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DELAYED EFFECT OF MONSOON RAINS INFLUENCES LAYING DATE OF A PASSERINE BIRD LIVING IN AN ARID ENVIRONMENT[1]

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Much work has established that early spring temperatures modulate the onset of egg laying in resident birds of the north Temperate Zone. Most of this work has been done on the Great Tit (*Parus major*) and other parids in Holland (Kluijver 1951, VanBalen 1973), England (Lack 1958, Perrins and McCleery 1989) and other European countries (Dhondt et al. 1984, Barba et al. 1995). Little is known, however, about yearly variation in factors that affect the timing of laying in resident passerine species that inhabit different climatic regimes (but see Lambrechts and Dias 1993). We report here on some climatic correlates of laying date in a natural population of the Mexican Jay that has been studied for 24 years in the mountains of southeastern Arizona.

This region has a monsoonal climate that differs greatly from that in Europe and much of North America. A hot, dry spring with almost no precipitation is followed by heavy monsoon rains in July and August (39% of annual total, range 18–73%) and a cold winter, including snow. Annual precipitation on the study area averaged 562.1 mm (SD = 131.5, range 252.0–780.5). The pattern of leaf fall and regrowth in southeastern Arizona also differs considerably from that in northwestern Europe. The vegetation on the study area is Madrean evergreen woodland (Brown 1982). Nearly all trees on our study area are evergreen. In particular, the oaks, except in extreme drought years, retain their leaves through winter and grow new ones immediately after dropping the old ones in spring. In a first attempt to identify ecological factors that influence the date of laying and the frequency of second clutches in a natural population of the Mexican Jay, we examine here the importance of certain climatic factors.

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METHODS AND STUDY AREA

The population under study was located in the Chiricahua Mountains of southeastern Arizona, USA, at the Southwestern Research Station (SWRS) of the American Museum of Natural History. The population was color-banded and observed every year, 1969 through 1995. During the period of this study (1972–1995) the population varied in size between 63 and 141 jays. The birds lived in six to nine flocks, each occupying a stable group territory that varied little in location and size from year to year. Further details on this population are available elsewhere (Brown and Brown 1990, Brown 1994).

We observed the reproductive success of each female by monitoring the first and subsequent nests of each female in the population each year. For each nest we determined the mother from behavioral observations. Mexican Jays tend to be monogamous in that typically a single pair builds a nest and only the female builder incubates. Studies with allozymes (Bowen et al. 1995) and DNA microsatellites (in progress) have not revealed any cases of intraspecific multiple maternity.

We used as the date for our analyses the Julian day of the year for the third egg of the clutch, which is thought to be the date of initiation of incubation. Most clutches are of four or five eggs (Brown 1994). 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 behavioral observations. By tracking individually recognizable, color-banded females we were able to determine the order of their clutches. Clutches of unbanded females were not used in this analysis. We defined reproductive variables as follows: mean date of first clutch in Julian calendar days, accounting for leap years (LAYING) and fraction of laying females with a second clutch (FRACTION).

From 1972 through 1979 field work began in mid-March and lasted into June. Beginning in 1980 and continuing through 1995, with the exception of 1992, field work began in January. In most years observers were present through the end of June. In addition, there were always many scientists at SWRS all through the summer. 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.

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, AZ, published in Climatological Data, Arizona by the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Environmental Data Service. We simplified the data by dividing the 12 months into "seasons," as follows: previous monsoon (July–August), previous autumn and winter (September through February), and early spring (March–April). These periods were chosen to fit the monsoon pattern of rainfall and the breeding season of the jays (mainly March through June). All temperatures are in degrees Celsius. Precipitation is in millimeters. We defined the following climatic variables: precipitation in early spring (March and April), maximum temperature in previous monsoon (July and August), minimum temperature in early spring (March and April) of same year, minimum temperature in autumn (September–November), minimum temperature of winter (December–February; COLDEST), precipitation in monsoon (July and August) of previous year (MONSOON), precipitation in previous monsoon, autumn and winter combined (July through February; JULY–FEB), annual precipitation from previous July through June of same year, precipitation in previous autumn and winter (September through February), warmth sum for February through March (the mean of the average maximum and average minimum temperatures for each month was multiplied by the number of days in the month and the products for each month were added together [WARMTH23]), and warmth sum for February through April calculated as above (WARMTH24).

We used stepwise regression procedures (SPSS Inc. 1993) to analyze relationships between climate variables and laying. All variables were checked for normality and corrected by appropriate transformation when needed. Sample sizes were 24 years (1972 through 1995) for all analyses except where otherwise indicated.

