Group structure, within-group conflict and reproductive tactics in cooperatively breeding Galápagos mockingbirds, *Nesomimus parvulus*

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**Abstract.** Reproductive conflict within groups can be an important feature of cooperative breeding systems, especially when more than one individual of a sex breeds within a social group. Relationships between group structure, dominance, within-group conflict and reproductive tactics of cooperatively breeding Galápagos mockingbirds were examined on Isla Genovesa. Territorial groups of 2–24 adults included up to three breeding females, with 42% of the groups containing more than one (plural groups); females in most plural groups nested separately. Territory size increased with group size, but the area available per pair in plural groups was smaller than in singular groups (groups with only one breeding pair). Most pairings were monogamous, and males usually outnumbered females; high-ranking males obtained mates more frequently than subordinate males. In 3 relatively dry years, but not in a wet El Niño year, subordinate pairs in plural groups fledged fewer young than dominant pairs or pairs breeding in singular groups. Interference by dominant breeders, often leading to abandonment of nests by subordinate pairs, appears to account for these differences: through nest disruption in drier years, dominant individuals may reduce the cost of sharing their territories and increase the chances of recruiting helpers. Dominant males in plural groups may also father young through extra-pair copulations with subordinate females. Despite costs imposed by within-group conflict, subordinate breeders have higher long-term reproductive success than birds that defer breeding. Plural group structure is maintained because unpredictable climatic variation favours opportunistic breeding by subordinates.

Cooperative breeding systems can be defined by the presence of individuals (helpers) that participate in rearing young other than their own offspring (Brown 1987). Although cooperative breeding is of evolutionary interest because of the aid-giving behaviour of helpers, conflict is also conspicuous in many cooperatively breeding populations. Reproductive conflict may be expected if cooperative breeding is promoted by ecological constraints because if breeding opportunities are limited by ecological factors, individuals should compete for the chance to breed (Brown 1974, 1978; Zahavi 1974, 1976; Gaston 1978a; Emlen 1982a, b).

Reproductive competition can result in an association between dominance and reproductive success. In species where only one pair breeds in each group (singular breeding; Brown 1978), breeders are nearly always the most dominant individuals (e.g. Woolfenden & Fitzpatrick 1977; Rabenold 1985). Dominant birds may prevent lower-ranking group members from breeding by mate guarding (Mumme et al. 1983a), by inducing hormonal changes that make subordinates effectively sterile (Reyer et al. 1986), or by monopolizing resources essential for breeding (Woolfenden & Fitzpatrick 1977). In singular groups, conflict can be conspicuous when birds contest a vacancy caused by the death of a breeder (e.g. Koenig 1981; Hannon et al. 1985; S. Zack & K. Rabenold, personal communication) or during times of resource scarcity (Hannon et al. 1987).

The relationship between dominance and reproductive success is more complex, and reproductive conflict can be particularly conspicuous, when more than one bird of each sex breeds in each group. Competitive interactions can then take two forms. In the first, cooperative polyandry, multiple males may compete for matings with a single female and the frequency of mating may be correlated with dominance rank (Faaborg & Patterson 1981; Davies 1983, 1985; Mumme et al. 1983a). In the second, groups can include more than one breeding female (plural breeding; Brown 1978). Behaviour occurring in plurally breeding groups can include extra-pair copulation and intraspecific parasitism (Emlen & Wrege 1986), as well as destruction of eggs or chicks (Vehrencamp 1977; Trail et al. 1981; Mumme et al. 1983b; Mock 1984;...
Emlen & Wrege 1986). Such behaviour appears to represent reproductive tactics by which individuals attempt to maximize their fitness in a complex society.

The purpose of this paper is to investigate relationships between group structure, dominance-related conflict and reproductive tactics in the Galápagos mockingbird, *Nesomimus parvulus*. Four allopatric species of mockingbird are endemic to the Galápagos; they live in groups occupying collective territories on all islands studied to date (Hatch 1966; Curry 1987). Helping occurs commonly in *N. parvulus* on Isla Genovesa (Grant & Grant 1979; Kinnaird & Grant 1982; Curry 1988), as does in most other mockingbird populations in the archipelago (Curry 1987). This paper addresses three questions concerning interactions within groups of *N. parvulus* on Genovesa. (1) How does group structure and dominance influence reproductive success? (2) What forms of reproductive conflict occur within groups? (3) How do reproductive tactics vary with dominance status and sex, and what are the fitness consequences of status differences? Answers to these interrelated questions can be used to consider how mockingbirds maximize personal reproduction in a complex cooperative breeding system, and to explain how plural group structure is maintained.

**METHODS**

Group structure and breeding behaviour of mockingbirds on Genovesa were studied between 1980 and 1984. Genovesa is a small, low island situated at the northeast extreme of the archipelago (Fig. 1). Except for small areas of littoral vegetation, the island is covered with uniform scrub woodland; permanently resident mockingbirds are abundant throughout. Research on mockingbirds on Genovesa began in 1978 (Grant & Grant 1979) and continued in 1979 and 1980 (Kinnaird & Grant 1982), but observations during breeding in 1978 and 1979 were not sufficiently complete for an analysis of group structure. I monitored the population during breeding (January–May) in each year, 1981–1984. Additional observations were made by P. R. Grant and coworkers, primarily during June through August each year.

Marked mockingbirds were studied in a semi-circular plot measuring approximately 25 ha in 1980 and 40 ha in 1981–1984. Resident adults and juveniles were captured in mist nets or small wire traps and were weighed, measured and colour-banded. Nestlings were given complete colour combinations while still in the nest, 8 days after hatching. Sex was determined from measurements of length of the flattened wing of birds at least 6 weeks old, as in Kinnaird & Grant (1982), and from observations of breeding behaviour. Classifications based on measurements were confirmed by observations of breeding behaviour with few exceptions (less than 1%). Year of birth was known precisely for birds banded as nestlings or in immature plumage, which is retained for 6–9 months after fledging. Mockingbirds in this population are capable of breeding during their first year (Kinnaird & Grant 1982; Curry 1987), so I classified all birds in adult plumage, including those born during the previous breeding season (yearlings), as adults.

To investigate relationships between group structure and reproduction, I examined 21–38 group territories during breeding each year. I defined a group territory as the area occupied by a dominant (alpha) male and defended by him against other alpha males. All additional birds resident in each alpha male’s territory were classified as members of that male’s group. These additional group members remained within the group territory for most foraging and all breeding activity, and most assisted the alpha male in defending the territory. Territories were mapped on detailed study-area maps drawn from aerial photographs and on-site measurements. Territory borders were demarcated by the ranges of residents and, most clearly, by locations of ‘flick-fight’ displays (Kinnaird 1982), which occurred almost daily at many locations. Most borders remained stable through entire breeding seasons; a few remained unchanged after 5 years. Estimates of territory size were calculated from counts of dots of known density on a computer-generated pattern superimposed on each year’s territory map.

Kin relationships within groups vary with sex because of differences in dispersal patterns (Curry 1987, 1988). Male mockingbirds belonging to the same group tend to be close relatives, because most males remain in their natal territory throughout their lives. Females more often disperse, but yearling females can breed in their natal territories before joining another group later in life. These patterns are loosely associated with sex differences in helping behaviour. Most helpers are young
males, predominantly non-breeders and breeders whose nests have failed, and they direct their help preferentially to nests containing closely related nestlings (Curry 1988). Most females breed and few act as helpers, even when living among close relatives.

During each breeding season all reproductive activity in the study area was monitored. All nesting followed periods of rainfall. A normal breeding season occurred between January and May in each year, 1980–1982, during which individual pairs produced up to three clutches. An unusually large amount of rain associated with El Niño–Southern Oscillation conditions fell between December 1982 and July 1983 (Grant & Grant 1987); some pairs initiated up to eight clutches during the prolonged breeding period that resulted (Curry 1985). In 1984, only eight pairs produced clutches following a small amount of rain, and all nest attempts failed, so I excluded these from subsequent analyses of reproductive success. Most nests in the study area were located during nest-building or incubation. Contents of active nests were checked at least every 3 days. I classified chicks as successfully fledged only if they were resighted after leaving the nest.

