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IMPACT OF CLIMATIC VARIATION ON GALAPAGOS MOCKINGBIRD SOCIAL ORGANIZATION

R. L. CURRY¹ and P. R. GRANT²¹ Archbold Biological Station, Lake Placid, FL 33852, USA*

*Present address: Dept. Biology, Villanova University, Villanova, PA 19085-1699, USA

² Program in Ecology, Evolution and Behavior, Department of Biology, Princeton University, Princeton, NJ 08544, USA

ABSTRACT. We studied cooperative breeding of *Nesomimus parvulus* over 13 years (1978-90) across a broad range of climatic conditions. Variation in annual rainfall strongly influenced demography, but had few direct effects on social behavior. Indirect effects were pronounced. The frequencies of polygyny and associated joint nesting decreased with adult sex ratio. Along with density, mate availability determined the proportion of males that bred and, secondarily, the proportion that helped. Sex ratio did not affect the proportion of females that bred, but the proportion helping decreased with availability of males because mate-sharing females most often acted as helpers. Polygyny benefits males but is usually rare because monogamous females have higher reproductive success than females sharing mates. The frequency of plural breeding varied with population age structure. By favoring flexible reproductive behavior, climatic and demographic variation ultimately accounts for the occurrence of polygyny, joint nesting, and plural breeding.

Keywords: Galapagos Mockingbirds, *Nesomimus parvulus*, cooperative breeding, mating systems, sex ratio, demography, El Niño.

INTRODUCTION

In the majority of cooperatively breeding species, most helpers are young non-breeders remaining in their natal groups. Consequently, investigators have focused on environmental and demographic factors that prevent individuals from dispersing and breeding. Why helpers help can be treated as a separate, though interdependent, question (e.g. Curry 1988a).

Despite considerable attention, ecological influences on dispersal and breeding in cooperative systems remain incompletely understood. At least eight different mechanisms have been proposed (Brown 1987: Table 5.1). Emlen (1982) argued that individuals in stable environments would be constrained mainly by the difficulty of acquiring territorial space necessary for breeding, whereas birds in variable environments would be limited by the difficulty of breeding successfully in poor years. Mate shortage (cf. Rowley 1965) could constrain breeding under either regime, especially where extrinsic factors produce sex ratio shifts.

Many environmental and demographic variables are not amenable to experimental study. Their effects nevertheless can be investigated given adequate natural variation. The Galapagos Mockingbird* *Nesomimus parvulus* on Isla Genovesa has provided an excellent opportunity to consider the impact of climatic variation on a territorial cooperative breeder. Our thirteen-year study included two droughts, two wet El Niño events, and eight years with intermediate conditions.

* Common and scientific names follow Swarth (1931)

Previously we documented relationships between climatic variation and mockingbird demography (Curry & Grant 1989). This paper further examines the impact of climatic change on mockingbird social organization. We focus on (1) direct influences of climatic conditions on social behavior, and (2) indirect effects mediated through changes in population structure, especially a shift from an excess of males to an excess of females. Female-biased sex ratios are rare in bird populations, and no previous study of a cooperative breeder has considered whether mate shortage can constrain breeding, and promote helping, by females.

METHODS

Genovesa is a small (17 km²), low island in the extreme northeast of the Galapagos. We color-banded nearly every bird in our 50-ha study area and determined sex from wing measurements and breeding behavior. Most data were collected during the usual breeding season (January-May) and early part (June-August) of the non-breeding season. We measured rainfall daily; annual totals for four years (Figure 1) are minimal estimates because additional rain is known or suspected to have fallen when we were not present.

In each year, we determined the reproductive status of all resident adults (>1 year old) and found and monitored all nests. We identified breeders by courtship behavior, nest building, and egg-laying, and conducted one-hour nest watches at two- or three-day intervals to identify helpers, defined as birds that fed nestlings or fledglings that were not their own offspring. Non-breeders did not invariably act as helpers, and some birds in plural-breeding groups (containing more than one breeding female) both helped and bred (Curry 1988a). Data from 1989 and 1990 were sufficient for estimating population parameters but not for documenting helping behavior or reproductive success.