RESULTS

The earliest clutch date for our study area was 3 March, and the latest recorded date was 26 June. Most breeding females (79% of 411) had only one clutch a year, and the peak period of egg laying was in mid-April. Those who failed in their first brood sometimes had a second, usually in May, or even a third clutch in late May or early June. Females that fledged young from their first nest rarely attempted a second (17 of 234), but on eight occasions females succeeded with two broods in a season. The distribution of laying dates for the first through third clutches is shown in Figure 1.

The average date of the first clutch varied considerably during our study, from a minimum of 98.5 (April 8) to a maximum of 126.7 (May 7) with a mean of 109.9 (April 20) for all 27 years. In a stepwise regression with mean date of first clutch as the dependent variable, the first variable to enter the equation was the precipitation in the monsoon of the previous year (July and August, MONSOON, $P < 0.001$). A second variable also was significant, namely the minimum winter temperature (COLDEST, $P = 0.014$). Scatter plots of these relationships are shown in Figure 2. The regression equation was as follows: LAYING = 1,094.16 − 9.8036 COLDEST −0.6273 MONSOON ($R^2 = 0.573$, $F = 13.44$, $P < 0.001$). This model predicts that jays begin to breed earlier when precipitation was relatively high in the preceding July and August and the winter was mild.

Of 411 records of first clutches, 99 individual females had recorded second clutches. The fraction of laying females with a second clutch was positively related only to precipitation in the previous monsoon, autumn and winter combined (July through February, $P = 0.002$) as shown in Figure 3. The regression equation was as follows: FRACTION = −0.1148 + 0.6012 JULY–FEB ($R^2 = 0.361$, $F = 11.89$, $P = 0.002$).

DISCUSSION

A surprising result of our study was that the mean date of first clutches in spring was strongly determined by

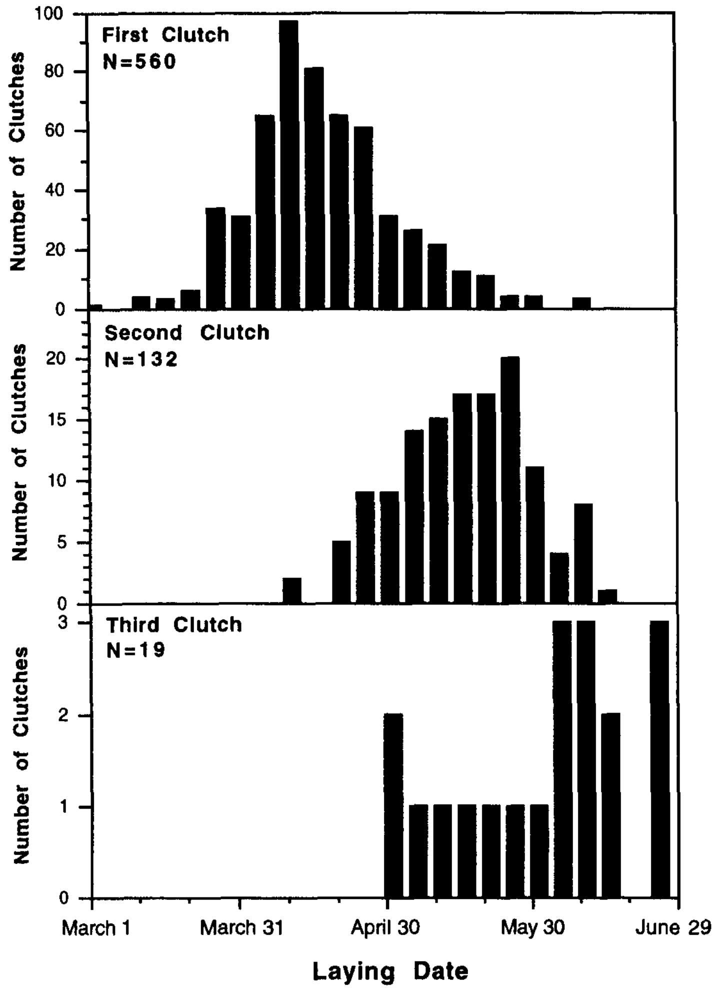

FIGURE 1. Dates and numbers of first, second and third clutches by banded female Mexican jays 1969–1995. Mean Julian day of first clutch was 109.5 (April 19, n = 451); second clutch, 137.4 (May 17, n = 105); third clutch, 151.9 (June 1, n = 13); all clutches, 115.8 (April 26, n = 687).

climatic events that occurred eight or nine months earlier in the preceding year, namely the monsoon rains. Furthermore, one might have expected a strong influence of temperature in the months just preceding laying, as in European titmice and flycatchers (see below), but we found no relationship of the mean date of laying of the first clutch with the minimum temperature in March–April before removal of the previous monsoon rains or after. Neither did we find a significant relationship between the mean date of laying of first clutches with our two variables expressing warmth sum (WARMTH23 and WARMTH24).

