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INFLUENCE OF CLIMATE ON REPRODUCTIVE SUCCESS IN MEXICAN JAYS

SHOU-HSIEN LI AND JERRAM L. BROWN[1]

Department of Biological Science, State University of New York, Albany, New York 12222, USA

ABSTRACT.—In the arid southwestern United States, many birds initiate breeding in the driest months of the year, March to May, long before the monsoon rains arrive in July and August. Although breeding success in these species is thought to be sensitive to precipitation, the relationships have not been rigorously described based on long-term study of a single species. We studied the relationships among reproductive success, precipitation, and temperature in Mexican Jays (*Aphelocoma ultramarina*) in the Chiricahua Mountains, Arizona. We identified three orthogonal factors that accounted for 85.8% of the variance in the 11 reproductive-success variables. Factor 1, the most important, was associated with production of young and with the fraction of females that were breeding. Because the Mexican Jay is a plural breeder (more than one breeding female per group), reproduction in the population can be influenced not only by the success of individual females, but also by the proportion of females in each flock that breed in a given year. This factor was positively related to the amount of precipitation both at the onset of breeding in March and April and during the previous eight months. Brood size at banding (14 to 15 days), which was strongly associated with Factor 2, was negatively related to the number of adult females per flock and relatively insensitive to yearly variation in climate. Success of the youngest females was associated with Factor 3 and depended on a different set of variables than that of older females. Although production of young was predictably depressed in drought years, the significant relationships between reproductive success and climate did not otherwise enable precise predictions based on climate alone. Because predation appears to be highly correlated with the number of nestlings per unit, the lack of strong predictability of reproductive success using climate variables alone may be caused by the independence of predation from climate variables. *Received 3 August 1998, accepted 25 January 1999.*

BECAUSE OF ALMOST DAILY ATTENTION in the scientific and mass media to El Niño and global climate change, especially in 1997–1998, ecologists and even the general public are becoming more attentive to the effects of climatic variation on a variety of biological phenomena, including geographic range (Parmesan 1996), global photosynthesis (Myneni et al. 1997), community composition (J. H. Brown et al. 1997), and timing of reproduction (Beebee 1995, Crick et al. 1997, Forchhammer et al. 1998, McCleery and Perrins 1998). This paper focuses on relationships between reproductive success and yearly climatic variation. Many short-term studies document that climate affects reproductive success, but such studies are limited by small sample sizes. Fortunately, long-term studies of birds have become a rich source of data for the study of climate effects on reproduction (e.g. Brown and Li 1996, Skinner et al. 1998). Such studies are needed to assess the influence of climate change on avian populations.

The most dramatic effects of climate on reproductive success have been reported from coastal Ecuador (Marchant 1959, 1960; Lloyd 1960) and the Galapagos Islands (Grant 1985, 1987; Curry and Grant 1989, 1991; Grant and Grant 1989). Effects of El Niño on this region have long been known. Recently, however, atmospheric scientists have demonstrated that variations in climate associated with oceanic phenomena, such as El Niño and the North Atlantic Oscillation, actually have more far-reaching statistical effects (Taylor et al. 1998). The realization that global climate changes dramatically on a decadal scale, and that these changes may affect bird populations (Crick et al. 1997, Forchhammer et al. 1998, McCleery and Perrins 1998), provides a new stimulus for the study of effects of climate on breeding biology of North American birds. However, before we can appreciate the possible effects of El Niño and global climate change on a particular species,

[1] Address correspondence to this author. E-mail: jlb81@cnsvax.albany.edu

we need detailed information on how that species reacts to yearly variation in climate. Therefore, in response to the need to evaluate effects of global climate processes on North American birds, we undertook a comprehensive examination of the statistical effects of climate on reproduction in the Mexican Jay (*Aphelocoma ultramarina*).

In warm, arid climates, reproductive success of birds is related to rainfall because most species do not breed until rains arrive and success is diminished when rain is insufficient. Breeding success tends to be sensitive to the duration and amount of precipitation in Galapagos finches (Grant 1986, Grant and Grant 1989), resident passerines of East African (Sinclair 1978, Dittami and Gwinner 1985), White-fronted Bee-eaters (*Merops bullockoides*; Wrege and Emlen 1991), wrens of the Venezuelan llanos (Piper 1994), and desert birds of Australia (Keast and Marshall 1954, Nix 1976). In Arizona populations of the Mexican Jay, however, breeding occurs not in the rainy season of July and August (monsoon), but in the driest months of the year, namely March through June (Brown and Li 1996). The purpose of our study was to determine more precisely how reproductive success in these jays is correlated with climatic variables in the months and years preceding a breeding season.

METHODS

Study population.—The study area is on the Southwestern Research Station of the American Museum of Natural History, adjoining private lands, and the Coronado National Forest in Cave Creek Canyon on the east side of the Chiricahua Mountains, Arizona (31°53′N, 109°12′W). The habitat is pine-oak-juniper woodland (see Brown and Brown 1990, Brown 1994).

The number of flocks (also termed "groups" or "units") under study increased from six in 1972 to nine in 1994. This led to an increase in the area under study by about 20%. Individuals that were known by direct observation to be living in the study flocks on 1 May of a given year were defined as the census population for that year. Birds hatched in the same year as the census were excluded as flock members that year. The population was color banded and observed every year from 1969 through 1996. During the period analyzed here (1972 to 1996), the population varied in size between 63 and 141 jays. Each flock occupied a stable group territory that varied little in location and size from year to year. Therefore, we indexed density on a per-flock basis rather than in relation to a fixed study area, which would be awkward because it would entail fractions of flocks. Further details on this population are available in Brown and Brown (1985, 1990) and Brown (1994).

