

DEMOGRAPHY OF THE COOPERATIVELY BREEDING  
GALAPAGOS MOCKINGBIRD, *NESOMIMUS PARVULUS*,  
IN A CLIMATICALLY VARIABLE ENVIRONMENT

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SUMMARY

(1) The Galápagos mockingbird is a group territorial and cooperatively breeding species. We studied its demography on Isla Genovesa for 11 years (1978–88), a period that included 7 years with moderate rainfall, 2 extremely wet years when El Niño–Southern Oscillation (ENSO) events occurred, and 2 drought years.

(2) Annual survival of adults ( $\bar{x} = 61\%$ ) was high during average conditions but lower in both drought years and during an epizootic. Males survived slightly better than females. Survival did not vary with age among adults, but survival of juveniles was lower ( $\bar{x} = 35\%$ ) and twice as variable as adult survival.

(3) Mockingbirds bred in response to rainfall, producing up to 5.2 fledglings per breeding female each season ( $\bar{x} = 2.3$ ). Clutch size, number of clutches and total production of fledglings increased in wet years. Helpers attended 34% of all nests and increased production of fledglings by 19%.

(4) Differential mortality produced variation in the adult sex ratio. Breeding by males was constrained by the relative scarcity of females, and the proportion of males acting as helpers varied correspondingly because non-breeding males most often helped. The proportion of females breeding did not vary with adult sex ratio, because polygyny occurred in 2 years when females predominated, and most of the few females that helped also bred.

(5) Variation in natality and survival caused substantial variation in population density, but the density of breeders remained relatively constant (C.V. = 21%) compared to density of non-breeders (C.V. = 93%). Group territories, which were defended year-round, filled all available habitat throughout virtually the entire study.

(6) Group size averaged 4.2 adults, with up to four breeding females in each group. Groups were larger and plural groups more frequent in years when density was high and when yearlings predominated in the population; 67% of yearlings remained in their natal territories, where 47% of females and 62% of males also first bred.

(7) Climatic variation influences mockingbird social organization mainly through its effects on natality and survivorship, which indirectly influence the population's density, age structure, and sex composition. Plural breeding is maintained in this species because climatically-induced demographic variation favours the tendency of young birds to breed without establishing independent territories.

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## INTRODUCTION

In cooperative breeding systems some individuals, termed helpers, provide care for young that are not their own offspring. Among birds, helpers are most commonly young, non-breeding, individuals remaining in their natal territories (reviewed by Brown 1987). Consequently, efforts to understand the ecological basis of cooperative breeding have focused on identifying factors preventing or inhibiting some birds from breeding and causing them to remain in their natal social groups. Why helping occurs within social groups can be considered a separate, though not entirely independent, question (Emlen & Vehrencamp 1983; Brown 1987; Koenig & Mumme 1987).

Ecological and demographic factors contributing to the development of cooperative breeding (Brown 1987) fall into four general categories. First, territorial behaviour may prevent some individuals from breeding if population density is high in relation to available space suitable for breeding (Selander 1964; Brown 1969, 1974; Koenig & Pitelka 1981). This 'habitat saturation' mechanism has been emphasized for populations in stable, predictable environments, where adult survival is high and habitat suitable for breeding remains constantly filled with territories (Emlen 1982a; Emlen & Vehrencamp 1983; Woolfenden & Fitzpatrick 1984). Second, poor environmental conditions may cause a pool of non-breeders to form by making breeding by some birds, particularly young, inexperienced, and unskilled individuals, prohibitively difficult or risky (Orians, Orians & Orians 1977; Brown 1987). Prohibitive costs of breeding could account for the occurrence of cooperative breeding in unpredictably variable environments (Emlen 1982a). Third, lack of available mates may prevent birds from breeding in populations with skewed adult sex ratios (Rowley 1965; Brown 1978; Emlen 1982a; Emlen & Vehrencamp 1983). This mechanism does not provide an adequate general explanation for cooperative breeding, because males outnumber females in many bird species that do not breed cooperatively (Breitwisch 1988), but it could apply in specific cases. Fourth, living in groups could confer sufficiently large direct or indirect advantages, such as might be obtained through improved defence from predators (Austad & Rabenold 1985; Ford *et al.* 1988) or communal foraging (Bednarz 1988), to cause some individuals to defer breeding, in order to remain in a group. These different mechanisms are not necessarily exclusive, and they may be expected to interact (Brown 1987) and, as a result, to produce conflict within social groups (Emlen 1982b; Curry 1988a).

The Galápagos mockingbird, *Nesomimus parvulus* (Gould), on Isla Genovesa provides an excellent opportunity to investigate ecological and demographic influences on cooperative breeding, because all four classes of factors appear to be applicable. In particular, mockingbirds on Genovesa defend territories throughout the year (Grant & Grant 1979; Kinnaird & Grant 1982), but they also inhabit a climatically variable environment, in which rainfall varies greatly and unpredictably among years (Grant & Boag 1980; Grant 1985). Mockingbird groups on Genovesa frequently contain more than one breeding female (Curry 1988a), a condition termed plural breeding (Brown 1978). Plural groups usually arise when young birds begin breeding while remaining in their natal territories with their parents. Most helpers on Genovesa are young non-breeders remaining in their natal groups, though breeders sometimes also act as helpers at other nests in plural groups (Curry 1988b).

The primary purpose of this paper is to examine the influence of climatic variation on the demography of *N. parvulus*. Our 11 years of study on Genovesa, 1978–88, have included two El Niño–Southern Oscillation (ENSO; Philander 1983) events, during which

extraordinarily large amounts of rain fell, 2 drought years, and 7 years with intermediate rainfall. Here we expand on earlier preliminary analyses (Grant & Grant 1979; Kinnaird & Grant 1982; Curry 1985) to examine the effects of these changes in climatic conditions on mockingbird survival, reproduction, and social behaviour. A second purpose is to examine demographic influences on breeding structure in order to interpret the evolution of plural breeding. We contrast the demography of the Galápagos mockingbird with that of the Florida scrub jay (*Aphelocoma c. coerulescens*), a singularly-nesting species whose demography in a climatically less variable environment has been thoroughly examined (Woolfenden & Fitzpatrick 1984; Fitzpatrick & Woolfenden 1986), and that of the gray-breasted (Mexican) jay (*A. ultramarina*), the only plurally-nesting and territorial cooperative breeder whose demography has been studied in comparable detail (Brown 1985, 1987).

### STUDY AREA AND METHODS

Genovesa, is a low, arid island (17.4 km<sup>2</sup>) in the north-east of the Galápagos Archipelago. The study area on the south side of the island included roughly 20 ha in 1978 and 1979 and then was increased to 30 ha in 1980 and to about 50 ha (approximately 3% of the island's area) from 1981 onwards. Additional details concerning the island and study area are given by Grant & Grant (1980, 1987) and Curry (1988a).

We studied mockingbirds in the usual breeding season (January–May) of each year from 1978 to 1988, and in part of the non-breeding season (June–December), except in 1978 and 1981. Observations lasted only 3 weeks in March 1979, and in February 1988, but they spanned 4–7 months in all other years. Daily rainfall was measured during all periods of study.

Adult ( $n = 377$ ) and fledged juvenile ( $n = 287$ ) mockingbirds were captured in nets or traps, weighed, measured, ringed, and released. One to three colour rings were used on each bird from 1978 to 1981; uniquely numbered aluminium rings and three colour rings were used on all birds from 1982 onwards. Nestlings ( $n = 1011$ ) were ringed at 8 days of age. Year of birth was known for birds ringed in juvenal or immature plumage because birds retained juvenal plumage, characterized by extensive spotting on the breast, until about 4 months of age, and immature plumage, characterized by small amounts of spotting on the throat, from 4 to 6 months of age. Birds in adult plumage but of unknown age were assigned to minimum-age cohorts (i.e. classified as  $\geq 1$  year old in year ringed) because reliable indicators of age among adults were lacking. In this paper, all birds less than 8 months old are termed juveniles. Birds are considered yearlings from their first January, when actual ages ranged from 8 to 12 months, until the following December.

Sex of birds at least 6 weeks old was determined from the length of the flattened wing; birds with wing lengths  $< 114$  mm were classified as females and those with wing lengths  $> 114$  mm were classified as males (Swarth 1931; Kinnaird & Grant 1982; Curry 1988a). Later breeding behaviour confirmed these identifications with few exceptions (2%). Fledged young were recaptured for sex identification from measurements. Sex could not be determined for birds with intermediate wing length (114 mm) that did not breed (6% of birds banded as adults or juveniles), nor for birds that died before being measured (61% of chicks fledged in the study area).

