

# BREEDING AND FEEDING OF GALÁPAGOS MOCKINGBIRDS, *NESOMIMUS PARVULUS*

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**ABSTRACT.**—Galápagos Mockingbirds (*Nesomimus parvulus*) were studied on Isla Genovesa, January to May and November 1978. They started egg-laying 1 week after the first rainfall of the wet season and produced an average of  $3.2 \pm 0.5$  fledglings per pair from two broods. Breeding characteristics were similar to those of the related *Mimus longicaudatus* on the mainland, although breeding success was slightly higher and the nestling period distinctly longer. Adult foraging and nestling diets were varied; most food items were arthropods taken from the ground. Nestlings were fed by parents and one or two helpers at seven nests. In two instances young of the first brood helped their parents in the feeding of the second brood. Cooperative behavior within families probably facilitates the formation of territorial groups, composed of one or more families, outside the breeding season. *Received 22 January 1979, accepted 21 May 1979.*

GALÁPAGOS Mockingbirds clearly are related to *Mimus longicaudatus* of the South American mainland, yet are sufficiently distinct to be placed in a separate genus, *Nesomimus* (Swarth 1931, but see Abbott and Abbott 1978). Four allopatric species are recognized currently (Harris 1974). The most widespread species, *N. parvulus*, is represented by seven subspecies (Swarth 1931). Breeding and feeding characteristics of Galápagos Mockingbirds are known in a general way from observations by Gifford (1913), Beebe (1924), Venables (1940), and others. Recent interest has centered on their egg-eating habit, which may vary from island to island (Hatch 1965, Harris 1968, Bowman and Carter 1971), and their habit of banding together in groups of up to 40 individuals outside the breeding season and collectively defending a territory (Hatch 1966).

None of the studies to date has quantified the breeding characteristics of Galápagos Mockingbirds throughout a breeding season as Marchant (1958, 1959, 1960) has done for the related species in a climatically similar region of mainland Ecuador. Here we present the results of such a study on Isla Genovesa (Tower), and compare them with Marchant's results where possible. The information is useful for two reasons: to explore the possibility of evolutionary change in breeding habits on the islands, and to give perspective to the habit of holding collective territories outside the breeding season. With regard to the last point, Hatch (1966) wrote, "It is difficult to evaluate the ecological significance of the collective territories without a series of observations of marked birds extending through the breeding season." Elsewhere other species of collectively territorial birds have been studied in detail (e.g. Brown 1974, Woolfenden 1976, Emlen 1978), but for Galápagos Mockingbirds only an unpublished study on Española in 1974 by Sarah Groves (pers. comm.) exists, and this study was not continued into the nonbreeding season to follow the fates and behavior of individually marked birds.

## METHODS

We stayed on I. Genovesa continuously from 19 January to 2 May 1978, except for 3–5 April when we visited I. Wolf. We also visited I. Pinta 6–17 January and returned to I. Genovesa 10–26 November. 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. In connection with a study of finches, we captured

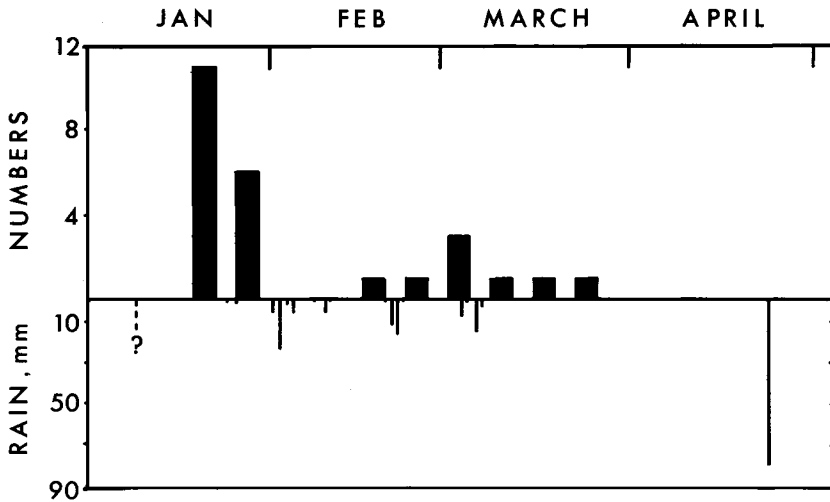


Fig. 1. Phenology of egg laying by *Nesomimus parvulus* in relation to rainfall. Numbers of completed clutches are grouped in weekly intervals.

mockingbirds in mist nets on all three islands, weighed them to the nearest gram, took measurements of wing, leg, and beak, placed one or two colored bands on their legs (except on Wolf) for later recognition, and released them.