Sex and age.—Most birds were banded as nestlings or when age could be determined reliably (i.e. 0 to 2 years). Jays in their first two years of life were assigned an age using the methods of Pitelka (1945), which we have confirmed using birds banded as nestlings and trapped at later ages (Brown 1994). Remiges, rectrices, the alula, and some greater and middle secondary coverts are retained beyond the first prebasic molt. These feathers are distinctly duller and more worn than the newer plumage. Reduced areas of light color on the bill persist to age two, rarely to age three. A few birds were age three or older when initially banded (5 to16% per year). These were assigned the age of three at the time of banding and used in this analysis. Females were birds known to have incubated. Males were birds that built nests with a female. We determined sex for all birds of age 8 or older, 96.4% of the birds at the most common breeding ages (4+), and 93% of birds age 3 or older; the rest were not sexed and were assigned half to each sex for calculation of certain variables. Further details of determination of age and sex are given elsewhere (Brown 1994, J. L. Brown et al. 1997, Brown and Bhagabati 1998).

Reproductive success.—We observed reproductive success in the population by monitoring nests of each female each year. Field work began in mid-March or earlier and lasted into June except in the years 1980 to 1991 and 1993 to 1995, when field work began in January. Observers were present through the end of June or close to it. In addition, many scientists were at SWRS all through the summer each year. If a nest had been discovered by observers in July or August, it is likely that the nest would have been brought to our attention; however, none were. From March to July, we located nearly every nest in our study population and determined the individual who incubated the eggs and the identity of her mate. We do not know of any nests that we missed, but because finding nests is difficult, it is possible that we missed a few, especially ones that failed early in incubation. However, we found no fledglings from undiscovered nests. Mexican Jays tend to be socially monogamous in that typically a single pair builds a nest, unless usurpation occurs, and only the female builder incubates. Studies using allozymes (Bowen et al. 1995) and DNA microsatellites (Li and Brown unpubl. data) have not revealed any cases of intraspecific multiple maternity. We monitored the reproduction of every nest until the young were banding age or until they left the nest (i.e. fledged). The seasonal pattern of breeding has been described in detail by Brown and Li 1996.

We employed 11 measures of reproductive success for each year in a factor analysis (Appendix). We chose these variables because they are components of

TABLE 1. Summary statistics for variables expressing reproductive success in Mexican Jays in southeastern Arizona, 1972 to 1996.

Variables	$\bar{x}$	SD	Min.	Max.	CV
1. Fraction of females 3+ years with eggs	0.52	0.13	0.23	0.68	23.9
2. No. young/banded female 2 and 3 years	0.49	0.52	0.00	1.60	106.0
3. No. young/banded female 4+ years	1.28	0.63	0.18	2.56	49.2
4. Brood size at banding	3.18	0.50	2.00	4.38	15.7
5. No. young/successful nest	3.18	0.51	2.00	4.37	16.0
6. No. nests with eggs per unit	3.05	0.91	1.33	4.78	29.8
7. No. nestlings/unit	4.91	1.81	1.11	8.50	36.9
8. No. successful nests/unit	1.36	0.54	0.22	2.38	39.7
9. No. fledglings/unit	4.37	1.85	0.56	8.50	42.3
10. No. fledglings/nest with eggs	1.46	0.64	0.29	2.92	43.8
11. Fraction of nests successful	0.45	0.17	0.12	0.71	37.8

population growth. We did not know *a priori* which, if any, variables would be sensitive to climatic factors or how they would be related to each other, so we included a variety. Some variables are expressed as the values for the population divided by the number of social units, or flocks. Thus, some of the variables are the averages per unit for each year (variables 6 to 9 in Table 1).

In the Mexican Jay, which is a plural breeding species, the number of breeding females per group is variable and typically more than one, unlike the more common singular breeders. Therefore, climate could affect the number of birds breeding per unit (variables 1 to 3, 6 to 9, and 11) and the success of those that do breed (variables 4, 5, and 10).

Reproductive timing variables.—Because timing variables are related to climate (Brown and Li 1996), we examined only their relationships to reproductive success. For each year, we calculated the mean date of first clutch for all females that bred, accounting for leap years. Subsequent clutches were not included. We used as the date for each clutch the Julian day of the year for the third egg of the clutch, which is the date of initiation of incubation (Brown 1994). Most clutches contain four or five eggs. We did not inspect most nests at the time of laying but instead calculated laying dates from the ages of eggs or nestlings, making supplementary use of observations of eggs and incubation. By tracking individually color-banded females, we were able to determine the order of their clutches. Clutches of unbanded females were not used in this analysis. We also examined the fraction of females with a second clutch each year.

Climatological data.—The climatological data used in our analyses were recorded daily by employees of the Southwestern Research Station within our study area. We obtained these data from the monthly station summaries for Portal, Arizona, published by the Environmental Data Service of the National Oceanic and Atmospheric Administration, United States Department of Commerce. Climate variables were chosen to cover a range of periods from the same breeding season to two years earlier. We suspected that the various types of food used by jays, including acorns, arthropods, and small vertebrates, would be influenced by various environmental factors at different times of the year.