We did, however, find a significant relationship between the mean date of laying of first clutches and the minimum temperature in the preceding winter (December–February, COLDEST) both before removal of previous monsoon rains and after. This suggests that birds emerging from a colder than usual winter were in less good condition and that this retarded their breeding. Unusually cold weather in winter was associated with temporarily lowered body mass when birds were weighed daily (unpubl. data).

Can these findings be reconciled with the work on European titmice? Before offering an interpretation we first review the work on these species. Research on the determinants of the mean day of first clutches in Holland found a correlation with average temperature in the interval January 1–April 30 (Kluijver 1951, 1952). When this relationship was expressed as a "warmth sum," high correlations with laying date were obtained (up to r = 0.94). In England, Lack (1958) found that "the mean date of laying was two days earlier for every degree that the mean March temperature was higher . . . ." Similar findings on the importance of warm temperature in the period just before laying were reported by later authors for the Great Tit (Perrins 1970, 1995,

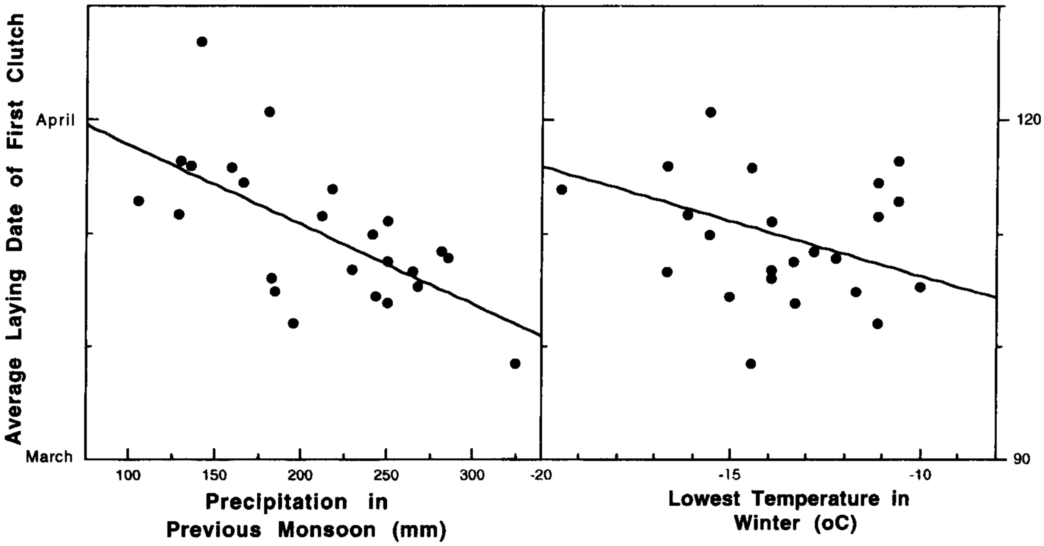

FIGURE 2. Mean date of first clutch was negatively related to precipitation in the previous monsoon and to the lowest temperature in the preceding winter ($R^2 = 0.57$, $P < 0.001$). Regression lines are shown separately for each independent variable.

VanBalen 1973, Perrins and McCleery 1989) and even for migrant species of flycatchers (Lack 1966) that were absent from the study area at the time. Other early studies on a variety of species are in agreement with this interpretation (Nice 1937).

The next stage was to link early spring temperatures with emergence of larvae of the principal prey species of the Great Tit during its breeding season. Mean laying date was strongly correlated with the "half-fall date" of the caterpillars of the winter moth (*Operophtera brumata*; Perrins 1965, Perrins and McCleery 1989). "Their breeding is timed so as to have their young in the nest when the caterpillar population on the oak trees is at its peak." (Perrins 1995: 49), although Lack (1966) thought this a "fortunate coincidence" (p. 24). Therefore, Great Tits initiate laying when food is not at peak