On Genovesa nests were checked every other day. A sample of nestlings was weighed and measured at each check. Nestlings were banded on about day 9–10 after hatching, at which time they were approximately 70% of adult weight, i.e. 40–45 g. On Genovesa and Wolf, foraging was recorded with a stopwatch in the same manner as that used in the study of finches (Abbott et al. 1977). An upper limit of  $300 \text{ s} \cdot \text{bird}^{-1} \cdot \text{day}^{-1}$  was set to avoid conspicuous individuals dominating our records. Visits to the nest by adults, and the food they brought for nestlings, were registered during 1-h or 2-h watches at a distance of 3–5 m from the nest in the periods 0800–1000 and 1400–1600. P. R. Grant measured and banded birds and made the feeding observations in November; N. Grant made all remaining feeding observations and performed the nest watches. A rain guage installed at the top of the beach on 19 January was checked daily.

## RESULTS

### BREEDING

*Timing in relation to rainfall.*—The first rain of the wet season on Genovesa fell on about 8–10 January (P. R. Grant and K. T. Grant, MS). By 19 January leaves were fully developed on most individuals of the principal tree species, *Bursera graveolens* and *Croton scouleri*. By calculating backward from hatching dates and known incubation period (see below), we estimate that the first mockingbird egg was laid on about 17 January, i.e. about 1 week after the first rainfall. The first hatching occurred on 1 February and the first fledging on 17 February (Fig. 1).

This phenology differs from that of *Mimus longicaudatus* on the mainland. Marchant (1959) found some nests with eggs in December and January, before the first rainfall at the end of January.

*Duration.*—Nesting continued until 9 April, the date of the last observed fledging. Two peaks in nesting activity, corresponding to two clutches, were evident (Fig. 1). A large amount of rain fell on 23 April (Fig. 1), which was followed immediately by nest-building activity by at least five pairs, but no eggs were laid before our

departure on 2 May, nor were occupied nests found from 31 May to 2 June (D. Schluter pers. comm.). One banded immature bird, 85 days old (from hatching), was seen alone rotating in the cup and adding twigs to a nest in its parents' territory on 2 May.

The incubation period was 12–13 days, as in *M. longicaudatus* (Table 1). The nestling period was distinctly longer than the period recorded for the mainland species; the modal value for *N. parvulus* was equal to the maximum value for *M. longicaudatus*. The shorter nestling period on the mainland was apparently not induced by more frequent visits by the observer, as Marchant (1958) visited nests every other day, or occasionally at longer intervals, while we also visited nests every other day.

The mean interval ( $\pm$  one standard error) between fledging of brood 1 and the first egg laid of clutch 2 was  $11.8 \pm 7.6$  days ( $n = 5$  pairs). There are no comparable mainland data. New nests were used for the second clutch, as usually happens with *M. longicaudatus*.

*Nesting and breeding success.*—Of 24 nests followed to completion, 7 (29%) suffered predation, none was deserted, and the remaining 17 were at least partially successful (Table 1). At some nests eggs were lost one or two at a time, while at others they all apparently disappeared together. Other mockingbirds may cause some of the egg disappearances, as they are known to feed on the eggs of seabirds and doves (Harris 1968) and are suspected of feeding on finch eggs (Harris 1974, P. R. Grant and B. R. Grant, MS). In one instance a parent was known to have been killed on the nest, for several feathers were left there. The eggs had disappeared when this was discovered. A Short-eared Owl (*Asio flammeus*) probably was responsible. Yellow-crowned Night Herons (*Nyctanassa violacea*) also may be nest predators, as on two occasions we observed mockingbird parents attack these birds close to the nest and follow them, chattering, until they were out of sight from the nest.

Although the loss of clutches is substantial, it is less than that recorded for *M. longicaudatus* (Table 1). The difference between the species is significant ( $\chi_1^2 = 6.77$ ,  $P < 0.01$ ) and is perhaps attributable to the presence on the mainland of egg-eating snakes and mammals, as well as the brood parasite *Molothrus bonariensis* (Marchant 1960), and their absence on Genovesa.

