fluttered his wings rapidly. Copulations averaged 5.4 ± 0.3 s (n = 27, range = 3—9 s). Most copulations (73%; n = 47) were observed in the early morning (> 08:30), with a lesser peak in the late afternoon (12%; < 16:30).

After copulation, the male *Coo*-called, performed a series of neck-jerk displays ("Aiming", Goodwin 1970: 23), then rested on the perch. Both birds regularly autopreened and occasionally allopreened. Females were usually (79.4%; n = 39) the first member of the pair to leave the copulation area. The other member flew off 0.05 to 7.3 min later (males — 0.05—2.1 min; females — 0.5—7.3 min). Males usually left in apparent defense of their territory.

*Breeding chronology.* — Male doves marked as nestlings were first observed performing aerial and ground courtship displays at 10 months of age. The youngest female I observed produce eggs was 11 months old.

Bent (1932) reported Zenaida Dove egg dates (n = 10) from 6 April to 8 December; the median 5 records were from 13 May to 12 June. Danforth (1935) found many nests with eggs

TABLE 9a. Zenaida Dove nesting chronology in lower montane second growth forest and pasturelands at Cidra, east-central Puerto Rico, 1974—1982. Data are for first egg laid.

| Month | Year 1974 | 1975 | 1977 | 1978 | 1980 | 1981 | 1982 | Total | % |
|---|---|---|---|---|---|---|---|---|---|
| Jan | 2 | 1 | 0 | 1 | X[a] | 1 | X | 5 | 5.5 |
| Feb | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 6 | 6.6 |
| Mar | 4 | 3 | 3 | 3 | 3 | 4 | 3 | 23 | 25.3 |
| Apr | 8 | 7 | 4 | 2 | 3 | 3 | 4 | 31 | 34.1 |
| May | 3 | 3 | 2 | 2 | X | 2 | 1 | 13 | 14.3 |
| Jun | 2 | 0 | 2 | 1 | X | 0 | X | 5 | 5.5 |
| Jul | 0 | 0 | 1 | 0 | X | 1 | X | 2 | 2.2 |
| Aug | 0 | 1 | 0 | 2 | X | 0 | X | 3 | 3.3 |
| Sep | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 2.2 |
| Oct | 0 | 0 | 0 | 1 | X | 0 | 0 | 1 | 1.1 |
| Nov | 0 | 0 | 0 | 0 | 0 | X | 0 | 0 | 0 |
| Dec | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Totals | 21 | 15 | 12 | 14 | 7 | 13 | 9 | 91 | 100.1 |

X[a] = period not sampled.

and chicks on Little Saba Cay in June. In Dominica, Zamore (1981) reported nests from March through December, with a peak in breeding activity in May. Nellis *et al.* (1984), summarizing Zenaida Dove breeding records for the Virgin Islands, reported the main nesting period as May to August, but eggs were found throughout the year. Although Maldonado Colon & Pérez-Rivera (1977) reported active nests in the dry forest zone at Guánica only from July through September, they found nests throughout the year in the moist lower montane zone of east-central Puerto Rico (Cayey, peak activity February—May).

TABLE 9b. Zenaida Dove nesting chronology in subtropical dry and moist forests, southwestern Puerto Rico (Guánica and Susua forests), 1973—1975. Data are for first egg laid.

| Month | Year 1973 | 1974 | 1975 | Total | |
|---|---|---|---|---|---|
| Jan | X[a] | 1 | 2 | 3 | 11.1 |
| Feb | X | 0 | 1 | 1 | 3.7 |
| Mar | X | 2 | 0 | 2 | 7.4 |
| Apr | X | 3 | 3 | 6 | 22.2 |
| May | X | 0 | 2 | 2 | 7.4 |
| Jun | X | 2 | 0 | 2 | 7.4 |
| Jul | X | 0 | 0 | 0 | 0 |
| Aug | X | 0 | 0 | 0 | 0 |
| Sep | X | 0 | 1 | 1 | 3.7 |
| Oct | 3 | 1 | 0 | 4 | 14.8 |
| Nov | 2 | 0 | 2 | 4 | 14.8 |
| Dec | 0 | 1 | 1 | 2 | 7.4 |
| Totals | 5 | 10 | 12 | 27 | |

X[a] = period not sampled.

Similarly, I found new dove nests in all months of the year (Tables 9a—c). However, the peak activity period for nesting was April or May in each of my study areas. One major breeding period occurred at Roosevelt Roads (March through July) and Cidra (March through May). Doves in the southwestern study areas perhaps had two breeding peaks: March through June, and October through January. However, I collected few data from the southwestern areas and further observations are needed to determine if the two breeding periods are normal for most years. Nellis *et al.* (1984) reported annual variation in breeding activity on Little Saba Cay, Virgin Islands. In some years only one breeding peak was observed, whereas in other years they noted two peaks in activity. A breeding peak occurred from August through October in only one of their five study years.

I found only slight correlation between dove breeding and rainfall patterns in my study areas (Fig. 7). Breeding activities (new nests) moderately corresponded with rainfall in the principle breeding months at Cidra (Spearman's Rank Correlation, $r = 0.64$, $n = 6$; $0.20 \leqq P < 0.05$) and Roosevelt Roads ($r = 0.74$, $n = 6$; $0.10 < P < 0.20$). However, a negative correlation was evident between year-long rainfall and nesting activities in these study areas, as little breeding activity occurred during the fall, the period of

TABLE 9c. Zenaida Dove nesting chronology in mangrove and leadtree-scrub forests of dry subtropical forest zone at Roosevelt Roads Naval Station study area, eastern Puerto Rico, 1974—1983. Data are for first egg laid.

