Oecologia (2002) 133:315–324
DOI 10.1007/s00442-002-1040-3

POPULATION ECOLOGY

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Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes

Received: 29 November 2001 / Accepted: 23 July 2002 / Published online: 7 September 2002

Abstract From 1997 to 1999, we monitored the reproductive success of individual rufous-crowned sparrows (*Aimophila ruficeps*) in coastal sage scrub habitat of southern California, USA. Annual reproductive output of this ground-nesting species varied strongly with annual variation in rainfall, attributed to the El Niño-Southern Oscillation. Birds fledged 3.0 young per breeding pair in 1997, when rainfall was near the long-term mean, 5.1 offspring per pair in 1998, a wet El Niño year, and 0.8 fledglings per pair in 1999, a dry La Niña year. Variation in many components of reproductive output was consistent with the hypothesis that food availability was positively correlated with rainfall. However, the factor most responsible for the high reproductive output in 1998 was low early season nest predation which, combined with favorable nesting conditions, enabled more pairs to multiple-brood. Cool, rainy El Niño conditions may have altered the activity of snakes, the main predator of these nests, in the early season of 1998. Overall, more of the annual variation in fecundity was attributable to variation in within-season components of reproductive output (mean number of nests fledged per pair) than to within-nest components (mean brood size). Annual variation in rufous-crowned sparrow fecundity appears to be driven primarily by food resource-mediated processes in La Niña years and by predator-mediated processes in El Niño years.

Keywords *Aimophila ruficeps* · Arid ecology · California coastal sage scrub · ENSO · Snake predation

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Introduction

Abiotic factors influence demographic rates (Davidson and Andrewartha 1948), particularly in variable environments (Nicholson 1958; Sinclair 1989). In arid regions, where rainfall is generally low and unpredictable, water is a strong limiting factor on population processes (Noy-Meir 1973). Many arid-region species respond opportunistically to episodically available resources (Evenari 1985; Shmida et al. 1986; Wiens 1991). Consequently, variation in rainfall can be accompanied by pronounced responses in arid community productivity and dynamics (Polis et al. 1997), prompting some to argue that arid ecosystems are subject to "bottom-up", or food-mediated, control (Jaksic et al. 1997; but see Meserve et al. 1999).

Because water limits primary productivity in arid regions (Noy-Meir 1973; Dillon and Rundel 1990), it is often assumed that fluctuations in consumer abundance with rainfall are caused by changes in food supply (Turner and Chew 1981). Dramatic increases in abundance of arthropods (Fuentes and Campusano 1985; Polis et al. 1997), rodents (Dickman et al. 1999; Lima et al. 1999a; b; Hjelle and Glass 2000) and songbirds (Hall et al. 1988; Rau et al. 1998; Jaksic and Lazo 1999) during relatively wet years have been hypothesized to result from increases in fecundity or survival made possible by heightened food availability. Similarly, population declines in drier years may result from adverse effects of food scarcity on demographic rates (Boag and Grant 1981). Yet, factors other than food supply may mediate the relationship between rainfall and demographic rates. Abiotic factors can also modulate a species' demographic rates through interactions with its predators (Ostfeld and Keesing 2000). Relative to food-mediated processes, however, direct predator-mediated climatic effects on terrestrial vertebrates have received little attention.

Annual variation in arid region songbird fecundity has generally been attributed to fluctuations in food availability with rainfall (Gibbs and Grant 1987; Blancher and Robertson 1987). Food-mediated effects on avian fecundity, however, can arise through a variety of pathways (Boutin 1989) that may differ even among similar, co-occurring species (Rotenberry and Wiens 1991). And, for species capable of raising multiple broods, annual fecundity is determined not only by "within-nest components" of reproductive output (e.g., clutch size, hatching rates), but also by "within-breeding season components", such as the number of nesting attempts or of broods produced (Pease and Grzybowski 1995). Rainfall, through its effect on food, can affect both the within-nest and within-season components of reproductive output. If, however, rainfall affected nest predation rates, the principal determinant of avian reproductive success (Ricklefs 1969), it could impact reproductive output through a process independent of food.

The principal driver of precipitation variation in a number of arid regions, including southern California, is the El Niño-Southern Oscillation (ENSO; Schonher and Nicholson 1989; Pavía and Badan 1998). The ENSO is an irregular inter-annual oscillation of tropical Pacific sea surface temperatures, characterized by El Niño and La Niña phases (Latif et al. 1998). Southern California coastal sage scrub is a predominant, drought-deciduous plant community in southwestern California and northwestern Baja California, Mexico. This mediterranean climate region is characterized by winter rains and summer drought. El Niño usually brings more winter rain, whereas La Niña brings less winter rain (Pavía and Badan 1998). For a 3-year period that encompassed both phases of the ENSO cycle, we monitored the reproductive demography of a coastal sage scrub resident passerine, the rufous-crowned sparrow (*Aimophila ruficeps*). In this paper we examine which components of reproductive output were most responsible for the annual variation in fecundity in this species, and whether food- or predator-mediated processes most influenced annual variation in fecundity.