Population variables.—Because reproduction might be density dependent, we tried to control for various density variables when necessary. Because the area under study was not constant but was defined by the territories of the groups, we used measures that were independent of the size of the study area, such as numbers of yearlings, adults, males or females per group, as defined below. Population increases were reflected in increases in group size. The origin of new groups and the loss of existing groups were rare and apparently were not directly related to population density or climate. We also tried to control for age structure, because reproductive success increases with age in this species (J. L. Brown et al. 1997), and we investigated possible effects of sex ratio on reproduction.

Statistical analysis.—All variables were normally distributed except precipitation in May and June and the number of young banded per female of age 2 to 3 years. We applied a square-root transformation to the former variable, but the latter variable, which had many zeros, could not be transformed to a normal distribution. Because the effect of deviation from normality is mainly to weaken the power of the test, we left it in the analysis; however, this variable was not critical for our results. Sample sizes were 25 years (1972 to 1996) for all analyses except where indicated.

Because the 11 measures of reproductive success that we used were often correlated with each other, we used the principal components method of factor analysis in SPSS to reduce the number of variables, an approach used in other studies of avian reproductive success (Skinner et al. 1998). We rotated the factor matrix orthogonally by the Varimax method. We then used the scores of the rotated factors instead of the original breeding variables as dependent var-

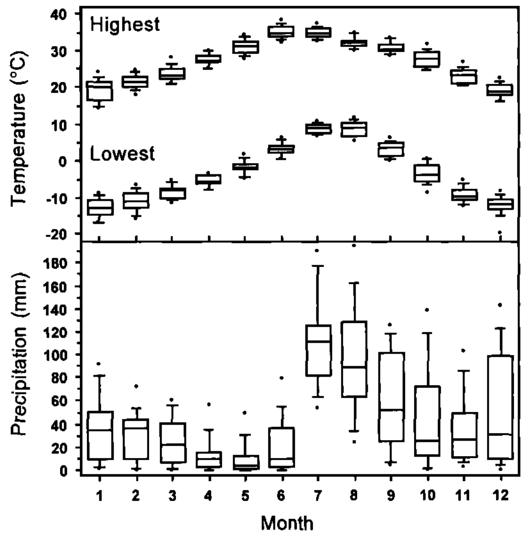

FIG. 1. Monthly pattern of temperature and precipitation on the study area from 1972 to 1996. Highest = highest temperature of month, and lowest = lowest temperature of month. Box = median, 25th, and 75th percentiles, whiskers = 5th and 95th percentiles, and dots = range.

iables to study the relationship between reproductive success and climate. We used multiple linear regression models to examine the statistical effects of climatic variation on the three principal factors representing annual reproductive success. We used the stepwise selection procedure to reduce the number of independent climate variables in the regression models.

Because reproduction may be influenced by factors such as population density, sex ratio, and age structure, we used a multiple linear regression model to detect possible relationships of these variables before we examined the climatic variables. Variables that had linear relationships with the reproduction of Mexican Jays were controlled using partial regression when examining statistical effects of climate variables.

RESULTS

Seasonal patterns of precipitation and temperature.—In the Chiricahua Mountains, the heaviest rains of the year occur during the monsoon months of July ($\bar{x}$ = 112.4 mm) and August ($\bar{x}$ = 97.7 mm; Fig. 1). In September, mean precipitation drops to 59.9 mm, and monthly precipitation gradually declines to 32.5 mm by February. The driest season is between March and June, when Mexican Jays breed. The mean monthly precipitation in this period was always below 30 mm. The largest fractions of annual precipitation were monsoon (41% of total) and winter rains (December to February; 51%). Precipitation from March to June made up only 8% of annual precipitation. Annual precipitation varied greatly (from 252 to 781 mm; $\bar{x}$ = 560 ± SD of 129.2 mm), as did precipitation in the critical months of early spring and July to February (Fig. 2). Snow occurred regularly in winter and could reach 15 to 25 cm in depth.

The coldest temperatures of the year typically occurred in January (mean lowest daily minima for January = −12.6°C; Fig. 1). Although the desert was only about 10 km away, maximum temperatures on the study area in most years were below 38°C. June and July were the hottest months, when the average daily maxima typically ranged from 29 to 34°C. The hottest single day of the month typically was between 35 and 37°C.

Annual variation in breeding-success.—Annual production of nestlings varied greatly from year to year (Fig. 2), but measures relevant to reproductive success did not always vary together. Altogether, we examined 11 measures of reproductive success. Descriptive information for each variable is shown in Table 1. Most variables had a coefficient of variation between 20 and 50, but brood size (of those nests that reached the nestling stage) was relatively constant (15.7), and the highest coefficient of variation belonged to the per capita success of young females (106).

The breeding-success variables can be summarized by three independent factors that together explained 85.8% of variation in annual reproductive success (Table 2). These three factors were the only ones with eigenvalues >1.0.