| | Year | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Month | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | Total | % |
| Jan | 0 | 1 | X[a] | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 6 | 1.9 |
| Feb | 0 | 2 | X | 2 | 1 | 3 | 2 | 1 | 0 | 0 | 11 | 3.4 |
| Mar | 0 | 5 | X | 1 | 1 | 5 | 9 | 3 | 2 | 4 | 30 | 9.3 |
| Apr | 2 | 7 | X | 8 | 5 | 13 | 13 | 5 | 4 | 5 | 62 | 19.2 |
| May | 8 | 13 | X | 9 | 7 | 12 | 17 | 7 | 3 | 8 | 84 | 26.0 |
| Jun | 9 | 11 | X | 6 | 5 | 6 | 5 | 4 | 0 | 2 | 48 | 14.9 |
| Jul | 11 | 2 | 6 | 5 | 2 | X | 2 | 4 | 1 | 2 | 35 | 10.8 |
| Aug | 6 | 1 | 4 | 4 | 0 | X | X | 5 | X | 0 | 20 | 6.2 |
| Sep | 2 | 0 | 2 | 3 | 1 | X | X | 4 | 0 | 1 | 13 | 4.0 |
| Oct | 1 | 0 | 0 | 2 | 0 | X | 0 | 2 | 0 | 0 | 5 | 1.5 |
| Nov | 1 | 0 | 1 | 2 | 0 | X | 0 | 0 | 0 | 0 | 4 | 1.2 |
| Dec | 3 | 0 | 0 | 1 | 0 | X | 0 | 1 | 0 | X | 5 | 1.5 |
| Totals | 43 | 42 | 13 | 44 | 22 | 41 | 49 | 36 | 10 | 23 | 323 | 99.9 |

[a] = period not sampled.

greatest rainfall: Cidra — $r$ = -0.21, Roosevelt Roads — $r$ = -0.32. Doves on the southwestern study areas showed two peaks in breeding activities (Fig. 7), but the number of new nests showed no correlation with rainfall patterns ($r$ = -0.32, n = 12). In contrast, Rivera Milán (1989) found a positive correlation between rainfall and timing of Zenaida Dove breeding activity in Puerto Rico.

I followed renesting behavior of pairs in which one or both members were color marked or had unique physical characteristics. Dove pairs whose first nests failed typically renested. Pairs that lost nests during the incubation stage laid replacement clutches sooner ($\bar{x}$ = 13.7 ± 0.8 days, range = 7—23 days, n = 7) than pairs whose nests failed during the chick stage ($\bar{x}$ = 20.3 ± 1.2 days, range = 9—31, n = 21; $P < 0.05$, Fisher-Behrens $t$-test). Others have reported much shorter intervals for replacement clutches of the closely related Mourning Dove. Harris *et al.* (1963) found that the renesting

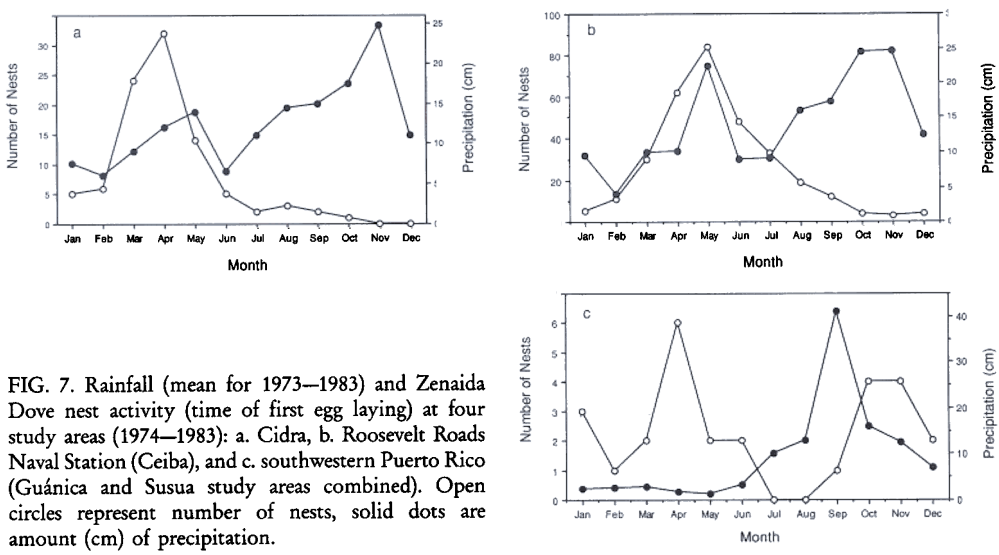


FIG. 7. Rainfall (mean for 1973—1983) and Zenaida Dove nest activity (time of first egg laying) at four study areas (1974—1983): a. Cidra, b. Roosevelt Roads Naval Station (Ceiba), and c. southwestern Puerto Rico (Guánica and Susua study areas combined). Open circles represent number of nests, solid dots are amount (cm) of precipitation.

interval for pairs whose nests failed during incubation was 9.8 days, the same as that for pairs whose nests failed during the nestling stage. Swank (1955) reported an interval of two to five days for relaying after an original Mourning Dove nest (n = 3) was destroyed. Maldonado Colon & Pérez-Rivera (1977) reported that Zenaida Doves in captivity will produce replacement clutches on an average of 8.8 days after loss of the first clutch.

I observed marked Zenaida Doves raising up to four broods in one year (n = 3). Most successful pairs (69%; n = 54) produced at least two broods per year and many (26%) fledged chicks from three attempts (all data from Roosevelt Roads and Cidra). These figures for recycling and replacement nestings are biased low, because pairs characteristically renested in a different site with each new attempt, and I probably did not relocate several of the marked, re-nesting pairs.