The two species produce clutches of similar size (Table 1). Five-egg clutches were not observed in our study, but one has been recorded on S. Cristóbal (Gifford 1913), so they may be produced rarely on Genovesa. The number of clutches produced in one season is probably the same in the two species. Two were produced in our study, and Marchant (1960) reported that second and third broods are "attempted" by *M. longicaudatus* in a good year.

The data in Table 2 indicate small differences in breeding success. *Nesomimus parvulus* has apparently lower success in the egg stage as a result of a higher frequency of hatching failure, though the frequency is not as high as Beebe's (1924) estimate of ~25% (sample size not given). On the other hand, *N. parvulus* has a higher success in the nestling stage. Marchant (1960) found annual variation in the breeding success of *M. longicaudatus* to range from 33 to 61%. As these figures lie to either side of our figure for *N. parvulus*, it appears that breeding success is approximately the same in the two species.

The total seasonal production (up to May) of 10 pairs observed continuously was  $3.2 \pm 0.5$  (SE) fledglings per pair. No figures exist from the mainland with which

TABLE 1. Breeding characteristics of *Nesomimus parvulus* on I. Genovesa and *Mimus longicaudatus* on the mainland of Ecuador.

	Clutch size				
	2	3	4	5	$\bar{x}$
<i>M. longicaudatus</i>	8	48	74	36	3.9
<i>N. parvulus</i>	0	3	18	0	3.9

	Duration	
	Incubation period <sup>a</sup>	Nestling period <sup>b</sup>
<i>M. longicaudatus</i>	12–13 days	12–15 days
<i>N. parvulus</i>	12–13 (12) days	11–17 (15) days

	Nesting success		
	Number of nests	% deserted <sup>c</sup>	% success
<i>M. longicaudatus</i>	184	7	51
<i>N. parvulus</i>	24	0	71

<sup>a</sup> Defined as the interval between the last egg laid and the last egg hatched (Marchant 1960). The modal value for I. Genovesa is given in parentheses.

<sup>b</sup> Defined as the interval between the last hatching and the last fledging (Marchant 1960). It is variable on I. Genovesa, because fledging from each nest occurs over a period of 1–5 days. The modal value is given in parentheses.

<sup>c</sup> Other failures are caused by predation, nest destruction, and starvation of young.

to compare ours. But because breeding success is comparable, and because *M. longicaudatus* lays two (sometimes three) clutches, as *N. parvulus* does, seasonal production perhaps is similar.

Second clutches were slightly less successful than first clutches. Seven out of 10 pairs were known to nest twice and were studied in both breeding attempts. They produced  $1.7 \pm 0.5$  fledglings on average from the first clutch and  $1.4 \pm 0.6$  from the second. Altogether, first-brood nests (February) produced  $2.4 \pm 0.3$  fledglings per nest ( $n = 15$ ), and second-brood nests (March–April) produced  $1.3 \pm 0.5$  per nest. The difference, although sizeable, can be attributed to chance ( $t_{23} = 1.87$ ,  $0.05 < P < 0.1$ ).

## FEEDING

*Adults.*—Table 3 shows how foraging activity changed throughout the wet season, January–April. In most periods the predominant feeding activity was picking up arthropods from the ground, as it was on Pinta and Wolf during our visits to those islands. Flowers were present on *Opuntia helleri* cactus and were exploited throughout the study. Other resource use was more or less restricted to certain periods. Thus, caterpillar-feeding was most frequent in the first four periods, when caterpillars were most abundant. In early March, when caterpillar numbers declined and fruits first appeared, foraging activity shifted to fruits. The response to a new food type in the environment was quick. We observed the first eating of *Lantana* fruits 6 days after we recorded the first ripe fruits, and the first eating of *Bursera* berries (arils) was noticed the day after the first exposed ripe aril was recorded.

Mockingbirds eat dove eggs (Table 3), and they also may eat finch eggs and nestlings, although we have no direct evidence of this. Outside the foraging study time, we observed two attacks through the roof of *Geospiza difficilis* nests and one similar attack on a *Certhidea olivacea* nest. One *difficilis* nest had eggs; the other

TABLE 2. Breeding success of *Nesomimus parvulus* on I. Genovesa and *Mimus longicaudatus* on the mainland of Ecuador.