We studied details of group structure in 1980-87 and in 1990. We classified breeding males as either dominant — including all those in singular-breeding groups, which contained only one nesting pair — or subordinate (Curry 1988b), and as either monogamous or polygynous. We classified breeding females as monogamous or mate-sharers, and categorized the latter as primary and secondary mates, depending on pairing sequence. We usually were unable to follow the fates of individual eggs from joint nests (in which multiple females laid eggs) so we assume contributing females shared parentage of fledglings equally.

Statistical tests were performed using JMP (SAS Institute Inc.). We used rank order correlation (r_s) for tests involving annual rainfall because of this variable's skewed distribution; other statistics are from parametric tests. F values are from two-way ANOVA with year as one factor, except where noted.

RESULTS

Climatic conditions and demography

Annual rainfall varied from 0 to 2408 mm (Figure 1). In most years, rain fell only during the January-April warm/wet season. In El Niño years (1983 and 1987) storms began as early as the preceding November and continued until as late as July. Most plants

were leafless throughout each annual cool/dry season and droughts. New foliage emerged soon after each year's first showers and persisted until a few weeks after the rains ended. Availability of caterpillars, often fed to nestlings, coincided with the presence of fresh vegetation (Grant & Grant 1989).

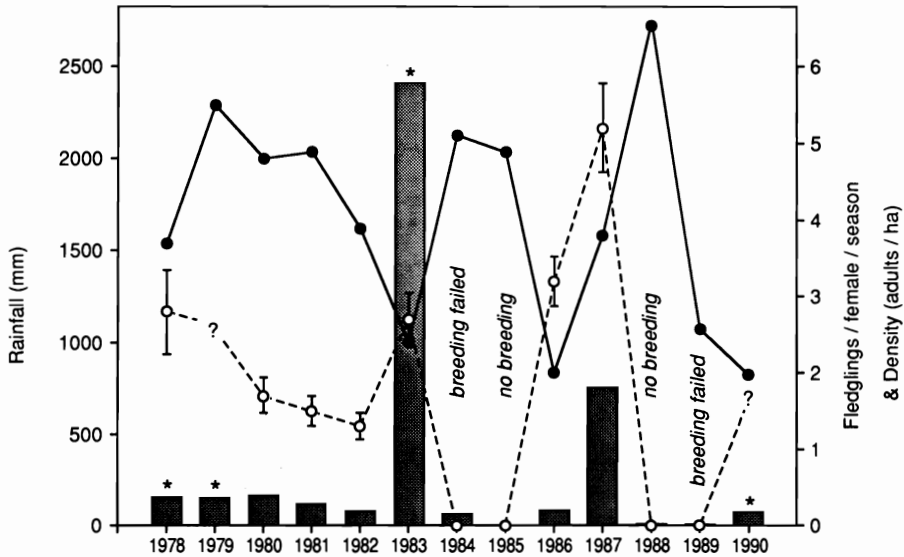


FIGURE 1 - Variation in annual rainfall, natality, and population density. Rainfall values (stippled bars) for four years (asterisks) are minimum estimates. Data on seasonal production of fledglings (open points, $x \pm SE$) in 1979 and 1990 were incomplete. In two drought years (1985 and 1988), no mockingbirds nested. In both 1984 and 1989, few pairs attempted to breed and none were successful. Moderately low adult density (solid points) in 1978 followed a drought in 1977.

