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BREEDING AND SURVIVAL OF GALAPAGOS MOCKINGBIRDS DURING EL NIÑO

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Summary

Mockingbirds began breeding on Genovesa in December 1982 following rain that first fell in November. Breeding occurred until July 1983, with a short break in late February and early March. Some females initiated as many as six clutches. Clutches were somewhat larger on average than in previous years. However, hatching success was unusually low. Fledgling success was normal. The net result was a typical number of fledglings per nest, but repeated breeding yielded a higher overall breeding success per female than in previous years. Most nest failures were attributable to heavy rainfall which killed eggs and newly hatched chicks. Some losses were due to predation by short-eared owls and to parental abandonment.

Population density on Genovesa was unusually low at the beginning of the breeding season. This may have been the result of heavy adult mortality caused by a pox-like disease that continued to appear in the population throughout the breeding season. In areas where disease-related mortality was high, group structure broke down. The incidence of helping at the nest was low, as many subordinate birds bred in

new territories instead of staying on the territories of the dominant birds and helping to raise their offspring.

Elsewhere in the archipelago the symptoms of a pox-like disease were observed on many islands; and population sizes did not increase greatly despite extensive breeding. For example, on the islet of Champion the breeding season apparently spanned eight months but the population size remained approximately stable at 45 birds.

Resumen

Los cucubes empezaron a reproducirse en Genovesa en Diciembre de 1982 después de las primeras lluvias que cayeron en noviembre. Hubo reproducción hasta julio de 1983, con una pequeña interrupción a finales de febrero y comienzos de marzo. Algunas hembras iniciaron hasta seis nidadas. El número de huevos por nido fue algo mayor en promedio que en los años anteriores. Sin embargo, el éxito de eclosión fue extremadamente bajo. El éxito en la salida del nido por parte de los juveniles fue normal. El resultado neto fue un número típico de juveniles por nido, pero la reproducción repetida produjo un éxito mayor por hembra que en los años anteriores. La mayor parte de fracasos de anidación son atribuibles a las lluvias que mataron a los huevos y a los pollitos recién eclosionados. Algunas pérdidas se debieron a predación por parte de lechuzas y a abandono del nido por parte de los padres.

La densidad poblacional en Genovesa fue extremadamente baja a comienzos de la estación reproductiva. Esto pudo deberse a una alta mortalidad de adultos causada por una enfermedad ("pox-like") presente en la población durante toda la estación reproducti-

va. En áreas en donde la mortalidad relacionada con la enfermedad fue alta, la estructura del grupo se alteró. La incidencia de ayuda en la anidación fue baja, ya que muchas aves subordinadas se aparearon en nuevos territorios en vez de quedarse en los territorios de aves dominantes y de ayudarles a éstas a criar su prole.

En otras partes del archipiélago los síntomas de la enfermedad se observaron en muchas islas, y los tamaños poblacionales no se incrementaron significativamente a pesar de la reproducción extensiva. Por ejemplo en el islote Champion, la estación reproductiva aparentemente duró ocho meses, pero el tamaño de la población se mantuvo relativamente estable con 45 aves.

INTRODUCTION

In this paper, I will describe the effects of the 1982-83 El Niño on the breeding biology and social organization of Galápagos mockingbirds (*Nesomimus spp.*). I will concentrate primarily on results from Isla Genovesa, where I have studied mockingbirds (*N. parvulus bauri*) since 1981 following earlier work by Peter Grant and colleagues from 1978 through 1980. I will supplement this information with results from Champion, where we have monitored the small mockingbird population (*N. trifasciatus*) since 1980, and with casual observations made on other islands.