I classified nest ownership and breeding roles on the basis of observations of pair bonds and nesting activity. I assigned maternity to the female(s) that built a nest and incubated its clutch. No nest containing a normal clutch (up to five eggs) was incubated by more than one female. Two females incubated at only four nests containing seven or eight eggs; at these joint nests, both females were classified as breeders. I classified each male paired to a maternal female as the nest owner and a breeder. Paired males remained physically close to their females prior to laying and interacted with her regularly; they also built and defended the nest, and nearly all fed the nestlings.

Dominance rankings within groups were determined from ad libitum observations of interactions. When approached or threatened by higher-ranking group members, subordinate Galápagos mockingbirds crouch and give loud, strident calls in a ritualized display similar to juvenile begging (Hatch 1966; Bowman & Carter 1971). Males sharing a territory interact frequently; low-ranking males give nearly continuous begging calls when in sight of the alpha male. Females interact less often with other group members but their relative dominance positions are obvious when they do. Because reversals of dominance rank occur rarely, I was able to determine intrasexual hierarchies within groups that persisted across entire breeding seasons and usually lasted several years. To test for associations between dominance, group structure and reproductive success, I divided breeding pairs into three categories based on the dominance status of males and the structure of their groups; classifications of females, in this analysis, correspond to those of their mates. Pairs in singular groups were termed singular breeders. In each plural group, the highest-ranking breeding male and his mate (or mates) were classified as dominant breeders. Other breeders in plural groups were classified as subordinate breeders; dominance relationships among them were discernible and were considered in some analyses. Comparisons of components of reproductive success were then made among pairs in the three categories.

I used similar classifications of breeding and dominance status to investigate relationships between status and both survival and transitions in status. In addition to the three breeding-status categories, resident birds that did not nest were classified as non-breeders. Survival was estimated from sightings of marked individuals. The study area was monitored continuously for the presence of residents, and a zone approximately two territories wide (about 200 m) peripheral to the study area was checked monthly for presence of marked dispersers. Birds were assumed to have died shortly after the last recorded sighting, so the survival values reported are minimal estimates. The proportions of birds in each dominance and breeding category that survived and remained in the study area in the following year were used to estimate transition probabilities between status categories as functions of sex and status. In calculating transition probabilities, I did not distinguish between singular and dominant breeders; both were classified as dominant breeders.

Kruskal–Wallis ANOVA was used to test for variation in group size among years and in reproductive success among dominance classes. Size of completed clutches was normally distributed, so for this variable I also used two-factor parametric ANOVA to test for effects of both year and dominance status simultaneously. For tests of association among categorical variables, statistics (G) include Williams's correction where appropriate (Sokal & Rohlf 1981). All tests are two-tailed unless otherwise noted.
RESULTS

Group Size and Structure

Most mockingbirds resident in the study area were members of groups that defended territories throughout the year; only 3% of the population consisted of floaters that were not associated with any group (total N = 844 bird-years). During each breeding season, group territories filled all habitat in the study area (e.g. Fig. 1) except late in 1983 following a period of heavy adult mortality (Curry 1985, 1987). Groups included 2–24 adults, (X ± se = 4·3 ± 0·21, N = 149 group-years). Mean group size varied among years (Fig. 2; Kruskal–Wallis H = 9·7, df = 4, P < 0·05), reflecting variation in survival of adults and in production and survival of young (Curry 1987). For example, groups were unusually large in 1984 because (1) breeding was prolonged in 1983, so many yearlings were present in 1984, and (2) several groups coalesced in late 1983 after all adults in some territories died from disease; surviving juveniles from these territories were incorporated into adjacent groups dominated by older adult neighbours not known to include close relatives.

Variation in group size among years was reflected in the proportion of territories occupied by simple pairs. Over all 5 years, 75% of the groups included more than two birds; this proportion varied annually, ranging from a low of 59% in 1983 to 90% in 1980 (G = 8·2, df = 4, P < 0·1). The proportion of birds living in groups larger than two totalled 88% for all years combined (N = 637 bird-years), but varied among years (G = 21·1, df = 4, P < 0·005); the proportion ranged from 77% (N = 85) in 1983 to 96% (N = 88) in 1980. Therefore, despite considerable annual variation, group living predominated in the Genovesa population throughout the study.

Regardless of group size, territorial residents occupied positions within stable dominance hierarchies in their groups. Relative status among males was strongly dependent on age. The alpha male was the oldest in its group in all cases where relative ages of all males in a group were known (N = 23 groups). Between 1980 and 1982, no group was led by a yearling male. Two yearling males in
1983 and another four in 1984 attained alpha status by replacing older males that died, but none of these displaced a surviving older male when acceding to the alpha position. Dominance relationships among males ranking below the alpha male also varied with age. Most beta males were at least 2 years of age, and yearling males were invariably lower-ranking than all older males in the same group. Status varied with age even among males born in the same year. Dominance relationships were determined during 1984 for 16 pairs of males living in the same group for which relative date of birth in 1983 was known; in every case, the older male was dominant over the younger male (binomial test, \( P < 0.001 \)). Dominance relationships among females were more complex, and less strictly age-dependent, because the status of mated females was correlated with the rank of their mates. Most females mated to alpha males were dominant over other females in the same group, displacing or chasing them, at least occasionally, and the reverse rarely occurred. Females were subordinate to males in their groups except that most older females remained dominant over their yearling and 2-year-old sons.

Up to three females nested within each group territory (Fig. 2). On average, each group in which breeding took place contained 1.5 ± 0.05 (SE) breeding females (\( N = 129 \) group-years). In all years
except 1984, when no birds bred in many groups, the number of breeding females increased with increasing group size. The few non-breeding females, however, resided in both small and large groups, so the association between group size and number of breeders is not due solely to different numbers of females. The proportion of groups with more than one female nesting (plural groups) totalled 42% for all years and ranged from 14% in 1984 (N = 7 groups in which at least one pair nested) to 52% (N = 21 groups) in 1980, but did not vary significantly among years (G = 5.5, df = 4, P > 0.1). In most plural groups, females nested separately in nests they built with the assistance of their mates and, less often, helpers. Two females laid jointly in only four (1.2%) of 341 nests belonging to birds of known status. One joint nest involved two females paired to different males. The three other joint nests, all in 1983, belonged to the same two females mated to a single male; earlier in the same season, these two females each nested once separately. All four joint nests failed; one was depredated before incubation began, and of the 23 eggs in the other three nests, only six (26%) hatched, and all the hatchlings disappeared before fledging age. Joint nests are excluded from the analyses of reproductive success below.

Both breeding-season group size and the number of breeding females per group were correlated with increasing territory size. Territory size increased significantly with group size over all years, 1980–1984 (Fig. 3a). The correlation was also significant (P < 0.01) in each year except 1983 (P = 0.1). Because the number of females breeding in each group also increased with group size, territory area occupied by each group increased with the number of breeding females. Mean territory size for groups with two breeding females was significantly larger than for groups with one, and was larger still for groups with three (Fig. 3b). Territories did not increase in size sufficiently, however, to compensate for the presence of multiple breeding females; on average, a female breeding alone in a singular territory occupied more area than did each breeding female in a plural group (Fig. 3b).

In the non-breeding season, each bird foraged throughout the entire territory occupied by its group, and most birds participated in territorial displays at all borders. During breeding, this pattern of territory use changed only slightly. Birds tended to forage near nests where they were actively feeding nestlings, but large dry-season groups did not split into smaller units during nesting. Residents continued to interact with most, if not all, other group members, and each could be observed at least occasionally at any given point in each territory. Observations of birds either helping at two nests or breeding at one and helping at another (Curry 1988) further demonstrate that groups frequently contained multiple nests.

