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EFFECTS OF WEATHER AND POPULATION DENSITY ON REPRODUCTIVE SUCCESS AND POPULATION DYNAMICS IN A SONG SPARROW (*MELOSPIZA MELODIA*) POPULATION: A LONG-TERM STUDY

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ABSTRACT.—We studied the relationships among weather, reproductive success, and population density over 21 years (1980–2000) in a resident Song Sparrow (*Melospiza melodia*) population in coastal scrub habitat. Our goals were to test potential relationships between annual variation in weather and reproductive success, to evaluate whether reproductive success is density dependent, and to explore the effects of weather and population density on population dynamics. We analyzed the following components of reproductive success: clutch size, hatching success, fledging success, number of young fledged per successful nest, nestling weight, number of fledglings produced per female, number of broods per female, and probability of nest survival. During the study period, several very wet El Niño–Southern Oscillation (ENSO) events as well as an eight-year period of below-average rainfall occurred. Annual reproductive success and population density showed strong positive relationships to annual rainfall levels. Song Sparrow reproductive success increased with increasing rainfall and peaked at above-average rainfall levels. However, no component of reproductive success was related to an index of variation in the ENSO (i.e. Southern Oscillation Index). The components of reproductive success most strongly associated with rainfall were probability of nest survival and length of the breeding season. Nest predation rates were lower in wetter years. Song Sparrows nested over a longer period in years with higher rainfall and lower summer temperatures, and there was an increase in the number of successful broods per female in wetter, cooler years. Nestling weight was not associated with annual rainfall. Neither clutch size nor the onset of laying was associated with spring temperatures. Warmer summer temperatures were associated with a decrease in number of young fledged per successful nest. We found no evidence for decreased reproductive success in years of higher population density, which suggests that reproductive success was limited primarily by density-independent factors, such as weather. Changes in population density from one year to the next were positively related to rainfall-associated variation in reproductive success and negatively related to population density in the previous year. Rainfall in the previous year explained at least 49% of the annual variation in population density. Thus, population dynamics appeared to be driven both by density-independent and density-dependent factors. Received 29 January 2004, accepted 15 November 2004.

Key words: breeding phenology, California coastal scrub, density dependence, density independence, El Niño–Southern Oscillation, *Melospiza melodia*, nest predation, nest success, population density, population dynamics, rainfall, reproductive success, Song Sparrow, temperature, weather.

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Efectos del Clima y de la Densidad Poblacional en el Éxito Reproductivo y la Dinámica Poblacional de una Población de *Melospiza melodia*: Un Estudio de Largo Plazo

RESUMEN.—Estudiamos la relación entre el clima, el éxito reproductivo y la densidad poblacional de una población residente de *Melospiza melodia* en un ambiente de matorral costero a lo largo de 21 años (1980–2000). Nuestros objetivos fueron evaluar las relaciones potenciales entre la variación anual en el clima y el éxito reproductivo, evaluar si el éxito reproductivo es denso-dependiente, y explorar los efectos del clima y de la densidad poblacional en las dinámicas poblacionales. Analizamos los siguientes componentes del éxito reproductivo: tamaño de la nidada, éxito de eclosión, éxito de emplumamiento, número de juveniles emplumados por nido exitoso, peso de los polluelos, número de volantones producidos por hembra, número de nidadas por hembra y probabilidad de supervivencia del nido. Durante el período de estudio ocurrieron varios eventos muy lluviosos de la Oscilación del Sur El Niño (ENSO por las siglas en inglés de El Niño–Southern Oscillation), y también un período de ocho años de lluvias por debajo de la media. El éxito reproductivo anual y la densidad poblacional se relacionaron fuerte y positivamente con los niveles de precipitación anual. El éxito reproductivo de *M. melodia* se incrementó con aumentos en las precipitaciones y presentó un pico con niveles de lluvia por arriba del promedio. Sin embargo, ningún componente del éxito reproductivo se relacionó con el índice de variación del ENSO (i.e. Índice de la Oscilación del Sur). Los componentes del éxito reproductivo que se asociaron más fuertemente con la precipitación fueron la probabilidad de supervivencia del nido y la duración de la estación reproductiva. Las tasas de depredación fueron menores en los años más lluviosos. *M. melodia* nidificó durante un período mayor en años con más precipitaciones y con temperaturas de verano menores, y hubo un aumento en el número de nidadas exitosas por hembra en años más lluviosos y fríos. El peso de los volantones no se asoció con la precipitación anual. Ni el tamaño de la nidada ni el fin de la puesta se asociaron con las temperaturas de primavera. Las temperaturas más cálidas de verano se asociaron con una disminución en el número de juveniles emplumados por nido exitoso. No encontramos evidencia de una disminución del éxito reproductivo en los años de alta densidad poblacional, lo que sugiere que el éxito reproductivo estuvo limitado principalmente por factores denso-independientes como el clima. Los cambios en la densidad poblacional de un año al siguiente estuvieron positivamente relacionados con las variaciones en el éxito reproductivo asociadas a la lluvia y negativamente relacionados con la densidad poblacional del año anterior. La lluvia del año previo explicó al menos 49% de la variación anual en la densidad poblacional. De este modo, la dinámica poblacional pareció estar guiada tanto por factores denso-independientes como denso-dependientes.

ANIMAL POPULATION GROWTH is influenced by extrinsic factors (e.g. weather) and intrinsic factors (e.g. population density) acting on birth and death rates (Andrewartha and Birch 1954, Nicholson 1954, Begon et al. 1990, Murdock 1994). Therefore, the study of how both weather and population density influence primary population parameters is a central focus of ecology. Density-dependent influences on fecundity have long been believed to have a regulatory effect on fluctuations in animal populations (Lack 1966, Sinclair 1989, Royama

1992). The influence of climatic variation on reproductive success and timing has gained increasing attention recently because of the effects of global climate change (Brown et al. 1999, Wuethrich 2000, Martin 2001, McCarty 2001). Also, ecologists are increasingly using data from long-term studies of animal populations to investigate the relative importance of intrinsic and extrinsic factors on population dynamics (e.g. Arcese et al. 1992, Forchhammer et al. 1998b, Krüger et al. 2002, Patterson and Power 2002).

In birds, much research has focused on detecting density dependence in reproductive success (Lack 1966, Newton 1998, Both et al. 2000, Sæther et al. 2000). A decrease in per-capita fecundity with increased population density—resulting from increased competition for food, territories, or nesting sites—may be an important cause of density dependence in bird populations (Sinclair 1989, Sherry and Holmes 1995, Krüger and Lindström 2001, Both and Visser 2003). However, the relative importance of competition to fecundity and population dynamics is likely to vary over time and space, because of variation in population densities, environmental conditions, and the frequency or magnitude of environmental changes (Wiens 1977, Sinclair 1989, Murray 1994, Sherry and Holmes 1995). Few studies have compared the factors influencing long-term variation in fecundity and population dynamics among populations of an individual bird species in different habitats (Martin 2001, Krebs 2002, Ringsby et al. 2002). Because those topics have been extensively studied in a population of Song Sparrows (*Melospiza melodia*) on Mandarte Island in British Columbia (Arcese and Smith 1988, Arcese et al. 1992, Wilson and Arcese 2003), our study provides a rare opportunity to compare the effects of density and weather in two populations. In the Mandarte Island population of Song Sparrows, density dependence strongly affects reproductive success and thus population dynamics (Arcese and Smith 1988, Arcese et al. 1992). However, further study is needed to determine whether that pattern exists in noninsular populations, or under different climatic conditions.

Many studies have demonstrated that weather influences avian fecundity (Järvinen and Väisänen 1984, Grant and Grant 1987, Rotenberry and Wiens 1991, Gende et al. 1997, Skinner et al. 1998, Sillett et al. 2000, Ringsby et al. 2002). However, few studies have analyzed avian reproductive success in relation to both weather and population density (Koenig and Mumme 1987, Nilsson 1987, Arcese et al. 1992, Krüger and Lindström 2001), and even fewer have also linked those demographic mechanisms to population dynamics (Arcese et al. 1992, Krüger and Lindström 2001, Wilson and Arcese 2003). Most previous studies of the mechanisms by which weather influences reproductive success have taken place in regions with either very dry or relatively cold climates (or both);

thus, the influence of weather on populations experiencing Mediterranean-type climates is not well known. In arid environments, rainfall has been found to be associated with such measures of avian reproductive success as clutch size, number of young produced, and date of initiation of breeding (Boag and Grant 1984; Rotenberry and Wiens 1989, 1991; Li and Brown 1999). Most authors have attributed that pattern to the influence of precipitation on primary productivity, which in turn promotes an increase in availability of seeds, insects, and other food items (Noy-Meir 1973, Cody 1981, Boag and Grant 1984, Grant and Grant 1987). Temperature has been shown to affect reproductive success through its effects on reproductive output and timing, especially in environments with relatively cold winters. Warmer spring temperatures have been found to be related to increased clutch size and earlier initiation of breeding in a number of species, including Song Sparrows (Nice 1937, Järvinen and Väisänen 1984, Arcese et al. 1992, McCleery and Perrins 1998, Brown et al. 1999). High summer temperatures may also influence timing of breeding—for example, by causing an early cessation of breeding because of an earlier onset of xeric conditions (DeSante and Baptista 1989).