*Nest building and pre-incubation behavior.* — Males selected nest sites and initiated nest building. Similar to Nice's (1922) observations for Mourning Doves, most nest building by Zenaida Doves was performed in the morning (74% of observations > 10:00). Doves gathered twigs up to 55 m from their nests and at heights ranging from the ground to 10 m at 3 nests I intensively studied. Materials were collected at a mean rate of 1 trip per 70 s (n = 45 trips) during bouts of nest building in the first 2 days of construction. The adult male did most of the building of the nest platform. After a foundation was established, the female played a more active role in building than in the initial construction stage. She occasionally sat in the nest bowl and the male, standing behind her, passed twigs over her shoulder, whereupon she worked the materials into the nest with her bill. These roles of male delivering and female building are typical among other columbid species (Goodwin 1970). In 15.1 hrs of early nestbuilding observations, males arranged nest twigs in 90.3% of the occasions (n = 23) and females in 9.7% (n = 3 nests). Both sexes participated in lining the bowl. Zamore (1981) observed that one Zenaida Dove (sex undetermined) gathered nest materials, whereas its mate performed all of the arranging of materials in the nest.

Nests were built of twigs, grass stems, and dried vines, and were lined with finer materials and leaves. Males molded the lining into place by walking and sitting in the bowl. Nest building took 3 to 7 days ($\bar{x}$ = 5.4 ± 0.3; n = 18).

Males were the first member of the pair to arrive at the nest during the pre-egglaying period (n = 9 observations). However, females left the nest first in most of my observations (61.5%; n = 13). During the pre-incubation period, both sexes were on the nest for extended periods (6.5 hrs [43.3%] of the 15.1 hrs I observed nests during that period at the Cidra study area), but males were in attendance more than females. While at the nest, males spent more time in the bowl than females (19.7% [179.0 min] *vs.* 3.4% [30.5 min] of observation time [15.1 hrs total], respectively), whereas females stood on the rim more often than males (13.9% [125.5 min] *vs.* 6.1% [55.5 min], respectively). Both members of the pair were in the bowl together 0.2% (2.0 min) of the time observed.

Nest cleaning was a common activity when the adults were at the nest. Males cleaned or arranged nest materials at a rate of 0.24 bouts per min (n = 128), whereas females cleaned at 0.02 bouts per min (n = 11).

Both sexes displayed with wing twitches when at the nest with their mate. Males exhibited this behavior in 97.6% (n = 40) of occasions when a female was at the nest. Females wing twitched whenever the male was present (n = 35; 15.1 hrs observation).

Allopreening was a frequent activity at the nest in the pre-incubation period. Females initiated allopreening bouts in 74.2% of my observations (n = 66). Males performed 21.7% (n = 13; 15.1 hrs observation) of the allopreening bouts, whereas females performed 78.3% (n = 47) of such bouts. Most preening bouts (95.8%; n = 118) occurred while the adult male was in the nest bowl and the female was on the rim. While males were in the nest bowl, they preened females less often (23 bouts, 20.4%) than females preened males (90 bouts, 79.6%; $P < 0.001$; $X^2$ one sample test). Few preening bouts occurred when the female was in the nest bowl; males preened females three times (60% of events), and females preened males twice. Females autopreened at the nest more often

(78.3%) than males (21.7%, n = 60 observations) during pre-incubation.

During the pre-incubation period, Zenaida Doves were active at the nests and frequently shifted position. Males shifted an average of 158.6 ± 13.3° (range = 20—360°, n = 33) per position change, whereas females moved an average of 153.8 ± 19.2° (30—180°, n = 8; $t$ = -0.171, $P > 0.05$). There was also no difference in the direction of shift on the nest between sexes. Males moved in a counter-clockwise direction in 63.6% of their position shifts (n = 22), and females did so in 46.9% of these movements (n = 32; $X^2 = 1.473$, $P > 0.05$).

*Eggs and incubation period.* — The first egg of the clutch was laid one to four days ($\bar{x}$ = 1.8 ± 0.3 days; n = 12) after the nest was completed. Zenaida Dove eggs from Puerto Rico averaged 29.5 ± 0.6 mm in length and 22.0 ± 0.2 mm in width (n = 21). Eggs from Culebra Island (n = 6) averaged 29.6 ± 0.7 x 21.9 ± 0.1 mm. Eggs from Puerto Rico and Culebra Island were comparable in size to those measured by Danforth (1935; 28.2 ± 1.4 [SD] x 21.8 ± 0.8 mm) and Nellis *et al.* (1984; 29.8 ± 1.4 x 22.5 ± 1.1 mm) in the Virgin Islands. Four eggs measured by Zamore (1981) in Dominica averaged 32.5 x 22.5 mm, and weighed an average of 14 g (range 12—16 g). Eleven eggs from Puerto Rico had a mean weight of 7.7 ± 0.6 g (range = 7.5—8.0 g).

Zenaida Dove eggs were usually laid on alternate days. At 27 Zenaida Dove nests, the mean interval between the laying of the first and second eggs was 1.1 ± 0.1 days; the 2 eggs were laid on the same day at 1 nest, at 1 day intervals at 23 nests, and at 2 day intervals at 3 nests.

The mean incubation period was 13.9 ± 0.5 days (range = 13—15 days, n = 14). Nellis *et al.* (1984), in their summary of Zenaida Dove ecology in the Virgin Islands, gave the incubation period as 14 days, whereas Zamore (1981) reported a mean incubation period of 15 days (range 14—16 days, n = 3).

Zenaida Doves follow the typical nest attendance pattern of columbids (Goodwin 1970); i.e., males were on the nest from mid-morning through mid-afternoon or early evening, when the female took over until the next morning. Zamore (1981) reported the male's attendance period as 09:00—15:00, whereas the female performed that task during the remaining period. In my study, morning nest exchanges during the incubation period took place from 08:10 to 09:00 ($\bar{x}$ = 08:34 ± 17.2 min; n = 13). Evening exchanges were between 15:30 and 16:40 ($\bar{x}$ = 15:53 ± 19.9 min; n = 13). Nests were attended by adults at all times during the incubation period; males were in attendance for an average of 7.3 ± 0.5 hrs and females for 16.8 ± 0.5 hrs.