**Influence of Dominance on Reproductive Success**

Dominance relationships among males influenced pairing and breeding patterns within groups (Fig. 4). Counting each group once for each breeding season, the alpha male bred in 99% of the subset of groups with more than one potential male breeder (N = 94), including all 54 plural groups. The single exception involved a group whose beta male bred (retaining his mate from the previous year) while a widowed alpha male remained unmated. Breeding by subordinate males in plural groups was more loosely associated with dominance. The beta male was paired in 85% of the
plural groups, but in eight of the groups, the beta male remained unpaired while one or more lower-ranking males bred.

Pairing patterns following mate losses also indicated a relationship between male dominance status and breeding. In 20 groups, an alpha male and one or more additional males were present as potential breeders following the death or departure of the alpha male’s mate. Immigrant females always paired with unpaired alpha males rather than with subordinate males (N=15). Even when no female joined the group, widowed alpha males usually acquired the former mates of lower-ranking males in their groups (N=4 of 5). Immigrant females also paired with widowed beta males in lieu of lower-ranking males in 11 of 13 cases where a beta male was widowed and either he or a subordinate male subsequently acquired a mate.

Dominance relationships among males rarely influenced the number of mates with which a male paired because nearly all pairings were monogamous (Fig. 4). In years other than 1983, bigamy occurred just once, when a widowed female paired with an already-mated male. In 1983, 14% of 55 breeding females paired with already-mated males at some point during the season. The alpha male was paired bigamously, leaving a beta male unpaired, in only one group containing multiple females; in all other such groups (N=49), the breeding females maintained pair bonds with different males.

Was breeding success correlated with dominance and group structure? Reproductive success is determined by the number of eggs produced in each nest and their subsequent survival to hatching, fledging and independence. Each of these components varies among years in Genovesa in association with changes in climatic conditions (Curry 1987). In 1980–1982, mockingbirds bred during wet seasons in which little rain fell (69–164 mm) over 2–4 months. In contrast, 2408 mm of rain fell during the 7 months in which mockingbirds nested in 1983. For this reason, I compared reproductive success among dominance classes in 1980–1982 separately from 1983. In subsequent analyses, I do not distinguish between subordinate pairs that bred in groups containing another nesting subordinate pair and those sharing their territory only with a dominant pair. Tertiary pairs (those ranking below two other breeding pairs in a plural group) produced 11 nests, and the remaining 66 nests of subordinates were those of secondary pairs (ranking immediately below the dominant pair). No component of reproductive success differed significantly between these two subordinate categories. One or more chicks fledged from 27% of the nests belonging to tertiary pairs compared with 38% of those of secondary pairs (G=4.4, df=1, P<0.05).

For nearly all components of reproductive success, singular and plural dominant pairs were more successful than subordinate pairs in the drier years (1980–1982), but not under wetter conditions (1983; Table I). Variation in reproductive success with dominance status arose at the earliest stages of nesting. Clutches that were not incubated, and therefore classified as incomplete, were smaller (\(\bar{X} \pm \text{SE} = 1.9 \pm 0.20\) eggs, N=14 nests) than complete clutches (\(\bar{X} \pm \text{SE} = 3.8 \pm 0.05\), N=152; Mann-Whitney U-test, \(P<0.001\), dominance categories combined). In 1980–1982, subordinate pairs produced fewer eggs per nest because more of them produced small, incomplete clutches than did higher-ranking pairs. In contrast, subordinate pairs in 1983 completed as many clutches as did singular and plural dominant pairs, and the number of eggs per nest did not vary with status. In most cases, clutches were not completed because the breeders abandoned the nest during laying. Therefore, factors influencing nest abandonment by subordinate pairs (e.g. interference by dominant birds; see below) may account for the difference, in dry versus wet conditions, in the relationship between status and the number of eggs produced per nest.

Additional variation with dominance status arose among those clutches that were completed. In 1980–1982, subordinate pairs had smaller complete clutches than higher-ranking pairs (Table I). In the same years, controlling for differences in clutch size between years in a two-factor ANOVA, singular pairs produced larger completed clutches than did plural dominant pairs (\(F=4.63, P<0.05\)). In 1983, subordinate pairs produced completed clutches that were slightly larger than those of singular pairs, and plural dominant pairs produced completed clutches that were even larger.

Hatching success (calculated as the percentage of eggs in completed clutches that hatched, excluding whole clutches lost to predators) also varied with dominance status (Table I). Subordinate pairs had lower hatching success than singular and plural dominant pairs in 1980–1982, but had higher success than higher-ranking pairs in 1983. Eggs were lost after the onset of incubation when
Curry: Plural breeding in Galápagos mockingbirds

Table I. Reproductive success in relation to dominance status of breeders in comparatively dry (1980–1982) and wet (1983) years

<table>
<thead>
<tr>
<th>Component of reproductive success</th>
<th>Status of pair</th>
<th>Year</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>1980–1982</td>
<td>1983</td>
</tr>
<tr>
<td>Eggs laid per nest*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Singular</td>
<td>3·8 ± 0·08 (73)</td>
<td>4·2 ± 0·10 (72)</td>
</tr>
<tr>
<td>Plural dominant</td>
<td>3·6 ± 0·10 (43)</td>
<td>4·3 ± 0·21 (27)</td>
</tr>
<tr>
<td>Plural subordinate</td>
<td>3·2 ± 0·14 (50)</td>
<td>4·2 ± 0·23 (20)</td>
</tr>
<tr>
<td>Kruskal–Wallis test</td>
<td><strong>H = 12·8, P &lt; 0·005</strong></td>
<td><strong>H = 1·9, P &gt; 0·1</strong></td>
</tr>
<tr>
<td>Percentage of clutches completed†</td>
<td>Sing.</td>
<td>96% (73)</td>
</tr>
<tr>
<td>Plural dominant</td>
<td>100% (43)</td>
<td>89% (28)</td>
</tr>
<tr>
<td>Plural subordinate</td>
<td>78% (50)</td>
<td>95% (20)</td>
</tr>
<tr>
<td>G-test</td>
<td><strong>G = 17·4, P &lt; 0·001</strong></td>
<td><strong>G = 0·7, P &gt; 0·5</strong></td>
</tr>
<tr>
<td>Size of complete clutches‡</td>
<td>Sing.</td>
<td>3·9 ± 0·07 (70)</td>
</tr>
<tr>
<td>Plural dominant</td>
<td>3·7 ± 0·10 (43)</td>
<td>4·6 ± 0·13 (25)</td>
</tr>
<tr>
<td>Plural subordinate</td>
<td>3·6 ± 0·11 (39)</td>
<td>4·4 ± 0·16 (19)</td>
</tr>
<tr>
<td>Kruskal–Wallis test</td>
<td><strong>H = 5·4, P &lt; 0·1</strong></td>
<td><strong>H = 4·8, P &lt; 0·1</strong></td>
</tr>
<tr>
<td>Hatching success§</td>
<td>Sing.</td>
<td>79% (272)</td>
</tr>
<tr>
<td>Plural dominant</td>
<td>77% (157)</td>
<td>46% (116)</td>
</tr>
<tr>
<td>Plural subordinate</td>
<td>61% (141)</td>
<td>64% (84)</td>
</tr>
<tr>
<td>G-test</td>
<td><strong>G = 15·4, P &lt; 0·005</strong></td>
<td><strong>G = 8·0, P &lt; 0·05</strong></td>
</tr>
<tr>
<td>Fledglings per nest**</td>
<td>Sing.</td>
<td>1·4 ± 0·15 (73)</td>
</tr>
<tr>
<td>Plural dominant</td>
<td>1·3 ± 0·20 (43)</td>
<td>1·1 ± 0·27 (28)</td>
</tr>
<tr>
<td>Plural subordinate</td>
<td>1·1 ± 0·15 (50)</td>
<td>1·0 ± 0·27 (22)</td>
</tr>
<tr>
<td>Kruskal–Wallis test</td>
<td><strong>H = 11·1, P &lt; 0·005</strong></td>
<td><strong>H = 0·4, P &gt; 0·5</strong></td>
</tr>
<tr>
<td>Fledglings per season††</td>
<td>Sing.</td>
<td>2·0 ± 0·19 (63)</td>
</tr>
<tr>
<td>Plural dominant</td>
<td>1·4 ± 0·20 (42)</td>
<td>3·2 ± 0·77 (16)</td>
</tr>
<tr>
<td>Plural subordinate</td>
<td>0·8 ± 0·17 (48)</td>
<td>2·2 ± 0·61 (13)</td>
</tr>
<tr>
<td>Kruskal–Wallis test</td>
<td><strong>H = 18·2, P &lt; 0·005</strong></td>
<td><strong>H = 0·6, P &gt; 0·5</strong></td>
</tr>
<tr>
<td>Percentage of pairs successful††</td>
<td>Sing.</td>
<td>76% (63)</td>
</tr>
<tr>
<td>Plural dominant</td>
<td>64% (42)</td>
<td>73% (16)</td>
</tr>
<tr>
<td>Plural subordinate</td>
<td>40% (48)</td>
<td>62% (13)</td>
</tr>
<tr>
<td>G-test</td>
<td><strong>G = 13·7, P &lt; 0·005</strong></td>
<td><strong>G = 1·2, P &gt; 0·5</strong></td>
</tr>
</tbody>
</table>