In addition to influencing food supply, weather may affect reproductive success by influencing nest predation rates (Woolfenden and Fitzpatrick 1984, Grant and Grant 1987). That may be attributable to the effects of weather on predator numbers or behavior (Rotenberry and Wiens 1989, Morrison and Bolger 2002), the characteristics of available nesting microhabitat, or nest-site selection behavior (Martin 2001). Although nest predation is the predominant cause of reproductive failure in many birds and probably interacts with food limitation to influence avian reproductive strategies (Martin 1992), we know relatively little about the effects of weather on nest predation. Here, we examine the effects of weather on both reproductive output and nest predation rates.

In California, the El Niño–Southern Oscillation (ENSO) is a major determinant of variation in precipitation (Schonher and Nicholson 1989). The ENSO is a periodic warming of the eastern equatorial Pacific Ocean with large-scale meteorological and ecological effects (Stenseth et al. 2002). Such large-scale climate patterns have been shown to affect

the reproductive success of terrestrial birds in many regions of the world (Silllett et al. 2000, Jonzén et al. 2002). For example, reproductive success of many songbirds breeding in western North America, including Song Sparrows, appears to be positively influenced by moist El Niño conditions associated with the ENSO (DeSante and Geupel 1987, Nott et al. 2002). In Rufous-crowned Sparrows (*Aimophila ruficeps*), the ENSO appears to influence reproductive success via its effects on both food availability and predation rates (Morrison and Bolger 2002).

Here, we present an analysis of data from a 21-year study of a nonmigratory Song Sparrow population. We examined the relationships among weather, reproductive success, and population density in an environment with a moist Mediterranean-type climate, characterized by moderate but highly variable rainfall and relatively stable, mild temperatures. This intensive long-term study allows us to study the effects of weather on multiple components of reproductive success. Here, we address three objectives: (1) to test whether annual variation in precipitation, spring temperatures, or summer temperatures are related to multiple components of Song Sparrow reproductive success, including reproductive output, timing, and rate of nest predation; (2) to test those components of reproductive success for evidence of density dependence; and (3) to evaluate the effects of population density and weather on population dynamics using time-series analysis.

METHODS

Study population and field methods.—Song Sparrows are territorial passerines found in a variety of brushy and moist habitats throughout most of North America (American Ornithologists' Union 1983, Arcese et al. 2002). We expected Song Sparrows to be particularly sensitive to rainfall, because they are strongly associated with moist habitats in the more arid portions of their range (Grinnell and Miller 1944, American Ornithologists' Union 1983) and evidence suggests that they are adversely affected by drought (Nice 1937). The *gouldii* subspecies is found in terrestrial habitats north of San Francisco Bay (Grinnell and Miller 1944) and is a year-round resident on the study site. Song Sparrows on the site are primarily socially

monogamous and produce multiple broods between late March and early August. Females build open-cup nests and are the sole incubators, whereas both sexes feed nestlings and fledglings.

From 1980 through 2000, Song Sparrows were studied at the Palomarin study area, located in the Point Reyes National Seashore, 20 km north of San Francisco, California. The 36-ha study area is made up of coastal scrub habitat adjacent to the Pacific Ocean. See DeSante and Geupel (1987) or Chase (2002) for a detailed description of the habitat. Between 29 and 57 pairs of Song Sparrows bred on the study area each year, and >90% of adults on the study area in each year were uniquely color-banded. Throughout each breeding season (March–August), three to four full-time observers mapped Song Sparrow territories using an intensive, standardized spot-mapping method (1980–2000). Additional details of the methodology can be found in Silkey et al. (1999). At the end of May, under the supervision of the same biologist in all 21 years (G.R.G.), mapped observations were compiled into detailed territory maps. We define a territory as the area used and defended by a single pair of birds during the breeding season. The total number of territories established on each site at that time was used as a measure of annual population density. We counted territories that extended beyond the boundaries of the study area by estimating whether the proportion of each territory that fell within the study area was 0.25, 0.5, or 0.75 of the total territory area. Because the study area is large in relation to the size of territories, those edge territories had little effect on the total number of territories.

Except for 1986, Song Sparrow nests were located in all years of the study, primarily by using behavioral cues (Martin and Geupel 1993). Standard procedures were followed to minimize human-induced mortality, and nests were checked every one to four days (Martin and Geupel 1993). Nestlings were weighed at approximately seven days of age (mean = 6.8 days, SD = 0.92, range = 5–10), with a Pesola spring scale or with a portable electronic scale. At the same time, nestlings were marked with a unique combination of three color bands and a numbered aluminium band. Nests were considered successful if they were found empty and intact after the nestlings had reached fledging age (mean = 10 days of age); in most cases,

fledging was confirmed by observations of parental behavior (e.g. food deliveries to fledglings, distress calls). Nests were classified as depredated if eggs disappeared or if nestlings disappeared at <10 days of age and parents were not observed feeding fledglings. Nests from which part of the clutch or brood disappeared were not counted as depredated unless a total loss occurred. Nests were classified as abandoned if eggs were deserted with no signs of predation or partial predation or if all young were found dead in the nest. A few successful nests were found on the day of fledging, and observers were unable to count the number of young fledged ($n = 26$ nests, 4.7% of successful nests). To include those nests in the calculation of the total number of fledglings produced per female, the number of young fledged in those cases was estimated as the mean number of young fledged per successful nest (mean = 2.92, SE = 0.037, $n = 503$ nests in which nestlings had been counted within four days of fledging).

As many nests as possible were found for each breeding pair. However, it is likely that some nests were not found, especially those failing early in the nesting cycle. Because we cannot say with certainty that all successful nests were found, we may underestimate the total number of young produced per female per breeding season. However, because nest-finding effort was generally constant across the years of the study, we believe this should not bias our results. Nest data were not collected in 1986 and were collected with reduced effort in 1987. Therefore, data for 1986 were omitted from all analyses, and data for 1987 were omitted from analyses concerning total number of young produced per female. Coincidentally, 1986 was also a year of extremely low reproductive success for Song Sparrows and most other bird species breeding at Palomarin (DeSante and Geupel 1987).

Reproductive variables.—Annual reproductive success in Song Sparrows can be decomposed into several components as follows:

$$r = n \times P \times a$$

where r = number of fledglings produced per female per year, n = number of fledglings produced per successful nest (defined as a nest producing at least one fledgling), P = probability of nest success, and a = number of nesting

attempts. Number of fledglings produced per successful nest (n) is itself a function of

$$n = c \times h \times f$$

where c = clutch size, h = proportion of eggs hatched (hatching success) per successful nest, and f = proportion of nestlings that survive to fledging (fledging success) per successful nest. Also, per capita reproductive success may be influenced by the probability of postfledging survival of offspring, which may depend in part on nestling condition. Thus, we analyzed the annual means of variables describing each of those components of reproductive success, as described below.

We measured annual reproductive success as mean number of fledglings produced per female per year. We estimated the number of young fledged per individual successful nest as number of young in the nest on the last visit before fledging. To describe the components of individual nest productivity, nests lost to predation at any stage were omitted from analyses of subsequent stages. When calculating mean clutch size, we ensured that clutches were complete when counted by including only clutches that were observed at least twice with the same number of eggs. Hatching success was calculated as the proportion of eggs that hatched (brood size divided by clutch size) and fledging success as the proportion of young that fledged (number of fledglings divided by brood size). Because the characteristics of multiple nest attempts by the same individual may not be independent, we calculated those annual means by first averaging their values on a per-female basis and then averaging the means for all females per year. Nestling weights were used as an index of nestling condition (Chase 2001) and were corrected for age at weighing using a preliminary regression (weight = 12.793 + [0.272 × age]). We could not accurately measure the number of nest attempts per female per year, because it was unlikely that we found every unsuccessful nesting attempt. However, we did analyze the number of successful nests produced by each female in a given year. In addition, we used length of the breeding season (described below) as an index of the number of nesting attempts possible in a given year.