The first factor accounted for 55.7% of the total variance. The most important variables for Factor 1 were the number of nests with eggs per unit, the number of successful nests per unit, the fraction of females with a nest, and the number of nestlings per unit. Each of these variables was highly correlated with Factor 1 ($r \geq 0.82$, $P < 0.0001$). High scores of this factor indicate that (1) a higher fraction of breeding-age females was engaged in reproduction, (2) more females built nests, (3) more had successful nests, (4) more nestlings were raised per flock, and (5) more fledglings were produced in a given year. Thus, the first factor represents the

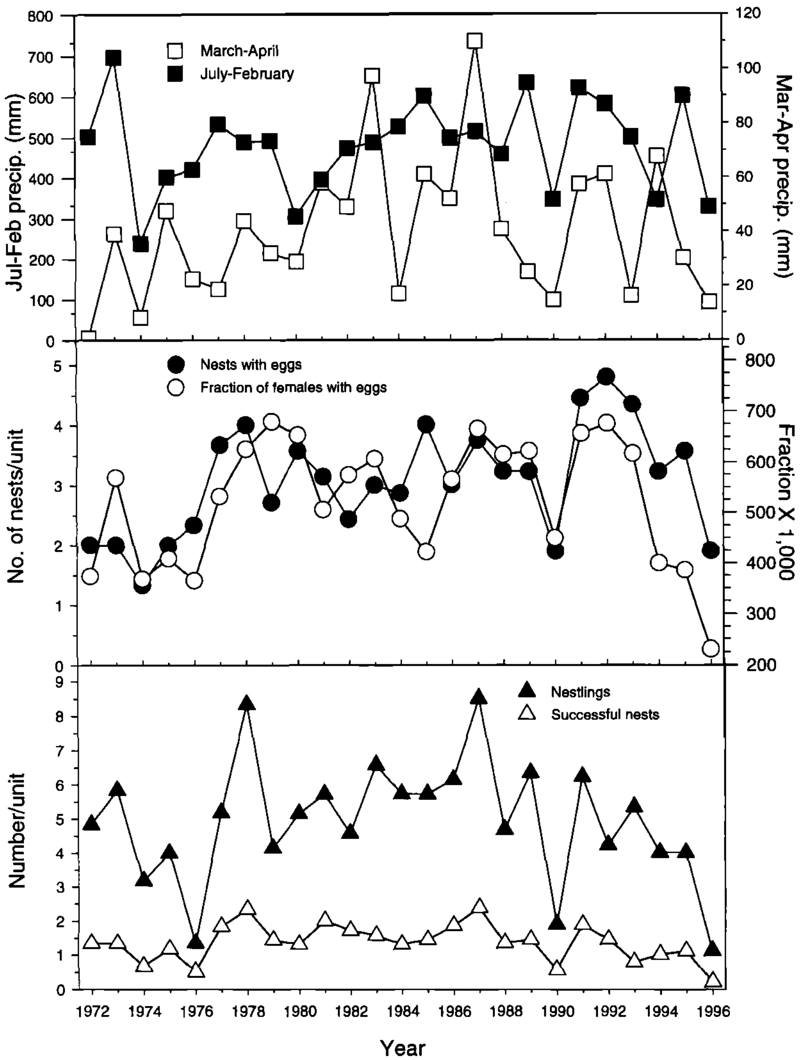

FIG. 2. Annual variation in two measures of precipitation and four measures of reproductive success in Mexican Jays.

TABLE 2. Rotated factor matrix of breeding variables with factor loadings. Highest values (above 0.8) are in bold. Variable numbers correspond to Figure 3 and Appendix.

Variable	Factor 1	Factor 2	Factor 3
1. Fraction of females 3+ years with eggs	**0.810**	0.036	0.122
2. No. young/banded female 2 and 3 years	0.033	0.102	**0.807**
3. No. young/banded female 4+ years	0.591	0.550	0.158
4. Brood size at banding	0.077	**0.944**	0.210
5. No. young/successful nest	0.035	**0.936**	0.257
6. No. nests with eggs per unit	**0.846**	−0.194	−0.348
7. No. nestlings/unit	**0.835**	0.393	0.282
8. No. successful nests/unit	**0.840**	0.083	0.484
9. No. fledglings/unit	0.748	0.368	0.505
10. No. fledglings/nest with eggs	0.214	0.580	0.771
11. Fraction of nests successful	0.270	0.336	**0.843**

variables that contributed most heavily to total production in the population. The main contributing variables to Factor 1, as listed above, are high when more than one female per unit breeds. Their maximum values in Table 1 reflect larger numbers than can be produced by only one breeding female per flock. Factor 1 was not, however, correlated with the number of females of breeding age (3+ years) per unit (r = 0.21, P = 0.313). As expected, the number of nestlings per unit was positively associated with the other variables having high loadings on Factor 1, namely, the fraction of females breeding, the number of nests with eggs per unit, and the number of successful nests per unit ($r \geq 0.539$, $P \leq 0.005$).

The second factor explained 20.4% of the total variance of the 11 reproductive-success variables. Variables having a high loading on Factor 2 were brood size and number of young per successful nest. This factor seems to reflect conditions for rearing young but not conditions conducive to initiating breeding.

The third factor explained 9.7% of the variance in the reproductive-success variables. Factor 3 had a positive relationship with the fraction of nests that were successful and the number of young per banded female for the youngest breeding ages (2 to 3 years).

When the factor loadings in Table 2 are plotted (Fig. 3), the 11 variables may be somewhat arbitrarily assigned to three clusters that reveal close affinities among the variables better than in Table 2. Those variables that loaded heavily on Factor 1 and low to medium on Factors 2 and 3 (1, 3, 6, 7, 8, 9) formed a cluster related to nestlings/unit and fraction of mature females breeding. The variables that loaded heavily on Factor 2 but low on Factor 1 (4, 5) formed a cluster related to brood size. A third cluster was formed by variables that loaded heavily on Factor 3 but low on Factor 1 (2, 10, 11). These reflected the breeding success of young females and the overall fraction of nests that were successful.