Materials and methods

The Southern California (or, "ashy") rufous-crowned sparrow subspecies (*A. r. canescens*) occurs in coastal sage scrub (Unitt 1984) between southwest California and northwest Baja California (Grinnell and Miller 1944). The birds generally begin breeding as the rainy season wanes, presumably because that coincides with increased arthropod food availability (Wolf 1977). The diet of nestlings and adults during the breeding season consists primarily of arthropods (Collins 1999). They are open-cup ground-nesters with a 13-day incubation period and a 10-day nestling stage. Females can renest within days of a failed nest, or within weeks of a fledged nest. Renesting tapers off with the onset of summer drought.

We established 15 study plots within three expanses of coastal sage scrub in San Diego, California. The plots were configured to investigate urban edge effects on rufous-crowned sparrow demography, but we found no significant differences in annual fecundity, patterns of inter-annual variation in reproductive output, or nest predation between edge and interior plots (Morrison and Bolger 2002). We therefore combined data from edge and interior areas in the analyses described below.

Each plot encompassed 2–5 focal pairs of breeding rufous-crowned sparrows. Birds were marked with a unique combination of colored leg bands. We monitored the breeding season activity, and attempted to locate all nests, of 41, 49, and 63 focal pairs in 1997, 1998, and 1999, respectively. We found a total of 79, 130, and 57 nests in the respective years. Each nest was visited every 2–3 days until it failed or fledged.

The occurrence and outcome of all nesting attempts was known for 36, 48 and 46 of the monitored pairs in the respective years. For the remaining pairs, we knew how many nests they fledged in a season through behavioral observations, but not how many nests they attempted. We included data from these pairs only in our estimate of the number of fledged nests per pair per year. If we failed to locate a nest of a pair, the pair would retain their focal status only if we could account for their entire breeding season history using observations of female behaviors and inference based on chronology of known nesting attempts. Data from nests of non-focal pairs located opportunistically in our plots were included in estimates of clutch and brood sizes, hatching success, and daily predation rates.

Measures of reproductive output

Multiple measures of reproductive output were compared between years. Clutch size was estimated by counting eggs in incubating nests, or by counting nestlings plus unhatched eggs in nests found during the nestling stage. Brood size was defined as the number of young fledged per successful nest. If multiple nests were found for a given pair during a season, we calculated the mean clutch or brood size for that pair. Egg hatching success was defined as the number of eggs hatched divided by the total eggs laid by a female over the season. The numbers of nest attempts and broods produced by each focal pair were also counted. Any nest in which egg laying had been initiated was counted as a nesting attempt. Any nest that fledged at least one offspring was counted as a successful brood.

Total annual reproductive output per focal pair was estimated by the mean number of fledglings produced per pair. Occasionally some pairs would fledge young from nests that had not yet been located. To remove such pairs from our sample of focal pairs would bias our sample toward pairs that fledged fewer nests. Instead, for any fledged focal nest that had not been found, we substituted that year's grand mean brood size for the offspring count.

Reproductive output data were collected from the same plots in each year, so data were compared using a repeated measures analysis, with Year as the within-subject factor. Data from breeding pairs were pooled to a plot mean, and tested with Site as the between-subject factor. Our 3-year data set was not complete for all plots for some measures. For example, no focal pairs attempted to nest in one plot in 1999, so for that plot and year no data were available for the analysis of clutch size, hatching success, or brood size. Thus, we performed these analyses using the MIXED procedure in SAS, because it can accommodate unbalanced and missing data (Littell et al. 1996). PROC MIXED requires the covariance structure of the data to be specified in the model (Littell et al. 1996). To determine the appropriate covariance structure for these data, we analyzed each measure using three candidate covariance structures: compound symmetric, autoregressive of order 1, and unstructured. Selection among these candidate models was based on model fit statistics (i.e., Akaike's Information Criteria, Schwarz's Bayesian Criteria, and –2 REML Log Likelihood values) provided in the model output (see Littell et al. 1996; UCLA Academic Technology Services, Los Angeles, Calif.).

Nest predation rate

To examine patterns of nest predation we estimated daily nest predation rates. We pooled data for monitored nests by year and nesting stage, and calculated annual mean daily nest predation rates, i.e., the total number of nest predation events divided by the total number of nest-days (Mayfield 1975), and standard errors (Johnson 1979). We also examined within-year patterns in predation rates by dividing the 1997 and 1998 breeding seasons into thirds based on the interval between the first and last clutch initiation dates, and comparing rates between intervals. A short breeding season in 1999 precluded a similar analysis with that year’s data. We tested variation in daily predation rates against a null hypothesis of homogeneity with a χ^2 statistic using the program CONTRAST (Hines and Sauer 1989; Sauer and Williams 1989). Nest survivorship over the entire nesting cycle was estimated by raising each stage’s daily survivorship rates (daily nest survivorship rate=1 – daily nest predation rate) to the exponent of each stage’s duration. The product of those two stage survivorship values provides an estimate of total survival over the nest cycle (Johnson 1979).