Probability of nest success in each year was estimated using the Mayfield (1975) method.

The Mayfield method calculates the rate of nest survival in relation to number of days nests are observed. Thus, it corrects for the upward bias that occurs when nest success is based on the observed proportion of successful nests and not all nests are observed over the entire nesting period. That upward bias occurs because nests that fail in the early stages of the nesting period are less likely to be found than nests that are successful. Daily nest-survival rates were calculated both for the whole nesting period (i.e. egg laying through fledging) and for the incubation and nestling stages separately, with variance calculated according to Johnson (1979). For failed nests, the exposure period was terminated at the midpoint between the last visit when the nest was active and the first visit after failure. Nests were assumed to have been depredated during the incubation period if eggs disappeared between two visits and the midpoint between visits was not later than the expected date of hatching. For successful nests, the exposure period was terminated at the midpoint between the last visits, with the following exception. If the last day the nestlings were observed in the nest was on or beyond the average day of fledging (mean nestling stage = 10 days), exposure was terminated that day. Nests with unknown outcomes (12% of nests) were included in survival analyses, with exposure terminated on the last observed active date, as recommended by Manolis et al. (2000) to minimize bias. The program CONTRAST (Hines and Sauer 1989) was used to compare daily-nest-survival estimates.

To examine the relationship between weather and reproductive timing, we calculated variables describing onset of nesting, end of nesting, and length of the breeding season in each year. For each nest, we determined the Julian date (1 January = 1) on which the final egg of the clutch was laid (clutch-completion date). We excluded nests for which we could not estimate the clutch-completion date (i.e. nests that were found with a full clutch and failed before hatching). Onset of nesting was defined as earliest date of clutch completion, and end of nesting as latest date of clutch completion. Length of the breeding season was defined as number of days between onset and end of nesting. Preliminary analyses indicated that the relationship between weather and reproductive timing was similar if onset and end of nesting were defined instead

as the tenth and ninetieth percentiles of clutch-completion date. We also analyzed the standard deviation of clutch completion as an index of the length of the breeding season in the general population.

Weather variables.—Rather than analyzing a large set of climatic variables, we chose variables that we expected *a priori* to likely influence reproductive success in our study system: annual precipitation, spring temperatures, and summer temperatures. Weather data were collected daily within the Palomarin study area by staff and interns of PRBO Conservation Science. Because 94% of annual precipitation (in the form of rain and fog) occurs between October and April at Palomarin (Fig. 1A), we defined annual

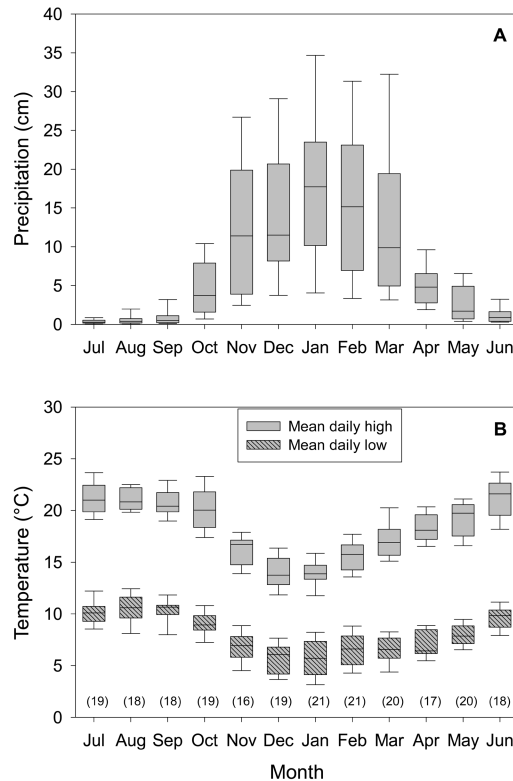


FIG. 1. Monthly variation in (A) precipitation at the Palomarin study area from 1980 to 2000 and (B) daily high and low temperatures at the Palomarin study area (numbers above *x* axis indicate number of years for which temperature data were available between 1980 and 2000). Boxes represent the 10th and 90th percentiles, the line within each box represents the median, and bars represent 5th and 95th percentiles.

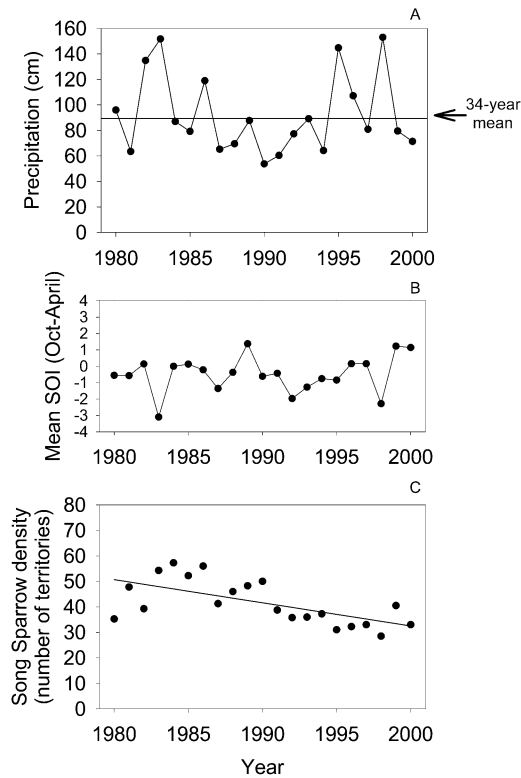


FIG. 2. (A) Annual variation in biowater (July–June) precipitation at Palomarin during the study period. Reference line indicates the average biowater rainfall from 1966 to 2000. (B) Annual variation in the mean monthly Southern Oscillation Index (SOI) for the period October–April. (C) Annual variation in number of territories established on the study area over 21 years. Solid line is the best least-squares fit to the data.

rainfall as the total precipitation in the July–June period (Fig. 2A). That period will be referred to here as the “biowater” and is equivalent to the “water year” commonly used by meteorologists to summarize precipitation in California. Preliminary analyses showed that we would have obtained qualitatively similar results if we had analyzed only the total precipitation occurring in the preceding “rainy season” (October–April). We used the standardized Southern Oscillation Index (SOI) to measure variation in the ENSO (Schonher and Nicholson 1989). The SOI is calculated on the basis of monthly values of air-pressure difference between Tahiti

and Darwin. Low values of the SOI are associated with moist El Niño episodes in California, and high values with dry La Niña conditions (Rasmusson and Wallace 1983). We obtained monthly values of the SOI and calculated the annual mean SOI values for the October–April period (Fig. 2B). Precipitation and daily high and low temperatures for each month of the year were summarized for descriptive purposes (Fig. 1B). Some temperature data were missing, so months in which there were five or more days with missing temperature data were not included in the summary or analysis. Daily high and low temperatures in spring (February and March) were available for the years 1981–2000, and the mean daily high and low temperatures during that period were calculated for analysis in relation to clutch size and onset of laying. Daily temperature data were also available for the months of May and June for 16 years and were used to analyze reproductive success and timing of cessation of breeding.

Statistical analysis.—We primarily employed regression analysis (STATA; Stata Corporation, College Station, Texas) to relate weather and reproductive success variables. Residuals of regression were screened for normality and for highly influential outlying cases, which we defined as cases with standardized residuals in excess of ± 3.0 . When such cases were detected, the analysis was repeated, omitting the outlying observation. Number of observations used in regression analyses is 20 (1980–1985, 1987–2000), unless otherwise stated. Where appropriate, the individual contribution of one independent variable to a multiple regression model is depicted in an adjusted partial residual plot. Those help to illustrate the effect of a single independent variable on the dependent variable while controlling for the effect of other independent variables.

Regression analysis assumes that errors of prediction (residuals) are independent of one another, an assumption that may not hold for data collected from a single population over time. Because autocorrelation of errors over time can bias the results of regression analysis, we screened for that potential problem in two ways. First, before conducting regression analyses, we evaluated all time-series variables for signs of temporal autocorrelation by inspecting autocorrelograms (Judge et al. 1988, Hamilton 1994), and we report any significant

autocorrelations in the results. Second, all regression models relating two time-series variables were tested for evidence of autocorrelation of residuals using the Durbin-Watson test (Judge et al. 1988). If the Durbin-Watson test identified temporal autocorrelation in a planned regression model, we instead performed a generalized least-squares regression correcting for first-order autocorrelated residuals using the Prais-Winsten transformed regression estimator in STATA. In the Prais-Winsten method, the autocorrelation coefficient is estimated first and is then used to calculate a corrected estimate of the regression coefficient for the variable of interest (Judge et al. 1988).