Statistical effects of density, sex ratio, and age structure.—To investigate the statistical effects of climatic variation on reproduction, we needed to control the statistical effects, if any, of population variables such as density, sex ratio, and various aspects of age structure (see Methods). To investigate the statistical effects of these seven population variables on the repro-

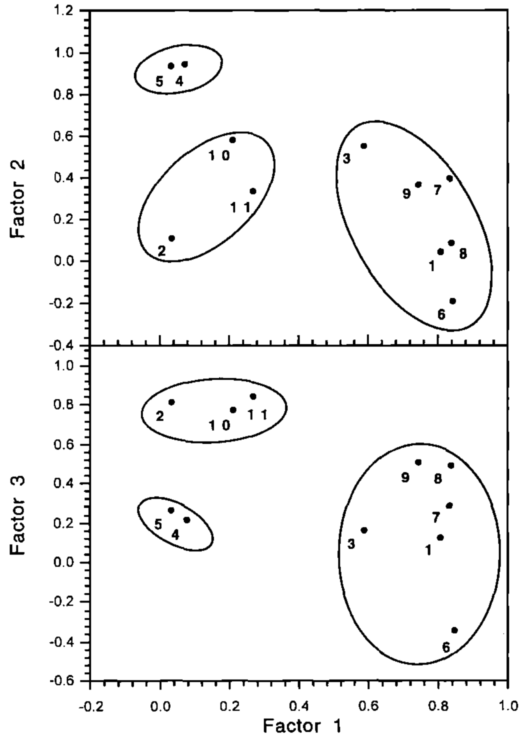

FIG. 3. Clustering of variables according to loadings on the three factors from Table 2. The ellipses facilitate comparison of the upper and lower figures and are purely arbitrary.

duction of Mexican Jays we used original scores of Factors 1, 2, and 3 as dependent variables in the multiple linear regression model. None of the population variables was selected for the regression model of Factor 1 ("fraction breeding"). Therefore, we used the original score of Factor 1 directly for climate analysis.

Factor 2 (brood size at banding) was negatively related to the number of mature (3+ years) adults per unit ($b = -0.4738 \pm 0.0999$; t = 4.74, P = 0.0001). Factor 3 was negatively associated with average unit size ($b = -0.2063 \pm 0.0900$; t = 2.29, P = 0.0231). Because Factors 2 and 3 were significantly related to the population variables, we used partial regression to control for the confounding effect of population variables on Factors 2 and 3 in our analysis of climate variables.

Statistical association of climate variables with reproductive success.—To investigate possible relationships between reproductive success and climate, we employed stepwise regression using each of the three factors as dependent var-

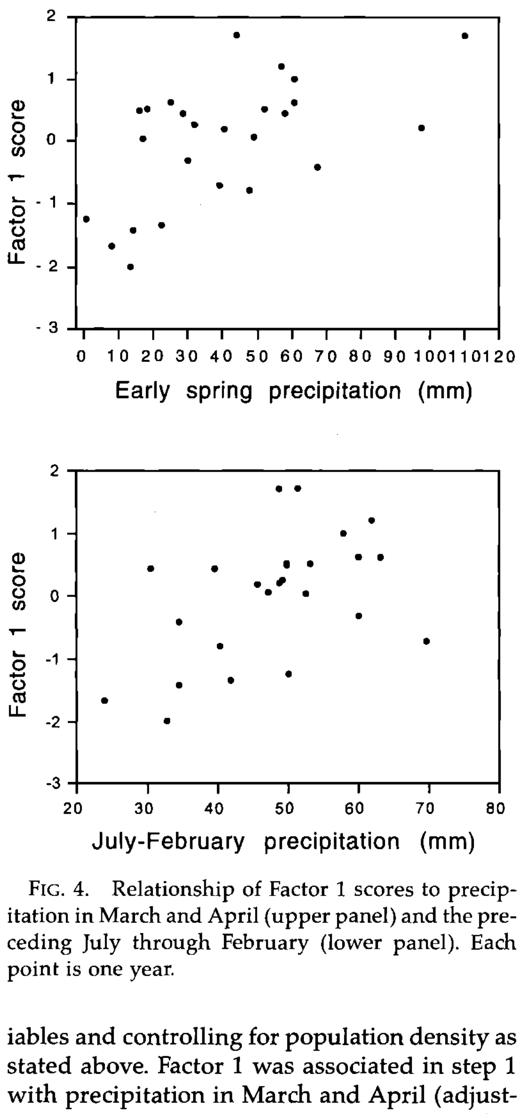

FIG. 4. Relationship of Factor 1 scores to precipitation in March and April (upper panel) and the preceding July through February (lower panel). Each point is one year.

iables and controlling for population density as stated above. Factor 1 was associated in step 1 with precipitation in March and April (adjusted $r^2 = 0.305$, $t = 3.15$, $P = 0.005$; Fig. 4) and in step 2 with precipitation the preceding July to February (adjusted $r^2 = 0.431$, $t = 2.46$, $P = 0.022$; full model, $F = 10.08$, df = 1 and 23, $P = 0.001$; Fig. 4). Although these two precipitation variables often vary together (Fig. 2), they were not significantly correlated with each other ($r_s = 0.329$, $P = 0.108$). Factor 1 was not associated with precipitation in the previous monsoon or any earlier period that we tested. As a check on these results, we ran separate stepwise regressions on each of the four reproductive-success variables with the highest loadings on Factor 1. As expected, each was significantly associated with one or more of the precipitation periods included in the period December to April ($P \leq 0.02$). For example, the number of nestlings per unit was positively associated with precipitation in March and April ($b = 0.0313$; $t = 2.87$, $P = 0.009$) and July to February ($b = 0.0066$; $t = 2.54$, $P = 0.0186$).