* X ± SE (N, nests), all nests included; statistics test for variation among the three status categories (df = 2).
† (N, clutches), clutches classified as completed if breeders initiated incubation.
‡ X ± SE (N, nests); only nests with completed clutches included.
§ Percentage of eggs hatching (N, eggs); nests with completed and not depredated clutches included.
** X ± SE (N, nests); all nests included.
†† X ± SE (N, pairs); all pairs producing one or more clutches during a season included.
††† Pairs producing one or more fledglings during a season classified as successful (N, pairs).

breeders abandoned their nests, when eggs disappeared and when the eggs survived but failed to hatch, but I was unable to determine the relative contribution of these sources. Complete hatch failure did account for some of the variation with status in 1980–1982; 93% of the nests with complete clutches of both singular (N = 70) and plural dominant pairs (N = 43) had at least one egg hatch successfully, compared with 77% of nests (N = 39) of subordinate pairs (G = 6·6, df = 2, P < 0·05). At least two subordinate pairs abandoned completed clutches in 1980–1982 following interference by dominant individuals. The proportion of nests with at least one hatching did not vary significantly with dominance status in 1983. It is not clear why hatching success was lower for high-ranking pairs.
Table II. Percentage of hatchlings that fledged successfully (N, hatchlings) in relation to status of pair and presence or absence of helpers

<table>
<thead>
<tr>
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<tbody>
<tr>
<td>Singular</td>
<td>Present</td>
<td>88% (64)</td>
<td>47% (45)</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td>47% (133)</td>
<td>46% (90)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>60% (197)</td>
<td>46% (135)</td>
</tr>
<tr>
<td>Plural dominant</td>
<td>Present</td>
<td>77% (52)</td>
<td>62% (24)</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td>42% (60)</td>
<td>52% (29)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>58% (112)</td>
<td>57% (53)</td>
</tr>
<tr>
<td>Plural subordinate</td>
<td>Present</td>
<td>71% (31)</td>
<td>56% (16)</td>
</tr>
<tr>
<td></td>
<td>Absent</td>
<td>25% (52)</td>
<td>33% (45)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>42% (83)</td>
<td>39% (61)</td>
</tr>
</tbody>
</table>

Tests of independence*

<table>
<thead>
<tr>
<th>Status</th>
<th>Percentage fledging (df = 4)</th>
<th>G = 11.7, P &lt; 0.05</th>
<th>G = 3.4, P &gt; 0.1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Helpers</td>
<td>Percentage fledging (df = 3)</td>
<td>G = 64.3, P &lt; 0.001</td>
<td>G = 3.8, P &gt; 0.1</td>
</tr>
<tr>
<td>Presence of helpers</td>
<td>Status (df = 4)</td>
<td>G = 9.8, P &lt; 0.001</td>
<td>G = 4.5, P &gt; 0.1</td>
</tr>
</tbody>
</table>

* Test of conditional independence between pairs of factors in three-way G-test (Sokal & Rohlf 1981); for both 1980–1982 and 1983, interaction terms among all three factors were not significant.

in 1983 (Table I), but in that year more nests were abandoned when storms occurred during incubation than in previous years (Curry 1985).

Survival of nestlings from hatching to fledging was influenced by dominance status, but it also varied in a complex way with climatic conditions and with the presence of helpers (which could be determined only for those nests where one or more eggs hatched; see Curry 1988). In 1980–1982, the percentage of hatchlings that fledged was higher for singular and plural dominant pairs than for subordinate pairs, independent of significantly higher fledging success of nestlings fed by helpers (Table II). At the same time, more hatchlings of plural dominant pairs (46%) and subordinate pairs (37%) received help than did nestlings of singular pairs (32%). In 1983, none of these relationships was statistically significant, though the overall pattern of variation in fledging success was similar. The results suggest that in comparatively dry years, helpers have a positive effect on the survival of hatchlings to fledging (Curry 1987; Curry & Grant, unpublished data), and that dominance also influences fledging success, largely because subordinate pairs without helpers fledge the smallest proportion of nestlings. In more favourable wet conditions, as in 1983, the effects of both dominance and helpers on fledging success are lessened.

Because subordinate pairs produced fewer eggs overall, hatched fewer eggs and fledged few hatchlings than singular and dominant pairs in 1980–1982 (but not in 1983), they consequently produced fewer fledglings per nest in the drier years. The total number of fledglings produced in a season followed the same pattern (Table I) because the proportion of pairs producing two or more clutches did not differ between dominance classes in any year (G-tests, df = 2, P > 0.05), despite large annual variation in the length of the breeding seasons and in the number of broods produced per pair (Curry 1985, 1987). In 1980–1982 the proportion of pairs successfully producing one or more fledglings varied significantly among the dominance categories, with singular pairs most often successful, followed by plural dominant pairs and subordinate pairs; a similar trend in 1983 was not significant (Table I).

**Interactions Within Groups**

Mockingbirds sharing each group territory
Table III. Outcome of within-pair and extra-pair copulation attempts in relation to dominance status of males

<table>
<thead>
<tr>
<th>Type of copulation</th>
<th>Attempt successful*</th>
<th>Attempt unsuccessful</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within-pair†</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dominant pair</td>
<td>13</td>
<td>5</td>
</tr>
<tr>
<td>Subordinate pair</td>
<td>6</td>
<td>13</td>
</tr>
<tr>
<td>Extra-pair, same group‡</td>
<td></td>
<td></td>
</tr>
<tr>
<td>With mate of lower-ranking male</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>With mate of higher-ranking male</td>
<td>0</td>
<td>19</td>
</tr>
<tr>
<td>Extra-pair, different group</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dominant male with mate of dominant male</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Dominant male with mate of subordinate male</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Subordinate male with mate of dominant male</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Subordinate male with mate of subordinate male</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Subordinate male with unpaired female</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>

* Cloacal contact observed or male mounted an acquiescent female for at least 10 s.
† G = 4.7 with correction for continuity, df = 1, P < 0.05.
‡ G = 8.6 with correction for continuity, df = 1, P < 0.005.

interacted continuously throughout the year. During the non-breeding periods, interactions were limited to displays of dominance status (e.g. chases or submissive posturing) and to communal territorial displays; birds in the same territory usually foraged independently of each other. Three kinds of more complex interactions during breeding are relevant in terms of understanding the relationship between dominance, group structure and reproduction: interference with mating, interference with nesting, and helping behaviour.