Nestling condition

We compared offspring condition among years to test for evidence of food-mediated effects of rainfall. Individual birds were measured on the morning of the 6th day of the nestling stage. We recorded mass to the nearest 0.1 g, and the lengths of the right tarsus and wing chord. Average length and mass measures were calculated for each brood and used in the following analyses. We corrected for body size by regressing mass against the first principal component score (PC1) of the wing and tarsus lengths (Marra and Holberton 1998). Residuals of that regression were considered estimates of the size-corrected body mass, and an index of offspring condition. We tested for differences among years in these corrected mass values with ANOVA.

Brood reduction

We estimated the rate that nestlings died due to factors other than predation of the entire brood, using a procedure similar to the daily nest predation rate calculation above. We were primarily interested in quantifying reduction in brood size due to poor nestling condition, e.g., starvation. We counted the number of nestlings found dead in their nests, but excluded from these counts any individuals that showed signs of injury, e.g., due to nest disturbance. We included in these counts nestlings that had disappeared prior to fledging age. Although some of the disappeared nestlings may have been removed by predators, we know from video surveillance that parent birds can also remove dead young from the nest. We divided the count of nestlings that died or disappeared by the total number of nestling-days for each year, i.e., the number of nestlings in a brood multiplied by the number of days that the brood was under observation (Mayfield 1975). We tested the resulting per day mortality rate for differences among years using CONTRAST.

Within-season versus within-nest components

We used a substitution-estimation procedure to assess the relative effect of within-nest versus within-season components of reproductive output on annual variation in fecundity. The procedure was based on estimating annual fecundity per pair by multiplying mean brood size (a within-nest component) by the mean number of fledged nests per pair (within-season). Data from 1997 were considered to represent baseline conditions (see Results). By alternately substituting 1997 values for each of the 1998 and 1999 values, we estimated the percentage change in fecundity attributable to changes in brood size versus that caused by changes in the number of fledged nests per pair.

Climatic conditions

Monthly rainfall records from 1950 to 1999 and daily temperature data were provided by the Weather Service Branch of the U.S. Marine Corps Air Station Miramar, located near the center of our study area. August and July are the 2 months with the lowest long-term mean precipitation (≤2 mm), so we considered those months to demarcate the beginning and end of the annual rainfall cycle (Fig. 1). Thus, we defined “bioyear precipitation” (Rotenberry and Wiens 1991) to be that which fell between August of the previous year and July. Approximately 82% of the long-term mean bioyear precipitation fell between November and March. Because rufous-crowned sparrows typically begin breeding near the end of this interval (Wolf 1977), we defined the rainfall over this 5-month interval as “prebreeding season precipitation”.

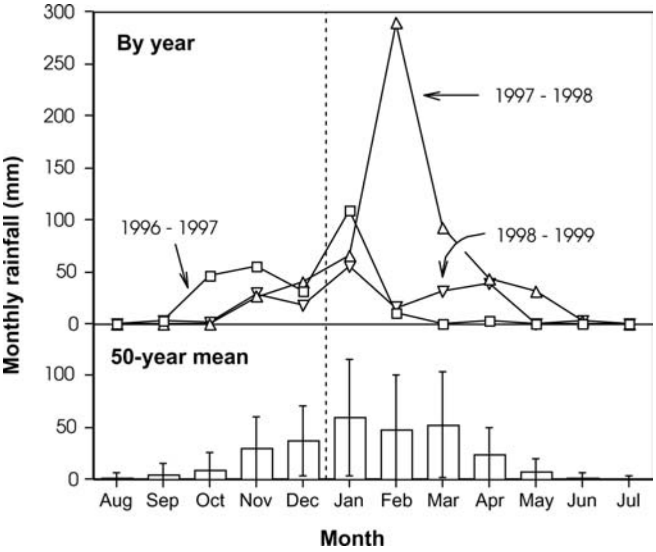

Fig. 1 Monthly rainfall totals for each bioyear of the study, and long-term means (±SD) based on a 50-year (1950–1999) climate record of Marine Corps Air Station Miramar. Long-term mean bioyear rainfall is 279 mm

To compare ambient conditions between 1997 and 1998, mean daily high temperatures were compared for 23-day periods (i.e., the duration of the nesting cycle) beginning with the median initiation dates of the first and last clutches of each year.