	Eggs				Young			
	Number		% success from eggs laid		% success from eggs hatched		Breeding total	
	Laid	Hatched	Total (losses excluded) included	Total (losses included) % infertile <sup>a</sup>	Total (losses excluded) included	Total (losses included)	% success <sup>c</sup>	
<i>M. longicaudatus</i>	477	341	93	71	4	86	86	47
Including all known losses <sup>b</sup>	562							41
<i>N. parvulus</i>	81	64	97	79	10	79	70	56
$\bar{x}$ /nest	3.9	2.7						
SE	0.1	0.3						

<sup>a</sup> Includes early death of embryos.  
<sup>b</sup> Includes data from nests where losses were known to occur but the stage at which they occurred was not known. The time of losses was known for all *N. parvulus* nests.  
<sup>c</sup> Numbers fledged as a percentage of eggs laid; first and second clutches are combined.

TABLE 3. Foraging activity of *Nesomimus parvulus* in seconds, 2 February–1 May 1978.

	Observation periods <sup>a</sup>										Totals ( $\Sigma = 9,470$ )	Proportions
	1	2	3	4	5	6	7	8	9	10		
Ground	675	665	510	480	540	345	20	20	25	630	3,910	0.413
Caterpillars on:												
<i>Croton scouleri</i>	430		25		20						475	0.050
<i>Cordia lutea</i>	380	60	315	300							755	0.080
<i>Cryptocarpus pyriformis</i>		485			15		300				1,100	0.116
<i>Bursera graveolens</i>	110	50			25						185	0.019
<i>Ipomoea tabelleana</i>				35	25						60	0.006
<i>Waltheria ovata</i>	25										25	0.003
Flycatching		5	10	90							105	0.011
Opuntia pad and stems				145	60				75		280	0.030
Opuntia flowers		10		75	85		65		50		285	0.030
Bursera berries						15	55	15	30		115	0.012
Lantana fruits					70	420	60				550	0.058
Cordia fruits							60				60	0.006
Probing into dead branches				65					85		150	0.016
Crabs								215			215	0.023
Dove eggs					300						300	0.032

<sup>a</sup> Observation periods are: 1 = 2–10 February; 2 = 11–19 February; 3 = 20–26 February; 4 = 1–8 March; 5 = 9–15 March; 6 = 21–26 March; 7 = 27 March–1 April; 8 = 7–14 April; 9 = 17–24 April; 10 = 25 April–1 May. All birds were adults, minimum number observed in a sampling period was 5.

TABLE 4. Food items brought to six nests in 2-h nest watches. Frequency refers to the proportion of nest watches in which the item was brought to the nest, where  $n = 19$  watches at first-brood nests and  $n = 22$  for second-brood nests.  $\bar{x}$  = mean and SE = standard error. Values of  $t$  have been calculated for differences between first- and second-brood means; the data were first transformed to  $\log_{10}(x + 2)$  to correct for skewness produced by large numbers of zeros. Significantly larger means are shown in bold-face.

Food type	First brood			Second brood			$t$	$P$
	Fre- quen- cy	$\bar{x}$	SE	Fre- quen- cy	$\bar{x}$	SE		
Spider	0.89	3.7	0.7	0.91	3.1	0.5	0.51	>0.1
Harvestman	0	0	—	0.09	~0.1	—	—	—
Ant lion	0.32	<b>0.6</b>	0.2	0	0	—	2.91	<0.01
Dragonfly	0	0	—	0.09	~0.1	—	—	—
Cricket	0.53	0.7	0.3	1.00	<b>8.2</b>	1.2	8.98	<0.001
Grasshopper	0.05	<0.1	—	0.50	<b>1.0</b>	0.3	3.49	<0.005
Beetle	0.53	1.6	0.5	0.77	2.1	0.4	1.18	>0.1
Moth	0.37	~0.5	—	0.23	~0.3	—	—	—
Lepidopterous larva (except <i>Sphingidae</i> )	0.89	5.1	0.9	0.73	3.0	0.6	1.61	>0.1
<i>Sphingidae</i> larva	0.53	<b>1.2</b>	0.3	0.23	0.4	0.2	2.08	<0.05
Other larva	1.00	<b>10.9</b>	1.0	0.59	0.7	0.2	7.10	<0.001
Pupa	0.68	<b>1.6</b>	0.4	0.27	0.4	0.2	2.93	<0.01
Isopod	0	<0.1	—	0.64	<b>2.1</b>	0.5	4.69	<0.001
Centipede	0	0	—	0.05	<0.1	—	—	—
Beetle larva	0.47	<b>1.4</b>	0.6	0.14	~0.1	—	2.80	<0.01
Aril of <i>Bursera graveolens</i>	0	0	—	0.59	<b>3.8</b>	1.2	3.81	<0.001
Fruit of <i>Croton scouleri</i>	0.11	~0.1	—	0	0	—	—	—
Fruit of <i>Lantana peduncularis</i>	0	0	—	0.09	~0.1	—	—	—
Eggshell	0	0	—	0.27	~0.3	—	—	—