Mockingbirds may interfere with mating by hindering birds attempting to join breeding groups. All adults transferring among groups were females; most such transfers occurred just after rainfall began and before nesting started. In groups containing an alpha male whose mate had died or left, the immigrant females quickly paired with the widower alpha male. In a few such groups, un-mated subordinate males aggressively chased the new female until her pair bond with the alpha male was established. Thereafter, the same subordinate males did not attack the female and they sometimes helped at the dominant pair’s nest. When a female attempted to join a group whose alpha male was already paired, usually both the alpha male and his mate attacked the newcomer. Some females moved on to other groups after such attacks, but most eventually settled into the group after pairing with a subordinate male. It is difficult to determine how frequently interactions of this kind prevented subordinate males from obtaining mates, because many females may have attempted and failed to join groups without being detected by observers. Other transfers among groups, including all the four known cases of males moving into a new group, were effected by juveniles. Most juveniles attempting to join groups were accepted by residents as low-ranking subordinates after a few days during which they were chased and mildly attacked.

A more conspicuous form of interference involved copulations. Between 1980 and 1984, 28 apparently successful copulations involving identified birds were observed along with another 53 attempts (Table III). Copulations involving two members of a subordinate pair were not successful as frequently as those involving dominant pairs. This difference may have been the result of interference; two copulation attempts involving subordinate pairs failed when a dominant male attacked the subordinate male and chased him from the vicinity. Subordinate males were not seen interfering in copulations of dominant pairs. Though most breeders maintained a pair bond with only a single mate, males also occasionally attempted to copulate with females paired with another male. Extra-pair copulations involving males in the same group were successful more frequently when the male attempting the copulation was ranked higher than the female’s mate (Table III). One reason for this was that the effectiveness of mate guarding varied with male dominance status. Dominant males remained close to their mates, especially just prior to egg laying, and attacked any lower-ranking mates that approached. Subordinate males attempted to copulate with dominant females only when the dominant males were not present, but even then dominant males may make the attempts costly to the subordinate male: on six occasions, a subordinate male was attacked by a dominant male while, or immediately after, the former attempted to copulate with the dominant male’s mate. Subordinate males were less able to guard their mates against dominant males. On six occasions, a sub-
ordinate male displayed submissively less than 3 m from a higher-ranking male copulating with the subordinate male's mate. Males obtaining these copulations had a high probability of fertilizing the female's eggs as five copulations took place 3–6 days before laying began (the sixth occurred a day after the female completed a clutch). The response of the female may also account, in part, for the difference in the frequency of successful copulations between males of different status: five females resisted, and only one did not, when approached by displaying males ranking lower than their mates, but only one female resisted and five did not when approached by a male ranking above their mate (Fisher's exact \( P = 0.08 \), two-tailed). Resisting females pecked at the males and backed into inaccessible positions in rock crevices. Therefore, dominant males may father young through extra-pair copulations with females paired with subordinate males, whereas the combination of female resistance and mate guarding by dominant males probably prevents subordinate males from fathering young through extra-pair copulations. A few males also attempted extra-pair copulations with females from another group, and were occasionally successful (Table III).

Females could also interfere with breeding by laying eggs in the nests of other females in their own or other groups, but my observations suggest that females did so rarely. In the absence of genetic information, intraspecific parasitism would be suspected if nests contained eggs differing greatly in appearance, eggs laid or hatching at irregular intervals, more eggs than are normally laid by a single female, or any combination of the three (Yom-Tov 1980). Mockingbird eggs are pale green with variable amounts of brown spots. Eggs differing in the pattern of spotting were found only in four joint nests. In each of these nests, two sets of different eggs were laid, with one egg of each kind laid on some days; both females incubated the joint clutches, often simultaneously. (The two females began laying on the same day in one, 1 day apart in two others, and 2 days apart in the fourth.) By checking nest contents immediately before and after each female laid eggs, I determined that eggs laid by the same female looked alike, and were consistently different from those laid by the other female. I did not detect variation in egg appearance that would indicate egg dumping in any nests belonging to only one female. Eggs were laid on successive days in most nests, and eggs were not added after an interruption of more than 1 day to any nest. Hatching occurred over a period of 24–48 h at nearly all nests; hatching separated by a longer interval (3 days) occurred only once. Mean clutch size varies among years in this population (Curry 1987), but individual females are not known to lay more than five eggs in a clutch. Except for joint clutches, which contained the equivalent of two normal clutches (i.e. a total of seven or eight eggs), only one nest contained more eggs (six) than were likely to have been laid by a single female.

The most conspicuous form of conflict within groups was interference with nesting. Interfering birds attacked laying, incubating, or brooding females, or chased breeding males, or both. Interference occurred at the nests of both dominant and subordinate pairs, but the types of interactions varied with the status of the target pair. Interference was observed at four (5%) of 87 nests of dominant pairs in plural groups; in all of these cases, the female paired with the alpha male was attacked by an older female from the same group. Interference was observed at 12 (15%) of 80 nests of subordinate pairs. Assuming that interference was equally detectable at all nests, nests of subordinate pairs received interference more frequently than did those of dominant pairs in plural groups (\( G = 5.2, df = 1, P < 0.05 \)). A typical example of interference in a plural group is summarized in Fig. 5. Interference was also observed at two (1%) of 182 nests of singular pairs: one male singular breeder was attacked by a male from an adjacent group, and a yearling female was chased briefly by her non-breeding mother. Excluding cases where the perpetrator was a bird from outside the group, a male interfered at three nests, a female at seven, and both a male and female at five nests; females therefore interfered at 80%, and males at 53%, of nests where interference was observed.

Eggs or nestlings were either abandoned or died in 76% of the 12 nests of subordinate pairs where interference was seen, suggesting that this form of conflict contributed to nest failure. However, I have no direct evidence of outright infanticide by nest disrupters. Only four cases of infanticide were observed, all involving parents rather than non-parental birds interfering with nesting. Three females ate their own eggs after abandoning nests; at least one did so after her eggs became chilled during a storm. The fourth incident occurred during poor conditions for breeding in 1984, when a presumptive father removed, killed and ate a
freshly hatched nesting from a nest also containing three eggs. These cases may be aberrant in that all followed nest abandonment, but the observations demonstrate that mockingbirds are physically capable of destroying eggs or nestlings at other nests as well.

Helping is a third category of behavioral interaction that occurs frequently with mockingbird groups, and which may be associated with other reproductive tactics. Because breeders in plural groups occasionally also acted as helpers, especially after their own nests failed (Curry 1988), dominant birds may interfere with the nesting of other pairs to influence the number of birds in their groups likely to help. Considering only subordinate males as potential helpers, 43% helped during a season in which their own nest failed ($N=28$), whereas only one of $11$ (9%) did so while breeding successfully ($G=4.4$, $df=1$, $P<0.05$). Eight (67%) of the 12 males whose breeding failed began helping only after their own nest failed; the other four were already helping when their nest failed. Interference was observed or suspected at least five of the eight nests where helping began after failure. It is therefore possible that nest disruption is a form of manipulation that influences the incidence of helping by subordinate individuals.

Fitness Consequences of Status Differences

Relationships between group structure, dominance status and reproductive success during a single season could lead to misleading conclusions about the fitness consequences of differences in breeding status. For example, breeding as a subordinate could be beneficial in the long term if subordinate breeders survive better, or are more likely to retain breeding status, than dominant breeders. I therefore examined the relationship between breeding status, survival between seasons and transitions among dominance classes in order to estimate reproductive output over 2 years as a function of breeding status in the first of those years.

Annual survival of adults varied among years as a result of changes in environmental conditions and the incidence of disease (Curry 1987), but differences between breeding-status categories were not large. Survival of male singular breeders from the start of one breeding season (January) to January of the following year was 58% ($N=100$ bird-years) over all years, 1980–1984, compared with 67% for male dominant breeders ($N=55$), 67% for male subordinate breeders ($N=60$), and 75% for male non-breeders ($G=8.4$, $df=3$, $P<0.05$). Combining the three breeder categories, survival of male breeders was lower than that of non-breeders ($G=6.6$, $df=1$, $P<0.05$), but survival did not vary significantly among breeding males differing in status. Among females, 63% of singular breeders survived to the next year ($N=99$), as did 63% of
dominant breeders ($N = 62$), 52% of subordinate breeders ($N = 56$), and 68% of non-breeders ($G = 3.1, df = 3, P > 0.1$). As among males, survival of female breeders overall was lower (60%) than that of non-breeders, but this difference was not significant. Therefore, breeding may confer a small cost in terms of survival to males, but otherwise, survival does not vary with breeding status.