Gifford (1919) was the first naturalist to describe the general aspects of mockingbird breeding in the Galápagos. He made observations on several islands during the California Academy of Sciences Expedition of 1905-06, and found that mockingbird nest-

ing occurred during the wet/warm season, which usually falls between January and May. This pattern of breeding is typical of small Galápagos landbirds (see Lack, 1950; Grant & Boag, 1980). Of later observers, only Venables (19140) happened to study mockingbird nesting during an El Niño year; his study during 1939 took place at the start of what was probably the most extreme El Niño in this century prior to 1982-83 (Grant, 1984; Grant & Grant, this volume). Despite this fact, nesting of *N. melanotis* on San Cristóbal that year began in January and ended by late February, matching the chronological pattern of a "normal" year. More recent studies of *N. macdonaldi* on Española (Hatch, 1966; Groves, 1974) and of *N. parvulus parvulus* on Santa Cruz (Vargas, 1980) have confirmed that mockingbird nesting usually does not begin until after the first heavy rains, and it ends before or soon after the rains cease; three clutches at most are produced under "normal" conditions.

Mockingbird breeding and feeding on Genovesa was first studied in 1978. During this roughly normal year, the Grants discovered that helpers were feeding young at many nests (Grant & Grant, 1979). The Genovesa mockingbirds, therefore, are cooperative breeders. Because cooperative breeding is currently an important topic in evolutionary biology, (see reviews by Brown, 1978; Emlen, 1978) the Genovesa study has continued. Mockingbirds on Genovesa live in groups that defend collective territories, and helping-at-the-nest is a regular feature of their social organization. The basic features of this system have been described by Kinnaird & Grant (1982). In my own work, I am attempting to answer questions about the evolution and ecology of cooperative breeding in Galápagos mockingbirds as a group. Study of *N. trifasciatus* on Champion was initiated in 1980 to see if cooperative breeding was common to other mockingbirds in Galápagos and to determine what aspects of social behavior differ among the islands (see N. Grant,

1983). The long-term study on Genovesa, and comparisons from less intensive study of the Champion mockingbirds, form the basis of my research.

The results I report here are particularly interesting for two reasons. First, we can determine the effects of El Niño on general aspects of mockingbird breeding biology by comparing 1982-83 results with those from five preceding years. Secondly, we can determine the effects of the heavy and prolonged rainfall of 1982-83 on the social behavior of the mockingbirds. Without the years of study leading up to the recent El Niño, we would not be able to assess adequately the full impact of this amazing climatic phenomenon on the mockingbirds of Galápagos.

BREEDING BIOLOGY

Mockingbirds on Genovesa probably began breeding in December 1982, following rain that began in November (see Grant & Grant, this volume. When I initiated fieldwork on 31 December, there were some recently fledged young in the study area, but none that had been out of the nest for more than a few days. Given that the nestling period averages about 13 days, incubation 12 days, and laying 4 to 5 days (Grant & Grant, 1979) it is likely that the nests that produced these young were initiated on or about December 1. Many territories at this time did not have fledged young; it is likely that many of the early nests were destroyed by heavy rain, especially during an archipelago-wide storm on 15 December. Pairs with and without fledglings immediately initiated second clutches, with some females overlapping the start of laying with the end of the nestling period of their preceding nest.

The distribution of nest starts and rainfall for the past four seasons is shown in Fig. 1. Some

