

## BREEDING AND FEEDING ECOLOGY OF THE GALÁPAGOS DOVE

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The Galápagos Dove (*Zenaida galapagoensis*) occurs on all of the major and several of the smaller Galápagos islands (Harris 1973, 1974). The species is better known taxonomically than ecologically (Goodwin 1977). Doves are larger on the two northernmost islands, Isla Wolf (Wenman) and I. Darwin (Culpepper), than on the others, and on this basis they are placed in two subspecies (Ridgway 1916, Swarth 1931).

Apart from repeated references to their tameness (Darwin 1845, Beebe 1924, Dampier 1927), little has been recorded of their habits. The most extensive observations were made by E. W. Gifford and other members of the California Academy of Sciences expedition to the islands in 1905-06. Gifford (1913) wrote, "Their chief food was seeds and occasionally pieces of green grass. Once some were seen eating cactus pulp from a fallen tree, and on another occasion several were seen feeding on the ocean-beach among the mangroves." With regard to breeding he wrote, "It appears that the breeding-season, taken as a whole throughout the archipelago, extends over seven months, from March to September inclusive" (Gifford 1913); Lévêque (1964) expanded this to 11 months, from January to November. The breeding season on any single island may be shorter, however, because several other species of birds were found breeding later on the northern islands of Wolf and Pinta (Abingdon) than on the others. On the other hand M. P. Harris (pers. comm.) has found active nests in most months of one year on I. Española. Gifford found several nests in rocky cavities or on the ground, containing one or two eggs, and he made some notes on adult behavior.

A visit to I. Genovesa (Tower) in 1978 gave us the opportunity to quantitatively study the feeding and breeding habits of this little-known species.

### METHODS

Our study area on Genovesa extended around Bahía Darwin, but most of our observations were made within 1 km of the centrally located landing beach. We stayed on I. Genovesa from 19 January to 2 May 1978,

except for 3-5 April when we visited I. Wolf. We also visited I. Daphne Major 23 November 1977 to 5 January 1978 and I. Pinta 6-17 January 1978, and returned to I. Genovesa 10-26 November 1978. Seventeen doves on I. Genovesa and six doves on I. Daphne were captured in mist-nets and color-banded.

On Genovesa, Daphne and Wolf, foraging was recorded with a stopwatch, used in the same manner as in a related study of finches (Abbott et al. 1977, Smith et al. 1978), except that on a few occasions on Genovesa our upper limit of 300s/bird/day was exceeded. We walked through a study area (Grant and Grant 1979) and attempted to encounter as many feeding doves as possible. All foraging activities were recorded. We divided the foraging results on Genovesa into 11 time periods. Based in part on our observations of banded birds, we estimated the minimum number of birds observed in each period to be 8, and the maximum to be about 20.

On Genovesa, nests were checked every other day. Visits to the nest by adults were registered during 1- or 2-h watches at a distance of 5 m from the nest, in the period 08:00-16:00. The first author made most of the feeding observations on Daphne and on Genovesa in November, and banded the birds; the second author made most of the feeding observations on Genovesa from January to May and performed the nest-watches. A rain gauge was installed at the top of the beach and checked daily.

### RESULTS

#### BREEDING

*Timing in relation to rainfall.* The wet season of the Galápagos starts in January or later in most years, rarely in December. I. Genovesa had received rain before our arrival on 19 January as indicated by the trees (*Bursera graveolens*) which were in leaf and flower, as were several shrubs. There was no sign of recent rain (standing water, damp soil, etc.). From later observations of rainfall, we judge this to indicate that rain fell no later than 14 January. The first rain must have fallen after 7 January; we learned this from guides of tourist boats who had visited the island in early January and found it dry and leafless. It seems likely that the first rain fell on 8-10 January, because Daphne Major received its first rainfall of the wet season on 8 January (P. T. Boag, pers. comm.), and Pinta received rain on 8 and 10 January, and no more until 15 January.

No breeding activity was observed until the first week of February (Fig. 1), when the first nests were started. The first egg was

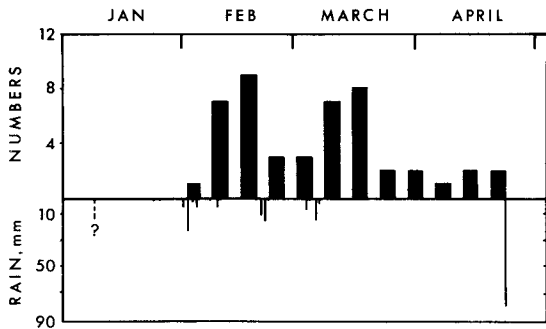


FIGURE 1. Phenology of egg-laying by Galápagos Doves in relation to rainfall. Numbers refer to nests in which clutches were started in a given week.

laid on about 6–8 February, the first hatching took place on 20 February and the first fledging occurred on 6 March. The interval of 28–32 days between first rain and first egg laid is similar to that for a similar species, the Gold-billed Ground-Dove (*Columbina cruziana*) on the mainland, where nests in pampa habitat are begun 21–35 days after the first rains (Marchant 1960).