Each territory was checked for nesting activity at least every 3 days, and nearly all nests in the study area were located during nest-building or incubation. A few nests in 1979, 1980, 1983, and 1987 were not found until after the young had fledged, but most juveniles

from these nests were captured while still dependent on their parents. We classified nestlings as having fledged only if they were seen alive away from their nest, and classified as independent young those birds surviving at least 1 month after fledging. Attendance of helpers at nests with nestlings was determined during 0.5 or 1 hour watches at 2 or 3-day intervals (Kinnaird & Grant 1982; Curry 1988b). Two females occasionally lay a total of six to nine eggs, twice as many as a female typically produces when nesting alone, in a joint nest (Curry 1988a). Females nesting jointly were not classified as helpers unless they also fed nestlings at one or more nests where they did not lay eggs.

Survival and dispersal were estimated from sightings of marked individuals. We defined each group territory as the area occupied and defended by a dominant male; all birds subordinate to that male and resident within his territory were classified as members of his group (Curry 1988a). We visited each territory at least once per week and recorded the identities of all birds sighted. We considered birds to have dispersed if they were regularly seen in a different territory and were tolerated by its residents, whether or not the disperser became a breeder. A zone roughly 200 m wide around the study area was checked once a month for the presence of marked birds. Ten ringed birds originating within the study area were seen in this region, and six were seen in more distant parts of the island. The survival values reported here are therefore minimum estimates, since additional birds from the study area probably dispersed to the interior of the island.

Group territories were plotted on detailed maps of the study area drawn from aerial photographs and on-site measurements. Areas were measured from computer-digitized tracings of each year's map. Total density and breeder density were calculated directly by dividing the number of resident adults and breeding birds respectively by the size of the area intensively studied in each year; birds in peripheral groups whose territory borders were not known with certainty were not included in the density estimations.

## RESULTS

### *Climatic variation*

Lowland sites in the Galápagos experience a warm/wet season and a cool/dry season in most years (Grant & Boag 1980). On Genovesa, rain began in January or February each year from 1978 to 1982 and in 1984 and 1986, and continued sporadically for up to 4 months, producing annual rainfall totals between 69 and 164 mm (Fig. 1) and hence varying by a factor of approximately two. Rainfall data for 1979 are incomplete, but the year was moderately wet, rain occurred from January through March, and the estimated total is close to the amount that fell in 1978 (Grant & Grant 1983). These can be considered climatically normal years. Once about 20 mm or more of rain had fallen at the start of each season, trees and shrubs rapidly produced flowers and leaves, and arthropod densities increased (see Grant 1986). Vegetation quickly dried out once the rains had ended, and for the remainder of each year the habitat was dry and leafless. Plant responses to rainfall are described in more detail in Grant (1986) and Grant & Grant (1987).

Both ENSO events during the study brought heavy and prolonged rainfall. The 1982–83 event was the strongest of the century (Cane 1983; Grant 1984). Unusual conditions recorded throughout the archipelago included torrential showers, high winds, elevated ocean levels, and higher than average ocean and air temperatures. Rain began falling on Genovesa in late November 1982 (Grant 1984) and showers continued almost daily through the first 7 months of 1983 (Fig. 1). The ENSO event of 1987 was less

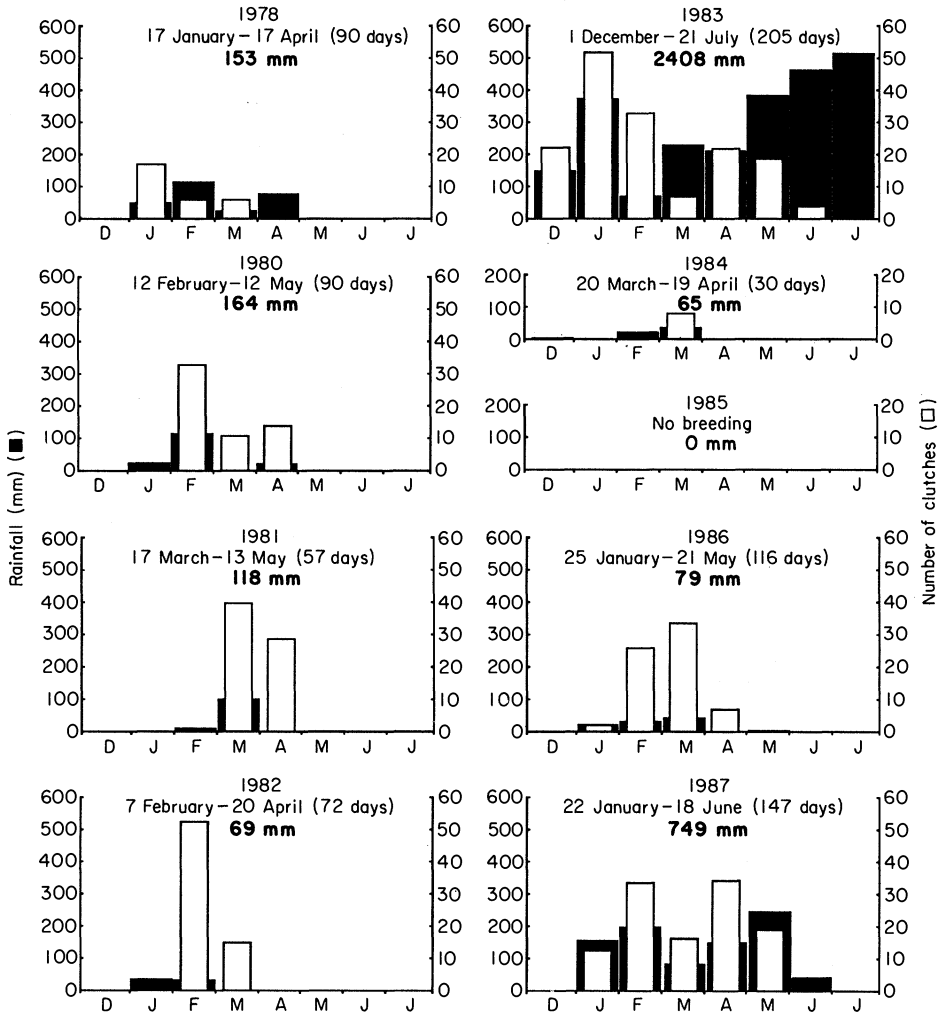


FIG. 1. Rainfall and breeding phenology. Solid bars show monthly rainfall totals; values for January 1978 and December 1982 are minimum estimates based on partial data. Annual rainfall totals (bold face) begin with December of the preceding year. Open bars show numbers of clutches produced, grouped in monthly intervals. Duration of breeding is indicated by dates of first egg and last fledging, with length of the interval shown in parentheses. Quantitative data for 1979 are lacking.

extraordinary: rains began in January and ended in May, yielding one-third of the total rainfall of the 1982–83 event.

No measurable rain fell during the study on Genovesa in 1985 (Fig. 1). Conditions were extraordinarily dry in the entire archipelago throughout the year. Green vegetation, which had been very thick by the end of the El Niño rains and which had been briefly replenished following rains in 1984, gradually died back during 1985; the habitat was dry and leafless when rains resumed in 1986. A second drought occurred in 1988 when only 13 mm of rain fell.

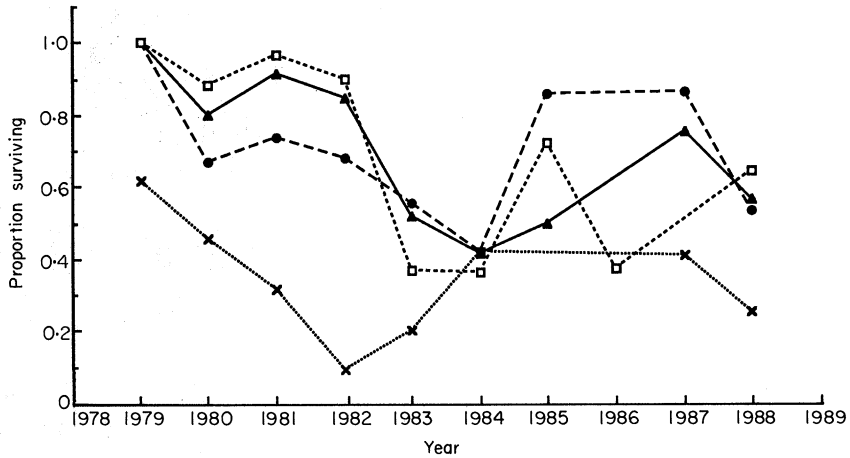


FIG. 2. Temporal variation in survival. Annual survival of male breeders (▲), female breeders (●), and non-breeding adults of both sexes (□) is estimated as the proportion of birds whose breeding status in the preceding year was known that remained alive as of January of the year indicated, or in March (1979) or February (1988) for years when no January census was made. Juvenile survival (×) is estimated as the proportion of all young fledged in the study area remaining alive in January of the year after birth.