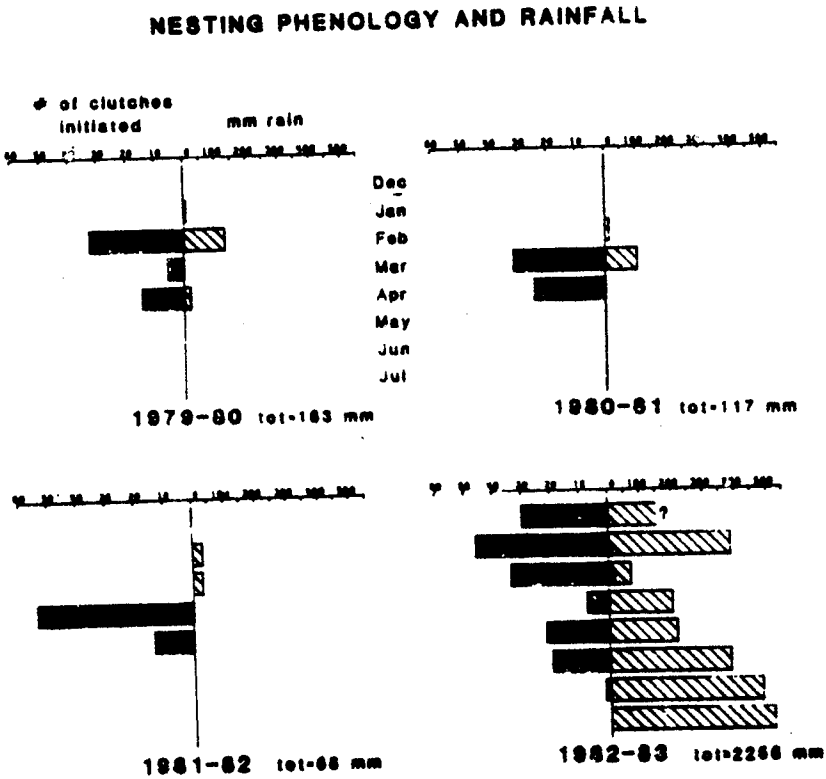

Figure 1. Clutch initiation in relation to rainfall on Genovesa during the years 1980-1983.

female mockingbirds initiated as many as six clutches during the extended 1982-83 season (Table 1). Breeding was nearly continuous between December and July. The only break during the season occurred in late February and early March, following a period of about two weeks with only trace amounts of rain in February. Though food supplies were not quantified throughout the season, it appeared that insect densities dropped quickly during this dry spell, particularly because it coincided with clear skies, intense

Table 1. Number of females attempting to breed 1-6 times on Genovesa in 1980-83.

N = total number of females breeding in the study area.

		Number of Nests Initiated					
	N	1	2	3	4	5	6
1980	74	59	14	1			
1981	60	55	5				
1982	54	41	13				
1983	58	22	7	10	9	6	4

Table 2. Mean (X) clutch size on Genovesa, with one standard error (SE), for the years 1980-83.

N = Sample size.

	Clutch Size		
	N	X	SE
1980	46	3.65	0.64
1981	62	3.87	0.59
1982	59	3.81	0.57
1983	113	4.36	0.64

solar radiation, and high temperatures. During this period, nestlings starved, and the mockingbirds delayed starting their next nests. Mockingbird nest-

Table 3. Percentage of 1983 nests on Genovesa in which some, all, or no eggs hatched.
N = sample size of nests.

		Eggs Hatched		
	N	None	Some	All
1980	51	9.8	21.6	68.6
1981	65	18.5	44.6	36.9
1982	63	19.0	39.7	41.3
1983	120	35.0	47.5	17.5

Table 4. Mean fledglings/female/season (X) for the years 1980-1983 on Genovesa.
N = sample size, SE = standard error.

	Fledglings/Female			
	N	X	SE	Range
1980	84	2.08	2.18	0 - 9
1981	60	1.42	1.46	0 - 5
1982	54	1.28	1.31	0 - 4
1983	58*	2.55	2.60	0 - 9

*Females that may have bred in December 1982, but who died shortly after study resumed, are not included in the 1983 totals.

ing resumed as soon as the rains returned in later march. The last mockingbird nest on Genovesa was initiated on 22 June, and all breeding had ceased when the final chick in this nest died on 22 July. The reason why breeding did not continue past this date is unclear, since more rain fell during the first three weeks of July than in any other equivalent period during the year. It is probable that the vegetation responded in a different way to this late rain than it had earlier, hence affecting insect abundance and mockingbird breeding (see Grant & Grant, this volume). Density-dependent effects may also have begun to predominate in the mockingbird population (see below).

Table 5. Percentage of nests failing or succeeding following hatch of at least one egg on Genovesa.

N = sample size of nests.