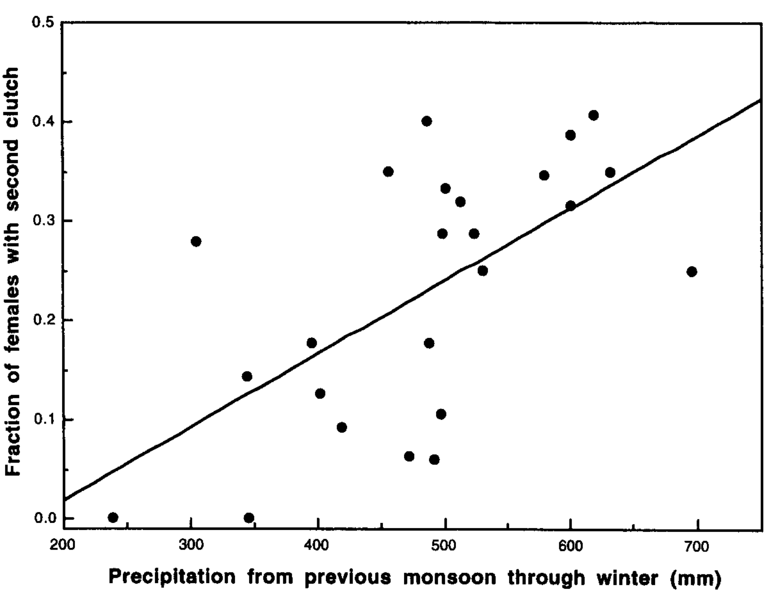

FIGURE 3. Fraction of females with a second clutch was positively related to precipitation in the previous monsoon and winter ($R^2 = 0.361$, $P = 0.001$). Regression line is shown.

levels but must be increasing rapidly. The positive results of most supplemental feeding experiments reinforce the view that food conditions influence laying date (reviewed in Martin 1987, Nilsson and Svensson 1993).

Could a similar explanation be true for the Mexican Jay? It seems reasonable to speculate that monsoon rains influence growth of insect populations in late summer, when insects are normally most abundant on our study area and just before many species of insect prepare for the winter. Some of these insects emerge in spring and become food for jays (Brown 1994, Siemens and Greene 1995). Thus, the biomass of insects in early spring could well depend heavily on conditions in the preceding year. A greater abundance of insects in early spring might induce earlier breeding in the jays. The timing of each insect species might still be determined by warmth sum or other factors.

A supplementary or alternative hypothesis is that monsoon rains influence the production of acorns, on which the jays depend in part during the winter, thereby affecting their condition at the end of winter. This may be true to a small degree, but acorns are formed in April and May before the monsoon season. Harvest begins in August during the monsoon rains. Thus, the contribution of monsoon rains to acorn growth is likely to be small.

Onset of laying is probably dependent on the physiological condition of the female. This could be enhanced by a high biomass of emerging insects and by the mildness of the preceding winter. Thus, warm temperatures in December–February were associated with earlier breeding. Presumably it is this effect that could cause a correlation with elevation. Laying date of this species was reported earlier to vary with elevation (Brown 1963). We did not study this systematically, but we observed a tendency for nests lower in the canyon off the study area to begin earlier.

The effect of climate on the frequency of second clutches might also be caused by effects on the insect population. The fraction of females having a second clutch was correlated with precipitation in the combined months from July to February, thus showing greater sensitivity to more recent conditions.

In warm, arid regions breeding tends to be initiated in conjunction with a rainy season, as in Galapagos finches (Grant 1986; Grant and Grant 1989), resident passerines (Sinclair 1978, Dittami and Gwinner 1985), White-fronted Bee-eaters (*Merops bullockoides*) of the East African savannah, wrens of the Venezuelan llanos (Piper 1994), and desert birds of Australia (Keast and Marshall 1954). In several of these cases breeding has been shown to be closely tied to food supplies that are governed by seasonal rains, although sometimes with a delay or slight anticipation. In these studies variation within years was the focus rather than variation among years. Statistical analyses based on many years of data were not used, and no attempt was made to analyze yearly variation in terms of precipitation or other climatic variables in previous years. Thus strict comparisons with the present study, which focuses on variation among years, cannot be made.

In the dry woodlands of Sonora, just south of Arizona, many avian species also breed during the monsoon of late summer (Short 1974), but in southern Arizona only a few species do so (Phillips et al. 1964). The Mexican Jay (Brown 1994), like many other species of pine-oak woodland, initiates breeding in the relatively dry months of March and April and feeds nestlings and fledglings in the driest months of the year, May and June. The period in which nestlings and fledglings are fed coincides with a peak of total arthropod biomass on two of the most common species of tree in the study area, the Emory oak (*Quercus emoryi*) and Alligator juniper (*Juniperus deppeana*), that occurs in early May of some years (Greene 1989). Except in extreme drought years the oaks renew their leaves in May at SWRS. Jays utilize some of these arboreal insects, but much of the food of nestlings is gathered on the ground. Newly emerging cicadas (*Tibicen duryi* and *T. chiricahuae*), for example, constitute roughly half the diet of nestlings in June (Brown 1994 and unpubl. data). Data with which to compare the relative magnitude of food available to jays in spring and the monsoon period are not available. Because the Mexican Jay in Arizona breeds in the dry spring rather than in the rainy season, a direct effect of the rainy season on breeding is precluded and the indirect effect of the preceding monsoon postulated here becomes possible.

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