Mean annual rainfall from 1978 to 1988, measured from December to December was 381 mm ( $\pm 744$  S.D., C.V. = 195%). These figures exclude data for 1979. We assume that rainfall outside our periods of study was negligible.

### Survival

#### *Variation with year, breeding status and age-class*

Annual survival of adults was high from 1978 to 1982, in 1984, and in 1986, years of climatically average conditions. It was lower in 1982–83, in 1985, and in 1987 (Fig. 2). Survival was therefore highest during intermediate climatic conditions and lowest during the extraordinarily wet 1982–83 ENSO and during the 1985 drought. Mean annual adult survival was 60.5% ( $\pm 0.18$  S.D.,  $n = 10$  years, C.V. = 28.7%). Adult survival did not vary significantly with breeding status. Mean annual survival was 70% for breeding females ( $\pm 0.18$  S.D.,  $n = 7$  years), 70% for breeding males ( $\pm 0.20$ ,  $n = 7$  years), and 62% for non-breeders of the sexes together ( $\pm 0.33$ ,  $n = 10$  years).

Survival of juveniles was lower and more variable than adult survival. Average annual survival of fledged young to the January of the year after their birth was 34.7% ( $\pm 0.16$  S.D.,  $n = 7$  years, C.V. = 47.3%). Juvenile survival varied significantly among years ( $\chi^2_1 = 55.1$ ,  $P < 0.001$ ), from 10% to 62%, and was as high as that of adults only in 1983 (Fig. 2). Overall, annual survival rates of juveniles were lower than those of adults (Wilcoxon matched-pairs test,  $P = 0.01$ ).

Because different cohorts experienced periods of high and low mortality at different ages, each had a somewhat different pattern of survival (see Fig. 2 for juveniles and Figs 2 and 3 for adults). Survival of adults did not vary systematically with age (Table 1). Through the first 4 years of life for which data are most extensive, survival did not decline with age in males or in females. Female survival values were lower than male survival values at all ages (up to and including 5 years, Wilcoxon matched-pairs test,  $P < 0.05$ ). As a result of small but consistent differences between the sexes in survival, synthetic

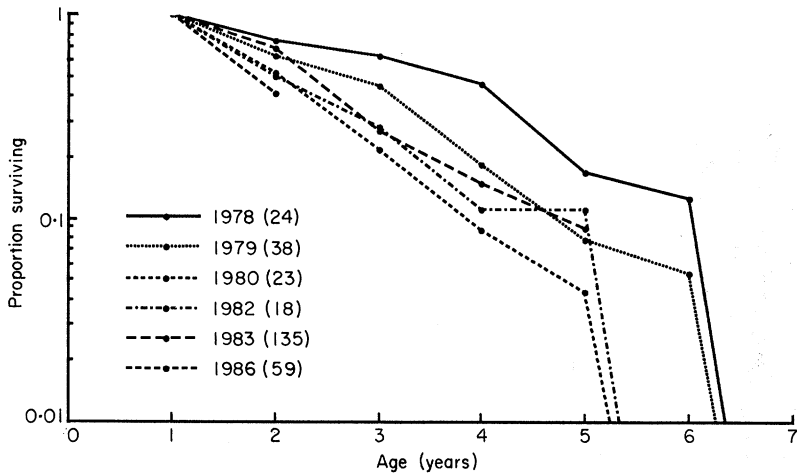


FIG. 3. Variation in survivorship among cohorts. Curves show proportion of birds (sexes combined) of seven cohorts that survived to adulthood (first January after birth) and that were sighted in successive January–February censuses.  $n$ , the number of yearlings in each cohort, is shown in parentheses.

survivorship curves for the separate sexes diverge with increasing age (Fig. 4). More frequent dispersal by females from the study area may in part account for their greater apparent mortality.

#### Causes of mortality

In the majority of cases, we do not know the cause of death. Starvation is a likely cause, particularly during harsh dry seasons and drought years. Short-eared owls (*Asio flammeus* Pontoppidan) occasionally eat mockingbirds on Genovesa, and herons (*Nycticorax violacea* Linnaeus) and *Butorides [striatus] sundevalli* Reichenow) also eat eggs and nestlings but are probably seldom capable of killing adult mockingbirds. There are no other predators on the island. Mockingbirds give alarm calls in the presence of owls and of herons near active nests, but we found no evidence of a coordinated system of anti-

TABLE 1. Age-specific survivorship of adults. Survivorship is estimated as the proportion of marked adults of known age present in each January ( $n$  is the number of birds) that had not disappeared by the subsequent January, with all cohorts (1978–86) combined

Age (years)	Males	Females	Total
1	0.607 (140)	0.585 (164)	0.593 (305)
2	0.606 (71)	0.419 (86)	0.503 (157)
3	0.581 (43)	0.500 (36)	0.544 (79)
4	0.560 (25)	0.500 (18)	0.535 (43)
5	0.857 (7)	0.000 (4)	0.545 (11)
6	0.167 (6)	—	0.167 (6)
$\bar{x} \pm \text{S.D.}$	$0.563 \pm 0.22$	$0.401 \pm 0.23$	$0.481 \pm 0.16$

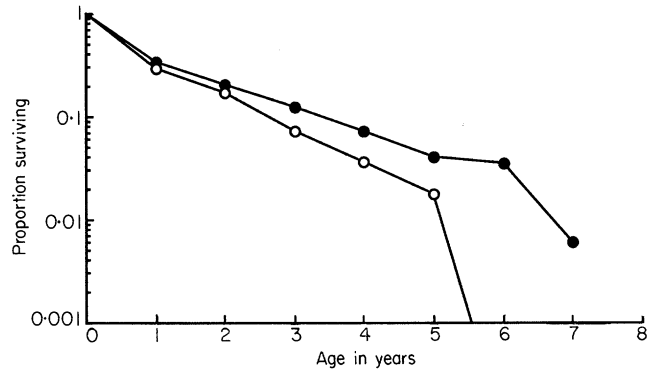


FIG. 4. Synthetic survivorship curves for males (●) and females (○). Survival from age 0 to age 1 year is estimated from the proportion of fledglings born in the study area that remained alive in January of the year after their birth, pooling all cohorts and assuming an even sex ratio at fledging. Subsequent survival estimates are based on all birds of known age and sex.

predator vigilance with mockingbird groups. Only three breeding females were killed at the nest, as indicated by the presence of many adult feathers and, in one case, the bird's head. Compared with other cooperatively breeding species that have been studied in detail (e.g. Woolfenden & Fitzpatrick 1984), this is a very low incidence.

Disease was an important cause of death: increased adult mortality in 1982 and 1983 (Fig. 2) was associated with an epizootic during the 1982–83 ENSO. We observed only three apparently-diseased individuals in 1978–82, but we saw eighty mockingbirds with conspicuous disease symptoms between January and June 1983. Affected birds had lesions on the eyelids, bill, head, wings, or feet, and some also suffered from growths or inflammation inside the mouth and throat. We suspect the cause was avian poxvirus (Karstad 1971) and that birds died as a direct result of the disease. Only 44% of adults and juveniles seen with symptoms between January and June of 1983 ( $n=80$ ) were still alive in July 1983, compared to 61% of those not seen with symptoms ( $n=342$ ;  $\chi^2_1=7.5$ ,  $P<0.01$ ). Several birds disappeared within a few days after developing severe symptoms, but others lingered for a month or longer. Some survivors suffered deformities that may have contributed to death later. One bird, for example, survived to July 1983 after losing its upper mandible in February, but then disappeared. Several others lived a year or more after losing an eye.