After controlling for the number of adults per unit, Factor 2 ("brood size") was not significantly associated with any climate variable that we examined. Factor 3, after controlling for the average number of birds in the group, was negatively associated in step 1 with precipitation from September to February two winters earlier (adjusted $r^2 = 0.178$; $t = 2.73$, $P = 0.012$) and in step 2 with minimum temperature from October to November (adjusted $r^2 = 0.291$; $t = 2.16$, $P = 0.042$; full model, $F = 5.92$, df = 2 and 22, $P = 0.009$).

Timing of laying.—Because the climate variables associated with reproductive success in this study differed partially from those that were associated with the timing of breeding in our previous analysis (Brown and Li 1996), we examined the relationship between two timing variables and reproductive success using the four reproductive-success variables that were most associated with Factor 1. Mean date of first clutch was positively associated with the number of nests with eggs per unit ($r = 0.617$, $P = 0.001$) and with the number of nestlings per unit ($r = 0.511$, $P = 0.011$) but not with the fraction of females breeding or with the number of successful nests per unit ($n = 24$; 1996 data excluded). Minimum temperature in winter was negatively associated with mean Julian date of first clutch (Brown and Li 1996) but was not associated with any of the three reproductive-success factors considered in this paper.

The second timing variable from our previous paper that we examined in relation to reproductive success was the fraction of females that had a second clutch. This fraction reflected the extent of breeding later in the season (May to June). Because this variable was already reported to be positively related to precipitation in the previous monsoon and winter, we wished to know how the fraction of females with second clutches was related to the reproductive-success variables that we use here. We found significant, positive Pearson correlations ($n = 26$ years) with five variables, including the four that were most strongly associated with Factor 1 (fraction of females with eggs, $r = 0.388$, $P = 0.05$; number of nests with eggs/

unit, $r = 0.661$, $P < 0.0001$; number of nestlings of banding age per unit per year, $r = 0.457$, $P = 0.019$; number of banding-age nests per unit per year, $r = 0.646$, $P < 0.0001$; and the fraction of banded males ages two years or older with a nest record, $r = 0.493$, $P = 0.011$) but not with other reproductive-success variables. These results suggest that one of the ways in which precipitation in July through February could influence Factor 1 is by extending the breeding season, thus allowing more second clutches by individuals whose first nest had failed.

Discussion

Precipitation.—Our finding that yearly variation in the amount of precipitation is related to annual reproductive success of Mexican Jays was not surprising considering the arid environment in which they live, but it was not clear *a priori* which months would be critical. Precipitation in March and April, at the beginning and peak of the laying season, had the strongest effect on Factor 1, which best reflected reproduction in the population. March and April are among the driest months of the year (Fig. 1). Therefore, even a little rain in this period could have a large effect on the food supply of jays by promoting growth of herbaceous plants and their animal dependents. Thus, precipitation at this time might influence the decision of a female jay to breed that year, thereby influencing the fraction of mature females that breed, which in turn affects the total production of nestlings per unit.

An additional statistical effect on Factor 1 came from the accumulated precipitation from the previous July through February, which we showed earlier to be related to the fraction of females with a second brood (Brown and Li 1996). Precipitation in this period should largely determine the level of the watertable in May. Therefore, through its effects on trees and other plants, accumulated precipitation should also influence the growth of biomass during the dry season, including food for jays.

Although in certain years (e.g. 1974, 1976, 1990, and 1996) drought appeared to depress reproductive success (Fig. 2), the percentage of variance of Factor 1 that is explained by precipitation variables is not impressive (adjusted $r^2 = 0.413$). Thus, although precipitation is important, especially in dry years, other variables must be involved to explain much of the observed variation in Factor 1 and the number of nestlings per unit. There may also be statistical effects of climate that do not show up in our analysis because of scale, nonlinearity, or the fact that climate is mainly a collection of variables whose statistical effects are likely to depend on other intervening variables that we did not measure, such as various kinds of jay food. Consequently, although we may conclude that precipitation has significant associations with reproduction, we cannot predict reproductive success precisely on the basis of precipitation alone except in severe droughts, like that in 1996, whose disastrous effects we did in fact predict accurately. The negative relationship between Factor 3 and the amount of precipitation two winters earlier is difficult to understand, and we can offer no obvious hypothesis that might explain it.

Predation.—Predation is a likely explanation for some of the variance in reproductive success because indirect evidence for it is frequently seen, but predation is virtually impossible to estimate directly because the predators are so diverse and difficult to observe. Major avian predators of Mexican Jays include Common Ravens (*Corvus corax*), three species of *Accipiter*, various owls, and other hawks. The most important mammal for the Mexican Jay is probably the coati (*Nasua narica*), which hunts in daylight, can probably hear begging nestlings, and can climb tall trees (Brown and Li unpubl. data). We also suspect that the ringtail (*Bassariscus astutus*), which is arboreal and occurs regularly on the study area, molests jay nests. The suite of predators on our study area is varied, and a simple connection with climate seems unlikely.