*Nestling period.* — Chicks hatched on alternate days, since the adults began incubating on the day that the first egg was laid (also see Zamore 1981). Hatching usually occurred in the morning, although I observed chicks hatching throughout the day ($\bar{x}$ = 08:13; Fig. 8). Few hatchings occurred overnight. Whitman (1919) generalized that most pigeon eggs hatched in the morning.

I observed a mean nestling period of 14.3 ± 0.6 days (n = 18, range = 13—15). Seaman (*in* Nellis *et al.* 1984) reported Zenaida Doves fledged after 15 days. Zamore (1981) found chicks fledged on the 14th day.

Adults were continuously at the nests during the first seven days of the nestling period. Thereafter, attendance dropped off steadily until, by day 14 after hatching, the chicks were not brooded overnight. From hatching (day 0) to day 5, males were on the nest an average of 7.8 ± 0.6 hrs and females 16.1 ± 0.7 hrs. The departing adult lingered on the nest for an average of 11.4 ± 7.8 min after the incoming bird arrived. Morning nest exchanges took place from 08:30 to 09:30 ($\bar{x}$ = 08:59 ± 7.0 min; n = 7) and

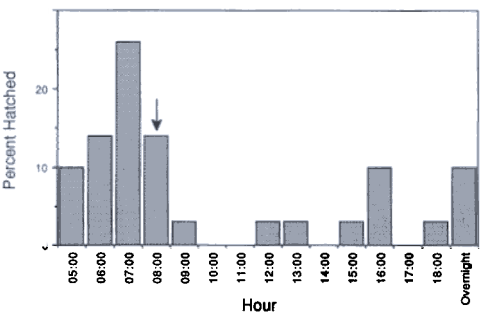


FIG. 8. Time of hatching of 23 Zenaida Dove chicks, Roosevelt Roads Naval Station, eastern Puerto Rico, 1974—1980. Mean hatching time shown by arrow.

evening changes from 16:00 to 18:10 ($\bar{x}$ = 16:53 ± 15.7 min; n = 7); essentially the same as during incubation.

From day 6 through day 10, adults tended chicks nearly continuously; from day 8 to 10, adults were gone from the nest for an average of 19.8 ± 5.4 min per day. Males were on the nest an average of 7.9 ± 0.7 hr and females 15.8 ± 0.5 hr. Morning exchanges took place from 08:30 to 09:30 ($\bar{x}$ = 09:09 ± 8.3 min, n = 6) and evening changes from 16:10 to 18:00 ($\bar{x}$ = 17:08 ± 14.7 min).

Nest attendance dramatically fell off after day 10. Nests were unattended an average of 3.3 ± 2.7 hrs from days 11 to 14 (n = 7 days of observation). Adults showed little overlap in attendance ($\bar{x}$ = 1.2 ± 3.0 min) and one adult often left far in advance of the arrival of its mate. Males were on the nest for an average of 5.3 ± 1.6 hrs and females 15.6 ± 0.5 hrs. Females left the nest from 07:10 to 08:55 hr ($\bar{x}$ = 08:46 ± 39.6 min; n = 6), and males arrived from 08:50 to 10:00 ($\bar{x}$ = 09:31 ± 27.0 min; n = 7). In the afternoons, males left the nest from 14:00 to 16:00 ($\bar{x}$ = 15:13 ± 46 min; n = 7) and females arrived from 16:10 to 18:10 ($\bar{x}$ = 17:15 ± 41 min; n = 7).

Zenaida Doves typically removed eggshells from the nest area. Shells were carried in the bill up to 100 m from the nest. The removal of eggshells may have an important function in avoiding chick predation at the nest (Tinbergen *et al.* 1962; Montevecchi 1974, 1976). I found that chicks at dove nests where eggshells were not removed or where shells were dropped near the nest were lost to predators more often than those where eggshells were removed from the area ($0.03 < P < 0.04$; Fisher exact probability test). At Zenaida Dove nests where adults removed eggshells, 45 (54.2%) were successful, whereas 38 (45.8%) failed because of predation. Where adults did not remove eggshells, only 9 (32.1%) nests were successful and chicks at 19 nests (67.9%) were taken by predators.

Both adults fed, although differed in their care of, the squabs. Males fed chicks for shorter periods ($\bar{x}$ = 54.3 ± 5.7 s, range = 10—180 s, n = 46) than did females (90.1 ± 10.8 s, range = 5—240 s, n = 47; $P < 0.001$, Fisher-Behrens *t*-test).

As they aged, chicks became increasingly more active in demanding food from adults (Table 10). From day of hatching through day 5, the chicks were largely passive and adults initiated feeding bouts. The adult reached down, touched the chick's bill in a side to side brushing motion of its own bill, then took the chick's bill in its own and regurgitated food. Beginning about day 5, the chick initiated some feedings by calling and nuzzling the adult's crop area. Chicks were initiating all feeding bouts by day 7. In addition to calling and nuzzling the adult's

TABLE 10. Adult Zenaida Dove feeding behavior of chicks at three nests during 60.5 hrs of observations, Roosevelt Roads Naval Station, eastern Puerto Rico, 1974 and 1975.