The incidence of disease during the 1982–83 ENSO varied with age and sex. Sixty (42%) of 142 banded adults present in 1983 were seen with disease symptoms, but only 7% of 275 juveniles had them ( $\chi^2_1=73.7$ ,  $P<0.005$ ). This difference arose in part because the disease was most prevalent in January and February, when forty-three of the eighty victims first developed symptoms and juveniles were relatively scarce. Males were victims apparently more often than females. Among adults, 50% of males ( $n=72$ ) but only 35% of females ( $n=70$ ) were seen with symptoms ( $\chi^2_1=3.4$ ,  $0.05 < P < 0.1$ ). Among juveniles, 9% of males ( $n=97$ ) and 2% of females ( $n=130$ ) had symptoms ( $\chi^2_1=5.5$ ,  $P<0.05$ ). The reason for the apparent sex difference in sensitivity to this disease is unknown, but it seems possible that males transfer a virus through fighting more frequently than would females since they are involved in boundary disputes and within-group aggressive behaviour more often (Curry 1988a).



Pox-like symptoms were extremely rare or absent in other years, including some ENSO events. For example, only two birds had conspicuous mouth and foot lesions in April 1987; one, a breeding male, disappeared soon after it was seen to be infected.

### *Longevity*

No birds are known to have survived through the entire study, but direct observations of longevity suggest a small difference between the sexes. One male ringed as an adult in 1981 remained alive in February, 1988, having lived at least 8 years. Two other males marked as adults lived at least 7 years. One male ringed as a nestling in 1981 was alive in 1988, having lived for 7 years, and five others lived for 6 years. Four females marked as adults survived to at least 6 years of age. Five females banded as nestlings survived 5 years but none attained 6 years of age.

As an alternative to direct observation, we can estimate maximum longevity, by extrapolating the survivorship curves of Fig. 4 to the horizontal axis (the point where 0.1% of a cohort of fledged young will remain alive), to be 12.1 years for males and 9.0 years for females. This assumes survival to adulthood of 34% for male fledglings and 29% for female fledglings and a constant rate of adult mortality of 59% for males and 50% for females, values which are taken from survival over the first 4 years of life (Table 1).

### *Breeding*

#### *Breeding phenology*

Rainfall is the primary determinant of breeding phenology in this population. Nesting in each year coincided with the onset of the wet season, beginning usually in January or February (Fig. 1). Birds sometimes carried nest material to old nests at other times of the year, when misty showers (*garúa*) occurred, but we found no evidence of breeding during the dry/cool season. For example, no nesting occurred after 6 mm of *garúa* fell in December, 1983. Breeding also did not occur in years when rains failed to arrive during the typical wet season; no mockingbirds nested in 1985 or in 1988. In its nearly complete dependence on rainfall for breeding, *N. parvulus* on Genovesa differs from *N. trifasciatus* (Gould) on Champion and *Mimus longicaudatus* (Lesson) in mainland Ecuador, both of which sometimes breed before rains begin (Marchant 1960; R. L. Curry & P. R. Grant, unpublished data).

Nest building increased in frequency immediately after the first heavy showers of each wet season. Females began laying eggs 9–10 days after about 40 mm of rain had fallen (see also Grant & Grant 1979). Breeding in the 1983 season began before the start of the calendar year; the earliest successful broods of the season fledged on 31 December 1982. Calculating backward using known nestling, incubation, and laying intervals (Grant & Grant 1979), we estimate that the first eggs of the season were laid on about 1 December 1982. Breeding started as late as 17 March in 1981.

Duration of breeding in each year was associated with the duration of rainfall and the pattern of rain throughout the season. The interval between the first egg laid and the last chick fledged ranged from 30 to 205 days (Fig. 1). This variable was correlated with total annual rainfall ( $r_s = 0.80$ ,  $P < 0.05$ ), and with the interval between the first and last days in the season with  $\geq 2$  mm of rain ( $r_s = 0.74$ ,  $P < 0.05$ ). The termination of breeding was less closely associated with rainfall patterns than was its onset. In 1981, 1982, and 1986, birds continued to produce clutches after the rains ended (Fig. 1), but incomplete information suggests that none did so after 79 mm of rain in April, 1978 (Grant & Grant 1979). Heavy rain continued until late July 1983, but no birds produced new clutches after late June; in

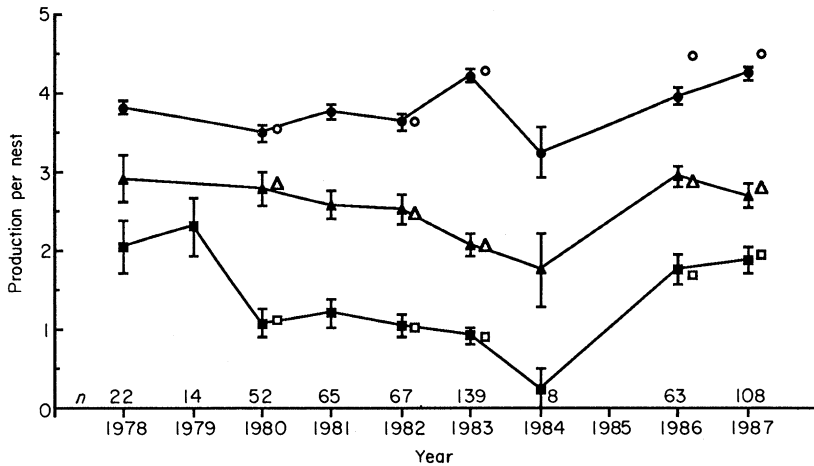


FIG. 5. Annual variation in reproductive success per nesting attempt. Solid symbols denote annual means ( $\pm$  S.E.) for eggs (circles), nestlings (triangles) and fledglings (squares) produced per nest, excluding nests in which two females laid eggs (joint nests). Open symbols indicate means with joint nests included. Sample sizes ( $n$ ) are given above the horizontal axis.

that year, arthropod abundance declined before the rains ended (Grant & Grant 1987). Changes in food resources, rather than rainfall, may therefore exert the strongest proximate influence on the cessation of breeding.

Amount and timing of rain does not completely account for variation in breeding phenology. Considerable rain (57 mm) fell during 2 weeks in February and March, 1984, but only eight pairs nested in an area usually containing fifty to sixty breeding pairs. This weak response to rainfall occurred when most potential breeders were yearlings (below). In contrast, breeding lasted longer in 1986, when 79 mm of rain fell, than in 1978, 1980, 1981, years when 118–164 mm of rain fell (Fig. 1). 1986 was also exceptional in that two females began laying 1 week before the first measurable rain. These unusually strong breeding responses took place at the end of the 1985 drought, after 2 years when no birds had nested successfully, and at a time when population density was unusually low (below).

#### *Reproductive success per nest*

Reproductive success at each nesting attempt varied among years, owing to different contributions of clutch size, hatching success and fledging success. This variation was only partially associated with variation in rainfall. Excluding joint nests, clutch size was highest in the two ENSO years (1983 and 1987; Fig. 5), when many females produced clutches of five eggs and one produced six eggs; five-egg clutches were rare prior to 1983 (Grant & Grant 1979; Curry 1985). Clutch size, however, was nearly as high in 1986, a comparatively dry year. Inclusion of the large combined clutches in joint nests magnifies these differences among years (Fig. 5). Joint nests, which constituted 4% of all nests and varied from none to 14% of the nests in each year ( $\chi^2_7 = 25.0$ ,  $P < 0.001$ ), were most frequent in the same years (1983, 1986, and 1987) when normal clutches were also largest.

Although large clutches are produced in years of heavy rainfall, hatching success is not always correspondingly high. The proportion of all eggs that hatched ranged from 48% in 1983 to 80% in 1980 (joint nests excluded;  $\chi^2_7 = 93.7$ ,  $P < 0.001$ ). Low hatching success in

TABLE 2. Effect of helpers on average fledgling production per nest. *n* is the number of nests with or without helpers during the nestling period; nests in which two females laid jointly are excluded

Year	Helpers present		Helpers present		% Helped
	$\bar{x} \pm \text{S.E.}$	<i>n</i>	$\bar{x} \pm \text{S.E.}$	<i>n</i>	
1978*	2.0 ± 0.5	8	2.2 ± 0.5	12	40
1979*	3.0 ± 0.7	4	2.0 ± 0.6	3	57
1980*	1.4 ± 0.3	20	1.4 ± 0.3	26	44
1981	2.1 ± 0.3	24	1.3 ± 0.2	34	41
1982	1.4 ± 0.3	24	1.3 ± 0.2	33	42
1983	1.8 ± 0.2	32	1.4 ± 0.1	79	29
1984	0.0 ± 0.0	2	0.7 ± 0.7	3	40
1986	2.5 ± 0.8	6	1.8 ± 0.2	51	11
1987	2.5 ± 0.2	33	2.3 ± 0.2	56	37
All years	1.9 ± 0.1	153	1.6 ± 0.1	297	34

\* Recalculated from raw data, excluding nests where presence or absence of helpers could not be determined because no eggs hatched; after Kinnaird & Grant (1982).