To analyze population growth rate as a function of direct density dependence, we used a regression model in which the logarithmic rate of change in population density (i.e. natural log of population density in year t – natural log of density in year $[t - 1]$) was related to the log of density in the previous year. In that model, negative, direct density dependence is indicated if the coefficient of the density term is significantly less than 0 (Berryman and Turchin 2001). That method is equivalent to conducting an autoregression (i.e. regressing the log of population density on the log of population density in the previous year) and testing whether the coefficient of the density term is significantly less than 1 (Royama 1992, Post and Stenseth 1999). To simultaneously control for the effect of density-independent factors on population change, we included rainfall in the previous year as a predictor variable in our regression model. Because population density declined significantly during the study period (i.e. the time series was nonstationary; Fig. 2C), we also “detrended” population density by including the variable “year” in the regression. In addition, we examined the partial rate correlation function (Berryman and Turchin 2001) for signs of delayed density dependence.

Results were considered significant if $P < 0.05$. Means and regression coefficients are presented with their standard errors (e.g. mean \pm SE).

RESULTS

Climate and weather patterns.—Monthly precipitation and temperatures at Palomarin during our study were typical of a moist Mediterranean climate, with wet, mild winters

and dry, moderately warm summers (Fig. 1). Precipitation was strongly concentrated in the winter months and was highly variable. During the 21 years of our study, coastal central California experienced a prolonged dry period as well as several extremely wet bioyears (Fig. 2A). The dry period at Palomarin lasted from 1987 to 1994; of those 8 bioyears, 6 were considerably drier than the average recorded over 34 years (34-year mean = 89.4 cm, SD = 30.7) and two were just below average. Although rainfall was not strongly correlated with the SOI overall ($r = -0.38$, $P = 0.09$, $n = 21$), the two bioyears with the strongest El Niño events (1983 and 1998) were also years of very high precipitation (Fig. 2A, B). Two other El Niño years (1987 and 1992) were not extremely wet. We found no evidence of temporal autocorrelation of annual rainfall (1980–2000) or spring (February–March) temperatures (1981–2000; all $P > 0.10$). Average daily spring temperatures increased significantly between 1981 and 2000 (coefficient = 0.103 ± 0.042 , $F = 6.06$, $df = 1$ and 18 , $P < 0.05$), primarily because of increasing daily high temperatures (coefficient = 0.335 ± 0.113 , $F = 8.82$, $df = 1$ and 18 , $P < 0.005$). Daily low temperatures and rainfall showed no trends over time (both $P > 0.10$).

REPRODUCTIVE SUCCESS, TIMING, AND WEATHER

Cumulative reproductive success.—Total number of young fledged over the breeding season by female Song Sparrows was greater in wetter years (Fig. 3A). Rainfall explained 30% of the annual variation in number of young fledged per female. Also, number of nests successfully fledged per female was positively related to bioyear rainfall (linear regression: coefficient = 0.0039 ± 0.0015 , $F = 6.56$, $df = 1$ and 17 , $P = 0.02$, $r^2 = 0.28$, $n = 18$ years). To better understand how rainfall is related to Song Sparrow productivity, we examined the components of annual reproductive output.

Productivity of individual nests.—An ANOVA of individual nest data showed that there was statistically significant variation among years in number of young fledged per successful nest (Fig. 4A), clutch size (Fig. 4A), hatching success (Fig. 4B), and fledging success (Fig. 4B). However, that annual variation was not significantly related to weather. Clutch size was not related to average daily low temperature or average daily high temperature during

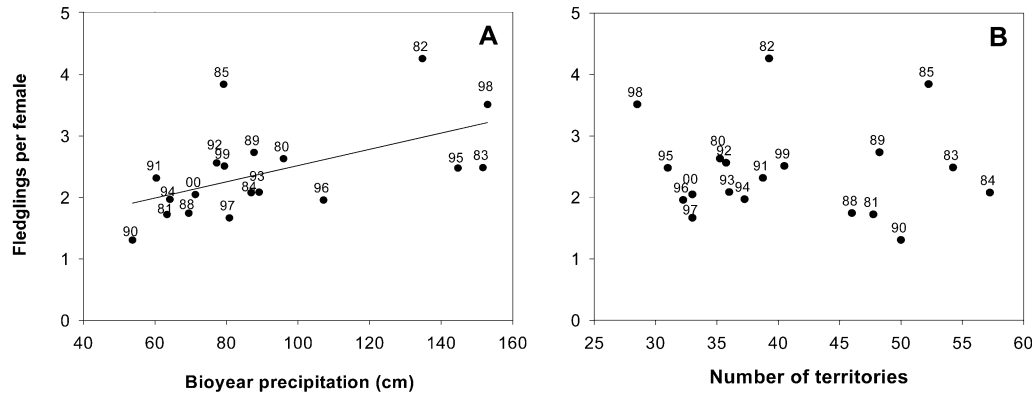


FIG. 3. Annual variation in number of fledglings produced per female Song Sparrow in relation to (A) biyear (July–June) precipitation (linear regression; coefficient = 0.013 ± 0.0049 , $F = 7.37$, $df = 1$ and 17 , $P = 0.015$, $r^2 = 0.30$, $n = 19$ years) and (B) population density, over 19 years (1980–1985, 1988–2000).

February and March (all $P > 0.10$). Biyear rainfall was not significantly related to any of the variables describing productivity of individual nests in linear regressions ($P > 0.10$ for clutch size, hatching success, and fledging success), though number of young fledged per successful nest approached significance (coefficient = 0.003 ± 0.002 , $F = 3.51$, $df = 1$ and 18 , $P = 0.08$, $r^2 = 0.16$). Nor was biyear rainfall related to nestling weight ($P > 0.5$). No quadratic regression terms were significant for those variables. That suggests that the main influence of rainfall on productivity was through its relationship to the number of successful nests produced in a season, rather than to the productivity of individual nesting attempts.

When 1996, a strong outlier in the overall relationship, was omitted from analysis, number of young fledged per successful nest was positively related to rainfall ($r^2 = 0.29$, $P < 0.05$). Similarly, 1996 is a strong outlier in the relationship between fledging success and rainfall, which approaches significance if 1996 is omitted ($r^2 = 0.17$, $P = 0.08$). Both the number of young fledged and fledging success were atypically low in 1996 (Fig. 4A, C), perhaps because summer temperatures were warmer than those in any other year for which they were recorded (see below for results concerning temperature).

Nest survival.—We found 1,168 nests and observed them for more than one day during the study (total observer days = 11,761). The daily nest-survival rate calculated over all years was 0.946 ± 0.002 , which corresponds to a total

nest-survival rate of 26.3% over the 24-day nest period (mean number of days from laying to fledging). Most nest failures appeared to be attributable to nest predation, rather than parasitism, abandonment, starvation, or exposure. A few predation events were observed directly. The predators were Western Scrub-Jay (*Aphelocoma californica*), gopher snake (*Pituophis melanoleucus*), garter snake (*Thamnophis* sp.), and western yellow-bellied racer (*Coluber constrictor mormon*). Other potential nest predators observed on the study site included Steller's Jay (*Cyanocitta stelleri*), Brown-headed Cowbird (*Molothrus ater*), rubber boa (*Charina bottae*), Sonoma chipmunk (*Eutamias sonomae*), dusky-footed wood rat (*Neotoma fuscipes*), deer mouse (*Peromyscus maniculatus*), bobcat (*Lynx rufus*), gray fox (*Urocyon cinereoargenteus*), coyote (*Canis latrans*), long-tailed weasel (*Mustela frenata*), domestic cat (*Felis domesticus*), and raccoon (*Procyon lotor*). Only 16 nests (2.5% of failed nests) were classified as abandoned (4 during laying, 7 during incubation, and 5 with young in the nest), and those events were not concentrated in any year (0–3 nests abandoned per year, mean = 0.8, SD = 0.95). Nests that were classified as abandoned included two nests in which the nestlings were found dead shortly after heavy rainstorms in June 1984. No nests were known to have failed because of nestling starvation. Eleven nests (0.9%) were parasitized by Brown-headed Cowbirds. Of those nests, four were depredated, four fledged both Song Sparrow young and Brown-headed Cowbirds,