Results

Climatic conditions

Rainfall was highly variable among years (Fig. 1). Prebreeding season and bioyear precipitation in 1997 totaled over 90% of the historic means of 229 mm and 279 mm, respectively. Rainfall was over twice the average amounts in 1998. In contrast, rainfall in 1999 was approximately two-thirds the historical means.

The mean daily high temperature during a hypothetical nesting cycle beginning on the median first-nest initiation date in 1998 (17.4 °C) was lower than that in 1997 (21.2 °C; t=3.14, df=44, P<0.005). There was no difference, however, between the mean temperatures during the nesting cycles beginning on the median initiation dates of the last nests (~24 °C; t=1.20, df=44, P>0.10).

Reproductive output

Rufous crowned sparrow reproduction varied strongly among years of our study (Tables 1, 2), and was positively

Table 1 Within-nest components of reproductive output for rufous-crowned sparrows. Mean (±SD) values for *n* monitored nests are provided, along with results of repeated measures analyses based on nest data pooled first by pair then by plot. Covariance structures (in parentheses) were modeled as autoregressive (*AR*) or unstructured (*UN*)

	1997	*n*	1998	*n*	1999	*n*	ANOVA	Source of variation		
								Year	Site	Year × site
Clutch size (AR)	3.26±0.57	78	3.59±0.57	128	2.91±0.45	53	*df*	2, 23	2, 12	4, 23
							F	21.64	0.96	0.87
							P	<0.0001	0.41	0.50
Hatching success (UN)	0.90±0.23	57	0.94±0.19	104	0.83±0.32	41	*df*	2, 12	2, 12	4, 12
							F	3.91	1.81	2.51
							P	0.05	0.21	0.10
Brood size (UN)	2.79±0.72	>25	>3.35±0.80	>65	>2.30±0.76	23	*df*	2, 12	2, 12	4, 12
							F	39.19	4.32	2.71
							P	<0.0001	0.04	0.08

Table 2 Within-season components of reproductive output for rufous-crowned sparrows. Mean (±SD) values for 36–63 focal breeding pairs are provided, along with results of repeated measures analyses. Covariance structures (in parentheses) were modeled as compound symmetric (*CS*), autoregressive (*AR*) or unstructured (*UN*)

	1997	1998	1999	ANOVA	Source of variation		
					Year	Site	Year × site
Offspring/pair (UN)	3.03±2.43	5.07±2.40	0.82±1.21	*df*	2, 12	2, 12	4, 12
				F	58.68	3.20	0.09
				P	<0.0001	0.08	0.99
Nest attempts/pair (AR)	3.56±0.88	3.67±0.97	1.25±0.69	*df*	2, 23	2, 12	4, 23
				F	60.56	3.04	2.86
				P	<0.0001	0.09	0.05
Fledged nests/pair (CS)	1.10±0.83	1.51±0.68	0.37±0.52	*df*	2, 24	2, 12	4, 24
				F	10.11	1.46	0.03
				P	<0.001	0.27	0.99

correlated with rainfall. Mean values of all demographic variables tended to be higher in 1998, and lower in 1999, compared to 1997 when precipitation was nearest the long-term average. Total annual reproductive output per pair ranged from 0.8 fledged young per pair in 1999 to 5.1 in 1998 (Table 2).

High inter-annual variation was observed in the within-nest components of reproductive output (Table 1); for example, mean clutch size ranged from 2.9 in 1999 to 3.6 in 1998. Only during the El Niño year of 1998 did we observe clutches of five eggs (*n*=3); four was the maximum clutch size in all of the other 263 nests found over the three years. In 1999, only 5% of the nests found had even a four-egg clutch, versus 29% in 1997 and 54% in 1998.

There was also high inter-annual variation in most within-season components of reproductive output (Table 2). For example, the median date of first-nest initiation was approximately 2 months later in 1999 than in the previous 2 years (Fig. 2). In 1999, 9% of the focal pairs failed to initiate any nest, whereas no pairs failed to initiate nesting in 1997 and 1998. Only 41% of the 1999 focal pairs that had an unsuccessful first nesting attempt attempted another nest, whereas all pairs nested more than once in the other years. Only 2% of the pairs in