two nests had young. In none of the attacks did we observe predation, but one nestling each from a *Geospiza* nest and the *Certhidea* nest fell to the ground.

In the dry season (November) mockingbirds were observed foraging for a total of 5,500 s. Of this time, 93% was spent on the ground foraging for arthropods, while the remainder was spent feeding on the soft tissue surrounding seeds extracted from fruits of *Opuntia helleri* but not on the seeds themselves.

*Nestlings.*—Our knowledge of nestling diets comes entirely from food items, which usually can be seen in the adults' beaks, delivered to the nestlings. More than 95% of the food items brought to nestlings during our nest watches could be identified, and these are listed in Table 4. Our identification was aided by the fact that they were brought singly in all but a few instances (>95%). Most items were arthropods. Our observations revealed a large taxonomic diversity of prey items; probably most are taken from the ground (Table 3).

Diets of first- and second-brood nestlings differed in ways expected from an observed but unmeasured change in prey abundance. For example, Orthoptera became abundant in March and were brought to the nest frequently at this time but rarely to first broods; the subsequent decline of Orthoptera and nonreplacement by other arthropods may have contributed to the early cessation of breeding of mockingbirds as compared with doves and finches. Caterpillar numbers declined after the fledging of first broods, and this too is reflected in a diminished supply to nestlings, although not to a statistically significant extent.

Differences also exist in nestling diets between second-brood families. We compared food items brought to two second-brood nests. Crickets and *Bursera* arils were each brought to one of the nests more frequently than to the other (in each case  $t_{16} = 3.46$ ,  $P < 0.005$ , where the combined number of 2-h watches is 18). Such

differences in prey composition are apparent from comparisons of proportions of the four common prey items (crickets, *Bursera arils*, caterpillars, and spiders) brought to the two nests in these 18 nest watches ( $\chi_3^2 = 45.56$ ,  $P < 0.001$ ). These quantitative data confirm earlier reports of varied diets and generalized feeding, including the eating of dove eggs (Harris 1968). The analysis of nestling diets shows both temporal and spatial components to the diversity of diets.

*Visits to the nest.*—We found no difference in the number of visits per h in morning and afternoon of the same day ( $t_{16} = 0.73$ ,  $P > 0.1$ ) and therefore combined the data for mornings and afternoons. There were no differences either between the number of visits at first- and second-brood nests ( $t_{39} = 1.37$ ,  $P > 0.1$ ), or between the two nests in our sample that contained first and second broods of the same parents ( $t_{17} = 1.55$ ,  $P > 0.1$ ). This lack of variation within the species contrasts with that between species. The average number of visits per h in 41 watches at mockingbird nests was  $15.6 \pm 1.0$  (SE). We can compare this figure with our data on finches. The mean number of visits during 8 watches at 2 *G. magnirostris* nests was  $3.5 \pm 0.3$ , and the average number of visits during 12 watches at 2 *G. difficilis* nests was  $4.1 \pm 0.4$ . The difference between the *Geospiza* species is not significant ( $t_{18} = 1.13$ ,  $P > 0.1$ ), but the difference between these two combined and mockingbirds is highly significant ( $t_{55} = 9.73$ ,  $P < 0.001$ ). Thus, a mockingbird appears at a nest on average once every 4 min, usually with a single food item, while the finches appear at their nests once every 15–20 min, usually with several food items (P. R. Grant and B. R. Grant, MS; see also Downhower 1978 for comparable finch data on I. Española).

