

Dependent vs. independent juvenile survival: contrasting drivers of variation and the buffering effect of parental care

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Abstract: Juvenile survival is often found to be more sensitive than adult survival to variation in environmental conditions, and variation in juvenile survival can have significant impacts on population growth rates and viability. Therefore, understanding the population-level effects of environmental changes requires understanding the effects on juvenile survival. We hypothesized that parental care will buffer the survival of dependent juveniles from variation in environmental conditions, while the survival of independent juveniles will respond more strongly to environmental variation and, in turn, drive the overall variation in annual juvenile survival. We tested this parental-care hypothesis using a 30-year mark–recapture data set to model the survival of juvenile Song Sparrows (*Melospiza melodia*) during the dependent and independent stages. We examined the effects of weather, density, and cohort mean fledge date and body mass on annual variation in survival during the first 12 weeks after fledging, as well as effects of individual fledge date and body mass on individual variation in survival. The primary driver of annual variation in juvenile survival was precipitation during the previous rainy season, consistent with an effect on food availability, which had a strong positive effect on the survival of independent juveniles, but no effect on dependent juveniles. We also found strong support for effects of body mass and fledge date on individual survival probability, including striking differences in the effect of fledge date by stage. Our results provided evidence that different mechanisms influence juvenile survival during each stage of fledgling development, and that parental care buffers the survival of dependent juveniles from variation in environmental conditions. Consequently, variation in juvenile survival was driven by independent juveniles, not dependent juveniles, and studies focused only on survival during the dependent stage may not be able to detect the major drivers of variation in juvenile survival. We recommend that future efforts to understand or project the population-level effects of environmental change not only examine the effects on juvenile survival, but specifically consider the survival of independent juveniles, as well as how the drivers of variation in juvenile survival may vary by stage.

Key words: California; juvenile survival; mark–recapture; *Melospiza melodia*; Palomarin; post-fledgling survival; Song Sparrow; weather.

INTRODUCTION

The survival of juveniles to reproductive age is a critical component of population dynamics, and variation in juvenile survival can have significant impacts on population growth rates and viability (Arcese et al. 1992, Gaillard et al. 1998, Finkelstein et al. 2010). Juvenile survival is also often found to be more sensitive than adult survival to fluctuations in environmental conditions, including weather, habitat structure, and population density (Powell et al. 2000, Coulson et al. 2001, Robinson et al. 2007, Oro et al. 2010). This heightened sensitivity may result from their relatively limited mobility and foraging skills (Marchetti and Price

1989), which make them more vulnerable than adults to variation in food availability and predation risk. Consequently, to better understand and predict the population-level effects of environmental change, including climate change, a growing number of studies have examined the response of juvenile survival to variation in environmental conditions (Robinson et al. 2007, Reid et al. 2008, Dybala 2012). However, few of these have examined whether the sensitivity of juvenile survival to environmental conditions changes as they transition from dependence on parental care to independence (but see Portier et al. 1998, Tarwater et al. 2011).

Across many taxa, juveniles pass through two distinct stages on their way to reproductive maturity: first, an initial dependent stage, during which they rely on parental care for food and protection and, second, an independent stage, during which they must fend for themselves, but may not yet have acquired adult-level

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foraging and predator-avoidance skills (Weathers and Sullivan 1989, Daunt et al. 2007). Although dependent juveniles are more limited in their abilities than independent juveniles, the skills of their adult parents may shield them from poor environmental conditions, while independent juveniles are fully exposed. Therefore, just as adult survival is buffered from variation in environmental conditions (Gaillard et al. 1998, Gaillard and Yoccoz 2003), we hypothesized that parental care will in turn buffer the survival of dependent juveniles from this variation (Erikstad et al. 1998, Cam et al. 2003, Proffitt et al. 2010), so that the survival of independent juveniles will be the most sensitive to environmental change.

We tested this parental-care hypothesis by using a 30-year mark–recapture data set to model the survival of juvenile Song Sparrows (*Melospiza melodia*) during dependent and independent stages of development. A previous study in this population identified prior rainy season precipitation as a major driver of overall variation in annual juvenile survival, consistent with an effect on food availability (Dybala 2012). In this study, we examined the strength of this effect on survival during the dependent and independent stages, as well as effects of several other variables that reflect annual and seasonal variation in environmental conditions. These included population density, fledge date, and body mass, an effect of which may reflect stored body fat and a need to withstand temporary food shortages (Perrins 1965, Magrath 1991, Perrins and McCleery 2001). If parental care buffered the survival of dependent juveniles from variation in these conditions, we expected (1) the strength and/or magnitude of each effect to vary by stage, (2) stronger effects during the independent stage, and (3) that the variables with the strongest effects on independent juveniles would contribute most to overall variation in annual juvenile survival.