**Duration.** Breeding continued uninterrupted from early February until early May, and showed no sign of ceasing at our time of departure. The heavy rainfall on 23 April probably helped to provide suitable conditions for breeding in May and June, and doves were breeding in the first two days of June (D. Schluter, pers. comm.). Four months is therefore a minimum estimate of the breeding season in 1978. Doves were not breeding in November 1978.

**Nest characteristics.** We found dove nests on the ground and in old Galápagos Mockingbird (*Nesomimus parvulus*) nests. One ground nest was exposed and the remainder were placed beneath plate-like pieces of lava. One nest in *Opuntia* cactus was entirely built by doves. Harris (1974) thought that the doves' habit of using old mockingbird nests was rare on Genovesa, but we found about as many dove nests in old mockingbirds nests (34) as on the ground (36), with an approximately equal effort spent searching the two habitats.

Nests in both habitats were approximately 15–20 cm long (i.e., maximum, external diameter) and the internal depth of the nests was 2–3 cm. The average height above ground of mockingbird nests used by doves, measured to the nearest 25 cm, was approximately 75 cm. We compared the sizes and heights of mockingbird nests used by doves with those empty and not used by doves, but could find no significant differences by *t* tests. We conclude that doves do not select

a particular type of mockingbird nest. All six pairs that were observed to breed twice nested in the same habitat during their two breeding attempts.

**Breeding success.** Seventy completed clutches were found. All but three comprised two eggs; there was one clutch of one egg and two of three eggs. The mean number of nestlings in 62 nests was  $1.5 \pm 0.1$ . Fifty-six nests were followed through from egg-laying to fledging or loss, and these were used for the calculations of breeding success given in Table 1.

Most losses occurred in the egg stage, most likely due to predation by mockingbirds. We observed mockingbirds apparently hunting in crevices in the lava where doves were nesting and once saw a mockingbird eat a dove egg and feed two juveniles with it (see also Harris 1968, Grant and Grant, in press). Other possible predators were gulls, Short-eared Owls (*Asio flammeus*) (on nestlings), and Yellow-crowned Night-Herons (*Nyctanassa violacea*). There are no snakes on Genovesa. Eggs disappeared from 16 of 56 nests (28.6%). In addition to these losses, 3 of 110 eggs (3%) were infertile or died early in development.

Below-ground nests would appear to be better protected against predators, particularly against owls, than above-ground nests. However, ground nests were preyed upon more (34.5%) than were old mockingbird nests (22.2%), although the mean number of fledglings per nest was the same in the two habitats ( $t_{54} = 1.56$ ,  $P > 0.1$ ; Table 1), and the proportions eaten did not differ significantly ( $\chi_1^2 = 1.03$ ,  $P > 0.1$ ).

Few adults were banded, and pairs changed nest locations between clutches. These factors made it hard for us to follow the fates of pairs. Nevertheless we can estimate the production of young per pair during our 14-week study from six identifiable pairs under continuous observation. The estimate is  $2.8 \pm 0.7$ . These all came from two clutches per pair. The bimodality in Figure 1 indicates a degree of synchrony in breeding. We saw nests being built at the time of our departure, which suggested that third clutches were imminent. It was confirmed by observations in early June of nestlings ready to fledge (D. Schluter, pers. comm.). Marchant (1960) gave no figures on seasonal production per pair for *Columbina cruziana*, but suggested that a pair may breed three times in quick succession and then rest for 2–3 months. Our data are consistent with the first part of this suggestion, but are insufficient to explore the second part.

TABLE 1. Breeding characteristics of Galápagos Doves in contrasting nest locations, and breeding success.