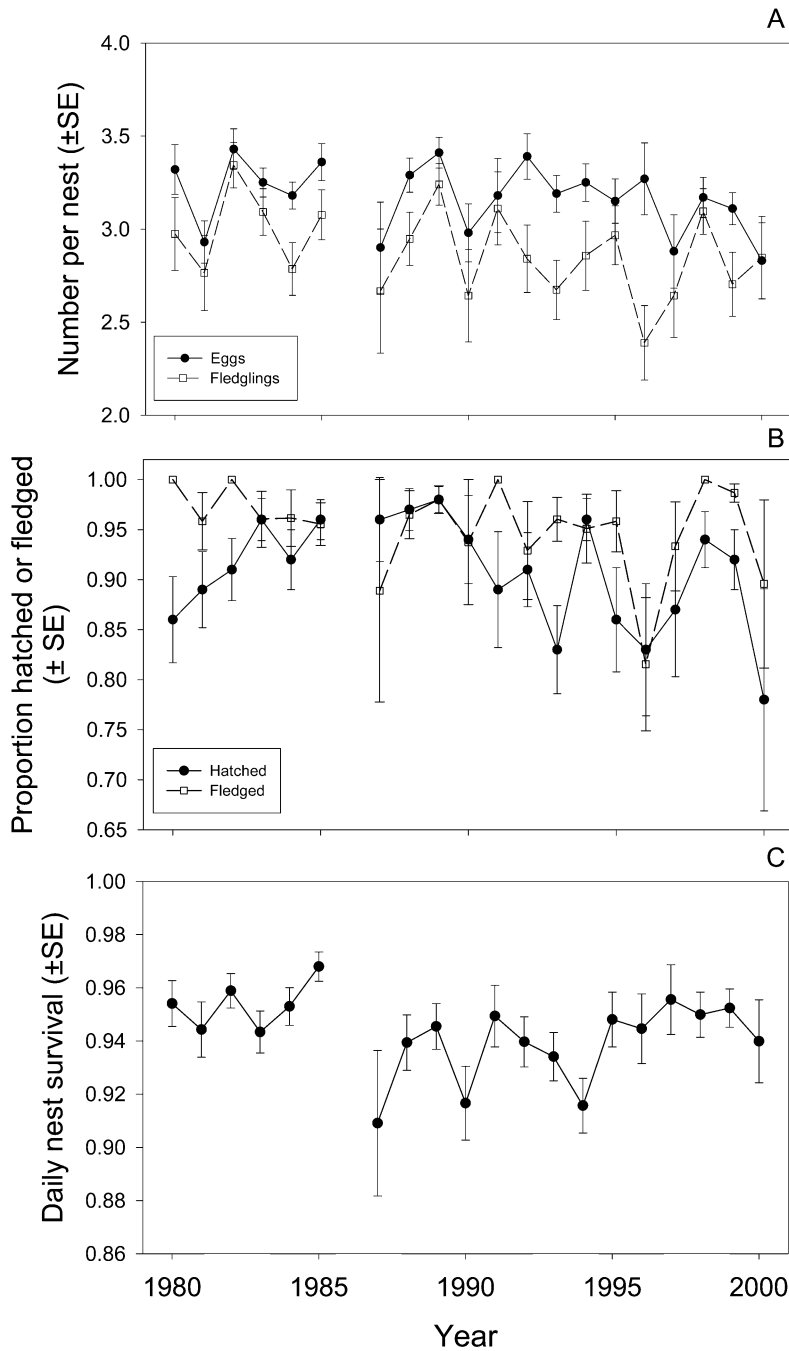


FIG. 4. (A) Annual variation in clutch size and number of fledglings per successful nest, (B) annual variation in hatching success and fledging success, and (C) annual variation in nest success. Among-year variation was statistically significant for clutch size ($F = 1.979$, $df = 19$ and 450 , $P < 0.01$), number of fledglings ($F = 2.059$, $df = 19$ and 396 , $P < 0.01$), hatching success ($F = 1.801$, $df = 19$ and 343 , $P < 0.05$), fledging success ($F = 1.734$, $df = 19$ and 335 , $P < 0.05$), and nest survival ($\chi^2 = 39.26$, $df = 19$, $P < 0.005$).

two fledged only Song Sparrows, and one fledged only a Brown-headed Cowbird.

Daily nest survival estimated over all years did not differ significantly between egg-laying stage (0.950 ± 0.010), incubation stage (0.947 ± 0.003), and nestling stage (0.944 ± 0.003 ; $\chi^2 = 0.54$, $df = 2$, $P > 0.50$). Daily nest survival varied significantly among years (Fig. 4C) and was significantly lower during the eight-year dry period (1987–1994) than in the other years of the study ($\chi^2 = 12.19$, $df = 1$, $P < 0.001$). Daily nest survival showed a significant quadratic relationship with bioyear precipitation ($F = 4.70$, $df = 2$ and 17 , $P = 0.024$, $r^2 = 0.36$, $P_{\text{quadratic}} = 0.035$). Because rainfall may influence nest success differently in the different stages of the nesting period, we also analyzed incubation- and nestling-stage survival separately. Precipitation explained a significant proportion (44%) of the annual variation in incubation-period survival (Fig. 5). Precipitation was also related to nestling-period survival, though it explained a smaller proportion of variation in survival (quadratic regression; $F = 3.18$, $df = 2$ and 17 , $P = 0.067$, $r^2 = 0.27$, $P_{\text{quadratic}} = 0.048$). Nest survival was not related to precipitation in any of the individual months February–April (all $P > 0.30$). However, the relationship between nest survival and May rainfall was negative, and was statistically significant if 1987, a strong outlier in the relationship, was omitted (coefficient = -0.0023 ± 0.0011 , $F = 4.76$, $df = 1$ and 17 , $P = 0.043$, $r^2 = 0.22$).

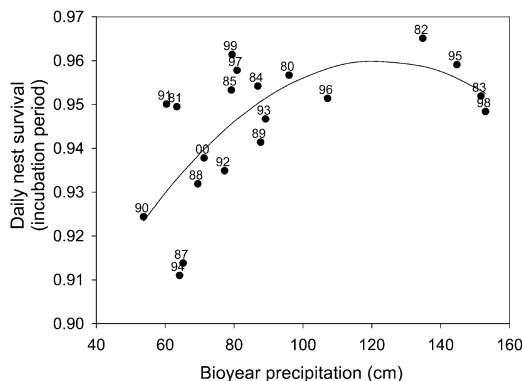


FIG. 5. Annual daily nest-survival estimates for the incubation period in relation to bioyear precipitation (1980–1985, 1987–2000): quadratic regression, $P_{\text{quadratic}} < 0.05$, $F = 6.80$, $df = 2$ and 17 , $P < 0.01$, $r^2 = 0.44$.

Reproductive timing.—Song Sparrows at Palomarin nested over a longer period (latest clutch-completion date – earliest clutch-completion date) in years with higher bioyear precipitation (linear regression: coefficient = 0.365 ± 0.094 , $F = 15.16$, $df = 1$ and 18 , $P < 0.005$, $r^2 = 0.46$). A similar relationship appeared when the standard deviation of clutch-completion date was used as an index of the length of the breeding season to reduce the influence of extreme values (coefficient = 0.088 ± 0.027 , $F = 10.86$, $df = 1$ and 18 , $P < 0.005$, $r^2 = 0.38$). Nesting started significantly earlier in the spring and continued significantly later into the summer in wetter years (Fig. 6A). Date of onset of nesting was not related to average or minimum daily low temperature, or to average or maximum daily high temperature, during February and March (all $P > 0.20$, $n = 19$ years). The SOI was not related to any measure of reproductive success or timing (all $P > 0.2$).

Average daily temperature in May and June was significantly related to the date at which nesting ceased (Fig. 6B). A multiple-regression model including both summer temperature and bioyear rainfall as predictor variables also indicated that nesting ended significantly earlier in years with high summer temperatures (coefficient = -4.83 ± 2.005 , $P < 0.05$, $F = 9.20$, $df = 2$ and 13 , $P < 0.005$, $r^2 = 0.59$, $n = 16$ years). Bioyear rainfall was not significant in that model ($P = 0.095$), probably in part because rainfall and summer temperatures were negatively correlated ($r = -0.50$, $P < 0.05$). Given the correlative nature of our analyses, we cannot disentangle the relative importance of rainfall and temperature as potential influences on when Song Sparrows stop nesting, but both results are consistent with our expectation that the end of the breeding season would occur earlier when conditions are drier.

Warmer summer temperatures were associated with fewer fledglings per successful nest (coefficient = -0.111 ± 0.047 , $F = 5.58$, $df = 1$ and 14 , $P = 0.033$, $r^2 = 0.29$, $n = 16$ years) and lowered fledging success (Fig. 7). It is interesting to note that the year of the study with the warmest summer (1996), in addition to having the lowest fledging success, also had low hatching success (Fig. 4B), fewest young fledged per successful nest (Fig. 4A), and a shorter nesting period (see the rightmost vertical line in Fig. 6B).