The relative importance of predation and climate may, however, be examined using the fraction of nests that were successful (fledged at least one young) as a proxy variable for predation, as done by Woolfenden and Fitzpatrick (1984). Use of this approach depends on our observations that loss of entire broods through starvation was rare and that predation often resulted in loss of entire broods. The fraction of nests that were successful loaded heavily on Factor 3, which collectively explained only 9.7% of variance in reproductive-success variables. To examine the importance of predation more directly, however, we ran a stepwise regression analysis using the number of nestlings per unit as the dependent variable (more representative in our study than fledglings because of larger sample sizes). Independent variables were the fraction of nests successful and the two climate variables previously shown to be significant. The first variable to enter the equation was the fraction of nests that were successful (adjusted $r^2 = 0.303$), the second was precipitation in March and April (combined adjusted $r^2 = 0.441$), and the third was precipitation from July to February (combined adjusted $r^2 = 0.541$). The final equation was highly significant ($F = 10.44$, $P = 0.0002$):

$$y = -0.711 + 4.352\, x_1 + 0.00553\, x_2 + 0.0245\, x_3, \quad (1)$$

where y = number of nestlings per unit, x_1 = fraction of nests successful, x_2 = precipitation in March and April, and x_3 = precipitation from July to February. These results suggest a strong association of predation with production of nestlings, but one that is relatively independent of our climate variables. As a check on the independence of the predation proxy variable we did an additional analysis. In a stepwise regression, the fraction of nests successful was not correlated with any of our 15 climate variables except minimum temperature in autumn (adjusted $r^2 = 0.392$, $F = 5.85$, $P = 0.0006$), a relationship that is not easy to explain.

Brood size.—Although we expected brood size to group with the variables in Factor 1 because of its direct relationship with reproductive success, it grouped with the variables in Factor 2. Nevertheless, brood size was significantly correlated with two of the variables in Factor 1, number of nestlings per unit ($r = 0.583$, $P = 0.001$, $n = 27$) and number of fledglings per unit ($r = 0.576$, $P = 0.002$, $n = 27$). Brood size was the least variable of our reproductive-success variables (Table 1) and was not associated with climate variables in the manner of Factor 1.

Although without strong statistical support, we found a positive relationship between precipitation and brood size in certain years, such as 1976. Mexican Jays had the lowest brood size ($\bar{x} = 2$) in 1976. In that year, jays also had the lowest number of successful nests per group (0.5) and the second lowest nesting success rate (0.21) of our study period. In 1976, precipitation in early spring and in the previous monsoon-to-winter was only 55.2% and 86.4%, respectively, of average precipitation in the same periods in all years. Therefore, prolonged drought lasting into early spring might still have some influence on brood size in some years.

Other acorn-eating species.—Birds that rely heavily on stored acorns for winter food should be influenced by the size of acorn crops in the preceding year, which in turn may be influenced by precipitation at the time acorns are produced. Woolfenden and Fitzpatrick (1984) examined annual variation in the "average number of fledglings produced per pair" in the acorn-eating Florida Scrub-Jay (*Aphelocoma coerulescens*). They estimated the importance of four factors that might influence reproduction by a female territory owner, namely clutch size, hatching failure, nestling starvation, and nest predation. Although mean clutch size in first nests was strongly correlated with rainfall in the previous summer, a significant association between fledglings per pair and mean size of first clutch was absent. However, using "the proportion of nests that survive to fledging" as an index of predation, they showed an "overwhelming" association with the number of fledglings per pair. Therefore, they concluded that "the annual level of nest predation determines the mean number of young that fledge" (Woolfenden and Fitzpatrick 1984:181). The proportion of nests that produced fledglings was also correlated with rainfall during the preceding 10 months, but the mechanism by which predation is influenced by climate is still obscure. Because the effect of density of breeding pairs on total production in the population was not considered, direct comparison with our study is not possible; but because the scrub-jay has only one breeding female per territory, density effects should be smaller than in the Mexican Jay. The variable of ours that most resembles that used with the scrub-jays is fledglings per nest with eggs (no. 10); this variable does not reflect the fraction or number of females breeding. In our study, fledglings per nest with eggs was highly correlated with the proxy predation variable (no. 11; $r = 0.696$, $P < 0.0001$, $n = 25$). Thus, by this measure also, yearly variation in predation is strongly associated with reproductive success.

Relationships between reproduction and climate have also been examined in the Acorn

Woodpecker (*Melanerpes formicivorus*), a species which, like the Mexican Jay, relies on stored acorns for much of its food (Koenig and Mumme 1988). In contrast to the two open-nesting *Aphelocoma*, predation in Acorn Woodpeckers was not an important cause of nestling loss, whereas starvation was an important factor. A strong correlation occurred between three measures of reproduction (clutch size, young/group, young/breeding female) and winter rainfall two years earlier. The authors felt, however, that this result was not explicable in terms of either acorn crop or insect abundance, and they concluded that "reproductive success . . . appears to be independent of any directly interpretable effect of the weather" (Koenig and Mumme 1988:124).

Their data do show, however, that the two best years for reproduction (in a 10-year data set) were preceded by the two years of good acorn crops, lowest insect damage to acorns, and highest levels of autumn breeding. Dependence of reproductive success on acorn quantity and quality would explain the lag time of two years between rainfall and breeding success if an abundance of high-quality acorns enabled woodpeckers to breed in autumn, overwinter in good condition, and enter the next breeding season with a surplus of stored acorns. In fact, the authors reported a strong correlation between the number of fledglings per breeding female and "total maximum kJ per individual stored in granaries during the prior winter." Such a scenario is also feasible for the Mexican Jay, but we have no data on acorn crops.