1983 was associated with nest abandonment during prolonged rains, nest destruction by high winds and deaths of incubating females from disease (Curry 1985). These effects were smaller in the other wet year, 1987, in the absence of disease. As a result of the non-concordance of clutch size and hatching success, the number of nestlings per nest peaked in a year, 1986, when clutch sizes were not at their largest (Fig. 5). Hatching success in joint nests was lower (40%) than in all other nests (64%;  $\chi^2_1 = 78.8$ ,  $P < 0.001$ ).

Average fledgling production varied among years (Fig. 5) as a result of variation in clutch size and hatching success, but also as a result of variation in the number of helpers. Helpers fed nestlings at 34% of all nests (Table 2). The proportion of nests helped varied among years ( $\chi^2_8 = 22.7$ ,  $P < 0.005$ ); the greatest source of this variation was an exceptionally small proportion of nests with helpers in 1986, when most birds in the population were breeding. Nests with helpers yielded an average of 1.9 fledglings compared to 1.6 fledglings for nests without helpers (Table 2;  $t_{488} = 2.11$ ,  $P < 0.05$ ). A significant effect of helpers on fledgling production is also detectable (two-factor ANOVA,  $F = 5.4$ , 1 d.f.,  $P = 0.02$ ; excludes the years 1978, 1979 and 1984, when few nests were studied) when variation among years in the number of fledglings produced per nest is controlled statistically.

#### *Seasonal reproductive output*

Though breeding lasted longer in the wetter years, the average number of fledglings produced per female was not a simple function of rainfall. The number of fledglings produced in each season was determined mainly by the number of clutches produced per female (Fig. 6). In 1983, the year of greatest rainfall, some females produced as many as six clutches, but many others died from disease during the breeding season, reducing the average to 2.6 clutches per female. Females produced more clutches on average in 1987, and nearly as many in 1986, even though each female produced at most four and three clutches in 1987 and 1986, respectively. Seasonal production of fledglings peaked in 1987, whereas poor hatching success caused lower average fledgling production in 1983.

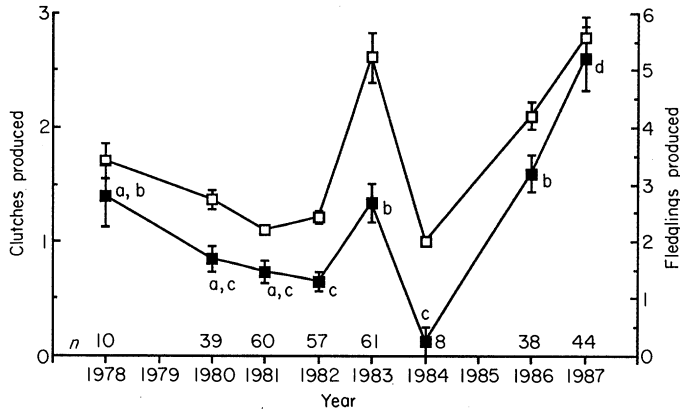
*Galápagos mockingbird demography*

FIG. 6. Annual variation in seasonal reproductive success. Solid squares denote mean number of fledglings ( $\pm$  S.E.) produced by each breeding female ( $n$  is the sample size). Means that share no letters differ significantly (Fisher's Least Significant Difference test,  $P < 0.05$ ). Open squares denote the mean number of clutches ( $\pm$  S.E.) produced per breeding female in each season.

Including only years in which breeding took place, mean seasonal production was 2.3 fledglings per breeding female ( $\pm 1.49$  S.D., C.V. = 64%,  $n = 8$  years, excluding incomplete data from 1979). With the drought years included, mean seasonal production was 1.8 fledglings per breeding female ( $\pm 1.69$  S.D., C.V. = 92%,  $n = 10$  years).

*Breeding in relation to age*

During the study, fifty-four males and forty-two females of known age attained breeding status (Table 3). Age at first breeding did not differ between the sexes (3- and 4-year-olds combined;  $\chi^2 = 2.0$ , N.S.). None bred in their year of birth, not even in the El Niño year of 1983, when some finches (*Geospiza* spp.) on Daphne Major bred at ages of 3 months (Gibbs, Grant & Weiland 1984). The youngest mockingbird to breed was a female born in May 1983 that nested in 1984 at 8 months of age. The lack of birds first breeding at age 2 years is more apparent than real. It is the result of a strong influence of year of birth on age at first breeding. No birds in the large 1983 and 1986 cohorts, for example, were able to breed as 2-year-olds, because drought conditions in 1985 and 1988 prevented breeding.

TABLE 3. Age at first breeding. Table includes all birds of known birth year that became breeders (produced at least one clutch) during the study

Age at first breeding (years)	Males		Females	
	$n$	% of total	$n$	% of total
1	27	50.0	27	64.3
2	5	9.3	3	7.1
3	21	38.9	12	28.6
4	1	1.9	0	0.0

TABLE 4. Breeding status in relation to age. Tabled values are the proportion of residents of known age and sex ( $n$  in parentheses) that nested one or more times in each year

Year	Age 1 year		Age 2 years		Age $\geq$ 3 years	
	Males	Females	Males	Females	Males	Females
1980	0.22 (9)	0.60 (10)	0.57 (7)	0.75 (4)	—	—
1981	0.25 (8)	0.57 (7)	0.33 (9)	0.75 (8)	0.86 (7)	1.00 (2)
1982	0.00 (4)	0.00 (3)	0.14 (7)	0.75 (4)	0.65 (17)	1.00 (7)
1983	0.67 (6)	0.86 (7)	1.00 (1)	0.00 (1)	0.64 (11)	0.80 (5)
1984	0.00 (42)	0.02 (49)	0.00 (1)	0.20 (5)	0.43 (7)	0.00 (1)
1986	—	—	—	—	1.00 (28)	0.97 (37)
1987	0.70 (23)	0.67 (15)	—	—	1.00 (19)	1.00 (26)
Total	0.26 (92)	0.30 (91)	0.36 (25)	0.59 (22)	0.83 (89)	0.96 (68)
$\bar{x} \pm$ S.D.	0.31 $\pm$ 0.31	0.45 $\pm$ 0.36	0.41 $\pm$ 0.39	0.49 $\pm$ 0.36	0.76 $\pm$ 0.29	0.80 $\pm$ 0.40

Dashes indicate years in which no birds of an age category were known to be present.

The proportions of both males and females that bred increased with increasing age (Table 4). The proportions of birds of different ages that bred were also influenced by changes in breeding opportunities among years. Prior to 1983, when many older birds were present (see below), only 19% of male yearlings and 50% of female yearlings bred. More yearlings bred in 1983 when increased mortality among older birds created territorial vacancies. The relatively large proportion of birds first breeding as yearlings (Table 3) results primarily from favourable conditions in 1987, when many birds from the large cohort of 1986 were able to breed. In contrast, in 1984 only one of the 112 yearling residents bred, compared to 22% of sixty-three older residents ( $\chi^2_1 = 19.6$ ,  $P < 0.005$ ). We attribute the failure of many yearlings to breed in 1984 to comparatively poor climatic conditions.

#### *Sex ratio, breeding and helping*

The sex ratio of adult residents in the breeding season period varied from 64% males in 1979 to 39% in 1985 (Table 5). A deviation from an even sex ratio could arise at birth, or could be produced by differential mortality later in life. We did not determine the sex of nestlings, but the sex ratio of fledged young is close to unity: 50.8% of 394 birds ringed as nestlings and sexed by recapture and measurement were males. Shifts in adult sex ratio therefore resulted from differential mortality among juveniles and adults.