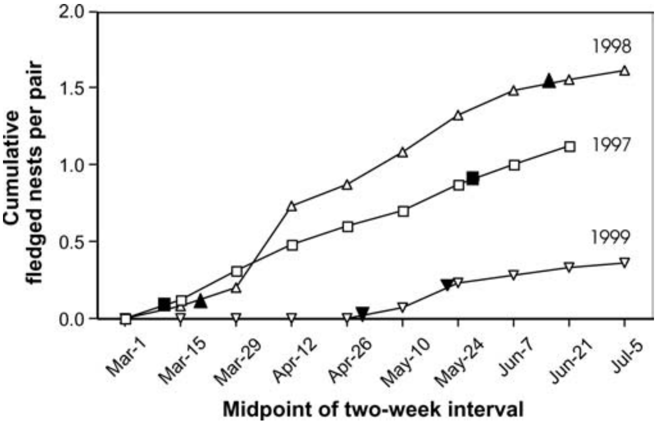

Fig. 2 Within-breeding season phenology of nesting rufous-crowned sparrows (*Aimophila ruficeps*). Seasons were divided into 2-week intervals. Figure depicts the number of nests of focal pairs that fledged during each interval, added to the total number of fledged nests to date, and divided by the number of pairs monitored. *Solid symbols* indicate the median clutch completion dates of the first and last nests attempted each year by focal breeding pairs. The interval between those medians, i.e., the duration of the breeding season, is 76 days, 88 days, and 24 days for 1997, 1998, and 1999, respectively. Initiation of breeding was equally synchronous among years; standard deviation of each year's first-nest initiation dates ranged from 7.9 to 9.1 days

Table 3 Mean daily nest predation rates (±SE) for rufous-crowned sparrows during the incubation and nestling stages, 1997–1999

Year	Incubation stage	Total nest days	Nestling stage	Total nest days
1997	0.066±0.015	275	0.102±0.018	274
1998	0.037±0.009	482	0.050±0.009	617
1999	0.029±0.009	343	0.042±0.012	283

1999 that had fledged one nest attempted a subsequent nest, versus 56% in 1997 and 92% in1998. Consequently, the interval between the median first clutch initiation date and the median last clutch initiation date in 1999 was less than a third of that for 1998 and 1997 (Fig. 2).

Although 1997 and 1998 breeding seasons were of similar duration (Fig. 2), the number of broods produced in those years was markedly different (Table 2). In 1998, 21% of focal pairs attempted, and 8% succeeded, in fledging a third brood. In 1997, only one of 41 focal pairs attempted to fledge a third brood. Higher success of first nesting attempts in 1998 facilitated this increased multiple-brooding; 71% of first nests in 1998 were successful, versus 47% and 38% in 1997 and 1999, respectively. High early-season nest success in 1998 resulted in a high nest fledging rate; by midseason, however, the fledging rate had declined to the 1997 rate (Fig. 2). By the end of the season in 1998, 46% of the focal pairs fledged at least two broods, versus 36% in 1997.

Nest predation rates

Mean daily nest predation rates varied among years (Table 3). Daily predation rates were not different among years for the incubation stage (χ^2=4.37, *df*=2, *P*>0.10), but were different for the nestling stage (χ^2=8.04, *df*=2, *P*<0.05). Orthogonal contrasts indicate that the nestling stage daily nest predation rate was higher in 1997 than in either of the later years (both *P*≤0.01), but did not differ between 1998 and 1999 (χ^2=0.28, *df*=1, *P*>0.50).

Daily nest predation rate during the incubation and nestling stages increased over the 1998 breeding season (both *P*<0.05; Fig. 3). In 1997, a year of comparable season duration, there was no similar trend in either stage's rate of nest predation (both *P*>0.50). As a consequence of this difference, early nests in 1998 had an estimated nest success rate of 71%, whereas early nest success in 1997 was only 14%. The breeding season was too short to identify trends in 1999.

Nestling condition

Nestling condition varied significantly among years. PC1 accounted for 93.7% of the variation in the mean tarsus and wing lengths of clutches, and did not vary among years ($F_{2,111}$=1.85, *P*>0.10). However, body-size corrected nestling mass varied significantly among years ($F_{2,110}$=9.99, *P* <0.0001). Mean size-corrected mass (±SE) in the wet El Niño year was 11.15±0.15 g, versus 10.23±0.27 g and 10.42±0.25 g in 1997 and 1999, respectively.

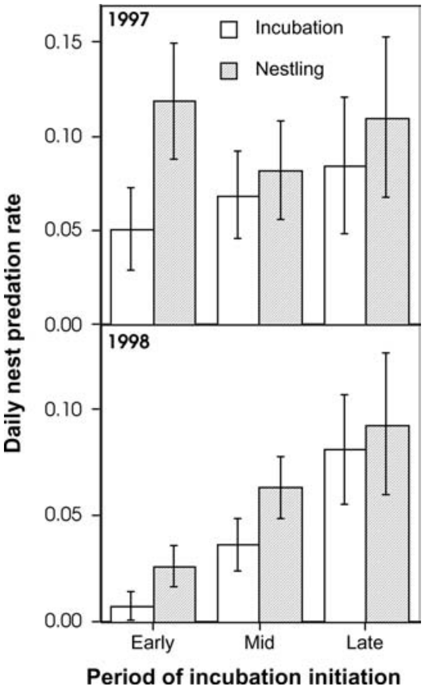

Fig. 3 Within breeding season variation in daily nest predation rate, 1997 and 1998. *Bars* depict daily nest predation rate (±1 SE) for monitored nests. Seasons were divided into thirds based on the interval between the incubation initiation dates of the seasons' first and last nests, and all nests were categorized by when their incubation had begun. The calendar dates of each interval roughly correspond between years. A shorter breeding season duration in 1999 precluded similar comparisons with that year; e.g., no breeding occurred until the latter half of the "Mid Period".