Wet years were generally favorable, and dry years poor, for breeding. In most years, nesting began approximately one week after >20 mm of rain had fallen. Duration of breeding varied with rainfall: individual females produced up to six clutches in El Niño years. Natality consequently increased with total rainfall (Figure 1). Three years were extraordinary. In 1984 a moderate amount of rain (57 mm) fell, but most residents did not breed, and no nesting pairs ($N = 8$) produced independent young. In 1989 at least two pairs attempted to nest, though only 7 mm of rain fell; we suspect they failed. In both 1986 and 1989, single pairs began nesting before any rain had fallen. These unusual breeding responses may have been influenced by extreme climatic conditions in the preceding year.

Adult density increased after wet years and declined after droughts, mainly because of variation in natality (Figure 1). Survival was highest under intermediate conditions, dropping during droughts and during an epizootic associated with the 1983 El Niño (Curry & Grant 1989).

Adult sex ratio varied dramatically (Figure 2). Prior to 1983, males outnumbered females because of marginally higher survival. For unknown reasons, more males than females died in the 1982-83 epizootic. Sex ratio then increased following renewed

reproduction and higher survival of males in 1986-89, but an excess of females reemerged in 1990 when they survived better (79%) than males (66%).

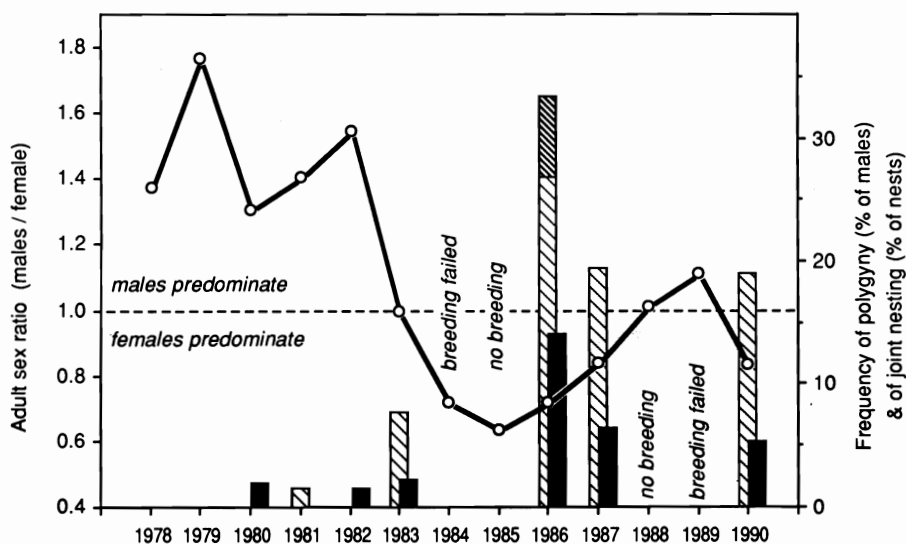


FIGURE 2 - Variation in adult sex ratio and in the frequencies of polygyny and joint nesting. Sex ratio values (open points) for 1988 and 1989 are estimates because the sex of up to 20% of residents was undetermined; sex was known for >95% of residents in other years. Frequency of polygyny is shown as the percentage of breeding males having two (light hatching) or three mates (heavy hatching). Frequency of joint nesting (black bars) is shown as a percentage of each year's nests.

Direct effects

GROUP SIZE AND STRUCTURE. Group size did not vary with annual rainfall ($r_s=0.05$, $N=11$ years, N.S.) but increased with density (Table 1) because the number of groups changed little. The proportion of yearlings dispersing from their natal territories was also independent of rainfall ($r_s=0.38$, $N=7$, N.S.), but decreased with adult density ($r_s=-0.76$, $N=7$, $P<0.05$). The impact of climatic conditions on dispersal and group size therefore appears to have been slight relative to that of competition for territorial vacancies. The frequency of plural breeding increased with annual rainfall ($r_s=0.83$, $N=7$ years, $P<0.05$), but was more strongly associated with variation in population age structure (Table 1 and below).

HELPING BEHAVIOR. Helpers attended 34% of nests ($N=450$). Nearly half (48%) of all helpers ($N=151$ helper-seasons) were non-breeding adult males. Other helpers consisted of 25% breeding males, 9% breeding females, 5% non-breeding females, 9% juvenile males, and 3% juvenile females (Curry & Grant 1990).