| | | Number (%) of observations | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Behavior of chick | | | | | | Behavior of adult | | | | |
| Chick age (days) | Hours observ. | No. events | Initiates feeding | Calls | Orients toward adult | Nuzzles adult's crop | Flutters wings | Sex | No. events | Reaches down | Breaks off | Broods after |
| 5 | 7.0 | 2 | 1 | 2 | 0 | 2 | 0 | M | 2 | 2 | 2 | 2 |
| | | (50) | (100) | (0) | (100) | (0) | | | | (100) | (100) | (100) |
| 7 | 13.5 | 12 | 12 | 9 | 12 | 12 | 3 | M | 8 | 8 | 8 | 8 |
| | | (100) | (75) | (100) | (100) | (25) | | | | (100) | (100) | (100) |
| | | | | | | | | F | 4 | 4 | 4 | 4 |
| | | | | | | | | | | (100) | (100) | (100) |
| 10 | 14.6 | 6 | 6 | 6 | 6 | 6 | 5 | Both | 6 | 6 | 6 | 6 |
| | | (100) | (100) | (100) | (100) | (83) | | | | (100) | (100) | (100) |
| 12 | 10.8 | 4 | 4 | 4 | 4 | 4 | 4 | M | 1 | 1 | 1 | 1 |
| | | (100) | (100) | (100) | (100) | (100) | | | | (100) | (100) | (100) |
| | | | | | | | | F | 3 | 2 | 3 | 3 |
| | | | | | | | | | | (67) | (100) | (100) |
| 14 | 14.6 | 7 | 7 | 7 | 7 | 7 | 7 | M | 3 | 0 | 3 | 0 |
| | | (100) | (100) | (100) | (100) | (100) | | | | (0) | (100) | (0) |
| | | | | | | | | F | 4 | 0 | 4 | 0 |
| | | | | | | | | | | (0) | (100) | (0) |

crop, the 7 day old chick oriented toward the adult and occasionally fluttered its wings. Adults still controlled the bouts by reaching down for the chick's proffered bill and broke off the bouts by backing away or lifting its bill out of the chick's reach.

By day 12, the begging bouts of the chick consisted of all components: calling, orienting toward adult, nuzzling adult's crop, and fluttering its wings. At this age, chicks could easily reach the adult's bill, so the chick vigorously probed at the adult's mouth rather than waiting until the adult reached down to the chick. Whereas all feeding bouts culminated in the adult brooding the chicks up to day 12, thereafter neither adult brooded the nestlings after the feedings.

Ten and 12 day old chicks frequently called with a "*Peeting*" vocalization. These calling bouts were performed during periods when the adults were less than 10 m from the nest and within sight of the chick, and perhaps served as contact calls or to beg for food. The distance of the adult from the nest during a chick's calling bouts averaged 3.6 ± 0.5 mm (range = 0.5—10 m; n = 32 calling bouts) in 24.4 hrs of obser-

TABLE 11. Highlights of development of Zenaida Dove chicks from day of hatch (day 0) to fledging (day 14), Puerto Rico.

| Day of age | Description of chick |
|---|---|
| 0 | Down dense, long, and ivory colored on body, wings, legs, crop; sparse on head; none on belly. Skin maroon-gray; crop skin yellowish. Legs and feet gray-charcoal. Orbits and eyelids charcoal. Cere charcoal, becoming light horn. Culmen tip white, with a band of reddish gray, then section of light horn. Mandible with hook (lower tooth) on underside of tip. Cannot hold head up steadily. Rights itself with head and legs. Frequently "Peep's". |
| 1 | Skin of back lighter, more reddish than older chick. Holds head up more steadily. |
| 2 | Crop skin pinkish. Blood vessels still visible through belly skin. Strong grasping reflex. Skin of wings becoming blue in color. |
| 3 | Eyelids brownish-gray, with some blue. Eyes sometimes partly open; eyes dark gray-brown. White toenails. Legs and feet medium gray. Skin of ventral side brown to medium gray, with drab red on belly to yellow-brown around crop. Wing skin dark blue. Down cream colored, with very faint yellow or orange tint. Sheathed primaries erupting. Pants in heat. |
| 4 | Orbit dark charcoal. Eyelids dark gray. Eyes half open; charcoal brown, with gray-charcoal pupil. Sheathed secondaries emerging. |
| 5 | Primaries begin to erupt from sheaths. Sheathed body feathers emerge on upper breast. |
| 7 | Secondaries begin to erupt from sheath: brown with light rust tips. Sheathed retrices and head feathers emerge. Yellowish down still over most of dorsal surface of body. Legs and feet gray. Skin lighter gray-pink under wing and on belly. Culmen tip light gray, then a narrow dark brown band, a horn colored section, and a proximal portion of dark brown around cere. Gives weak "Squeak" or "Peep". Maintains perch grip and balances well. Flutters wings when looses balance. Raises wings above back and snaps them at human intruder when hand moves toward squab. |
| 8 | Yellowish down covers most of dorsal surface of body. Most body feather sheaths well emerged, but only few feathers have erupted from sheaths. Secondaries begin to erupt from sheath: brown with light rust tip. Skin dark gray; lighter gray-pink under wings and on belly. |
| 10 | Legs and feet light to medium gray with pinkish soles. Cere dark brownish-gray. Secondaries and primaries well out of sheaths. White bar on wings visible. Some of feathers on back and rump erupting from sheaths. Retrices breaking out of sheaths. Yellow curly down persists on crown. |
| 10-12 | Eggtooth lost. |
| 11 | Feathers erupting from sheaths in ventral tract of abdominal area. May fledge if frightened. |
| 12 | Back and rump feathers sleek. Rest of body well covered with erupted feathers, which appear neater than on day 10. Cinnamon-colored feathers of auricular and crown tracts and darker brown feathers of eyeline tract conspicuous. |
| 14 | Fledges with strong flight. |

vations. Chicks gave no calls when the adult was farther than 10 m from the nest, but 78.1% (n = 25) of the calls (n = 32 bouts) were given when the adult was 10 m or less from the nest and 21.9% (n = 7) were given by chicks when the adult was on the nest.