Nestling ages of mockingbirds and finches at these nests ranged evenly from 3 to 13 days. We found no significant relationship between the number of visits and nestling age at four mockingbird nests (data combined,  $r = 0.241$ ,  $df = 25$ ,  $P > 0.1$ ). The data, however, were heterogeneous. At 1 nest a strong positive correlation occurred ( $r = 0.873$ ,  $df = 7$ ,  $P < 0.005$ ); at 2 of the 3 others the correlation coefficient was negative but not significant ( $P > 0.1$ ). Some tendency may exist, therefore, for the nest visit rate to increase with nestling age, but the absence of significant positive correlations at three of four nests carries the interesting implication that parents meet the assumed daily increasing energy needs of their nestlings by bringing larger food items per visit rather than by bringing food more often.

*Visitors to the nest.*—More than two birds were known to feed young at seven of 29 nests (~25%). Because we visited some nests only briefly, the real percentage may have been larger. At 6 of the nests 3 birds visited, and at 1 nest 4 visited. All of these birds were observed to feed the young, and we therefore refer to the additional birds as helpers. At five nests, both of the parents and the helpers were banded. At the other two nests, the presence of (unbanded) helpers was established by keeping all three birds at each nest in sight simultaneously. Some details of the visitors and visits are given in Table 5.

Two of the helpers were siblings of the first brood associating with their parents at the second brood, demonstrating a close genetic relatedness between helper and helped in at least these instances. The other two banded helpers were in adult plumage, and their genetic affinities with other members of the population are unknown. Probably both were males, as their wing lengths were 119 and 120 mm respectively, which fall within the range of 5 known males (115–121 mm) and above the range of 5 known females (108–111 mm). One adult-plumaged helper assisted a banded pair in raising two broods. Another helped one pair with its first brood,



TABLE 5. Characteristics of visits and visitors to nests. Nests 1 and 28 belonged to the same pair. Helpers are identified by their leg bands; in all cases here they were placed on the left leg.

Nest number	Brood	Number of watches	Number of hours	Helpers	Number of visits				$\bar{x}$ visits per h	Number of nestlings fledged
					Adult	Juvenile	Total	Parents		
							♂	♀		
1	First	9	16	—	—	—	103	183	17.9	2
13	First	5	10	L-Orange	0	12	54	115	18.1	3
2	Second	8	15	L-Blue/Orange	20	20	124	187	20.9	3
28	Second	10	19	L-Orange, L-Yellow/Green	4	60	59	106	11.8	2

then a different pair with its second brood. The two helpers at one nest never appeared at that nest in the same period of observation. Males or helpers fed either the nestlings or the female parent at the nest. The female then either fed the nestlings or, rarely, herself. At second-brood nests siblings always fed the nestlings directly.

Table 5 shows that feeding visits of helpers were as numerous as or fewer than the number of visits of the adult male, while female parents consistently visited more frequently. Helpers did not increase the frequency of total visits to the nest uniformly. We tested for a difference in fledging success between broods with and without helpers. Although no significant differences occurred for first broods, for second broods, or for the two combined (Fisher's Exact Test,  $P > 0.1$  in each case), broods with helpers had a higher recorded success. Thirteen of 14 nestlings (93%) fledged from first broods attended by a helper, and 6 of 8 (75%) fledged from second broods aided by a helper. At nests without helpers, the comparable figures are 23 of 30 (77%) and 3 of 8 (38%).

Helpers did not increase the rate at which nestlings gained weight. Nestling weight is an approximately linear function of age for the first 10 days of the nestling's life. We regressed untransformed weights on age for this period, treating each nestling separately, and used the regression coefficient (slope) as an estimate of each individual's growth rate. Five nestlings from 2 nests with helpers had the same average growth rate as did 17 nestlings from 6 nests of comparable brood sizes without helpers ( $t_{20} = 0.52$ ,  $P > 0.1$ ). We are thus unable to detect short-term gains to the brood as a consequence of receiving help (cf. Emlen 1978).

Helping at the nest is not known to occur in the mainland species but is suggested by a single remark of Marchant's (1960: 381): "Amicable associations of more than two birds were often noted in the breeding season." He appears to have interpreted this, however, as evidence of polygamy. He found 1 nest with 8 eggs, 4 each of 2 different types, which he attributed to 2 females. We found no evidence of polygamy in *N. parvulus*.