To evaluate whether the length of the breeding season is correlated with overall reproductive

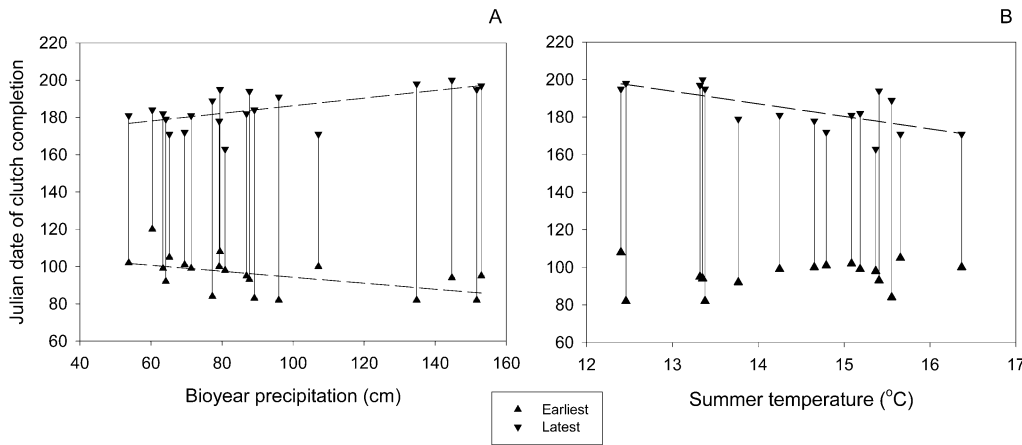


FIG. 6. Annual variation in onset of nesting (earliest clutch-completion date) and end of nesting (latest clutch-completion date) in relation to (A) biyear rainfall over 20 years, with the regressions of onset and end of breeding on rainfall represented by the lower dashed line (coefficient = -0.161 ± 0.064 , $F = 6.28$, $df = 1$ and 18 , $P < 0.025$, $r^2 = 0.26$) and the upper dashed line (coefficient = 0.205 ± 0.062 , $F = 10.99$, $df = 1$ and 18 , $P < 0.025$, $r^2 = 0.38$), respectively; and (B) average daily temperatures in May and June over 16 years, the dashed line indicating regression of end of nesting on temperature (coefficient = -6.690 ± 1.850 , $F = 13.08$, $df = 1$ and 14 , $P < 0.005$, $r^2 = 0.48$).

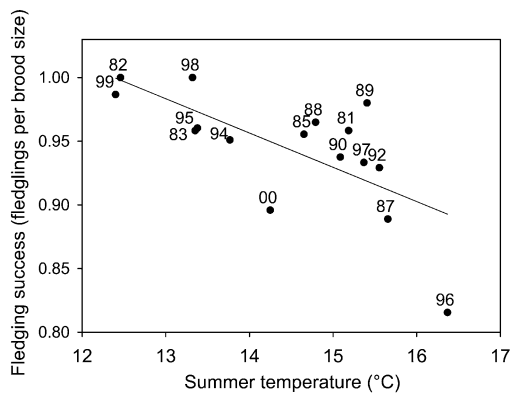


FIG. 7. Annual fledging success in relation to average daily temperatures in May and June over 16 years (linear regression; coefficient = -0.027 ± 0.0076 , $F = 12.60$, $df = 1$ and 14 , $P < 0.005$, $r^2 = 0.47$).

success, we performed a multiple regression of the total number of young fledged per female on the number fledged per successful nest, nest-survival rate, and the length of the breeding season (indexed by the standard deviation of clutch-completion date). Total number of young fledged was positively associated with breeding-

season length ($P < 0.01$), controlling for nest survival ($P < 0.005$) and the number fledged per nest ($P = 0.18$; model $r^2 = 0.80$, $F = 19.89$, $df = 3$ and 15 , $P < 0.001$, $n = 18$ years). That suggests that the number of young fledged per female was greater in cooler and wetter years because of increases in both rate of nest survival and length of the breeding season (i.e. number of nesting attempts).

REPRODUCTIVE SUCCESS AND POPULATION DENSITY

We analyzed two aspects of the relationship between population density and reproductive success. First, we explored whether there was evidence for density-dependent variation in reproductive success. We examined the relationship between population density in a given year and the various components of reproductive success in that year using multiple-regression models that included population density and biyear precipitation as explanatory variables. Of the variables describing productivity of individual nests (clutch size, hatching success, fledging success, and number of young fledged per successful nest), only hatching success was significantly related to population density, and that relationship was moderately positive

TABLE 1. Prais-Winsten regression analyses relating population density to average number of young fledged per female in the previous year (18 years), rainfall in the previous bioyear (20 years), rainfall in the previous bioyear (excluding 1986), and year (21 years). Results are presented from separate univariate regressions (models A–D) and from a multivariable regression (model E: 18 years).

Model	Variables	Coefficient ± SE	F	df	P	r ²
A	Young fledged per female	4.167 ± 1.031	42.05	1 16	<0.001	0.72
B	Bioyear rainfall	0.082 ± 0.036	16.95	1, 18	<0.001	0.49
C	Bioyear rainfall (1986 excluded)	0.119 ± 0.023	30.64	1, 17	<0.001	0.64
D	Year	-0.833 ± 0.311	6.55	1, 19	<0.05	0.26
E	Model		29.43	3, 14	<0.001	0.86
	Young fledged per female	2.624 ± 1.210			<0.05	
	Bioyear rainfall	0.070 ± 0.032			<0.05	
	Year	-1.021 ± 0.346			<0.05	

(density coefficient = 0.0039 ± 0.0013, *t* = 2.97, *P* = 0.009, model-adjusted *r*² = 0.27). Population density was not significantly related (all *P* > 0.3) to nest survival, nestling weight, or number of young fledged per female (Fig. 3B).

Second, we examined whether the density of Song Sparrows breeding on the study area is a reflection of reproductive success in previous years. Population density showed significant temporal autocorrelation, with a one-year time lag (linear autocorrelation coefficient = 0.61, $\chi^2 = 9.86$, *P* < 0.005). Therefore, to analyze population density in relation to reproductive success in the previous year, we used the Prais-Winsten regression method (see above). Annual variation in population density was strongly positively related to the number of young fledged per female in the previous year (Table 1: model A; Fig. 8A). Those results suggest that breeding-season population density is primarily influenced by production of young in the previous year, which in turn is influenced by rainfall. Indeed, rainfall in the previous bioyear explained at least 49% of the variation in population density between 1980 and 2000 (Table 1: models B and C; Fig. 8B). Song Sparrow population density at Palomarin decreased significantly over the 21 years of study (Table 1: model D; Fig. 2C), though number of young fledged per female did not (*F* = 0.89, *df* = 1 and 17, *P* > 0.4, *r*² = 0.05, *n* = 19 years). Reproductive success, rainfall, and year each explained a significant amount of the variation in population density in a multivariable model (Table 1: model E).

Although we found no evidence for density-dependent fecundity, results of the time-series analysis of population growth rate suggest that some density-dependent factor has influenced

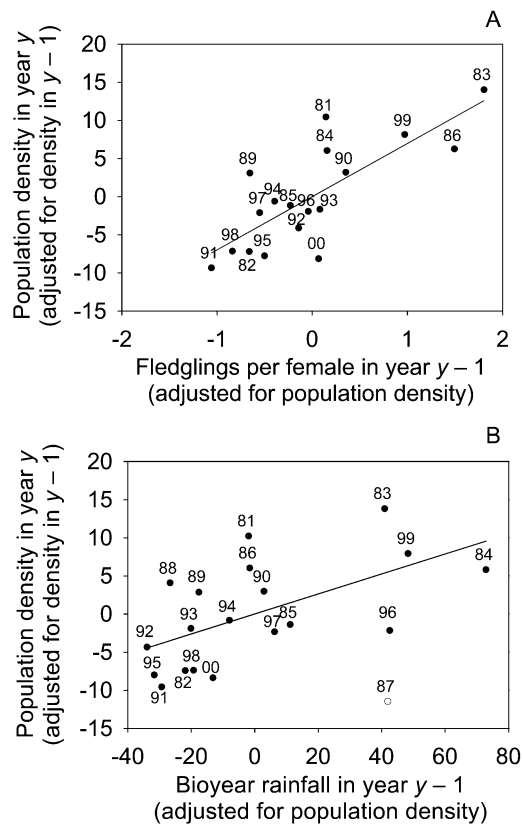


FIG. 8. (A) Adjusted partial residual plot of the relationship between population density and reproductive success in the previous year, with both variables adjusted for population density in the previous year (*P* < 0.001; Table 1). (B) Adjusted partial residual plot of the relationship between population density and rainfall in the previous year, excluding 1986, with both variables adjusted for population density in the previous year (*P* < 0.001; Table 1).