Among those birds that survived, breeding status was associated strongly with status in the preceding season (Fig. 6). Most males remained in the same status category from one year to the next, but females changed status more frequently. More females than males changed from non-breeder to subordinate breeder ($G = 9.2, df = 1, P < 0.005$) and from subordinate to dominant breeder ($G = 6.6, df = 1, P < 0.02$). Fewer females than males became non-breeders after breeding as a subordinate ($G = 3.9, df = 1, P < 0.05$). Differences between the sexes in transition frequencies reflect demographic patterns in the population. Annual survival of males was slightly higher (68%, $N = 383$ bird-years, 1980–1984) than that of females (62%, $N = 328$; $G = 3.0, df = 1, P < 0.1$). Females therefore had more frequent opportunities than males to replace breeders that died. Sex differences in mortality and accession to breeding status were also correlated with differences in resident patterns. Except in 1983, when high mortality enabled some males to replace neighbouring breeders that died, all adult males remained in the same territory from one year to the next, where they advanced in status only after higher-ranking males in the same group died. Females changed groups more frequently, for two reasons. First, groups in which a female breeder died often did not contain a replacement female because males predominated in the population; such vacancies were filled by females from other groups. Second, unpaired males courted females that wandered into new territories, facilitating transfer of females among groups. In contrast, adult males were attacked if they left their territories, and none was accepted into groups containing other males.

I used the long-term averages of observed seasonal production of fledglings, annual survival and frequencies of changes in status to estimate reproductive success over 2 years in relation to breeding status in the first of those years. For males and females separately, the number of fledglings produced over two seasons was estimated as

$$RS_i = S_i (P_{r-Dom})RS_{Dom} + (P_{r-Sub})RS_{Sub}$$

where $RS_i$ is reproductive success as a function of status, $S_i$ in the first of 2 years; $S_i$ is the status-dependent survival to the second year; $(P_{r-Dom})$ and $(P_{r-Sub})$ are the conditional probabilities of breeding as a dominant and subordinate, respectively, in
the second of 2 years, as a function of $s$ and $RS_{Dom}$ and $RS_{Sub}$ are the average number of fledglings produced per season by dominant and subordinate breeders (2-1 and 1-1 fledglings, respectively).

Breeding initially as a dominant confers higher long-term reproductive success than breeding first as a subordinate or not breeding, but birds that breed as subordinates are nevertheless more productive than birds that do not breed initially. Both males and females that breed initially as dominants can expect to produce 3-2 fledged young over 2 years. Males and females breeding first as subordinates should produce 1-8 and 1-9 fledged young, respectively, over 2 years. Lower survival of female subordinates is offset by their higher probability of breeding as a dominant in the second year. Non-breeding status does not confer a sufficiently large survival benefit to counterbalance the loss of even the low seasonal reproductive success obtained by subordinates. Because few females remain non-breeders through successive years, females that do not breed in the first of 2 years can be expected to produce 0-7 fledglings, nearly twice the projected 2-year success (0-4 fledglings) of males that do not breed in the first year.

DISCUSSION

Patterns of Social Complexity

Galápagos mockingbird society is richly complex in terms of variability in group structure, mating patterns and within-group conflict. Singular groups in which there is little conspicuous reproductive conflict exist side by side with plural groups in which extra-pair copulations and nest disruption occur. Added to this variation is flexibility in helping behaviour; mockingbirds can revert to helping after becoming established breeders, and they occasionally help and breed at the same time. Group structure is as variable, and interactions within groups as complex, in only a few other cooperatively breeding birds studied to date. These include groove-billed anis (Crotaphaga sulcirostris, Vehrencamp 1978), white-fronted bee-eaters (Merops bullockoides, Emlen 1981; Hegner et al. 1982), grey-breasted (Mexican) jays (Aphelocoma ultramarina, Brown 1963, 1970; Brown & Brown 1980), acorn woodpeckers (Melanerpes formicivorus, Stacey 1979; Koenig 1981; Jost et al. 1982; Koenig et al. 1983, 1984; Mumme et al. 1983a; b; Hannon et al. 1985; Jost et al. 1985), noisy miners (Manorina melanocephala, Dow 1978), long-tailed tits (Aegithalos caudatus, Gaston 1973; Glen 1985) and pukeko (Porphyrio porphyrio, Craig 1980).

The complexity that characterizes Galápagos mockingbird society arises because individuals within the population employ a variety of reproductive tactics depending on their sex, their dominance status, the structure of their groups and prevailing climatic conditions. Relationships between these variables and reproductive tactics are reflected in three elements of mockingbird social organization: (1) pairing patterns; (2) extra-pair reproductive activity; and (3) interference with reproduction. Understanding how alternative tactics (Caro & Bateson 1986) are used by individuals in reproductive competition with other mockingbirds can help explain patterns of complexity of their cooperative breeding system.

Pairing patterns of Galápagos mockingbirds are dependent primarily on dominance relationships. In nearly all groups, dominant males pair and breed, while many lower-ranking males do not obtain mates. Because dominance is correlated with age, most unpaired males are young. Pairing is less obviously dependent on dominance and age among females because most breed under normal conditions. Females may still compete, however, for pairings with high-ranking males; most females that paired with dominant males were dominant over, and usually older than, other females in their groups. These relationships alone would not account for the complexity of mockingbird society; pairing may be linked to dominance in nearly all cooperative breeders (Brown 1987), including species that breed singularly. However, the influence of dominance on pairing within plural groups demonstrated for Galápagos mockingbirds has not been documented clearly for any other plurally breeding species. Dominance interacts with other variables to increase the variability in pairing patterns. Because dominant male mockingbirds nearly always obtain mates, the proportion of subordinate males that pair is dependent on the population sex ratio, which ultimately varies with climatic conditions. For females, pairing is affected differently by changes in mate availability because females can pair bigamously with already-paired males. As a result, subordinate females are able to breed even when females predominate in the population, as they did in several years following this study (R. L. Curry & P. R. Grant, unpublished data).
Once they are paired, individuals may further increase their reproductive success by obtaining additional matings or by parasitizing the parental effort of other breeding individuals. Assuming eggs are sometimes fertilized as a result of extra-pair copulations, male mockingbirds probably gain reproductive benefits by copulating with females in the same group or in nearby territories. Available evidence suggests that the benefits gained using this tactic are dominance-dependent. Dominant males are able to copulate with females paired to lower-ranking males in the same group; subordinate males seem unable to prevent these matings. In contrast, subordinate males probably rarely achieve successful extra-pair copulations because dominant males actively guard their mates; these females also resist copulation attempts by subordinate males. Among cooperatively breeding birds, the tactic of obtaining extra-pair copulations seems to be limited to species with plural groups. Extra-pair copulations are thought to be rare in singular breeders (e.g. Woolfenden & Fitzpatrick 1984; Rabenold 1985), and Reyers et al. (1986) argued that in some cooperative societies, non-breeding subordinate males may be physiologically incapable of mating. Some low-ranking male mockingbirds, including both subordinate breeders and non-breeders, may occasionally father young through extra-pair copulations, but observed frequencies suggest that dominant males are more likely to do so. Mating patterns in the Genovesa population may therefore be dependent on dominance among males in a way comparable to that suggested for cooperatively polyandrous species (Faaborg & Patterson 1981; Stacey 1982; Davies 1983), but with the difference that more than one female is involved. Males have been reported to seek extra-pair copulations in other plurally breeding species (e.g. Emlen & Wrege 1986), but it is not known whether only dominant males are successful in fertilizing females through extra-pair copulations.