#### OTHER OBSERVATIONS

*Post-fledgling survival and development.*—Of 50 banded nestlings, 36 (72%) from 18 nests were seen as fledglings. These comprised 27 of 36 first-brood nestlings and 9 of 14 second-brood nestlings. Of these 36 observed fledglings, 23 (64%) were present in November. In the wet season all fledglings were observed within 100 m of their birth site, on their parents' territory (usually) or a neighbor's territory. In the dry season (November) all but five were still on their parents' territory; four of these were on neighboring territories and the other, a male, was on the north coast approximately 3 km from its birth place. Two young birds remaining on home territories were judged from wing lengths to be females, and two others were judged to be males.

Fledglings not seen in November generally disappeared early from their territories. They were last seen an average of  $39.4 \pm 9.6$  (SE) days after fledging. In contrast, those present in November were last seen in the wet season an average of  $65.5 \pm 6.5$  days after fledging. This large difference is therefore brought about by disappearance, by death or dispersal, in the first 1–2 months after fledging. The single instance of long-distance dispersal indicates that dispersal may occur early. This bird was last seen only 16 days after fledging in March, before being recorded on the north coast of the island in November.

The feeding of at least 20 juveniles by parents was observed on days 1 to 33 after

fledging. Parents therefore continue feeding their young up to 5 weeks after the young have left the nest and while the parents are attending a second clutch. We noted the following additional developmental characteristics: The first juvenile song occurred at day 36 after fledging, full pigmentation of the lower mandible was seen by day 36, and the beginnings of a color change in the iris from gray to yellow-green were noted by day 66.

*Territorial behavior.*—On several occasions in the breeding season we observed agonistic behavior that could be interpreted as defense of territories. These disputes never involved more than two breeding pairs. Near our camp displays and physical encounters frequently occurred within an area of 3 m<sup>2</sup>. One banded pair repeatedly contested possession of the area with an unmarked pair. Two fledglings of the first pair attended their parents but did not take an active part in the displays. In the nonbreeding season, however, the same banded pair and two of the offspring (males) collectively defended this territory boundary against an unmarked pair. We assume that this was the same unmarked pair as the one involved in disputes in the breeding season, because 16 of the 17 banded adults studied in the breeding season were present and on their territories in the nonbreeding season. A third offspring of the banded pair, another male, also participated, but on the side of the unmarked pair and hence against its relatives. In the breeding season it had always been with its parents during such disputes.

Away from the camp we observed only one other territorial dispute involving more than 2 pairs, a conflict in the dry season between 3 birds and 2 birds. These observations suggest that territories are rarely defended by more than a pair on Genovesa.

*Nest characteristics.*—Seventeen of 27 nests were situated in *Opuntia* bushes; the remainder were in *Croton scouleri*, *Cordia lutea*, and *Bursera graveolens*. The height of the nest above ground appears to be governed by the height of the shrub or tree used for nesting, because the two are highly correlated ( $r = 0.724$ ,  $df = 19$ ,  $P < 0.001$ ). The average height of nests,  $1.11 \pm 0.09$  m, was approximately half the height of the shrubs or trees (mean height  $2.19 \pm 0.14$  m). On other islands where trees are taller, nests are placed as high as 6 m above the ground (e.g. San Cristóbal; Gifford 1913).

## DISCUSSION

*Comparison of island and mainland mockingbirds.*—The possibility of evolutionary change in life history features on the islands can be examined by comparing breeding data of *N. parvulus* and *M. longicaudatus*. For example, one might anticipate reduced clutch sizes in *N. parvulus*, because this is predicted for insular populations that experience seasonal climates by Cody's (1966) theory of optimal clutch size. In fact, we observe no difference between the species in clutch sizes and small differences in other features of the breeding cycle. The most noticeable difference is in the nestling period, which is longer on the islands than on the mainland. This difference is not restricted to mockingbirds, for we found it in our parallel studies of doves (P. R. Grant and K. T. Grant, MS) and finches (P. R. Grant and B. R. Grant, MS). If the difference in nestling period is determined by different sets of genes in the two mockingbird species, it may be said to have evolved on the islands. The argument would be strengthened if our findings were replicated on other islands, and on Genovesa in other years.