		Failed	Successful
	N	(0 Fledglings)	(≥ 1 Fledglings)
1980	46	41.3	58.7
1981	53	37.7	62.3
1982	51	39.2	60.8
1983	79	46.8	53.2

Success of individual nesting attempts by mockingbirds on Genovesa was not greatly affected by the El Niño conditions. Clutch size was higher than in previous years (Table 2), particularly for clutches initiated early in the season. Mockingbirds appeared

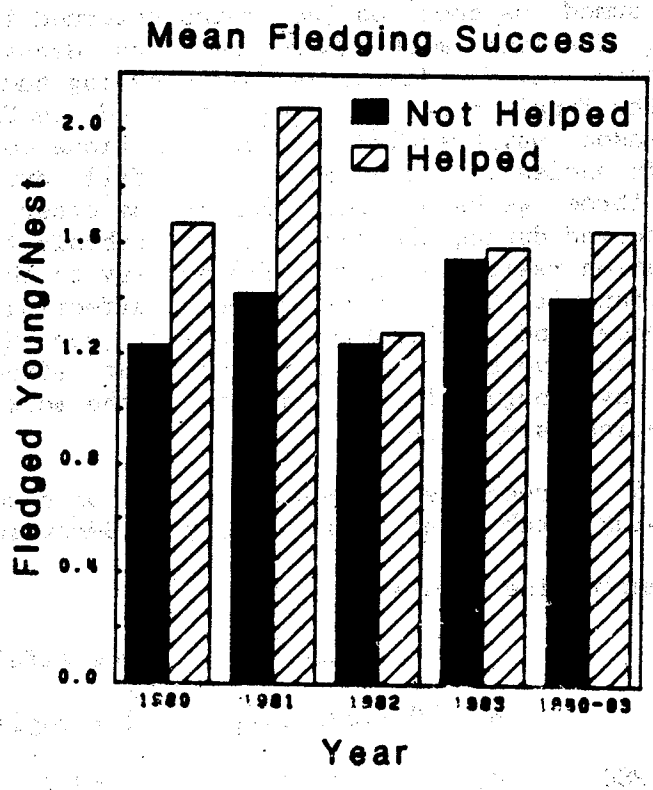

Figure 2. **Mean annual fledging success at nests with and without helpers, Isla Genovesa.**

to adjust their clutch size to exceptional rainfall to a greater degree than do Darwin's finches (Grant & Grant, this volume).

Increased clutch size was, however, largely offset by decreased hatching success. The proportions of nests in which all, some, or none of the eggs hatched differ significantly among the years 1980 through 1983 (Table 3). Decreased hatching success was followed by a normal fledgling of hatched

young (Table 4). The proportion of nests fledgling at least 1 young following successful hatch did not differ significantly among years (Table 5), although it was lowest in 1983. The final result was that the mean number of fledged young per nesting attempt was comparable with previous years (Fig. 2). This contrasts with the decreased number of fledglings per nest in Darwin's finches. Most mockingbird nest failures were attributable to heavy rainfall, especially when eggs or newly hatched chicks were chilled during prolonged showers. Other losses were due to predation by short-eared owls or parental abandonment. Mockingbirds did not appear to suffer heavily from intraspecific predation (infanticide), though I did observe wandering immature mockingbirds inspecting nests. These birds were usually chased away immediately by the resident birds, and probably seldom had opportunities to break or steal eggs, or eat nestlings. The absence of this mortality factor in the mockingbirds appears to explain the difference in success per nest between mockingbirds and Darwin's finches on Genovesa (see Grant & Grant, this volume).

Because most females nested repeatedly throughout the season and had good reproductive success per nest, the average success per female was significantly higher for the 1982-83 season than in previous years (Table 4). This success had direct effect on the size of territorial groups and on the density of the mockingbird population as a whole. These results are described in the following section.

DEMOGRAPHY

Early in the season, population density in the study area on Genovesa was as low or lower than at any previous point in this study. Some mortality is expected during any dry season; juvenile survival is

usually low but adult losses are not great, averaging about 20 percent from year to year. As soon as I arrived on Genovesa in December, it became apparent that many adults in the study area had disappeared while recruitment of 1982 juveniles had been typically low. About 100 adult mockingbirds were present in 24 groups. I attribute the bulk of the adult mortality to a pox-like disease that was affecting many mockingbirds in December. I observed birds with lesions symptomatic of this infection throughout the season, and many affected birds subsequently disappeared and are presumed to have died. Avian pox virus has been observed on Santa Cruz and another islands, especially those inhabited by humans and their domestic animals, since at least 1905, when affected birds were common on San Cristóbal (Gifford, 1919). Lesions are found especially about the bill, eyes, and mouth, but many other parts of the body can also be affected (e.g. the skin on the wings and chest and the feet).