Changes in adult sex ratio influenced the proportion of birds breeding and acting as helpers at the nest, but the effects on males and females differed (Table 5). As the adult sex ratio increased, the proportion of males that bred decreased (Spearman's  $r_s = -0.95$ , 7 d.f.,  $P < 0.001$ ; data for the atypical 1984 breeding season excluded) and the proportion that helped at one or more nests during a season increased ( $r_s = 0.74$ , d.f.,  $P < 0.05$ ). A lack of available mates for males therefore increases the pool of non-breeding males, which are the birds that most often act as helpers at the nest (Curry 1988b). Sex ratio influences helping by females differently. The proportion of females that helped decreased as females became relatively more abundant ( $r_s = -0.91$ , 7 d.f.,  $P < 0.005$ ), but not because their breeding was prevented by lack of mates: the proportion of females that bred did not vary

TABLE 5. Variation in adult sex ratio and in proportions of birds breeding and helping

Year	All adults*	Males	Females	Sex ratio†	Proportion breeding		Proportion helping	
					Males	Females	Males	Females
1978	19	11	8	0.58	0.73	1.00	0.18	0.00
1979	36	23	13	0.64	0.44	0.77	0.30	0.00
1980	113	64	49	0.57	0.67	0.88	0.27	0.02
1981	172	100	71	0.58	0.61	0.87	0.29	0.00
1982	159	96	62	0.61	0.59	0.92	0.24	0.00
1983	119	60	59	0.50	0.87	0.92	0.20	0.07
1984‡	169	70	97	0.42	0.12	0.08	0.00	0.02
1985	140	54	85	0.39	—No breeding—			
1986	62	26	36	0.42	1.00	0.94	0.04	0.08
1987	94	42	50	0.46	0.83	0.88	0.21	0.12
1988	65	59	124	0.52	—No breeding—			
$\bar{x} \pm$ S.D.				0.52 $\pm$ 0.1	0.65 $\pm$ 0.3	0.81 $\pm$ 0.3	0.19 $\pm$ 0.1	0.03 $\pm$ 0.1

\* Includes adults of unknown sex.

† Percentage of males among adults of known sex.

‡ Only eight pairs nested in the study area in 1984.

with adult sex ratio ( $r_s = -0.43$ , 7 d.f., N.S.). Most females were able to breed at all times because many paired polygynously when females predominated. These polygynously paired females also most often acted as helpers, whereas few non-breeding females did so (Curry 1988b and unpublished data).

#### Population density and use of space

Changes in both natality and mortality caused a threefold variation in the total density. Following an initial increase in 1979, density declined gradually as a result of

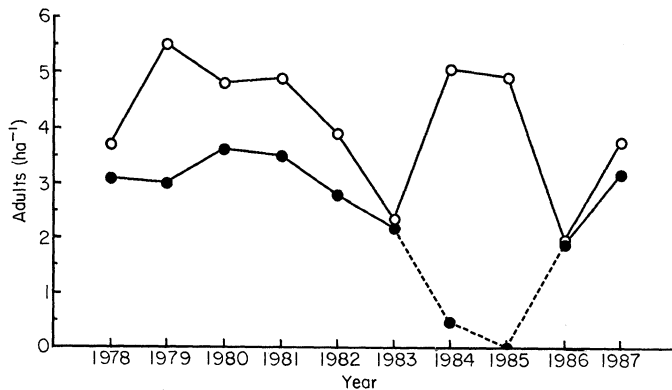


FIG. 7. Population density of adult residents (○) and breeders (●), based on census data from February to March of each year (breeding season). Breeders are defined as members of pairs that produced one or more clutches in a season. Dashed line indicates years when few (eight pairs in 1984) or none (1985) of the paired residents within the study area produced eggs.

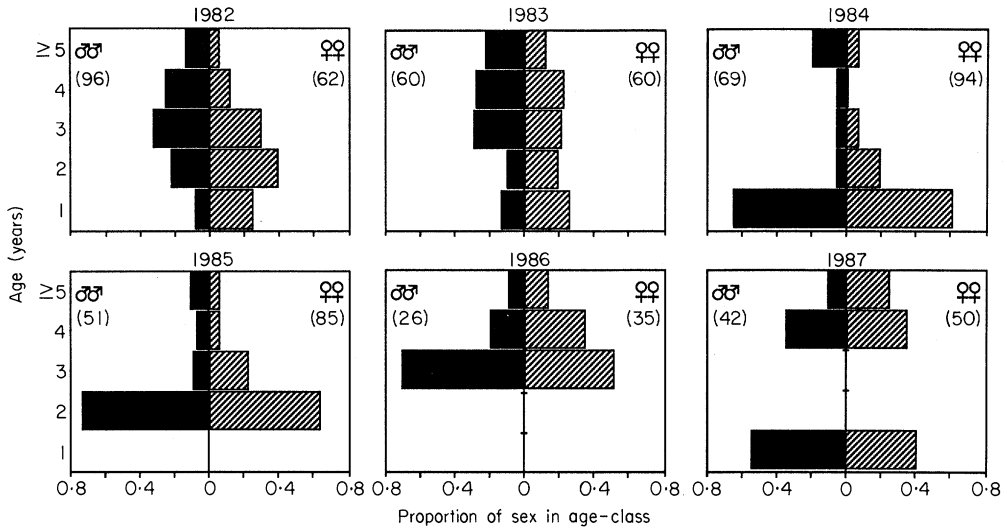


FIG. 8. Variation in population age structure, 1982–87. Bars shows proportion of residents of each sex in different age-classes during the usual breeding season (February–March). Adults of uncertain age have been divided equally into minimum-age cohort and the next older age class. Because breeding failed in 1984 and 1985, birds of unknown age marked in 1985 and 1986 were assumed to have been born in 1983 or before.

comparatively low seasonal reproduction until the first ENSO event in 1983, when density increased sharply (Fig. 7). This pattern was repeated between 1984 and 1987. Density reached its lowest level of  $2.0 \text{ birds ha}^{-1}$  in 1986, following 2 years of reproductive failure and low adult survival. Increased density in 1987 reflected successful reproduction in 1986 coupled with moderate juvenile survival and high adult survival.

Variation in total density resulted largely from changes in the numbers of non-breeders present, because density of breeding birds remained relatively constant. Omitting the exceptional years when few (1984) or no birds (1985 and 1988) bred, we calculate that mean breeder density was  $2.9 \pm 0.6 \text{ birds ha}^{-1}$  (C.V. = 21%). Variation in density of non-breeding adults was much greater (C.V. = 93%) over the same years. The density of breeders did not vary with increasing total density. Consequently, the proportion of residents breeding (sexes combined) was negatively correlated with adult density ( $r_s = -0.81$ ,  $n = 8$  years,  $P < 0.025$ ).

Mockingbird territories occupied all terrestrial habitat on Genovesa throughout nearly the entire study. The only exception occurred during 1983, when mortality eliminated some entire groups. Some areas occupied by these groups were left vacant for as long as a month before being occupied and defended by adults and juveniles from other parts of the study area and from other parts of the island (Curry 1985, 1989).

#### *Age structure*

Population age structure varied dramatically among years (Fig. 8). In 1982 and 1983, when ages were known for most birds in the study population, the age distribution was relatively even. Age structure was similar in 1979 through 1981 according to our less complete data. Mortality among older birds combined with recruitment of birds born during the 1983 ENSO resulted in a bottom-heavy age distribution in 1984. The 1983

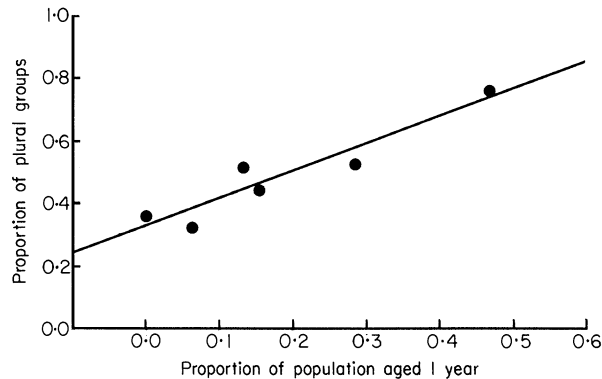


FIG. 9. Relationship between population age structure and the frequency of plural breeding. Omitting 1984, when few pairs nested, the proportion of groups containing more than one breeding female (plural groups) is correlated with the proportion of residents of known age that were yearlings ( $r_s = 0.87$ ,  $n = 6$  years,  $P < 0.05$ ).

cohort continued to dominate the population until recruitment occurred again in 1987 from the 1986 cohort.