METHODS

Study site, species, and data collection.—This study was conducted at the Palomarin Field Station, located in the Point Reyes National Seashore, 20 km north of San Francisco, California, USA (37°56' N, 122°45' W). The study area, flora, and field methods have been described in detail elsewhere (Ballard et al. 2004, Jennings et al. 2009), and are summarized here. The climate is Mediterranean, typically with cool, rainy winters and warm, dry summers; total precipitation and high and low temperatures are collected on site daily. The habitat in the 36-ha study area is coastal scrub with a steadily increasing abundance and density of Douglas firs (*Pseudotsuga menziesii*), which has coincided with a steady decline in the density of Song Sparrow breeding territories (Chase et al. 2005). Song Sparrows are a common, open-cup-nesting passerine found throughout North America, and the local subspecies (*Melospiza melodia gouldii*) is non-migratory (Arcese et al. 2002).

Year-round, constant-effort mist-netting at Palomarin began in 1979 and, since 1980, field biologists have used standardized methods to intensively search the entire study area each year for passerine territories and nests (DeSante and Geupel 1987, Martin and Geupel 1993). Biologists record the body mass of each Song Sparrow nestling approximately 1–4 days prior to fledging, and mark them with a unique combination of colored leg bands and a U.S. Department of the Interior aluminum band (see Plate 1). Nestlings are returned to their nests, and fledging success is later determined from a combination of nest condition, parent behavior, and direct observation of fledglings. We excluded from the survival analysis all nestlings known not to have fledged.

Juvenile survival.—We modeled juvenile survival using R 2.14.1 with the package RMark 2.1.0 to write Cormack-Jolly-Seber models for Program MARK 6.1 (Lebreton et al. 1992, White and Burnham 1999, R Core Development Team 2011, Laake 2012). We first constructed weekly capture histories for all individuals marked as nestlings from 1980 through 2010, extending to 13 weeks after fledging. We also included an additional, 14th encounter occasion that indicated whether the individual was later recaptured or identified in the field by their unique color band combination, up to 31 December of the year following fledging. This approach maximizes the final recapture probability, increasing the power to estimate survival rates during the first 12 weeks (Reid et al. 2011). We initially modeled survival (ϕ) and recapture (p) probabilities solely in terms of year (t) and fledgling age, measured in weeks after fledging (week), to establish a baseline model structure. Our data were too sparse to estimate survival in each week of each year, so our most general model included additive effects of week and year on both survival and recapture probabilities: $\phi(\text{week} + t) p(\text{week} + t)$. We used the median- \hat{c} method implemented in Program MARK 6.1 to test the fit of this model, and overdispersion was low ($\hat{c} = 1.09$), indicating this model fit the data well.

We expected juvenile survival during the first 12 weeks after fledging to vary by year and by stage of fledgling development. Juvenile Song Sparrows become independent during the fourth or fifth week after fledging (Hochachka and Smith 1991, Dybala 2012). Thus, we classified weeks 4–5 as “transitional,” a group composed of a mix of dependent and independent juveniles, while we classified weeks 1–3 and 6–12 as “dependent” and “independent” stages, respectively. Within the dependent stage, we always included separate intercepts for week 1 and weeks 2–3, based on widespread evidence that survival is lowest during the first week after fledging (Naef-Daenzer et al. 2001, Adams et al. 2006, Whittaker and Marzluff 2009), including in this population (Dybala 2012). We defined six survival models that included effects of week or weeks grouped into stages ($w_1 + w_{2-3} + w_{4-5} + w_{6-12}$), with or without an added effect of year (t) or trend in year (T). The effect of t

allowed survival to vary by year, while the effect of T constrained this variation to a linear trend in survival over the study period. We also defined two recapture probability models, including effects of week (week), or week and year (week + t). We did not consider effects of stage for recapture probability, because we expected fledgling mobility, and hence recapture probability, to change more gradually from week to week, rather than in a step-wise fashion from stage to stage.