Song Sparrow population dynamics. The change in population density from year y to year $y + 1$ was negatively related to population density in year y (Fig. 9) and positively related to rainfall, while controlling for the negative trend in density over time (Table 2). The partial rate correlation function showed no evidence of delayed density dependence (i.e. there were no significant partial correlations of population growth rate and population density for time lags greater than one year; Berryman and Turchin 2001).

DISCUSSION

Weather and reproductive success.—Song Sparrow reproductive success increased with increasing rainfall and peaked at above-average rainfall levels (Fig. 3A). Rainfall has been associated with increased reproductive success in several other species of songbirds, including Brewer's Sparrows (*Spizella breweri*) and Sage Sparrows (*Amphispiza belli*) breeding in shrub-steppe habitat (Rotenberry and Wiens 1991), Mexican Jays (*Aphelocoma ultramarina*; Li and Brown 1999), and several species in the Galapagos Islands (Boag and Grant 1984, Grant and Grant 1987, Curry and Grant 1989). Those studies were conducted in arid environments where the climate is considerably drier and warmer (in summer) than in coastal central California. However, rainfall also influences primary and secondary productivity in Mediterranean-type ecosystems (Specht 1981; Hobbs and Mooney 1995; Pereira and Chaves 1995; Jaksic et al. 1996, 1997). Our results, together with those of DeSante and Geupel (1987), suggest that rainfall also can have an important and positive influence on avian demography in Mediterranean-type shrub habitats, as well as in other areas with moderate annual rainfall and year-round mild temperatures (also see Woolfenden and Fitzpatrick 1984).

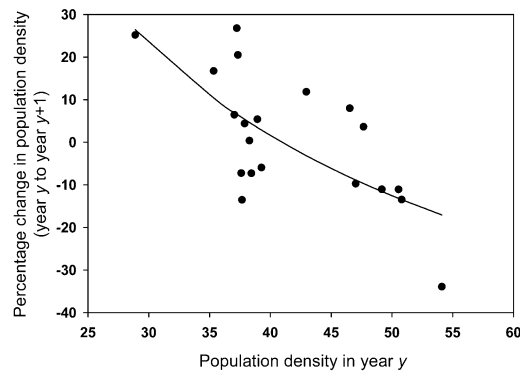


FIG. 9. Annual variation in the percentage of change in population density (number of territories) in relation to density in the previous year, while controlling for the effect of rainfall and the trend in density over time, 1980–2000. Effect of density is significant ($P < 0.005$; see Table 2 for regression statistics).

The components of reproductive success most strongly associated with rainfall were probability of nest survival, especially in the incubation stage, and length of the breeding season. Nest-survival rates peaked in years with average or above-average rainfall and appeared to decrease slightly in the wettest years, though nest survival in the wettest years was still above average (Fig. 5). We suggest that rainfall may influence nest survival at Palomarin in two general ways. Increased rainfall may affect nest survival positively by influencing predation rates. By contrast, adverse weather during the nesting period may occasionally lower nest survival by causing exposure, starvation, parental neglect, or desertion. The slight decline in nest success in the wettest years and the trend toward lowered nest survival in years with wetter May weather may be attributable in part to the abandonment of nests during late-spring rainstorms. Similarly, DeSante and Geupel (1987) found a negative

TABLE 2. Results of log-linear regression analysis of annual change in Song Sparrow population density in relation to population density and rainfall in the previous year ($F = 8.69$, $df = 3$ and 16 , $P = 0.001$, $r^2 = 0.62$, $n = 20$ years).

Predictor variable	Coefficient	SE	P
Density in year $t - 1$	-0.672	0.183	0.002
Rainfall in year $t - 1$	0.201	0.093	0.046
Year	-41.147	12.559	0.005

correlation between May rainfall and the combined mist-net capture rate of 51 species of juvenile birds at the Palomarin study area.

However, because >95% of nest failures appeared to be attributable to predation, the general trend toward increased nest survival in wetter years was probably a result of lowered nest predation rates. Some nests that we classified as depredated actually may have failed because of other causes (e.g. desertion), followed by the scavenging of their contents. However, the small number of deserted nests observed and the relatively high frequency of nest checks suggest that such misclassification was rare and unlikely to have had a strong influence on our results. Furthermore, nest parasitism by Brown-headed Cowbirds in the population was also rare (<1% of nests) and thus is unlikely to have influenced nest survival as it has in other Song Sparrows populations (Smith et al. 2003). Few other studies have demonstrated rainfall-dependent nest predation. In Florida Scrub-jays (*A. coerulescens*), nest success increased with increasing rainfall in the months preceding the nesting season (Woolfenden and Fitzpatrick 1984). By contrast, nest predation was independent of rainfall in Mexican Jays (Li and Brown 1999). Predation on nests of shrubsteppe birds peaked during a ground squirrel (*Spermophilus townsendi*) irruption that followed two years of increased rainfall (Rotenberry and Wiens 1989). Grant and Grant (1987) documented lowered nest success in the Large Cactus-Finch (*Geospiza conirostris*) in an extremely wet El Niño year, which may have been in part because of increased nest predation. Several other studies have linked increased rainfall to lowered nest success, but nest predation was not considered as an explanation of those patterns (Marzluff and Balda 1992, Gende et al. 1997, Skinner et al. 1998, North et al. 2000).

Rainfall may influence nest predation via several mechanisms (Woolfenden and Fitzpatrick 1984). First, it may affect the density of nest predators. Rotenberry and Wiens (1989) provide an example of a time-lagged increase in mammalian predator density and nest predation following increased rainfall. Second, rainfall may affect either the availability of alternate food for predators or predator food selectivity (or both). Changes in both predator numbers and food selection in response to rainfall have been reported in Mediterranean-type

scrub communities in Chile (Jaksic et al. 1997). Effects of weather on predators at Palomarin is likely complex, given the diversity of predators present. Third, rainfall may influence time budgets or nest vigilance of Song Sparrow parents, either directly or via food availability (Martin 1992). Song Sparrow nest success on Mandarte Island was improved by food supplementation, which suggests that well-fed parents may be better able to guard their nests. But that increase in nest success occurred primarily through a decrease in the rate of Brown-headed Cowbird related nest failure rather than through nest predation (Arcese and Smith 1988, Arcese et al. 1992). Also, female nest defense did not appear to be correlated with nest success in the same population of Song Sparrows (Hatch 1997). Fourth, rainfall may affect the vegetation cover surrounding nests and the overall availability of nest sites, which in turn may influence the probability of nest predation. Song Sparrow nests with greater vegetative cover from below tend to have a lower rate of predation on our study area (Chase 2002). Fifth, birds may modify their nest microhabitat selection in response to climatic variation, and that may influence their risk of nest predation (Martin 2001). We currently lack the data necessary to distinguish among those proposed mechanisms, but we believe that the influence of weather on nest predation is an interesting area for further research.

The Song Sparrow breeding season began earlier and continued longer in years with more rainfall (Fig. 6), as would be expected if food resources were greater in wetter years and if the food-resource levels necessary for breeding persisted longer in wetter years. Later breeding was also associated with cooler summer temperatures, as we expected. Summer temperatures probably influence how long moist conditions prevail in the scrub habitat by altering the rate of evapotranspiration, especially because cool days at our study site are also often foggy. Primary productivity declines because of dehydration stress in Mediterranean-type vegetation as the summer drought proceeds (Pereira and Chaves 1995). It is reasonable to suppose that insects and other invertebrate food items may also become less abundant (Atkins 1977). However, availability of annual grasses and other dense vegetation that provide nest cover may also be related to rainfall and temperature and may also influence the timing

of nesting. Longer breeding seasons probably contributed to the increase in average number of successful broods per female in cooler, wetter years, through increases in both renesting following nest failure and attempts to produce a second or third successful nest. Nice (1937) reported that Song Sparrows stopped nesting early in a drought year in Ohio, and our results suggest that this may be a general pattern in Song Sparrows. Breeding phenology is related to rainfall in a number of other bird species as well. This has been better documented in very arid climates, where some species breed only after rains occur, breed for longer periods when rains are prolonged, and may not breed at all in very dry years (Boag and Grant 1984, Curry and Grant 1989). In Mexican Jays breeding in a more temperate climate, earlier breeding is associated with higher rainfall in the previous summer (Brown and Li 1996), and second broods are more common in years with wetter weather in July–February (Li and Brown 1999). We also found that Song Sparrow fledging success declined in years with warmer summer temperatures (Fig. 7).