Variable environments.—Long-term studies have been conducted on two other passerine species that inhabit unusually variable environments. The Pinyon Jay (*Gymnorhinus cyanocephalus*) is well adapted to use seeds of pinyon pine (*Pinus edulis*), whose yearly crops are erratic (Marzluff and Balda 1992). Reproductive success in this jay was positively related to the size of the preceding crop of pinyon seeds and negatively to precipitation during the breeding season (Marzluff and Balda 1992:209). Paradoxically, although the Pinyon Jay lives in a colder climate than does the Mexican Jay, it often initiates breeding much earlier (e.g. February), apparently relying mainly on stored pinyon seeds. Very early breeding places Pinyon Jays at risk to snowstorms and thus appears to explain the negative relationship between reproductive success and spring precipitation. Even summer precipitation was negatively related to fledging success. Thus, the relationship between reproduction and precipitation just prior to and during breeding in this closely related species (Espinosa de los Monteros and Cracraft 1997) is opposite that of the Mexican Jay.

The Galapagos Mockingbird (*Nesomimus parvulus*) lives in the region most strongly affected by El Niño and consequently is subjected to extreme variation in precipitation. Like some Galapagos finches (Grant 1985, 1987; Grant and Grant 1989), this mockingbird produces many young in wet years and relatively few in dry ones (Curry and Grant 1989, 1991). It does so, however, by a different mechanism than in the Mexican Jay. The breeding season in the Galapagos is extended during wet years, but success per nest is relatively constant. Unlike the situation in the Mexican Jay, "Breeding density is among the least variable . . . of the population's demographic characteristics" (Curry and Grant 1989:457) and "the density of breeding birds remained relatively constant." Thus, with the exception of some very dry years, the fraction of females breeding was insensitive to precipitation in a given year but increased as density decreased. Plural breeding was mainly a function of the proportion of yearling females in the population, again in contrast to the Mexican Jay, in which plural breeding is regular in all flocks and years and involves females of all mature ages. One factor that may be partly responsible for these differences is that breeding seasons in Arizona are curtailed by extreme dryness in May and June and by the onset of cold weather in September, whereas breeding in the Galapagos can continue for 205 days if the rains persist. Evidence for a modest extension of the breeding season of the Mexican Jay resulting from precipitation in the previous July through February is the positive relationship between precipitation in this period and the fraction of females with a second clutch in the subsequent breeding season (Brown and Li 1996).

Conclusions.—Renewed attention to climate change, human-caused or otherwise, has reawakened interest in its possible effects on avian populations. Comparison of our results with those from other long-term studies, however, has suggested that generalizations about the effects of climate variables on populations will be difficult. Although the matter is far more complex than the simple statistical associations between climate and reproduction that we have identified in this and in our previous paper (Brown and Li 1996), perhaps knowledge of these phenomena will someday be more useful than presently appreciated. Long-term studies of avian populations currently harbor a large amount of relevant data whose value in relation to effects of variation in climate has just begun to be realized. Studies that attempt to identify more precisely how climate variation affects reproduction will be needed in a variety of species to evaluate the potential effects of global warming on North American birds (Brown et al. 1999). This paper is part of a planned series of studies on the Mexican Jay that may lead to a more comprehensive understanding of the complex relationships between climate and the health of avian populations.

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APPENDIX. List of variables used to assess the effects of weather on reproductive success in Mexican Jays in southeastern Arizona.

Reproductive success

1. Fraction of females of age 3+ years (breeding or not) recorded with a nest and eggs.
2. Number of nestlings per banded female of ages 2 and 3 years, breeding or not. This is the number of banding-age nestlings produced by females of these ages divided by the number of females of these ages.
3. Number of nestlings per banded female of age 4+ years, breeding or not. This is the number of banding-age nestlings produced by females of these ages divided by the number of females of these ages.
4. Mean brood size at time of banding (14 to 15 days). Fledging occurs at 24 to 27 days.
5. Number of fledglings per successful nest (fledged at least one young).
6. Number of nests per unit (flock or group) that reached the egg stage.
7. Number of banding-age nestlings per unit.
8. Number of nests per unit that reached banding age.
9. Number of fledglings (i.e. leaving nest) per unit.
10. Number of fledglings per nest with eggs.
11. Fraction of nests that reach the age of banding for females of age 3+ years.

Precipitation

Precipitation in late spring, May and June, of same year.
Precipitation in early spring, March and April, of same year.
Precipitation in previous winter, December through February.
Precipitation in previous autumn and winter, September through February.
Precipitation in the previous monsoon, July and August.
Precipitation in previous monsoon, autumn and winter combined, July through February.
Precipitation in previous monsoon, autumn, winter and early spring combined, July through April.
Precipitation in December through February, two years earlier.
Precipitation in September through February, two years earlier.
Precipitation in September through November, two years earlier.
Precipitation in monsoon two years earlier.
Precipitation in monsoon and winter (July through February), two years earlier.
Annual precipitation was calculated from July through June.

Temperature

Minimum temperature in early spring, March and April of same year.
Minimum temperature in preceding December through February.
Minimum temperature in preceding autumn, September, October, November.
Maximum temperature in previous monsoon, July and August.
Maximum temperature in May and June of same year.

Population characteristics

Number of yearlings (second calendar year) per unit.
Number of yearlings and second year jays (third calendar year) per unit.
Number of adults (3+ years old; 4th calendar year) per unit.
Number of adult males per group of age three or older. Number of adult females per group of age three or older.
Average group size during the breeding season on May 1.
Fraction of males in the population of age three or older.