Chicks became increasingly active in nests as they matured. The frequency of position shifts and stretches per hour increased up to fledging: on day 7 chicks shifted an average of 0.3 times per hours and stretched 0.5 times per hour; day 10 — 0.6 shifts/hr and 0.5 stretches/hr; day 12 — 2.8 shifts/hr and 1.4 stretches/hr; day 14 — 10.5 shifts/hr and 13.4 stretches/hr. Chicks vigorously autopreened beginning about day 10; 10- to 12-day old chicks autopreened an average of 1.5 ± 0.3 times per hour (24.4 hr of observation, n = 41). Chicks autopreening activity was independent of adult presence; adults were off the nest during 51.2% (n = 21) of chick autopreening bouts.

Male adults were more active in nest sanitation than females during the nestling period. I saw males clean nests in 75.6% of my observations (n = 45; 50.5 hrs of observation). Zamore (1981) observed an adult Zenaida Dove removing droppings from its 3-day old chicks and depositing them 12 m from the nest. By day 10, chicks made an effort to drop their excreta over the nest edge, although most material was deposited on the nest rim. By the 12th day after hatching, most chicks were proficient at backing to the nest edge and unloading their excreta over the rim.

*Growth and development.* — I have summarized the development of Zenaida Dove chicks from day of hatching through day 14 (Table 11). Chicks (n = 14) weighed an average of 8.4 ± 0.3 g at hatching. They achieved a mean daily weight increase of 18.3% and attained a 14.2-fold increase in weight by fledging (Fig. 9). Weight increase peaked at day 14, then declined through the time of fledging. Chicks weighed approximately 120 g at fledging, or about 81% of adult weight. Culmen growth averaged 4.0% per day from days 0 to 14 and achieved the greatest growth rate from days 5 to 6 (13.2%; Fig. 9). Ulna growth averaged 9.8% daily and attained greatest relative growth from days 2 to 3 (20.4%; Fig. 9). Tarsometatarsus growth was also greatest

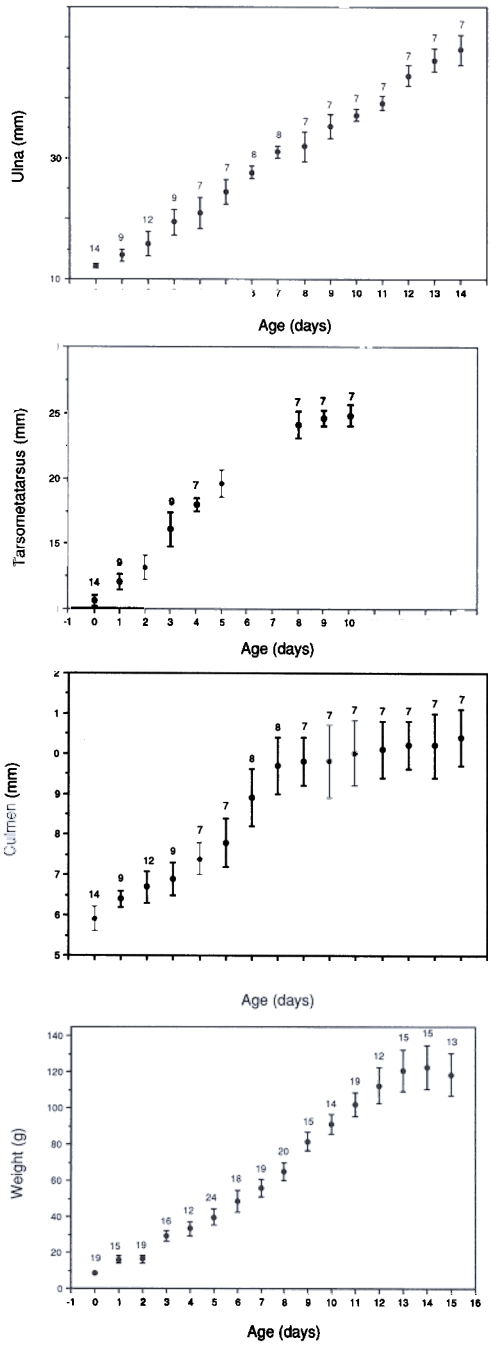


FIG. 9. Growth of Zenaida Dove chicks. Solid dots are means, vertical bars represent 1 standard deviation. Numbers above bars are sample sizes.

from days 2 to 3 (20.6%) and averaged 6.5% daily (Fig. 9). Ulna, culmen, and tarsometatarsus growth continued through the time of fledging.

*Productivity and nest success.* — Zenaida Doves lay two eggs as a rule, although I occasionally found clutches of one or, more rarely, three eggs (Table 12). Nellis *et al.* (1984) reported a mean clutch of 2.01 [± 0.01] (n = 405) for Zenaida Doves in the Virgin Islands; they found one nest with a 3-egg clutch (0.2%) and one with 4 eggs. Zamore (1981) found Zenaida Doves in Dominica normally produced two eggs ($\bar{x}$ = 1.97 ± 0.16, range = 1—2; n = 37). Maldonado Colon & Pérez-Rivera (1977) reported a substantially lower mean clutch size (1.25) for 68 nests studied in east-central Puerto Rico. Burger *et al.* (1989b) also reported smaller average clutch sizes for doves on islets off Culebra Island than those I observed there or on mainland Puerto Rico: 1.29 for Cayo Raton and 1.67 for Cayo del Agua.