Reproductive success of female birds is limited by the number of eggs they produce that result in surviving young, barring effects of mate choice. Mated female mockingbirds, therefore, would be unlikely to increase their reproductive success through extra-pair copulations. Females could, however, lay eggs in nests in addition to their own. Intraspecific nest parasitism has been reported recently in the cooperatively breeding white-fronted bee-eater (Emlen & Wrege 1986). Though parasitism of this kind may be detected in several ways (Yom-Tov 1980), I found no evidence to indicate that female Galápagos mockingbirds parasitize other clutches on any regular basis. Joint nesting (or communal breeding, Emlen & Vehrencamp 1983), however, can also be considered a form of intraspecific parasitism in which “parasitizing” females remain to help raise the offspring (Emlen & Wrege 1986). Galápagos mockingbirds do nest jointly, but only in a small minority of groups; invariably, both females that lay eggs incubate and care for the young. Joint nesting may be prevented from becoming more common because hatching success in joint nests is lower than in separate nests, perhaps because females are unable to incubate enlarged joint clutches effectively.

Reproductive Conflict in Plural Groups

In a plural breeding system, conflict between breeders can occur whether females nest jointly or separately. Females nesting jointly may be expected to manipulate their ultimate contribution to the combined clutch through preferential infanticide of eggs or nestlings of other females; this can be viewed as resistance to parasitism (Emlen & Wrege 1986) or ‘skewing’ of reproductive contribution (Vehrencamp 1979, 1983). Removal of eggs (egg tossing) by breeding females has been reported in most species in which joint nesting occurs regularly, including smooth-billed anis (Crotophaga ani, Köster 1971), groove-billed anis (Vehrencamp 1977, 1978; Vehrencamp et al. 1986), ostriches (Struthio camelus, Bertram 1979), acorn woodpeckers (Mumme et al. 1983b) and white-fronted bee-eaters (Emlen & Wrege 1986). However, eggs did not disappear from any of the few joint mockingbird nests in this study, suggesting that females nesting jointly do not invariably destroy each other’s eggs. In this respect, the mockingbirds resemble white-winged choughs, Corcorax melanorhampus, in which females lay eggs jointly in at least 15% of the nests, apparently without egg tossing (Rowley 1978). The failure of mockingbirds nesting jointly to manipulate clutch composition may reflect the aberrant nature of joint nesting in the Genovesa population. There is likely to be little selection favouring egg tossing because females nest jointly only when rare shifts in the adult sex ratio result in a shortage of mates (R. L. Curry & P. R. Grant, unpublished data).
Though mockingbirds nesting jointly seem to share their nests amicably, outright conflict is evident in plural groups with pairs nesting separately, and its pattern of occurrence is associated with dominance. Dominant birds are capable of exerting some degree of control over the reproduction of lower-ranking birds by interfering with the nesting attempts of subordinate pairs. Because dominance among females is not invariably correlated with relative status among their mates, in a few cases a female paired with a subordinate male was in conflict with another female mated to a higher-ranking male, but no subordinate male was seen performing any kind of interference at a dominant pair's nest. Conflict among pairs nesting separately has been reported in a few other cooperative breeders, including grey-breasted jays (Brown 1963; Barkan et al. 1986), Arabian babblers (Turdoides squamiceps, Zahavi 1974), common babblers (Turdoides caudatus, Gaston 1978b) and whiteheads (Mohoua albicilla, MacLean et al. 1986). However, an association between disrupted nesting and dominance has been suggested only for grey-breasted jays (Barkan et al. 1986) and common babblers (Gaston 1978b).

Though conflict is conspicuous within many Galápagos mockingbird groups, it is not yet clear whether nest disrupters even destroy eggs or kill chicks directly. In addition to egg tossing from joint nests, infanticide by birds other than parents has been observed or suspected in several cooperatively breeding species (Trail et al. 1981; Stacey & Edwards 1983; Whitmore 1986). The direct observations of infanticide by parents on Genovesa demonstrate that Galápagos mockingbirds are capable of killing chicks. The same observations show that victims can be close relatives, as would often be the case during within-group interference. Nevertheless, outright destruction of eggs or chicks may be constrained if selection has acted to suppress intraspecific infanticide in group-living birds, as suggested by Trail et al. (1981). Strong selection for parental care may impose additional constraints on breeders, preventing the evolution of discriminative infanticide of non-descendant young. A possible example is the behaviour of dominant female 178, who aggressively disrupted nesting by two different females in her group in each of 2 successive years (Fig. 5). This female's repeated attacks were directed toward the incubating subordinate females; 178 did not destroy eggs in any of the disrupted nests, though she had opportu-

nities to do so after chasing off subordinate females. Females that have already laid eggs have been reported to destroy selectively the eggs or chicks of other females only in ostriches (Bertram 1979) and, possibly, grey-breasted jays (Trail et al. 1981); in several other species, females stop tossing eggs once they begin laying (Vehrencamp 1977, 1978; Mumme et al. 1983b; Emlen & Wreege 1986; Vehrencamp et al. 1986), presumably because they cannot distinguish their own eggs from other eggs.

Regardless of whether dominant mockingbirds destroy eggs and nestlings or just disrupt nesting, their behaviour is correlated with, and probably causes, low reproductive output by subordinate breeders under relatively dry conditions. Several nests of subordinate pairs clearly failed as a direct consequence of interference (e.g. Fig. 5). Interference was not observed directly at many other nests, but patterns among the components of reproduction support the hypothesis that their low reproductive success is attributable to interference. Lowered output from the nests of subordinate pairs is most evident at three stages: laying, incubation and hatching. Subordinate pairs lay smaller clutches than dominant pairs and fewer of their eggs hatch successfully. Most observed interference took place during the same nest stages. The proportion of nestlings that fledged was lower for subordinate pairs than for dominant pairs, but nestling survival also varied with the presence of helpers. Sufficient data are not yet available to separate the effects of additional factors, such as age or breeding experience, from the influence of dominance status on survival of nestlings.

Climatic Variation and Within-group Conflict

Why should dominant mockingbirds disrupt nesting by subordinate pairs in the same groups? Emlen (1982b) suggested that interference of this kind (his Type II conflict) constitutes manipulation by dominant birds. According to Emlen’s model, subordinate birds may benefit most under favourable environmental conditions by breeding independently rather than helping at their parents’ nests. If dominant birds would benefit more from receiving help than they would indirectly through the breeding success of their offspring, the dominant birds can be expected to disrupt the nests of subordinate birds, increasing the chances, as a result, that the failed subordinate breeders will act as helpers for the dominant pair. When environ-
mental conditions are less favourable, resource limitations are more likely to prevent young, subordinate birds from attempting to breed; a large pool of non-breeding subordinate birds will then be available to help dominant breeders, without any need for disruption of subordinate nesting. The model therefore predicts that conflict involving manipulative disruption by dominant breeders of nesting by subordinate pairs should be most frequent when conditions are favourable for independent breeding by subordinate birds (Emlen 1982b).

Emlen’s model addresses the type of conflict that occurs within mockingbird groups, but the relationship between prevailing environmental conditions on Genovesa and the incidence of disruption appears to be counter to the foregoing prediction. Helping does confer benefits to breeders (Table III and Curry 1987), and failed subordinate breeders do frequently become helpers for dominant breeders in their groups. However, interference by dominant birds and subsequent nest abandonment and redirection of help by subordinate birds are most conspicuous in relatively dry years when conditions are least, rather than most, favourable for successful independent nesting by subordinate pairs. When resources for breeding are abundant, as they appear to have been during El Niño conditions in 1983, interference is rare and subordinate reproductive success is as high as that of dominant breeders.

Although the prediction emphasized by Emlen (1982b) is not upheld, the model cannot necessarily be rejected (Emlen, personal communication). Conditions in 1983 may have been so good that dominant birds received larger fitness benefits when their offspring bred independently than they could have received by disrupting nesting by subordinates, and inducing help from their offspring. In this view, conditions were sufficiently good to favour attempted breeding by subordinate pairs in all of the years of this study, but were sufficiently poor for Type II conflict to arise only in the first 3 years (1980–1982). The model predicts that conditions conceivably could be so bad that resource limitation or other constraints might prevent all subordinate pairs from breeding while permitting older, dominant pairs to do so; Type II conflict would also be rare under such conditions.