Song Sparrows did not appear to alter their clutch size in response to annual variation in rainfall. Clutch size has been found to increase in wet years in several bird species (Boag and Grant 1984, Curry and Grant 1989, Rotenberry and Wiens 1989); but in other species, clutch size is independent of annual precipitation (Grant and Grant 1987, Koenig and Mumme 1987, Rotenberry and Wiens 1989). If rainfall influences food availability, one might expect to observe an association between rainfall and clutch size, especially given that food supplementation was found to influence clutch size in another population of Song Sparrows (Arcese and Smith 1988). Similarly, one might expect the fledging success and weight of nestlings to be increased in wetter years. However, Rotenberry and Wiens (1991) showed that reproductive success can be associated with weather occurring over two different time scales: the entire breeding season or the period of days in which eggs are laid or young are fed. Patten and Rotenberry (1999) also found that rainfall during egg formation was a better predictor of clutch size than annual rainfall in California Gnatcatchers (*Poliophtila californica*), which breed in southern California coastal scrub habitats. Thus, although annual variation in rainfall was

unrelated to clutch size or the number of young eventually fledged from Song Sparrow nests that escaped predation, we do not rule out the possibility that short-term variation in weather might influence the productivity of successful nests.

In Song Sparrows at Palomarin, clutch size and onset of egg-laying were unrelated to spring temperatures. By contrast, Song Sparrows started nesting earlier and laid larger clutches following warmer springs on Mandarte Island, Canada (Arcese et al. 1992, Wilson and Arcese 2003), and Nice (1937) found the start of laying for Song Sparrows in Ohio to be closely correlated with spring temperatures. Also, there is increasing evidence of long-term trends toward both warmer winter and spring temperatures and earlier onset of breeding in a variety of birds and other organisms (Forchhammer et al. 1998a, Brown et al. 1999, Wuethrich 2000). A possible explanation for the discrepancy between our results and those of previous studies of Song Sparrows is that food availability is less strongly limited by temperature in our study location, because of the milder winter and spring temperatures in coastal central California.

Some of the variation in rainfall that we observed was associated with the ENSO. Although variation in the ENSO was not strongly correlated with rainfall or reproductive success over the entire study period, the two strongest El Niño events of the past two decades coincided with two of the three wettest years during the study (1983 and 1998). Our results suggest that the ENSO primarily influences Song Sparrow reproduction in strong El Niño years, whereas weaker variations in the ENSO have little effect. The intermittent effects of strong El Niño events on pelagic (Schreiber and Schreiber 1984, Wilson 1991) and terrestrial (Grant and Grant 1987, Hejl et al. 1988, Curry and Grant 1989, North et al. 2000) bird populations have been extensively documented. Continuous variation in the ENSO has been shown to influence winter survival and nestling weight over 12 years in the migratory Black-throated Blue Warbler (*Dendroica caerulescens*; Sillett et al. 2000). In a population of Rufous-crowned Sparrows in Southern California, an El Niño event appeared to lower nest predation rates early in the breeding season, possibly via the effects of wet, cool weather on the predatory ability of snakes

(Morrisson and Bolger 2002). In Song Sparrows on Mandarte Island, ENSO affected the timing of breeding and reproductive success over 32 years via its effect on spring temperatures (Wilson and Arcese 2003). Clearly, the effects of ENSO on bird populations in different regions of the Pacific Coast vary, depending on how ENSO affects regional weather and on how weather influences reproduction in a population.

Density, reproductive success, and population dynamics.—Years in which larger numbers of juvenile Song Sparrows fledged were followed by years with higher population density, and rainfall in the previous year explained about half the variation in population density. The potential for strong effects of weather on population dynamics can be illustrated by comparing the annual values of reproductive success observed here to what would be needed to sustain a stable population. The minimum number of fledglings that must be produced to maintain a stable or increasing population (in the absence of net immigration or emigration) can be estimated from a simple population model (Pulliam 1988, Sherry and Holmes 2000) and has been termed the “source–sink threshold” (Trine 1998). Given that annual adult mortality in Palomarin Song Sparrows is 40% (estimated from capture–recapture analyses of both mist-net and color-band observations; Nur et al. 2000) and juvenile mortality is estimated to be between 60% and 70% (from simulations of on- and off-site recruitment; Chase 2001), the minimum number of fledglings necessary to sustain a viable population is between 2.0 and 2.7 per pair per year. Our estimates of fledgling production fell below that threshold range in 6 out of 19 years, and exceeded that range in 4 years (Fig. 3). Although our estimates of the number of young fledged per pair may be slightly lower than the actual number (because of nests that escaped detection), it appears that in many years the Palomarin Song Sparrow population does not produce enough young to offset mortality. Those results suggest that the effect of weather may be strong enough to push reproductive success across the source–sink threshold.

We found no evidence of depressed reproductive success when the number of Song Sparrow territories on the Palomarin study area increased. Thus, our results are consistent with the hypothesis that reproductive success

was limited primarily by density-independent factors such as weather. At Palomarin, the influence of rainfall on reproductive success may be partially independent of population density if, as our results suggest, variation in rainfall primarily alters nest predation pressures and the time-span over which high-quality food is available for breeding birds, rather than altering the general level of competition for resources. However, it is still possible that reproductive success may be density-dependent in years with unusually poor environmental conditions, and it may require many more years of data to demonstrate such an interaction between weather and density. By contrast, Arcese et al. (1992) found strong evidence of density-dependent reproductive success in Song Sparrows on Mandarte Island: increasing density was correlated with a decrease in clutch size, an increase in the rate of nest failure, and a decline in the number of independent offspring produced per female. Two factors may account for that difference between the populations. First, density-dependent nest failure on Mandarte was associated with nest parasitism by Brown-headed Cowbirds (Arcese et al. 1996). By contrast, Brown-headed Cowbirds had little effect on Song Sparrows at Palomarin, where parasitism was relatively rare. Second, levels of population density and the magnitude of variation in density observed at Palomarin may have been too low to trigger density-dependent reproductive success. Density-dependent declines in birth rate may occur within a population only when density has reached a critical level, above which interspecific competition intensifies with increasing density (Murray 1994). Thus, the strength of density dependence may be nonlinearly related to population density (Sæther et al. 2002, Sibly and Hone 2002). Experimental evidence supports the idea that reproductive success on Mandarte Island declines at high densities in part because compression of territories causes a reduction in the amount of food available per breeding pair (Arcese and Smith 1988). However, reproductive success on Mandarte was not strongly depressed with increasing density when the population was at low levels (<5 females per hectare; Arcese and Smith 1988). In the Palomarin study area, where the habitat was not saturated, density may have increased without greatly compressing most territories, and thus without decreasing the

average suitability of territories. That hypothesis is consistent with the patterns observed here and by Arcese et al. (1992). The average density of Song Sparrows on our study area was 85% lower than density on Mandarte Island (mean = 1.2 territories per hectare here vs. 7.8 females per hectare on Mandarte; Arcese et al. 1992), and much of what appeared to be suitable habitat at Palomarin was unoccupied in many years.

In our study, population dynamics showed signs of density dependence, while also being related to weather via its effects on reproductive success. By contrast, on Mandarte Island, population growth appeared to be influenced by density-dependent juvenile recruitment, but not by the increase in reproductive success associated with El Niño (Wilson and Arcese 2003). There, density-dependent factors appeared to regulate the population, thus outweighing the effects of climatic variation on reproductive success. Because population growth was negatively related to density at Palomarin, some factors may have been acting in a density-dependent manner to regulate Song Sparrow density on our study area. Future research can evaluate whether other demographic parameters, such as mortality, emigration, or immigration, may be related to population density (Sinclair 1989). Immigration and emigration rates of juveniles are high in the Palomarin population (Chase 2001) and thus may have a large effect on population dynamics. Although the proportion of locally produced fledglings that recruit into the breeding population is not related to population density (Chase 2001), the overall rate of recruitment of new breeders into the population shows signs of density dependence (PRBO unpubl. data). Therefore, continued long-term study of the Palomarin Song Sparrow population—including analysis of survival, immigration, and emigration—should lead to additional insights into the mechanisms relating weather, population density, and population dynamics.

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