	Ground			Old mockingbird nests		
	Eggs	Nestlings	Fledglings	Eggs	Nestlings	Fledglings
Total	57	38	37	53	45	40
Clutches	29	29	29	27	27	27
$\bar{x}$	2.0	1.3	1.3	2.0	1.7	1.5
$S\bar{x}$	0.1	0.2	0.2	0.1	0.1	0.2
CV	16.52	71.52	73.83	17.22	46.14	60.13

Hatching and fledgling success

Eggs			Young		Total percent success
Laid	Hatched	% Hatched	Fledged	% Fledged	
(A)	(B)	(B/A × 100)	(C)	(C/B × 100)	(C/A × 100)
110	83	75.4	79	95.2	71.8

Marchant (1960) found one nest of *C. cruziana* with three eggs, but did not record its fate. Three-egg clutches have been recorded in studies of other species of doves (cited by Marchant 1960; also Goodwin 1977), although rarely. They may be produced by two females. We followed two clutches of three eggs. When one egg disappeared from one of them, that nest was abandoned. In the other nest all three eggs hatched and all three nestlings fledged. The young were fed, on separate occasions by one banded male and one or two unbanded females.

FEEDING

*Wet season.* Table 2 shows patterns of variation in foraging activity. For orientation, the first egg was laid just before period three, the first egg hatched in period four, and the first young fledged in period five. In the first three periods, doves fed mainly on caterpillars and on flowers of the cactus *Opuntia helleri*. For the next five periods, foraging was concentrated on the ground; the principal item was seeds of a bush, *Croton scouleri*, which were large enough for us to identify as the doves picked them up. In the last three periods, doves fed on a variety of small seeds and fruits from the plants themselves, all low herbs and shrubs, as well as from the ground and on other plant parts.

Foraging followed available resources. Although caterpillars were present in all periods they were never so abundant as in the first three periods. The same was true for *Opuntia* flowers. The doves preferred *Croton* seeds when they became available, even though caterpillars and *Opuntia* flowers were still present, although declining. *Croton* seeds are a rich source of energy (Downhower and Racine 1976). The diet

switched again in April (period 9), when seeds and fruits were maturing.

When feeding nestlings, adult doves, both males and females, gleaned most of their food from the ground. Nestlings were fed at about one-hour intervals (13 times in 14 hours of observation at six nests). Crop samples from nestlings of various ages, and observations through the crop wall of 45 others, revealed only croton seeds with or without the seed coat intact, in addition to parental "milk."

Two items in the diet deserve special mention. Foraging upon caterpillars from croton bushes required some perching skills which the birds barely possessed. Many caterpillars, perhaps as many as one in two, were dropped or dislodged and lost in the attempt to secure them. Yet the birds persisted and spent much time at this activity (Table 2), presumably because they were able to harvest enough of the abundant caterpillars to make it worthwhile. Their inefficiency probably was important in causing the change in diet when caterpillars became scarcer.

Foraging upon *Opuntia* flowers was not noted by previous ornithologists (Gifford 1913, Beebe 1924, Harris 1974). Stamens, and possibly nectar, were first removed from flowers; then the petals were eaten. Unlike the more agile finches, the doves were constrained by their body proportions to feed on flowers on the top and sides of *Opuntia* pads, those on the lower surfaces being out of reach. This unusual feeding habit is certainly not exhibited by all populations. We observed it on Wolf but not on Pinta or Daphne. P. T. Boag (pers. comm.) was on Daphne in 1976-78 in the seasons that we were on Genovesa, yet never saw the habit there.

TABLE 2. Foraging activity of Galápagos Doves (in seconds), 23 Jan.-1 May 1978.

Foraging category	Numbers of foraging observations during 11 time periods*											Total	Proportions
	1	2	3	4	5	6	7	8	9	10	11		
Ground	175	1,270	700	2,460	3,040	1,290	1,660	2,100	570	3,315	1,380	17,960	.626
Caterpillars on:													
<i>Croton scouleri</i>	90	1,935										2,025	.071
<i>Cordia lutea</i>	420	240	125									785	.027
<i>Cryptocarpus pyriformis</i>	30	415	1,900		600			300				3,245	.113
<i>Bursera graveolens</i>		30										30	.001
<i>Ipomoea habeliana</i>						75						75	.003
<i>Waltheria ovata</i>									40			40	.002
<i>Cacabus miersii</i>					65							65	.002
Seeds/fruits on:													
<i>Heliotropium angiospermum</i>						10					5	15	.001
<i>Chamaesyce recurva</i>								280		135	30	445	.015
<i>Portulaca howelli</i>								235		10	50	295	.010
<i>Waltheria ovata</i>								60		5		65	.002
<i>Sesuvium edmonstonei</i>										100	20	120	.004
<i>Ipomoea linearifolia</i>											10	10	<.001
<i>Eragrostis ciliaris</i>										45	195	240	.008
Other:													
<i>Opuntia helieri</i> flowers			480						5			1,155	.040
<i>Opuntia helleri</i> pulp	670		125						300	745	160	1,330	.046
<i>Bursera graveolens</i> arils								10		50		60	.002
<i>Cyperus anderssoni</i>										75		75	.003
<i>Cryptocarpus</i> leaves										95		95	.003
<i>Lantana peduncularis</i> petals										475		475	.017
<i>Sida salvifolia</i> buds											30	30	.001
Termites											15	15	.001

\* Observation periods are 1, 23 Jan.-1 Feb.; 2, 2-10 Feb.; 3, 11-19 Feb.; 4, 20-26 Feb.; 5, 1-8 March; 6, 9-15 March; 7, 21-26 March; 8, 27 March-1 April; 9, 7-14 April; 10, 17-24 April; 11, 25 April-1 May.