Brood reduction

Rates of brood reduction differed among years (χ^2=8.78, *df*=2, *P*=0.01). The rate (±SE) in 1999 was 0.014±0.004 nestlings/nestling day, versus 0.001±0.001 and 0.004±0.001 in 1997 and 1998, respectively.

Within-season versus within-nest components

Fecundity estimated by the product of brood size (Table 1) and number of fledged nests (Table 2) was 3.07, 5.06, and 0.85 young per pair for 1997, 1998, and 1999, respectively, which was similar to realized fecundity of 3.03, 5.07, and 0.82. We estimated that an in-

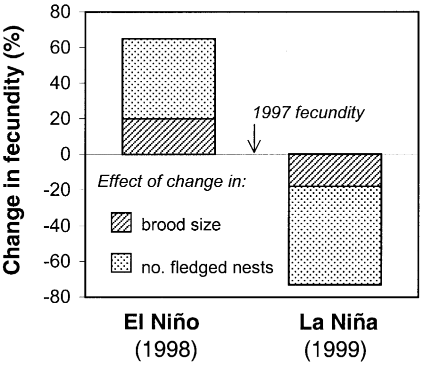

Fig. 4 The relative contribution of two components of reproductive output to annual variation in rufous-crowned sparrow fecundity. Figure depicts the percentage change in the number of fledglings per pair resulting from changes in mean brood size (Table 1) and in mean number of fledged nests per pair (Table 2), during a wet El Niño year (1998) and a dry La Niña year (1999), relative to an average rainfall year (1997). For each year (*t*), mean brood size (BS_t) × fledged nests per pair (FN_t) provided an estimate of fecundity that reproduced realized fecundity (Table 2). Relative to 1997's estimated fecundity, represented by the *horizontal axis*, the change in annual fecundity that resulted from the change in mean brood size was estimated as $(BS_t \times FN_{1997})-(BS_{1997} \times FN_{1997})$. The change in annual fecundity resulting from changes in the mean number of fledged nests per pair was estimated as $(BS_t \times FN_t)-(BS_t \times FN_{1997})$

crease in brood sizes relative to 1997 increased fecundity in 1998 by 0.62 fledglings per pair, whereas an increase in the number of nests fledged per pair increased fecundity by 1.37 fledglings (Fig. 4). We estimated that fecundity per pair in 1999 declined by 0.54 fledglings because of smaller brood sizes, whereas the reduced number of nests fledged per pair led to a reduction of 1.68 fledglings (Fig. 4). Thus, in both 1998 and 1999 the within-season component, nests fledged per pair, caused more of the deviation in fecundity from 1997 levels.

Discussion

Rufous-crowned sparrow fecundity varied strongly and positively with inter-annual variation in rainfall. While these findings are consistent with many other studies of arid region birds (Newton 1998), the patterns of variation in within-nest and within-season reproductive measures suggest that rainfall causes annual variation in sparrow fecundity through its effect on both food availability and nest predation. Moreover, the process primarily responsible for generating variation in fecundity in a given year appears to switch from a food-mediated process in drier years, to a predator-mediated process in wetter years.

Trophic mechanisms

Most of the inter-annual variation in fecundity was generated by variation in the within-season (Table 2), rather than the within-nest (Table 1), components of reproductive output (Fig. 4). In 1999, a lower number of fledged nests reduced fecundity 55% relative to 1997, whereas smaller brood sizes reduced fecundity only 20% (Fig. 4). In 1998, nearly 70% of the increase in fecundity relative to 1997 can be attributed to an increase in the number of fledged nests (Fig. 4).

Although the component of reproductive output that drove variation in fecundity was the same in both years, the trophic pathway was not. Few nests fledged in 1999 largely because few nests were attempted (Table 2). That apparently resulted from a shorter period of favorable nesting conditions (Fig. 2), and is consistent with food limitation. In contrast, both the breeding season duration (Fig. 2) and the number of nesting attempts per pair (Table 2) were similar in 1997 and 1998. Thus, the difference between the number of fledged nests in 1997 and 1998 was primarily due to lower nest predation rates in early 1998 (Figs. 2, 3). Lower nest predation rates in the early season (Fig. 3) allowed almost half of the pairs to multiple-brood in that year (Fig. 2, Table 2).