Prevailing climatic conditions did not directly influence helping. Neither the proportion of nests attended by helpers, nor the proportion of birds that bred, nor the proportion that helped among birds of either sex varied with annual rainfall (all $r_s<0.50$, $N=8$ years, N.S.; data from the failed 1984 and 1989 breeding seasons are excluded from these and subsequent analyses).

On average, nests attended by helpers produced 19% more fledglings than nests without helpers (Curry & Grant 1989). In a variable environment, climatic conditions might influence the efficacy of help, with helpers providing a larger benefit in poor (dry) years (Orlans et al. 1977). However, the change in fledgling production attributable to helpers did not vary with rainfall ($r_s=0.08$, $N=7$ years, N.S.).

Indirect effects

MATING SYSTEM. Adult sex ratio strongly influenced the mating system (Figure 2). In 1978-82, when males outnumbered females, nearly all pairings were monogamous. (Genetic polyandry, however, may result from extra-pair copulations involving dominant males and subordinate females; Curry 1988b). In 1986 and later, when females predominated, polygyny was common, with individual males obtaining up to three mates. The proportion of males mated polygynously thus varied inversely with sex ratio (Table 1).

TABLE 1 - Correlation matrix (Pearson r) for population breeding parameters (N, maximum number of years for which data are available). Significance levels are indicated by ^a, $P<0.05$; ^b, $P<0.01$; ^c, $P<0.005$. (Parameter codes: SR, sex ratio; AD, adult density; pYg, % yearlings; GS, group size; pMB, % males breed; pMH, % males help; pFB, % females breed; pFH, % females help; pMP, % males polygynous; pGP, % groups plural.)

Code	N	AD	pYg	GS	pMB	pMH	pFB	pFH	pMP	pGP
SR	13	.28	-.17	.01	-.96 ^c	.76 ^a	-.45	-.89 ^c	-.90 ^c	-.05
AD	13	.	.65	.84 ^c	-.93 ^c	.88 ^c	-.65	-.61	-.75 ^a	.52
pYg	12		.	.77	-.19	.35	-.72	.51	-.09	.95
GS	11			.	-.77 ^a	.84 ^b	-.66	-.16	-.53	.81 ^a
pMB	9				.	-.87 ^b	.60	.78 ^a	.85 ^c	-.24
pMH	8					.	-.63	-.54	-.81 ^a	.29
pFB	9						.	.11	.23	-.74
pFH	8							.	.84 ^b	.53
pMP	9								.	-.06
pGP	9									.

Mating patterns in turn influenced the mode of nesting. Females laid eggs in separate nests in 98% of plural-breeding groups where they had different, monogamous mates ($N=59$). In contrast, two females laid eggs in a joint nest at least once in 71% of groups that included a polygynous trio ($N=17$; $\chi^2=39.5$, $P<0.001$). Consequently, the frequency of joint nests increased with the frequency of polygyny (Figure 2).

FITNESS CONSEQUENCES. Both mating type and dominance status affected reproductive success. Polygyny was beneficial for breeding males (Table 2). In each of three years, dominant polygynous males produced more fledglings than dominant monogamous

males; both had higher success than monogamous subordinate males. Reproductive success of the two subordinate males that mated polygynously in 1987 was similar to that of dominant males, and higher than that of monogamous subordinate males.

TABLE 2 - Mean number of fledglings produced per season, \pm SE (N, breeders), in relation to sex, dominance status, and type of mating.