#### Group size and structure

Demographic changes influenced group size through the effects of both density and population age structure. Groups contained two to twenty-four adults ( $\bar{x} = 4.2 \pm 2.5$  S.D.,  $n = 221$  group-years), varying annually over a nearly threefold range from 2.6 adults in 1986 to 6.1 in 1984 (group size was not measured in 1978–79; see also Curry 1988a). Mean group size increased with total adult density ( $r_s = 0.76$ ,  $n = 8$  years,  $P < 0.05$ ), because the number of territories defended remained relatively constant. Group sizes also tended to increase with the proportion of yearlings in the population ( $r_s = 0.5$ ,  $n = 8$  years,  $P < 0.1$ ). Groups were larger, for example, when most birds present were yearlings (1984, 1987) than when the age structure was comparatively even (1980–82), though total density was similar in these years.

The population's age composition also influenced group breeding structure. Up to four females in each group bred ( $\bar{x} = 1.6 \pm 0.7$  S.D.,  $n = 175$  groups in which at least one female nested), and 46% of groups containing more than one. The proportion of plural groups varied from 14% ( $n = 7$  actively-breeding groups) in 1984 to 76% ( $n = 21$ ) in 1987 and increased significantly with the proportion of yearlings in the population (Fig. 9;  $r_s = 0.89$ ,  $P < 0.01$ ,  $n = 6$  years, excluding data from 1984, 1985, and 1988). This correlation resulted from the low dominance status of yearlings, which induced most of those that bred to do so as subordinates. In 1987, for example, 35 of 36 yearlings resided in groups dominated by an older adult, and 22 of 23 yearlings that nested did so as subordinate breeders.

#### Dispersal

Of all birds born in the study area and alive as yearlings, only 33% had left their natal territory (Table 6). The proportion of yearlings dispersing was negatively correlated with total adult density ( $r_s = -0.74$ ,  $P < 0.05$ ,  $n = 8$  cohorts, sexes combined). An association between dispersal and density was especially apparent among males. For example, the high proportion of yearling males (67%) dispersing in 1983 coincided with a drop in density that enabled more yearling males than usual to fill vacancies off their natal



TABLE 6. Dispersal of yearlings from natal territories, expressed as proportion of yearlings living off their natal territory in the breeding season (February) of the year after birth,  $n$  is the number surviving as yearlings; none were present in 1985 or 1986

Cohort	Males	$n$	Females	$n$	Total*	$n$
1978	0.09	11	0.20	5	0.11	19
1979	0.20	5	0.50	2	0.29	7
1980	0.25	12	0.67	6	0.43	21
1981	0.25	4	0.50	4	0.33	9
1982	0.67	6	0.56	9	0.60	15
1983	0.16	25	0.44	27	0.29	63
1986	0.36	25	0.31	13	0.34	38
All cohorts	0.26	88	0.44	66	0.33	172

† Includes birds of unknown sex.

territories. Dispersal by females was less dependent on density because females moving into new territories were courted by resident males, whereas males leaving their territories were usually not accepted (Curry 1988a). In five of seven yearling cohorts, more females than males left their natal territories (Wilcoxon matched-pairs test,  $P < 0.05$ ) and the total proportion of dispersers was higher among females (Table 6).

Dispersal patterns among older birds were similar to those among yearlings. Most females eventually dispersed from their natal territories, even though 47% of females first bred there ( $n = 34$ ). Most males remained in their natal territories throughout their lives, and 62% of males first bred there ( $n = 45$ ).

## DISCUSSION

Strong seasonality and annual variation in rainfall govern the demography of Galápagos mockingbirds. Average values for demographic parameters, and their interaction with the species' use of space and dietary requirements, determine most of the basic features of social organization. Variation in those values caused by changes in climatic conditions result in fluctuations in the size and composition of the population. The changes in social behaviour that follow help to illustrate how climate, through demography, influences sociality.

### *Demographic context of cooperative breeding*

Though they inhabit a climatically variable environment, Galápagos mockingbirds share many of the demographic characteristics of territorial cooperative breeders inhabiting less variable environments. These characteristics include high survival of breeders, stable density of breeders, delayed age of first breeding and reduced dispersal (Brown 1974, 1978, 1987; Ricklefs 1975; Woolfenden & Fitzpatrick 1984). Breeder survival in the mockingbird averages 70%, which is near the middle of the range of values for all cooperative breeders (Brown 1987). Breeding density is among the least variable (C.V. = 21%) of the population's demographic characteristics. Some mockingbirds breed in their first year, but many yearlings and some older birds are unable to do so, and these non-breeders most often act as helpers at the nest. Mockingbird groups are maintained through retention of young whose dispersal is delayed or reduced.

High rates of adult survival cannot alone account for the occurrence of regular cooperative breeding in Galápagos mockingbirds. Adult survival is at least as high, for example, in Darwin's finches (*Geospiza* spp.) inhabiting the same arid lowlands in the Galápagos. Average annual survival in *G. fortis* on Daphne is almost identical (69%; Gibbs & Grant 1987a) to that of *N. parvulus* breeders, and survival is even higher among some cohorts of *G. conirostris* on Genovesa (81% for males and 78% for females; P. R. Grant & B. R. Grant, unpublished data), and in *G. scandens* on Daphne (82%; Gibbs & Grant 1987a). These finches do not maintain social groups for breeding, though helpers have been reported under unusual circumstances on one island (Price, Millington & Grant 1983). Factors other than adult survival must be considered to explain the differences in social structure between these genera.

A critical difference between Galápagos mockingbirds and finches is their territorial behaviour and its effects on breeding density. Use of space by both mockingbirds and finches is determined ultimately by the distributions of food resources. Galápagos mockingbirds subsist on a broad range of arthropods, fruits and other food, which they also feed to their nestlings (Grant & Grant 1979, 1987; R. L. Curry, unpublished data). Because they can find these foods in all available habitats in both breeding and non-breeding seasons, and in wet and dry years, mockingbirds on Genovesa maintain permanent territories over virtually the entire island. Sympatric Darwin's finches also raise their young on arthropods, but during the dry seasons when most are predominantly granivorous they abandon breeding territories to varying degrees (Schluter 1984; Grant 1986); territories in some species (e.g. *G. conirostris*) are usually restricted to areas with high density of cactus (Grant & Grant 1987). Juvenile finches also leave their places of birth 2–4 weeks after fledging and range widely (Grant & Grant 1980) whereas juvenile mockingbirds remain in their natal territories. These differences suggest that seeds are more patchily distributed than are foods used by the mockingbirds, and that the finches are subject to greater seasonality in their food supply. If so, the differences in social organization between the finches and mockingbirds are consistent with the view (Ford *et al.* 1988) that cooperative breeding most often arises in species experiencing reduced seasonality. The differences in social organization between the mockingbirds and finches parallels a general paucity of cooperative breeders among granivorous birds in comparison with insectivores and omnivores (Brown 1978; Ford *et al.* 1988).

Year-round use of all available space by territorial mockingbirds will directly influence survival and breeding characteristics. In an environment saturated with territories, dispersal and breeding must occur amid severe competition within and between social groups. Breeding density may represent a maximum determined by resource availability in wet years: if conditions cannot be predicted even after rains begin, as many mated birds as the habitat will support should attempt to breed on the chance that it will be a wet year (Curry 1988a). Competitive interactions between breeding pairs in plural groups subsequently determines breeding success in drier years; subordinate pairs then have poor success because their nesting is frequently disrupted by dominant birds (Curry 1988a). Annual conditions influence breeding density of finch populations differently because their breeding territories usually do not fill all habitats. Many young *G. conirostris* on Genovesa, for example, live as non-breeding floaters in drier years in areas lacking cactus, but in wet years they establish territories and breed in these same habitats (Grant & Grant 1987).

The lack of available space suitable for new territories, therefore, appears to represent a limiting ecological constraint on breeding in these permanently territorial mockingbirds,

just as it does in other territorial cooperative breeders (Brown 1974, 1987; Koenig & Pitelka 1981; Emlen 1982a; Woolfenden & Fitzpatrick 1984). The relative stability of breeding density is consistent with this conclusion, as is the presence in nearly all years of non-breeding females (Brown 1969). Comparative evidence provides additional support (Curry 1988c). On two other low and arid islands, Champion and Española, habitat diversity is low and mockingbird territories fill all available space. On these islands, groups average 3.5 and 8.9 adults respectively. In contrast, on San Cristóbal, where habitat diversity is much greater and territories do not fill all habitats, groups average only 2.3 adults and the proportion of birds not breeding is correspondingly reduced. Groups are therefore smaller where more space for territories is available. Differences in resource distributions among habitats and high rates of predation by introduced mammals are two possible reasons why territories on San Cristóbal do not fill all available space (Curry 1988c).