An important selective factor governing the nestling period is predation. Fewer

nest predators exist on Genovesa than on the mainland, and our data indicate fewer losses from the nest. We suggest that natural selection has favored longer nestling periods on the islands, primarily because individuals remaining in the nest are at lessened risk from predators, and secondarily because they are at an energetic advantage over those that leave earlier. Alternatively, the food supply may be less plentiful on the islands than on the mainland, and it may be physically impossible for the parents to supply the nestlings with food at the rate they do on the mainland. In the absence of information on feeding and growth rates of nestlings, we cannot address this second hypothesis directly, but it is not supported by the observation that many mainland nestlings died, apparently of starvation (Marchant 1960.)

*Cooperative breeding and group territories.*—One stimulus for this study was Hatch's (1966) suggestion that the behavior of mockingbirds in the breeding season may help to interpret the significance of group territories outside the breeding season. Our observations indicate that group territoriality is facilitated by behavior expressed in the breeding season. Cooperative behavior is shown by the presence of helpers at the nest. Some of the helpers were known to be offspring of the helped. Hatch (1966) once observed a juvenile feeding nestlings on Española, and Sarah Groves (pers. comm.) observed the same at one nest on Española and identified the helper as a male. The switch of one helper in adult plumage from one pair to another in our study suggests that helping also occurs outside the immediate family unit. It is also possible, however, that its parents were mated to other birds in this breeding season, and that it helped one of its parents with the rearing of the first brood and the other with a second brood.

We suggest that the dominance behavior within family groups, which permits the groups to form and regulates the activities of the members, is the basis of extra-familial associations observed outside the breeding season. Helpers were always subordinate to the parents. The transmitting of food from helper to parent, rather than always directly to the nestlings, is a form of subordinate behavior that indicates social as well as nutritional significance in the bringing of food to the nest (see also Woolfenden and Fitzpatrick 1977). Territorial transgressions reveal how extra-familial associations may become established. When an adult crossed a boundary and came near a juvenile, the juvenile always approached the intruder, adopted a subordinate posture (see Venables 1940 and Hatch 1966 for description), and begged, always unsuccessfully, for food. The juvenile followed the adult unless attacked by it and even then often followed when the adult stopped attacking. That such persistence may lead to tolerance is shown by the young male that left its parents' territory near our camp after the breeding season and joined the neighboring pair that had previously harassed it repeatedly.

Evolution of behavioral traits permitting helpers to bring food to the nest may have proceeded because juveniles are at a severe risk from other mockingbirds if they leave their own territories permanently in the breeding season. Attacks on juveniles when in neighboring territories were observed occasionally; they were short, intense, and always resulted in the departure of the juvenile. It is noteworthy that juveniles remained on territories a long time compared with finches, were fed by parents for a long time, and were never seen more than one territory away from their birth place in the breeding season, and then never for long. Why then are mockingbirds so aggressive? Their frequent visits to the nest, as compared with finches, and their high nest losses suggest that their aggressiveness may have evolved in the context of nest defense.

Aggressive-submissive social systems that regulate the behavior of participants can be subverted (Wilson 1975). Zahavi (1976) has argued from observations of babblers (genus *Turdoides*), which are ecologically similar to mockingbirds, that additional birds may hinder rather than help the parents, thereby elevating their own relative fitness. We have no direct evidence for this. But it is possible that some of the egg and nestling losses are attributable to helpers, or to others masquerading as such. One unusual observation may be relevant. On the day the first egg of a second brood pipped, we found the other three eggs around and outside of the nest rim. Ejection of eggs was never observed at any other nests. We put all 3 back and 2 subsequently hatched, although eventually all 3 nestlings died. The parents at this nest did not have a helper, but at their first nest they did. It is possible that the helper returned to this pair and ejected the eggs. Of course several other possibilities exist, which is why the hindering hypothesis (Zahavi 1976) is so difficult to test.

Finally, we emphasize that group territoriality is not a conspicuous phenomenon on Genovesa, whereas it is conspicuous on Española. On Española, however, it is largely restricted to the mockingbirds inhabiting the seabird colony where they may gain a rich supply of food; elsewhere on this island mockingbirds occur singly or in pairs in the nonbreeding season (Hatch 1966). Our results may therefore be the norm for Galápagos Mockingbirds, and the large groups on parts of Española may be an exception fostered by an abundant and persistent food supply on the ground (Brown 1974, Woolfenden 1976). But the exception is potentially most interesting and useful. The variation in territoriality on Española suggests an investigation, either observational or experimental, of the role of food supply as a proximate factor in determining the nature of territoriality.

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