Some territorial mockingbird groups on Genovesa were not affected by disease, and the structure of those groups was comparable to previous years (see below). Losses due to disease were quickly offset by recruitment of fledged juveniles as the season progressed, despite the fact that both adults and young mockingbirds with pox-like symptoms continued to disappear. By July, approximately 400 marked mockingbirds were resident in the study area, compared to less than 200 at the end of the previous breeding season. The largest group at this time contained 15 birds, with 9 of them birds-of-the-year on their natal territory. Group size normally ranges between 2 and 10 birds on Genovesa (Curry, in prep).

SOCIAL BEHAVIOR

In territories where few birds died due to disease, group integrity was maintained throughout the season. Despite steady increase in group size as successful nesting continued, dominance hierarchies among the adults were sustained; no groups had fissioned by the end of the season.

As in the preceding years many subordinate males were able to attract mates into their groups. During El Niño, the nesting of these subordinate pairs was particularly successful - their breeding efforts were not disrupted by more dominant birds as they are during more typical years (Curry in prep). Nest of subordinate pairs seldom have helpers, so the increased breeding of subordinates added to the proportion of nests without helpers. In addition, no subordinate males helped and bred simultaneously, though this did not occur in other years (Curry, in prep). Furthermore, the number of 1- and 2-year old males that most frequently act as helpers (Kinnaird and Grant, 1982) was reduced by disease-related mortality. The combination of these factors resulted in a large, though not statistically significant, decrease in the overall incidence of helping (Table 6). Note that the proportion of nests with helpers in 1983 (31.9%) was still larger than the 28% reported by the Grants for 1978, but the real proportion of nests with helpers in that year was probably higher (Grant & Grant, 1979).

Those birds that did help during El Niño had little effect on breeding success; the average number of fledglings was similar for nests with and without helpers (Fig. 2). Though I have not yet analyzed

Table 6. Proportion of nests with helpers on Genovesa, 1980-83.

	Number of Nests		Percent
	Without Helpers	With Helpers	With Helpers
1980	26	18	40.9
1981	26	24	48.0
1982	29	25	46.3
1983	62	29	31.9

data on nestling diets and feeding rates by the different participants, suitable food appeared to be superabundant throughout most of the season, except in March (see above). Since reproduction was limited by losses during hatching (see above), helpers were unable to increase output of fledglings. Some juveniles helped at their parents' nests, but had no more effect on success than did adult helpers.

In areas where disease-related mortality was high, group structure broke down. This occurred especially, but not always when the highest ranking male was among those that died. Some adults and many juveniles, both from outside the study area and from neighboring territories, collected in these largely vacant areas. The adults eventually settled and nested, but the juveniles wandered singly or in loose bands. Territory boundaries were not reestablished, and the young birds, unrestricted by normal dominance interactions and territories, plundered many finch nests. Group structure had still not emerged by the end of the breeding season, but territory boundaries

and group affiliations were apparent among the same birds by December 1983 (pers. observ.).

OTHER ISLANDS

I do not have any data to indicate when breeding began on Champion. No fledglings were obvious on the islet in mid-January (G. Robinson, pers. comm.), though it is likely that the mockingbirds were nesting at that time. I made very brief visits to Champion in late March and late May. In March, there were fledglings as well as additional nests in progress in most of the islet's 10 territories. Vegetation here was very thick and the vines and herbs, especially *Mentzelia*, made walking nearly impossible. The mockingbirds, perhaps to avoid the clinging leaves of this ground layer, spent most of their time in the large *Opuntia* trees, and nestlings were being fed newly-molted locusts (*Sphignonotus tetranesiotis*). One nest with chicks was being attended by at least four adults; *N. trifasciatus* is certainly a cooperatively breeding species.