The mean number of chicks hatched per nest that held eggs ranged from 0.3 to 1.6 among years for 3 major study areas (Table 12). Hatch-

TABLE 12. Zenaida Dove productivity and nest success at 4 study areas and clutch size on 2 islands, Puerto Rico, 1974—1983[a]

| Locale & year | No. nests | No. with eggs | Mean number ± SE per nest | | | No. nests successful[b] | % nests successful |
|---|---|---|---|---|---|---|---|
| | | | Eggs | Chicks Hatch | Chicks Fledge | | |
| Guánica | | | | | | | |
| 1974 | 7 | 4 | 2.00 ± 0.0 | 0.50 ± 0.50 | 0.50 ± 0.50 | 1 | 25.0 |
| 1975 | 12 | 5 | 2.00 ± 0.0 | 1.60 ± 0.40 | 1.40 ± 0.40 | 4 | 80.0 |
| Susua | | | | | | | |
| 1974 | 22 | 6 | 2.00 ± 0.0 | 1.17 ± 0.40 | 0.50 ± 0.22 | | 50.0 |
| 1975 | 11 | 7 | 2.00 ± 0.0 | 0.29 ± 0.23 | 0.29 ± 0.23 | | 14.3 |
| Southwestern Puerto Rico (Guánica and Susua) | | | | | | | |
| 1974 | 29 | 10 | 2.00 ± 0.0 | 0.90 ± 0.31 | 0.50 ± 0.22 | 4 | 40.0 |
| 1975 | 23 | 12 | 2.00 ± 0.0 | 0.83 ± 0.30 | 0.75 ± 0.29 | 5 | 41.7 |
| 1974-75 | 52 | 22 | 2.00 ± 0.0 | 0.86 ± 0.20 | 0.73 ± 0.19 | 9 | 40.9 |
| Cidra | | | | | | | |
| 1974 | 25 | 21 | 1.95 ± 0.05 | 1.52 ± 0.18 | 1.14 ± 0.20 | 14 | 66.7 |
| 1975 | 17 | 15 | 2.00 ± 0.0 | 1.40 ± 0.24 | 1.20 ± 0.26 | 9 | 60.0 |
| 1977 | 13 | 12 | 2.00 ± 0.0 | 1.42 ± 0.26 | 1.08 ± 0.29 | 7 | 58.3 |
| 1978 | 22 | 14 | 2.00 ± 0.0 | 1.43 ± 0.25 | 1.29 ± 0.27 | 9 | 64.3 |
| 1980 | 7 | 7 | 2.00 ± 0.0 | 1.43 ± 0.37 | 1.14 ± 0.40 | 4 | 57.1 |
| 1981 | 16 | 13 | 2.00 ± 0.0 | 1.54 ± 0.22 | 1.15 ± 0.27 | 8 | 61.5 |
| 1982 | 10 | 9 | 2.00 ± 0.0 | 1.56 ± 0.29 | 1.22 ± 0.32 | 6 | 66.7 |
| 1974-82 | 110 | 91 | 1.99 ± 0.01 | 1.47 ± 0.09 | 1.18 ± 0.10 | 57 | 62.6 |
| Roosevelt Roads | | | | | | | |
| 1974 | 69 | 43 | 2.00 ± 0.0 | 1.33 ± 0.13 | 0.86 ± 0.13 | 24 | 55.8 |
| 1975 | 67 | 42 | 1.93 ± 0.04 | 1.29 ± 0.14 | 0.79 ± 0.15 | 17 | 40.5 |
| 1976 | 17 | 13 | 2.00 ± 0.0 | 1.54 ± 0.21 | 1.38 ± 0.23 | 9 | 69.2 |
| 1977 | 54 | 44 | 2.00 ± 0.0 | 1.20 ± 0.13 | 0.86 ± 0.13 | 21 | 47.7 |
| 1978 | 29 | 22 | 1.95 ± 0.05 | 1.45 ± 0.19 | 1.00 ± 0.21 | 12 | 54.5 |
| 1979 | 53 | 41 | 2.00 ± 0.0 | 1.20 ± 0.15 | 0.98 ± 0.15 | 21 | 51.2 |
| 1980 | 61 | 49 | 2.00 ± 0.0 | 1.61 ± 0.11 | 1.16 ± 0.14 | 30 | 61.2 |
| 1981 | 43 | 36 | 2.00 ± 0.0 | 1.36 ± 0.16 | 0.94 ± 0.17 | 17 | 47.2 |
| 1982 | 12 | 10 | 2.00 ± 0.0 | 1.40 ± 0.31 | 1.00 ± 0.33 | 5 | 50.0 |
| 1983 | 28 | 23 | 2.00 ± 0.0 | 1.48 ± 0.18 | 1.00 ± 0.21 | 12 | 52.2 |
| 1974-83 | 433 | 323 | 1.99 ± 0.01 | 1.32 ± 0.05 | 0.93 ± 0.06 | 168 | 52.0 |
| Mona Island | | | | | | | |
| 1974-75 | 19 | 18 | 1.83 ± 0.09 | | | | |
| Culebra Island | | | | | | | |
| 1974-75 | 15 | 15 | 2.07 ± 0.07 | | | | |

[a] Only nests that were found during egg laying are considered. [b] Success determined for nests that held eggs.

ing success was greatest at Cidra and lowest in the southwestern study areas.

The mean number of chicks fledged per nest ranged from 0.3 to 1.4 for the 3 major study areas, with fledging success lowest in the southwestern area ($\bar{x}$ = 0.7 chicks fledged/nest), highest at Cidra (1.2/nest), and intermediate at Roosevelt Roads (0.9/nest; Table 12). Nest success followed a similar pattern among the study areas: southwestern Puerto Rico, 40.9% of nests with eggs were successful; Cidra, 62.6% successful; Roosevelt Roads Naval Station, 52.0% (Table 12). I had expected higher nest success and productivity in the southwestern study areas because fewer mammalian predators and Pearly-eyed Thrashers (*Margarops fuscatus*) occur in that part of the island. Overall, nest success in my study areas averaged 53.6%. This was considerably higher than the 26% observed by Nellis *et al.* (1984) for Zenaida Doves in the Virgin Islands, but not as high as the 79.4% successful nests (n = 68) studied by Maldonado Colon & Pérez-Rivera (1977) in Puerto Rico or 97.3% (n = 37) reported by Zamore (1981) in Dominica.