Dominance status and mating type	Year		
	1983	1986	1987
MALES			
Dominant			
Monogamous	3.0 \pm 0.47(39)	3.9 \pm 0.53(19)	7.9 \pm 0.88(16)
Polygynous	5.0 \pm 0.58 (3)	5.2 \pm 1.36 (7)	10.0 \pm 0.55 (5)
Subordinate			
Monogamous	2.9 \pm 0.81(10)	3.0 \pm 0.58 (3)	2.3 \pm 0.81(13)
Polygynous	—	—	9.0 \pm 5.00 (2)
Mating type, dominants, $F_{1,83}=4.1$, $P<0.05$; Year, $F_{2,83}=13.1$, $P<0.01$			
Mating type, subordinates (1987 only), $F_{1,13}=6.6$, $P<0.05$			
Dominance status (monogamous only), $F_{1,94}=8.3$, $P<0.01$; Year, $F_{2,94}=4.4$, $P<0.05$			
FEMALES			
Dominant			
Monogamous	2.9 \pm 0.46(41)	4.1 \pm 0.51(18)	7.9 \pm 0.88(16)
1° mate-sharer	3.7 \pm 0.33 (3)	3.1 \pm 0.42 (7)	6.6 \pm 0.70 (5)
2° mate-sharer	1.3 \pm 0.88 (3)	1.6 \pm 0.62 (9)	3.4 \pm 1.13 (5)
Subordinate			
Monogamous	2.3 \pm 0.61(13)	3.0 \pm 0.58 (3)	2.3 \pm 0.81(13)
1° mate-sharer	—	—	4.2 \pm 2.25 (2)
2° mate-sharer	—	—	4.8 \pm 2.75 (2)
Mating type, dominants, $F_{2,98}=6.7$, $P<0.01$; Year, $F_{2,98}=9.4$, $P<0.01$			
Mating type, subordinates (1987 only), $F_{2,16}=0.8$, N.S.			
Dominance status (monogamous only), $F_{1,98}=11.1$, $P<0.01$; Year, $F_{1,98}=6.9$, $P<0.01$			

Mate-sharing did not benefit females (Table 2). Among the mates of dominant males, monogamous females produced significantly more fledglings than did mate-sharing females. Primary females with dominant mates had higher reproductive success than either secondary females ($F_{1,26}=12.9$, $P<0.05$) or females paired monogamously to subordinate males ($F_{1,38}=5.4$, $P<0.05$), principally because of differences in the number of clutches produced per season. Females in the latter two categories had roughly equal success ($F_{1,40}=0.6$, N.S.). Independent of mating type, females with dominant mates produced more fledglings than females with subordinate mates because the former initiated more clutches and more of their eggs hatched (68%, $N=511$ vs. 62%, $N=129$).

Mate-sharing females incurred costs because they often nested jointly. Most joint nests contained 7-8 eggs, with each female contributing 3-4 eggs (modal clutch size for separate nests was 4 eggs). Hatching success in joint nests was poorer (40%, $N=155$ eggs) than in nests where only one female laid (64%, $N=1935$; $\chi^2=33.6$, $P<0.001$). Joint nests consequently produced fewer fledglings per female ($x=0.8$, $N=19$) than separate nests ($x=1.4$, $N=290$; $F_{1,303}=5.6$, $P<0.05$).

BREEDING AND HELPING. The proportions of resident adults that bred and helped in each year varied (Table 1), and associations with sex ratio differed between the sexes. In the absence of polyandry, more non-breeding males were present when females were in short supply. Adult density had an additional influence; sex ratio and density together account for 98% (R^2) of the variation in the proportion of males that bred ($F_{2,6}=156.7$, $P<0.001$). Because non-breeding males most often acted as helpers, the proportion of males helping increased significantly with sex ratio.

The proportion of females that bred did not vary with adult sex ratio (Table 1) because polygyny made it possible for most females to obtain mates. The proportion of females that helped nevertheless decreased with mate availability, as it did for males. Female breeders most often also acted as helpers, especially if they shared mates: 32% of mate-sharing females with a chance to help at another's nest did so ($N=37$) compared with only 1% of monogamously-paired females with such an opportunity ($N=145$; $\chi^2=35.8$, $P<0.001$). The proportion of females helping thus increased with the frequency of polygyny (Table 1). Mate shortage therefore promoted helping by females by forcing them to share mates.