I suggest that for Galápagos mockingbirds, an alternative model to that of Emlen (1982b) can also explain the pattern of occurrence of nest disruption in relation to environmental variation. This model assumes dominant pairs in plural groups may incur costs by sharing the resources of their territories with other breeding pairs (see also Trail et al. 1981). The resources that a Galápagos mockingbird, a predominantly terrestrial omnivore, can gather for breeding are likely to depend on the amount of territorial space the bird can search. If so, pairs in plural groups are likely to suffer a cost by sharing their territory, because there is less space per pair in plural territories than singular territories. The costs of sharing their territory could explain why dominant females laid fewer eggs per clutch than singular-breeding females in dry years. Therefore, dominant pairs may disrupt the nests of subordinate pairs to reduce the costs of sharing their territory with other nesting pairs; such costs are not explicitly included in Emlen’s (1982b) model predicting Type II conflict. The hypothesis that conflict arises from reproductive competition for resources within plural territories does not preclude the possibility that interference might also enable dominant pairs to increase the pool of birds likely to act as helpers. Therefore, though based on different mechanisms, the two hypotheses do not make mutually exclusive predictions about the incidence of within-group conflict in relation to environmental conditions. The pattern of nest disruption and of redirected helping observed in this study is consistent with either hypothesis.

Regardless of whether disruption enables breeders to recruit helpers or reduce the costs of sharing territorial resources or both, within-group conflict may be influenced further by familial relationships. Dominant breeders may incur indirect fitness costs (Brown 1980) if they kill offspring of subordinated relatives (Trail et al. 1981). Therefore, dominant mockingbird pairs, often the parents or older siblings of subordinate male breeders, may maximize their inclusive fitness by allowing their offspring to reproduce (Brown & Brown 1984), even if to do so they must incur costs of sharing their territories. Two changes in familial relationships should further affect the probability of disruption of subordinate nesting. First, immigrant females that pair with widowed dominant males will be unrelated to the subordinate pair and their nestlings. Consequently, immigrant females may be expected to take the lead in disrupting the nests of subordinate pairs, assuming interference confers benefits to dominant pairs. Second, if dominant males may be the fathers of offspring through
extra-pair copulations with subordinate females, they should not disrupt the nests of subordinate pairs, as long as the benefits of additional matings outweigh the costs imposed by territory-sharing on the dominant pair’s nestlings. Both of these changes in familial relationships may produce additional conflict between members of dominant pairs. Immigrant females may attempt to disrupt nesting by subordinates when having a son breed successfully would benefit the dominant male. Alternatively, if the dominant female is the subordinate male’s mother, her genetic interest in the nestlings in the nest of a subordinate pair will decrease if the dominant male fathers the young, while plural breeding may be advantageous for dominant males by providing them with opportunities for obtaining such matings. In either case, the dominant male and female can be expected to have different thresholds for disruption, and conflict between them can be expected. I did not observe overt conflict between members of dominant pairs, but conflicts of interest between dominant breeders and subordinates are suggested since dominant females participated in nearly all incidents of disruption of subordinate breeding, including those in which the male subordinates were their sons, whereas few dominant males took an active role in disruption.

Why Breed Plurally?

Although conflict within groups reduces the reproductive success of subordinate individuals, analysis of reproductive output over 2 years suggests that subordinate breeders have greater long-term fitness than do birds that do not breed initially. In other words, a mockingbird should always attempt to breed if it can obtain a mate, but its success will be greater if it breeds as a dominant rather than as a subordinate. Deferred breeding would be beneficial only if the delay in reproduction were offset by higher survival to breed at a later date. However, the differences in survival between dominant breeders, subordinate breeders, and non-breeders are small. Deferral of breeding is less costly for a female than for a male because a female that survives can be virtually assured of attaining breeding status, but males are likely to remain non-breeders. However, the benefit of breeding as a subordinate must be revalued by the probability that the subordinate male does not father his mate’s offspring. Male mockingbirds that defer breeding would have higher long-term reproductive success if subordinate males father fewer than 2% of the offspring of their mates, assuming that male dominant breeders father all of the young produced by their mates. No data are currently available to test for the true level of mixed paternity, but the few observations of copulations suggest that confidence of paternity for subordinate males is likely to be higher than this level.

Why should a mockingbird ever breed as a subordinate and suffer the cost of interference from dominant individuals? The alternative would be to establish an independent territory, as occurs in most singularly breeding species (e.g. Woolfenden & Fitzpatrick 1978, 1984). The reason why Galápagos mockingbirds frequently opt for subordinate breeding is probably related both to ecological constraints influencing the Genovesa population and to climatic variability among years. Because all habitat on the island is occupied by mockingbird groups, a subordinate could only form a new territory at the expense of other, established groups, or by replacing breeders that die. Because plural groups have territories that are small in relation to the number of pairs in the group, the territories that would result even from an equal subdivision of a plural territory would be smaller, on average, than those of singular breeders. As a result, a subordinate that attempted territorial fission would meet resistance from older, more dominant group members, and, in consequence, it would obtain insufficient space for successful breeding.

However, climatic conditions (especially rainfall) vary unpredictably on Genovesa (Grant & Boag 1980; Curry 1987). The duration and amount of rainfall in a breeding season probably influences how many pairs can breed within a territory because rainfall in the Galápagos indirectly influences arthropod abundance (Gibbs & Grant 1987). When heavy rainfall produces plentiful resources, constraints on breeding are eased and interference from dominant breeders is reduced, which enables subordinate breeders to attain reproductive success equaling that of dominant breeders. If breeding-season conditions were consistently good, the habitat could provide sufficient resources to support a higher density of breeding pairs. Alternatively, if breeding conditions were always poor, dominant breeders would defend larger areas for their own breeding and subordinate individuals would not benefit from nesting because dominant breeders would never be willing to share
their territory. In either case, the benefits of breeding independently would be consistent and predictable, and young birds would be expected to begin breeding at an age where, because of demographic parameters such as survival among established breeders, the expected fitness gain from independent breeding would be higher than that obtainable through deferral of breeding (Emlen 1978, 1982a; Wiley 1981; Woolfenden & Fitzpatrick 1984).

On Genovesa, a mockingbird will be unable to predict whether a season will be good; there seem to be few cues by which a bird could know that rainfall will be heavy in a given year, even after the rains begin. Since wet years occur frequently but unpredictably (Grant & Boag 1980), a subordinate should always attempt breeding once rainfall begins if it can acquire a mate, on the chance that the rains will continue; by doing so, it will be spared the investment in territorial defense against the rest of its group that would be required to create a new, independent territory. If little rain falls, the subordinate will suffer only a small survival cost from breeding. This cost will be more than offset, on average, by the subordinate's reproductive success, even when the effects of within-group conflict in dry years are taken into account. Climatic variability in the Galápagos therefore functions to decouple mockingbird breeding opportunities from the physical constraints of limited island habitat in a manner similar to the way that colonial nesting relaxes constraints on breeding in bee-eaters (Hegner et al. 1982). The result in both systems is an increase in behavioral complexity that can be traced to shifting climatic conditions. These two kinds of systems differ, however, in the ways that climate influences the costs of plural breeding: a bee-eater may suffer little cost when other members of its group breed, because all feed away from the nesting area, but a mockingbird may compete directly with other group members for resources available in the plural territory.

Plural breeding and associated reproductive tactics in Galápagos mockingbirds derive from the combination of a competitive social environment and the influence of a variable climate. Disruption by dominant breeders of nests of subordinate pairs and extra-pair matings by dominant males appear to represent opportunistic tactics for increasing personal fitness. Despite the costs imposed as a result of the tactics of dominant individuals, subordinate individuals benefit from breeding because their reproductive success will be large in wet years, and better than non-breeding even in other years. The interplay among these ecological and social factors gives rise to an unusually complex society.

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