Of the sources that could be identified, Pearly-eyed Thrasher predation on eggs and chicks was the primary cause of nest failures in my study areas (Table 13). Roof rats were the second most important source of egg and chick loss. Zamore (1981) reported the Pearly-eyed Thrasher was the only Zenaida Dove predator observed in his study in Dominica. Dewey & Nellis (1980) reported that none of the Zenaida Dove nests they observed on rat-inhabited cays in the Virgin Islands were successful.

In all study areas, nestling Zenaida Doves incurred a low incidence (2.9%; n = 721) of warble fly (*Philornis [Neomusca] pici*) parasitism. Infested chicks normally survived (81%) warble fly infestations. Incidence of warble fly infestations of nestlings varied among the study areas. I observed no parasitized dove chicks on the offshore islands or in southwestern Puerto Rico (n = 174; some chicks included in these calculations were not included in calculations of productivity). Nestling doves at Cidra incurred the highest rate of parasitism (9.9%; n = 91). The Roosevelt Roads dove populations were parasitized at an intermediate rate (1.8%). Maldonado Colon & Pérez-Rivera (1977) reported that 3.7% of the Zenaida Dove chicks (n = 54) they examined in Puerto Rico were infested with warble fly larvae.

Zenaida Dove nests within the space defended (radius of 10 m) by nesting Gray Kingbirds (*Tyrannus dominicencis*) were more likely to fledge young than were dove pairs that nested distant from kingbird nests ($X^2$ = 5.82, d.f. = 1, n = 212; $P < 0.05$). Kingbirds aggressively defended their territories against intruders, including Pearly-eyed Thrashers, and nesting doves probably incidentally benefited from this as-

TABLE 13. Sources of egg and squab loss at 162 Zenaida Dove nests, Roosevelt Roads Naval Station, eastern Puerto Rico, 1974—1983.

| Nest contents | Number affected in nest | Number of losses (%) by source | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Rat | Pearly-eyed trasher | Weather | Nest falls | Nest mites | Warble flies | Unknown | Total |
| | | | | 0 | 0 | 0 | 0 | | |
| | | | | (0) | (0) | (0) | (0) | | |
| | 2 | | | 4 | 4 | 0 | 0 | | 86 |
| | | | | (5) | (5) | (0) | (0) | | |
| subtotal | | | | 4 | 4 | 0 | 0 | | 94 |
| | | | | (4) | (4) | (0) | (0) | | |
| | | | | 2 | 1 | 1 | 0 | | 14 |
| | | | | (14) | (7) | (7) | (0) | | |
| | | | | 1 | 1 | 0 | 1 | | 55 |
| | | | | (2) | (2) | (0) | (2) | | |
| | | | | 3 | 2 | 1 | 1 | | 69 |
| | | | | (4) | (3) | (1) | (1) | | |
| | | | | 7 | 6 | 1 | 1 | | 163 |
| | | | | (4) | (4) | (1) | (1) | | |

sociation. Blancher & Robertson (1982) have shown that aggressive Eastern Kingbirds (*T. tyrannus*) are effective in defending their nest sites against some predators. Although not statistically significant, White-crowned Pigeons had increased nest success at nests within active Gray Kingbird territories (Wiley & Wiley 1979). Burger *et al.* (1989b) found that Zenaida Doves nested closer to breeding terns than expected, which they suggested gave some antipredator advantage to the doves.

## MANAGEMENT RECOMMENDATIONS

Based on the data I collected from 1973 to 1983, I make the following recommendations for managing Zenaida Dove populations in Puerto Rico:

1. Breeding activities of dove populations should be monitored at about monthly intervals, in several study areas, representative of the different habitats preferred by the species in Puerto Rico.

2. Representative dove populations should be monitored for onset and termination of breeding activities, productivity, and nest success. Additional studies are needed to determine the importance and incidence of multiple nesting attempts per pair.

3. Hunting seasons should be set to exclude the period of greatest breeding activity. Based on early studies of Zenaida Dove populations in southwestern Puerto Rico, Danforth (1925) suggested the species should be protected at least from 15 February to 15 October to ensure adequate breeding for replacement. Based on data collected in my study, I suggest protection from March through June or July for east central and eastern Puerto Rico, but an additional closure from September through December for southwestern Puerto Rico.

4. Timing of hunting seasons should be set regionally to reflect dove population differences in breeding activities.

5. Hunting seasons should be adjusted each year based on breeding activities of doves that year.

6. Further climatic and Zenaida Dove breeding chronology data are needed to determine if rainfall patterns can be used to predict onset of dove nesting seasons. If a stronger relationship is determined, rainfall patterns may prove useful as an indicator on which to annually set initial hunting seasons, which can later be refined through monitoring dove populations.

Of course, management of the Zenaida Dove in Puerto Rico requires many other elements, especially the implementation of bag limits that reflect the harvest rates the population can absorb above the "natural" mortality rate. Productivity data are available from this and other studies (Maldonado Colon & Pérez-Rivera 1977, Nellis *et al.* 1984), but other data on population dynamics are lacking. These data are particularly difficult to gather using the traditional technique of banding because of several factors. Return rates from the Caribbean islands are poor relative to those in North America (Wiley, unpubl. data). Many bands are retained by individuals who hope to be rewarded someday by an United States government official or because they are not aware of the purpose of the banding program. Furthermore, Zenaida Doves undergo considerable inter-island movement, thereby complicating recovery in any banding scheme. Nevertheless, banding is probably the best method of determining certain population parameters of the Zenaida Dove. Any such program should be developed as a cooperative effort among Puerto Rico and the nearby countries (Dominican Republic, Virgin Islands) to improve data returns.

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