Breeding on Champion was still underway in May. I estimate that the nests then present were either third of fourth clutches. Several nests contained the combined clutches of two females, with both incubating; communal nesting of this kind occurs rarely but regularly on Genovesa as well (Curry, in prep). Though the data are not complete enough for detailed analysis, it appears that success per nest was low on Champion - several territories that had nests with eggs in March had no additional fledglings in May. Though there may have been other factors, some losses were probably due to disease. Mockingbirds with pox-like symptoms similar to those on Genovesa were present during both of my visits.

Subsequent work on Champion has revealed that breeding on the islet continued into at least late August, since we found mockingbirds in juvenile plumage in December 1983. The net effect of El Niño on Champion was neutral - the size of the relict mockingbird population on this islet remains stable at about 45 birds. The majority of the population now consists of young birds, as juveniles have replaced older birds that died from disease.

Fragmentary breeding data are available from only two other islands. There were no mockingbird fledglings in the vicinity of CDRS on Santa Cruz in late December 1982, but there was much green vegetation. Early nests here were probably rained out, especially by the intense storm on 15 December. Breeding near CDRS was still in progress in June 1983. On Española, there were still some active nests in late August (M. Iturralde, pers. comm.).

The pox-like disease was apparent on most islands. The outbreak near Puerto Ayore on Santa Cruz was particularly severe early in the season; there were far fewer affected birds by CDRS by June (pers. observ.). Mockingbirds with identical symptoms were also present on Santa Fe (A. Laurie, pers. comm.), and Española (P.R. Grant, pers. comm.). The disease thought to be avian pox is common during most breeding seasons on Santa Cruz, where 28% of chicks were affected in 1980 (Vargas, 1980), but previously affected birds had been seen only rarely on the arid, uninhabited islands.

The demographic shift towards young birds produced by the combination of repeated nesting and adult mortality seems to have taken place on most islands. By early June, the majority of mockingbirds present on Fernandina, Isabela, and Santa Cruz were juveniles (pers. observ), as on Genovesa and Champion.

DISCUSSION

The principal effect of the El Niño on Galápagos mockingbirds was the prolongation of conditions favorable for breeding. In a typical year, the wet, season is brief, beginning in January and often over by late February. In these years, few mockingbird pairs are able to raise more than one brood. Fledgling success of additional clutches is reduced by starvation of nestlings, since parents are unable to find adequate food as the vegetation quickly dries out. During El Niño, heavy rain resulted in an advance in the onset of nesting by about two months. Nearly continuous rainfall in the months that followed prevented the vegetation from drying and caused it to grow profusely. Without the normal decline in breeding conditions, the mockingbirds nested continuously. Breeding ended only when most females had attempted several clutches, some as many as six. Though rain continued to fall into July, it appears likely that insect abundance had begun to decline by June, coinciding with the last few nest starts on Genovesa. By the time the last nest terminated - its nestlings apparently starved - the breeding season for the mockingbirds had lasted at least eight months. The El Niño, then, had a largely favorable effect on Galápagos mockingbirds.

The advantageous continuation of breeding conditions, though, was offset in two important ways. One of these, decreased hatching success, is a direct result of weather conditions -severe storms with torrential rainfall and high winds - that destroyed nests outright or forced females to leave their nests. Highest losses appeared to result from storms lasting several hours; incubating females were eventually forced to leave their nest to forage, and

their eggs became chilled when they did so. Reduced hatching success offset the increase in number of hatchlings that would have been expected from the substantial increase in average clutch size.