TABLE 3. The number of seeds in the gizzards of five Galápagos Doves found dead on I. Daphne Major in December 1977.

Seed species	Specimen					$\bar{x}$
	1	2	3	4	5	
<i>Ipomoea linearifolia</i>	3	1	6	12		4.4
<i>Merremia aegyptica</i>	1		13	4		3.6
<i>Tribulus cistoides</i> *				1		0.2
<i>Opuntia echios</i>	27	30	23	12	20	22.4
<i>Chamaesyce</i> spp.			4	1	2	1.4
<i>Heliotropium angiospermum</i>		19	9		1	5.8
<i>Amaranthus sclerantoides</i>		18	6		2	5.2

\* Whole fruit.

*Dry season.* The predominant foraging activity of doves on Genovesa in November 1978 was picking up seeds from the ground (92% of 5,300 s of foraging observations). The remaining activities were feeding on *Opuntia* flowers (7%) and *Opuntia* pulp (1%). The food items picked up from the ground were not identified.

On Daphne a total of 2,130 seconds of foraging activity was recorded in December 1977. All foraging was on the ground: 85% was in the open and 15% was beneath bushes of *O. echios*. Doves were observed pecking on the surface or digging in the soil for seeds of *Merremia aegyptica*, *Ipomoea linearifolia* and *O. echios*, as well as for some small unidentified seeds. The three species mentioned all have hard seeds; finches ignored the first two, and the smaller finches had difficulty in cracking the third. Doves swallowed whole all three types. It is therefore surprising that they exercised some choice. We recorded the acceptance of 4 seeds of *Merremia aegyptica* and the rejection of 15 others after mandibulation, by four dove individuals. Possibly the doves assess the strength of seeds and swallow only the weakest. Despite a low overall density of seeds at this time (unpubl. data), many *Merremia* seeds were ignored. One dove, observed at a distance of less than 3 m, walked past 10 *Merremia* seeds and picked up another 6, accepting 2, rejecting 4.

Digging with the beak can be important. We estimated that one individual removed its own volume of soil beneath an *Opuntia* bush in 300 s of observation. It was still digging 700 s later.

Gizzard contents (Table 3) confirm that doves fed largely on the three species of hard seeds. The remaining seeds, except for those of *Tribulus cistoides*, were all small and soft and could not be identified when birds picked them up from the ground and swallowed them. The only large seeds not

exploited commonly were those of *T. cistoides*; its fruits have stiff spines which protect it more from birds that swallow, such as doves, than from those that crack the fruits before swallowing the seeds, such as finches.

The number of seeds in the five gizzards can be compared with what was available on the ground as determined by random sampling of 50 one-m<sup>2</sup> plots (Abbott et al. 1977, P. R. Grant and B. R. Grant unpubl. data). We calculate the similarity of diet and seed availability to be 0.480 using Whittaker's index (Whittaker 1960). However, the discrepancies between individual seed species available and consumed are more instructive. *Opuntia echios* is represented in the gizzards more frequently ( $P = 0.521$ ) than in the environment ( $P = 0.170$ ), whereas *Tribulus cistoides* is represented less frequently in the gizzards ( $P = 0.005$ ) than in the environment ( $P = 0.311$ ). If the figures for seed availability in December are similar to availability just before the doves died, and their last meals were representative of usual meals, these results show a strong preference for *Opuntia* seeds and a strong avoidance of *Tribulus* fruits.

Gifford (1913) recorded doves eating cactus pulp. Presumably they did this as much for the water as for nutrition. We observed this habit repeatedly on Daphne in the present study, but not during our systematic study of foraging there. Tj. de Vries (pers. comm.) has seen it on Santa Fe and Española. We saw it on Genovesa in November 1973 (unpubl.) and in the wet season and dry season in 1978. Presumably doves gain moisture as well as nutrition from the pulp. In addition, they may feed on the dipteran larvae and pupae that are found in the pulp of both pads and trunks of the cactus.