Helping behavior may facilitate joint nesting. In 80% of cases ($N=10$) where one female first acted as a helper at the nest of another female sharing the same male, the two subsequently nested jointly. When neither mate-sharing female first acted as a helper for the other, they less often nested jointly (27%, $N=11$; Fisher's exact test, $P=0.03$).

PLURAL-BREEDING GROUPS. The proportion of groups containing multiple breeding females varied from 14% in 1984 to 76% in 1987. The frequency of plural breeding increased with the proportion of yearlings in the population and, consequently, with group size but did not vary with other parameters (Table 1). Plural groups therefore were not an incidental product of polygyny, but arose when yearlings attempted to breed without establishing independent territories (Curry & Grant 1989).

DISCUSSION

Galapagos Mockingbirds inhabit an extraordinarily variable climatic environment. Nevertheless, reproductive decisions in this territorial species, whose groups fill all available habitat on Genovesa, are influenced principally by indirect effects of changes in population size and structure. Consequently, the social system varies greatly depending on prevailing demographic conditions.

Climatic variation may play a small direct role. Conflict between pairs in plural-breeding groups, for example, appears to be more intense in drier years, possibly because of competition for resources or for helpers (Curry 1988b). Total rainfall may also be an inaccurate index of resource levels. A thorough test of the hypothesis that climatic conditions influence helping by altering breeding costs (Orians et al. 1977, Emlen 1982) would require experimentation or direct measurements of food supplies. We lack these data.

Among demographic variables, mate availability has the strongest influence on mockingbird social organization. Mate shortage increases the pool of male non-breeders

available to act as helpers. This raises the question: Why do dominance interactions prevent polyandry? We hypothesize that young males cannot overcome age-dependent asymmetries in competitive ability, and that dominant males incur negligible costs by imposing a skew in reproductive success (Vehrencamp 1983), because subordinate males have few options in Genovesa's often crowded demographic environment.

Mate shortage also promotes helping by females, by influencing the way in which females must breed rather than the number able to do so. Because females that share mates suffer decreased reproductive success, they mate monogamously if possible. When an excess of males exists, most unpaired females wander in search of mates, rather than staying home and helping (Curry 1988a). Because of Genovesa's unpredictable climatic regime, females gain by breeding whenever conditions are favorable, even if they must pair with a subordinate male to do so (Curry 1988b). When males are in short supply, polygyny becomes the only available route to breeding.

Our results imply that mating decisions are primarily under female control. If males determined mating, polygyny would always occur because the reduced reproductive success of each female is more than offset by their combined fledgling production. Females paired with dominant males, however, should attempt to avoid the costs of mate-sharing. Their resistance may force additional females to pair with subordinate males, if available. When the supply of males is limited, excess females should employ tactics that facilitate polygyny, and to receive support from prospective mates. An unpaired female initially may act as a helper in order to form a social bond with the primary female, and thereby overcome her initial aggression. By laying in a joint nest, the secondary female may also protect her eggs from disruption on the part of the primary female (Curry 1988b). Joint nesting by mockingbirds, however, is not intrinsically advantageous, as in other species where it occurs more often (e.g. Koford et al. 1990).

Though variation in mate availability affects mockingbird breeding, we suggest that the relationship between population density and territory space has an overriding influence on social organization and reproductive strategies (Curry & Grant 1989, 1990). The weak negative correlation between density and breeding by females on Genovesa (Table 1, $P < 0.1$) supports this hypothesis, as does evidence that social organization varies with population density among the four allopatric species of *Nesomimus* (Curry 1989). We predict that under conditions of high density on Genovesa, many females are prevented from breeding, regardless of mate availability. This prediction remains untested because an excess of females and high density co-occurred only once in our study – during a drought year (1985) when no mockingbirds nested.

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