Food-mediated variation in output

All of the components of rufous-crowned sparrow reproductive output varied in a manner consistent with the hypothesis of heightened food availability in the wettest year and reduced availability during the driest (Tables 1, 2; Fig. 2). Availability of food resources can affect numerous components of avian reproductive output (e.g., Greenlaw 1978; Price 1985; Simons and Martin 1990; Rodenhouse and Holmes 1992). In arid ecosystems, the availability of seeds and arthropods that provide food resources for songbirds presumably parallels the tight correlation between rainfall and primary productivity (Noy-Meir 1985; Inouye 1991; Wisdom 1991). Although interactions between climatic conditions, avian foraging, and the life cycle and activity of invertebrate prey may be complex (Avery and Krebs 1984; Kingsolver 1989; Ayal 1994), our data support the hypothesis that rainfall affects the bird's reproduction in this semi-arid region through its effect on food resource availability.

Variation in arthropod abundance in response to precipitation has not been well-described in coastal southern California (Longcore 1999). On our study plots, however, the abundance the non-native generalist Argentine ant, *Linepithema humile*, increased 3–10-fold between spring 1997 and spring 1998 (D. Bolger, unpublished data). Similarly, dipterans were approximately 5 times more abundant in spring 1998 than in spring 1997 in vacuum and pitfall samples collected in similar habitat in adjacent Riverside County (M.A. Patten, personal communication). Additional indirect evidence of the hypothesized relationship comes from Laakkonen et al. (2001) who found a marked increase in abundance of an insectivorous shrew (*Notiosorex crawfordi*) in southern California in 1998.

Variation in nestling condition provided additional evidence that food availability varied among years. Nestling size-corrected mass was higher in 1998 than in the other years. Although mass did not decrease in 1999 relative to 1997, brood size did (Table 1), so total provisioning demands may have been lower. Brood sizes were lower in 1999 because clutch sizes were smaller and brood reduction was more frequent. During conditions of food scarcity, brood size may be reduced by partial brood starvation (Magrath 1990). In contrast, nestling mass was higher in 1998 despite larger brood size, suggesting higher food availability. Such variation in nestling condition may have important population implications. Fledglings in better condition may experience higher survival (Blancher and Robertson 1987; Ringsby et al. 1998). Because juvenile songbirds may be particularly sensitive to starvation (Weathers and Sullivan 1989), we suspect that juvenile survivorship of these birds might also positively covary with rainfall.

Predator-mediated variation in output

Climatic effects on predator behavior can be important determinants of survival (Spiller and Schoener 1995) and reproduction (Chalcraft and Andrews 1999) of prey species, and may underlie some patterns of nest predation in birds (Schmidt 1999). Few field studies, however, have demonstrated a direct predator-mediated climatic effect on vital rates of prey, such as through a direct effect of climate on predator foraging behavior or efficiency (Post et al. 1999). This differs from climate-induced predator-prey cycles, which may occur when predators respond with a time-lag to rainfall-induced increases in prey (Rotenberry and Wiens 1989; Jaksic et al. 1997). In those cases, the predator-mediated climatic effect on prey demography is indirect, and still a consequence of a food-mediated process.

We propose that early season rainfall in 1998 governed rufous-crowned sparrow reproduction by mediating interactions with its main nest predators. Video-surveillance of nests has implicated California kingsnakes (*Lampropeltis getula californiae*) and San Diego gopher snakes (*Pituophis melanoleucus annectens*) as the principal nest predators of this species, accounting for 90% of the predation events in which the predator could be identified; most events occurred in the early to mid afternoon (Morrison and Bolger 2002). Within-year variation in daily predation rate in 1998 (Fig. 3) was consistent with a hypothesis that foraging behavior of snakes was affected by weather conditions. High nest success in the early season of 1998 was coincident with heavy rainfall (Fig. 1) and lower daily high temperatures. Rainy and cooler conditions may have imposed thermoregulatory constraints on snake activity (Ford and Burghardt 1993; Peterson et al. 1993), and so suppressed nest predation by snakes. Activity of gopher snakes, for example, increases linearly with body temperature in the 18–27 °C range; at 18 °C, foraging activity is significantly impaired (Greenwald 1974). In contrast to 1997, ambient temperatures in the early season in 1998 were below 18 °C. Although the relationship between ambient and body temperature of actively foraging snakes is complex (Huey and Slatkin 1976; Blouin-Demers and Weatherhead 2001), it is interesting to note that in 1997, when conditions were more uniformly warm and dry, a window of reduced nest predation did not occur. Furthermore, in the late season of 1998, when weather conditions were again similar to 1997, the rate of nest predation was also similar (Fig. 3).