The limiting influence of territorial space on breeding in Galápagos mockingbirds differs from factors thought to constrain breeding in colonial cooperative breeders inhabiting climatically variable environments. In several such species, variation in resource availability, influenced directly or indirectly by climatic variation, may act as an ecological constraint by sometimes making costs of breeding prohibitively high (Emlen 1982a, 1984; Marzluff & Balda 1988). However, at no time in our study did groups coalesce or disintegrate as would be expected if dispersal were determined solely by prevailing conditions and their effects on costs of breeding. Yearling mockingbirds do seem to be more sensitive than older adults to the suitability of conditions for breeding: whereas most paired yearlings bred in 1983 and 1987 when conditions were clearly favourable, few yearlings nested in 1984, though many had formed pairs, during apparently poor conditions. Nonetheless, the structure of territorial groups was maintained in 1984 and throughout the drought in 1985.

Intrinsic advantages of group living on Genovesa do not appear to be sufficiently large by themselves to account for delayed breeding and reduced dispersal. The effect of helpers on breeder reproduction is smaller than in some other cooperative breeders (e.g. Rabenold 1984; Austad & Rabenold 1985), primarily because mockingbird helpers do not reduce rates of predation on nests (Kinnaird & Grant 1982; Curry 1987). Mockingbirds lack a sentinel system, they do not forage as a group, and they do not make improvements (e.g. for storing food) to their territories, factors which confer benefits to several other group-living birds (e.g. Woolfenden & Fitzpatrick 1984; Stacey & Ligon 1987; Koenig & Mumme 1987).

#### *Effects of climatically-induced demographic variation*

Changing climatic conditions have both direct and indirect effects on demography in the Genovesa population. The largest source of demographic variation is in the seasonal production of fledglings (C.V. = 92%), primarily attributable to variation in the length of breeding seasons. Large numbers of fledglings are produced in exceptionally wet years, whereas none are produced in drought years. Juvenile survival (C.V. = 47%) and adult survival (C.V. = 29%) vary less. Adult mortality is relatively high in some wet years, partly because of increased incidence of disease, and in extremely dry years, probably because of starvation. Variation in natality and survival produce variation in population density (C.V. = 29%). These levels of variation are not exceptional. Adult survival is similarly variable in *Geospiza scandens* (C.V. = 27%) and more than twice as variable in *G. fortis*

(64%; Gibbs & Grant 1987a). Population size also varies more in both *G. scandens* (C.V. = 42%) and *G. fortis* (C.V. = 82%; Gibbs & Grant 1987b) than in *N. parvulus*.

Demographic variation in the Genovesa mockingbird population is nonetheless sufficiently large to cause changes in social behaviour. Because breeding density appears to be limited by space for territories, changes in total density determine the proportion of birds able to breed and, inversely, the proportion acting as helpers. Nearly every bird breeds during density troughs, and with few non-breeders present the proportion of birds helping declines. At high density, the proportion of birds unable to obtain space for breeding is large, and so is the incidence of helping. These patterns arise because non-breeders most frequently act as nest helpers. The correlations are not trivial because some individuals neither breed nor help and some breeders also act as helpers (Curry 1988b).

Changes in adult sex ratio further influence relationships between breeding, helping, and density. A preponderance of males can be considered normal for the population, given that males tend to survive better on average than females. The reasons for this difference are not clear, but we can suggest two possibilities. First, females suffer higher mortality on territory during times of food scarcity because most are smaller and socially subordinate to males (Curry 1988a). Second, females disperse at an earlier age and further than males (this study; R. L. Curry & P. R. Grant, unpublished data). Dispersing females may suffer increased mortality by having fewer feeding opportunities, as a result of being chased more often.

When males predominate in the population some do not breed, because at these times mockingbirds pair monogamously and never polyandrously. This feature is consistent with previous studies suggesting that limited availability of mates is a constraint on breeding, and therefore is a factor maintaining helping behaviour (Rowley 1965; Emlen 1978, 1982a, 1984). In *N. parvulus*, however, the role of sex ratio as a constraint on breeding appears to be secondary to the limits imposed by lack of territorial space. In 1987, for example, some birds of both sexes did not breed (Table 2), despite a nearly even sex ratio, when density was high and extra space was not available.

A preponderance of females, such as arose during this study from differential disease-related mortality, might be expected to limit breeding by females, but it does not. When in the majority, females pair polygynously with already-mated males. Females sharing a mate but nesting separately more often act as helpers (for each other) than females that do not breed. Limited availability of mates therefore acts to maintain helping among females not by creating a pool of non-breeders, but by increasing the frequency of polygyny. We know of no previous study demonstrating a difference between males and females in the way that skews in the adult sex ratio influence breeding and helping behaviour. Females rarely or never predominate in populations of most other cooperative breeders.

Variation in demographic parameters may also account for the occurrence of plural breeding in *N. parvulus*. Plural breeding arises when young, subordinate birds attempt to breed without first establishing an independent territory (Curry 1988a). Subordinate breeding appears to be an opportunistic tactic used by birds too young to be able to defend space against older, socially dominant birds. Our hypothesis for plural breeding, then, is that changes in population size and age structure caused by climatic fluctuation or other factors, such as disease, allows birds to breed opportunistically as subordinates. The corollary of this hypothesis is that without variation in population age structure, birds attempt to breed at some constant age when individuals have acquired the ability to defend a territory. In a population with a constant age structure, birds attempting to breed at too early an age will fail in social competition with older adults, even when

environmental conditions are favourable for breeding. If demographic variability is large, on the other hand, changes in age structure will occasionally produce a permissive social environment (relatively few old birds) coincident with good breeding conditions.

This 'demographic variation' hypothesis differs from two other hypotheses for the evolution of plural breeding proposed previously (Brown & Brown 1984; Fitzpatrick & Woolfenden 1986). Both of these assume that the conducive condition for plural breeding is spatial variation in habitat quality, rather than climatic variation. They differ in the mechanism by which this variation influences group size and structure. The three hypotheses are not mutually exclusive. However, neither of the alternatives to our hypothesis specifies a connection between plural breeding and demographic variation caused by fluctuating climatic conditions.

The demographic variation hypothesis is supported by the patterns of breeding as a function of age on Genovesa. When yearlings predominate, plural groups increase in frequency (Fig. 9), because few yearlings can establish their own territories. Instead, those yearlings, and some older birds, that breed do so as subordinates.

The demographic variation hypothesis predicts that plurally breeding species should exhibit greater demographic variation than singularly-breeding species. Data are not available to test this prediction with other mockingbirds, but a preliminary test can be made with data from jays in the genus *Aphelocoma*. In accordance with our hypothesis, demographic variation is low for singularly-breeding Florida scrub jays, *A. c. coerulescens*: coefficients of variation are 11% for annual breeder survival, 26% for juvenile survival, and 38% for the annual proportion of the population that consists of yearlings (Woolfenden & Fitzpatrick 1984). *N. parvulus* is more variable in all respects (C.V. = 25%, 47%, and 106% respectively for the same three parameters). Variation in the proportion of yearlings in a plurally-breeding population of the gray-breasted (Mexican) jay is also more than twice as large (75%; calculated from Brown 1985) as in the congeneric scrub jay. This variation is the result of variation in the number of young produced and in their survival, which for both may ultimately be caused by variation in climatic conditions (Brown 1985). Yearling mockingbirds often breed, but breeding first occurs normally at 2 or more years of age in both *Aphelocoma* jays (Woolfenden & Fitzpatrick 1984; Brown 1985), a difference that complicates comparisons between the genera. However, the preliminary comparison made above remains valid as long as variation in the proportion of yearlings in jay populations in one year correlates with the proportion of 2-year-old mature birds in the next year. The proportion of yearlings present each year in *A. ultramarina* is correlated with group size (Brown 1985), as in *N. parvulus* also. This provides additional support for an association between population age structure and the size of social groups in both of these plurally breeding species.

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