The other factor that affected the Genovesa mockingbird population during El Niño was disease related mortality. It is not clear at this time if the incidence of pox-like disease on Genovesa during 1982–83 was directly associated with the El Niño. Avian pox can be transmitted by mosquitos, and mosquito density on Genovesa was certainly much higher than normal during El Niño (pers. observ.). Thus it is possible that the increased density of vectors led to an outbreak of a disease that previously had little effect on mockingbirds. This hypothesis, however, is difficult to reconcile with the observation that other landbird species on Genovesa, which elsewhere are commonly victims of avian pox, were hardly affected at all by the disease that afflicted the mockingbirds on Genovesa. Perhaps the strain of pox virus that was prevalent on Genovesa was specific to the mockingbirds. Alternatively, mockingbird behavior, especially fighting, might contribute to more rapid disease transmission than in the less social finches. We do not know its identity. Its effect was clear, however. Many adult mockingbirds in the study area, and across the entire island, were infected during the breeding season, and many of them disappeared, or were at least so sick as to be unable to raise their young. If so many adult mockingbirds had not been affected by this disease and had continued to breed, the net effect of the El Niño would have been even more favorable, and the resulting density of mockingbirds on Genovesa would have been greatly enhanced.

Aside from repeated nesting, there were few other important breeding responses by the mockingbirds. It appears that by increasing clutch size,

mockingbird females were trying to take advantage of the unusually favorable conditions in order to raise more young than usual. Most, however, were prevented from doing so by the severity of the weather. Another indication that the mockingbirds were doing all they could to maximize reproductive output was the initiation of new clutches before previous broods had fledged. This was particularly noticeable early in the season, when mockingbird density was still low and vegetative growth was increasing rapidly. In general, though, El Niño simply permitted the mockingbirds to keep nesting, rather than causing them to breed in a qualitatively different way.

Similarly, mockingbird social behavior on Genovesa was not greatly affected by the El Niño conditions. The two most important effects were the reduction in the number of nests with helpers and the fact that nests with helpers had no better fledglings success than those without helpers. In some years, helping appears to be the only way some young mockingbirds can achieve any degree of reproductive success, even if indirect. In the El Niño year, however, helping was a less favorable option, and those birds that chose to help rather than breed did not appear to gain as much as they would have done had they bred. This combined with the fact that many young birds, which in a normal year probably would have helped, chose instead to breed, and did so successfully, suggests that when conditions are extremely favorable for breeding, the cost-benefit balance between helping and breeding shifts toward breeding. This aspect of mockingbird biology on Genovesa will be dealt with in detail in forthcoming papers.

The combination of repeated successful breeding, maintenance of the social system, and disease-related mortality produced, by the end of the season, two different results. In those groups that happened to be spared the effects of disease, group integrity was

maintained and the size of these groups increased markedly due to recruitment of juveniles. In other parts of the study area, there were no structured groups by the end of the season: either whole groups had succumbed to disease, or their dominant birds had died and the groups disbanded. In these areas, a large number of juveniles, many produced in adjacent intact groups, settled but failed to establish groups. With adults to enforce dominance relationships, interactions among birds in these areas continued to be chaotic, though some older immature birds had begun to establish site dependent dominance by late in the season. Similarly, without adults to chase off intruding juveniles, these areas experienced a steady stream of wandering mockingbirds. One result of this situation was obvious: finches attempting to nest in these areas suffered very high nest predation by mockingbirds. Without the matrix of adult territories to limit the movements and density of juvenile mockingbirds, they were able to effectively scour large areas of all finch nests (see Grant & Grant, this volume).

It is impossible at this point to determine the extent to which the effects of El Niño on the Genovesa mockingbirds were typical of mockingbirds on other islands. The meagre data available suggest that pox-like disease was prevalent throughout the archipelago; this supports the idea that the prevalence of the disease was affected directly or indirectly by the unusually heavy rainfall. By June, juvenile mockingbirds appeared to outnumber adults on many islands, indicating that breeding was successful throughout the archipelago. None of the data from Champion differ substantially from those collected on Genovesa, though for unknown reasons, mockingbird breeding ended earlier on Genovesa than at some other islands, including Champion.

In 1984, I will conduct a comparative study of all four species of *Nesomimus*. Though it will not be

possible to fully assess the effects of El Niño in this way, I will at least determine whether or not the biology of the different mockingbirds varies substantially during the recovery period following this historic climatic phenomenon.

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