Weather-induced suppression of foraging by active-searching snakes is not the only mechanism that could have produced the observed pattern in nest predation. A variety of community interactions can mediate predator-prey relationships (Schmidt 1999). Early in 1998, for example, snakes could have exploited alternative prey (Murdoch and Oaten 1975) enhanced by rainfall (Jaksic et al. 1997). More rainfall in 1998 also may have increased vegetation structural diversity, which may lower foraging success of snakes (Mullin et al. 1998). Alternatively, parent birds may alter their activities in inclement weather (Johnson and Best 1982; Hilton et al. 1999), and perhaps reduce exposing their nests to nest predators that can visually cue on parental behaviors (Skutch 1985), like snakes (Eichholz and Koenig 1992).

Effects of timing of rainfall

In arid regions, the timing of rainfall, rather than total rainfall alone, has been shown to be an important influence on primary productivity (Ayyad 1981), and songbird reproduction (Rotenberry and Weins 1991; Brown and Li 1996; Lloyd 1999; Patten and Rotenberry 1999). Likewise, biotic responses to rainfall may be influenced by rainfall conditions in preceding years (Grant et al. 2000). As in many arid regions (Noy-Meir 1973), monthly rainfall in San Diego is relatively unpredictable; the standard deviation of monthly rainfall exceeds the mean in all but 3 months (Fig. 1). It is possible that the between-year variation in fecundity we observed may have been generated in part by idiosyncratic within-year rainfall patterns. Longer-term data will be required to evaluate the importance of within-year rainfall timing and the generality of the pattern we observed.

Population dynamics and conservation

The ENSO is the predominant driver of rainfall variation in the mediterranean climate regions of southern California and Baja California (Pavía and Badan 1998). Our data suggest that rufous-crowned sparrow reproductive success is coupled to the ENSO cycle. This may have important population implications. Global warming (Mahlman 1997) may cause an increase in El Niño frequency (Timmermann et al. 1999); indeed, El Niño conditions appear to occur more frequently in the latter half of the 1950–1999 climate record (Trenberth and Hoar 1997). That prediction might seem to bode well for this subspecies, a California Species of Special Concern (California Department of Fish and Game 1992), because it would suggest an increase in mean annual fecundity. However, too much rainfall could result in a decline in productivity (DeSante and Geupel 1987; Grant et al. 2000). Moreover, global warming may also result in stronger variation in ENSO conditions, and more intense La Niña events (Timmermann et al. 1999). Increased density-independent fluctuations in vital rates, such as those that would be produced by a more variable ENSO, can increase the risk of population extinction, even if the geometric mean population growth rate is increasing (Tuljapurkar and Orzack 1980).

Urban and agricultural development has reduced coastal sage scrub habitat to approximately 10% of its former coverage and caused extensive habitat fragmentation (Westman 1981). Nearly 100 plant and animal species that reside in a coastal sage scrub are listed as threatened, endangered, or of conservation concern by state and federal agencies (Atwood 1993). Many of the resident songbirds, including the rufous-crowned sparrow, appear sensitive to fragmentation, in that they are markedly less abundant in smaller habitat fragments (Bolger et al. 1997; Crooks et al. 2001; Bolger 2002). All coastal sage scrub biota are subject to a precipitation regime linked to ENSO, and it is unlikely that high responsiveness to the ENSO cycle is unique to rufous-crowned sparrows (e.g., Erickson and Miner 1998; Atwood et al. 1998). ENSO-driven variation could have implications for composition of communities (Westman and Malanson 1992), inter-specific interactions (Quinn and Karr 1993), and population persistence in fragmented landscapes. Because of ENSO's likely substantial population and community effects, a consideration of its effects should be an essential component of conservation planning in this region.

Acknowledgements We thank the tireless field assistants whose talents made this study possible: K. Ellison, B. Boehlert, D.M. Cooper, D.S. Cooper, W. Cover, T. DeMarco, M. DiGiorgio, K. Gayman, K. Hulvey, J. Knight, B. Langan, L. Lanwermeyer, D. LeFer, M. Lynes, R. Nagel, C. Nishida, K. Podolak, S. Prosser, N. Vulgares, and K. Wakelee. We are also grateful for the support of the staffs of Los Peñasquitos Canyon Preserve, Mission Trails Regional Park, the San Diego National Wildlife Refuge, and the Weather Service Branch of MCAS Miramar. We thank M. Ayres for lively discussions concerning this research and manuscript, K. Cottingham, J. Dykes, T.S. Sillett, and M.S. Zens for discussions concerning analyses, and R. Holmes, M. McPeek, M. Patten, J. M. Reed, and P. Vickery for helpful comments on earlier versions of this manuscript. Reviewing editor R. Moen provided suggestions that greatly improved this paper. I. Berry, J. Berry, G. Eaton, R. Lewis, W. Lowe, and P. Strasdin provided generous logistical support. This research was supported by NSF grant DEB94–24559, and a contract from the Metropolitan Water District of Southern California, to D.T.B.

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