## DISCUSSION

The breeding characteristics of the Galápagos Dove on Genovesa are strikingly sim-

ilar to those of the Gold-billed Ground-Dove recorded by Marchant (1958, 1959, 1960) in a region of the Ecuadorian mainland climatically similar to the Galápagos (Svenson 1946). These characteristics include a delayed breeding response of three to five weeks after initial rainfall; clutch sizes; nesting habits, including the use of old mockingbird nests; incubation periods; and overall breeding success. The chief differences between the species are a longer nestling period but a shorter interval between broods in the Galápagos Dove than in the ground-dove. The nestling period is 13–17 days in the island species but only 11 days in the mainland dove. The interval between fledging from brood  $i$  and egg-laying in clutch  $i + 1$  is usually 11–15 days in the mainland dove, but was only 6–10 days in the Galápagos Dove. Mainland doves also may be subject to more predation at the nest, particularly at the nestling stage of the breeding cycle, owing to a greater diversity and possible greater abundance of predators on the mainland than on the islands.

Doves start breeding later in the year than do mockingbirds and finches. Lack (1950:272) felt that the “later nesting season of the dove suggests dependence upon a food source which becomes common as a result of the rains, but rather late, as seeds or fruits might do.” Our results confirmed this idea and allowed us to be more specific. The hatching of dove eggs first occurred after the peak of caterpillar abundance and well before the maturation of seeds on a large variety of plants. It coincided with the ripening of croton fruits. *Croton* seeds are “shot” from the plant with an audible crack when the ripe fruits dry in the sun and split open. We recorded the “shooting season” as starting on 20 February, the same day the first egg hatched. From this time onward for more than a month, doves concentrated their feeding activity on the ground. They fed mainly on *Croton* seeds, and fed these seeds to their nestlings. In contrast, the first fledging did not coincide with the appearance of a novel food in the environment, nor with a noticeable increase in the abundance of any food type. On the Ecuadorian mainland, where the breeding of the Gold-billed Ground-Dove is likewise delayed, a related plant, *Croton rivinaefolius* occurs (Marchant 1960). Food for nestlings is an ultimate factor. The doves might respond to many possible proximate factors, including the flowering of *Croton*. However, other controlling influences must exist on islands

such as Santa Fe and Española where introduced goats have decimated these shrubs.

The diet of doves during the dry season appears to be at least as generalized as that in the wet season. Even in the dry season, however, when food is scarce, some degree of seed selectivity is exercised.

The most surprising feeding activity we observed was the eating of pollen and petals from *Opuntia* flowers in late dry season and early wet season. We saw this habit on Genovesa and Wolf but not on Daphne. One factor contributing to the difference may be the rigidity of spines on mature *Opuntia* pads. Spines on the cactus (*O. helleri*) on Genovesa and Wolf are soft and flexible, whereas those on *O. echios* on Daphne and other southern islands are stiff. Stiff spines may prevent doves from perching on the pads to reach the flowers. Dawson (1966), following Stewart (1911), interpreted the difference in spines as being related to differences in grazing pressures from tortoises (and presumably land iguanas). The southern islands, with *O. echios*, generally have numbers of these herbivores, whereas the northern islands, with *O. helleri*, do not.

Our observations on dove feeding suggest an additional, complementary, hypothesis to explain the difference in the spines. We suggest that non-rigid spines have been selected in northern cacti because the relatively unprotected flowers are more frequently visited and pollinated by birds, including doves. One necessary condition is that doves do not damage the stigmas when they feed on the rest of the flower. Another, sufficient, condition is that the usual pollinator of flowers in populations of *O. echios* (Rick 1966), a bee (*Xylocopa darwini*), is absent from the northern islands. Both of these conditions are met. Thus, although the Galápagos Dove has not differentiated to any marked degree in the archipelago, it may have influenced the differentiation of *Opuntia* cacti.

#### SUMMARY

We studied the feeding and breeding of Galápagos Doves on I. Genovesa (Tower) from January to May, 1978, and their feeding in the non-breeding season on I. Pinta, I. Wolf and I. Daphne. The first rain fell in early January but doves did not start breeding until early February. They laid two-egg clutches most frequently, fledged  $1.4 \pm 0.1$  young/nest and produced a maximum of three broods in four months. First hatching of eggs coincided with the onset of seed-

shedding in *Croton scouleri*. Nestlings were fed on *Croton* seeds. A functional relationship between the timing of *Croton* and dove reproduction is suggested. Breeding characteristics were generally similar to those of *Columbina cruziana*, a species of dove on the Ecuadorian mainland, although the nestling period was longer and the interval between broods was shorter in Galápagos Doves. Three young were successfully raised from three eggs in one nest. A feeding difference between island populations is documented and linked to the evolution of *Opuntia* cactus.

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