We fit all 12 combinations of the six survival and two recapture models to the mark–recapture data, and used the model-selection results to calculate model-averaged weekly survival and recapture probabilities. We also calculated the cumulative probability of surviving the first 12 weeks after fledging, using the Delta method to calculate 95% confidence intervals for these estimates. The model with the most support, which included effects of stage and year on survival and effects of week and year on recapture probability, hereafter Ref_t , became the primary reference model to which we compared models including effects of the candidate explanatory variables (Grosbois et al. 2008). We also refer to the nested models Ref_T , which is identical to Ref_t except that it constrains the variation in survival during each stage to a common linear trend, and Ref_c , which constrains survival during each stage to be constant.

Candidate explanatory variables.—Environmental variables hypothesized to contribute to annual variation in juvenile survival during the first 12 weeks after fledging included total precipitation during the previous rainy season (October–March) and population density. In the Mediterranean climate of central coastal California, primary and secondary productivity are limited by water availability (Roy et al. 1995). Wet years benefit plant growth and insect populations (Bale et al. 2002, Kreyling 2010), which can provide increased cover and food resources for birds throughout the following breeding season (Bolger et al. 2005). In addition, previous studies showed that prior rainy season precipitation was positively related to both fledging success and overall annual juvenile survival in this population (Chase et al. 2005, Dybala 2012). Therefore, we expected to confirm the positive relationship between prior winter precipitation and juvenile survival in this study. We also expected juvenile survival to be higher in low-density years, since density may reflect competition for food or territories. We measured density in terms of the annual number of Song Sparrow territories in the study area each breeding season. However, because the territory density has been steadily declining as the habitat has changed, we examined the effect of territory density relative to this declining trend, calculated as the residuals between the number of territories observed and the number predicted from the trend.

Individual variables hypothesized to contribute to variation in juvenile survival included fledge date and nestling body mass. Individual variables may influence survival in two ways. First, they may contribute to

variation in survival probability among individual juveniles. Second, if they have strong effects on individual survival, and if there is considerable variation among cohorts in their mean body mass or fledge date, these variables may also contribute to variation in survival among cohorts. For example, body mass may reflect stored body fat and an ability to withstand temporary food shortages (Perrins 1965, Magrath 1991, Perrins and McCleery 2001), so we expected individual survival to be higher for individuals with greater body mass. However, we also expected cohort survival to be higher in years with greater average cohort body mass. Similarly, we expected an effect of fledge date to reflect seasonal variation in food availability or predation risk (Naef-Daenzer et al. 2001, Fisher and Davis 2011), so that individuals and cohorts with earlier fledge dates may have different survival probabilities than those with later fledge dates.

We measured nestling body mass at the time of banding to the nearest 0.1 g. The age at which nestling body masses were recorded ranged from 5 to 10 days after hatching, although 70% of the nestlings were measured on days 6 or 7. Therefore, we first standardized body masses to a 7-day-old nestling, based on a quadratic regression between age and mass. We estimated individual fledge dates as the mid-point between the date of the last active nest check and the first inactive nest check, which were typically accurate to within 48 hours. We then calculated each cohort's mean body mass and fledge date.

We calculated the Pearson's correlation coefficient (r) between all of the variables under consideration, as well as identified any linear or quadratic trends in each of the variables (reported in *Results*). We then standardized each of the variables to have a mean of 0 and standard deviation of 1, so that the effect sizes could be compared on the same scale.

Annual variation in survival.—We first examined how well prior rainy season precipitation, relative territory density, and cohort mean fledge date and body mass accounted for the annual variation in juvenile survival during the first 12 weeks after fledging that was estimated by Ref_t , the primary reference model that included effects of stage and year on survival. Therefore, we compared the fit of Ref_t to models that replaced the effect of year with an effect of one of the candidate variables. However, rather than adding effects of candidate variables to Ref_t , the baseline reference model with an effect of stage and no effect of year on survival, we instead added effects of candidate variables to Ref_T , the baseline model that included a long-term trend in survival. We took this approach because Ref_T had much stronger support than Ref_c , indicating evidence for a long-term trend in survival underlying the annual variation in survival. None of our four candidate variables exhibited a strong trend, and we suspect this trend in survival may be related to the long-term habitat change at Palomarin. Therefore, we added the candidate



PLATE 1. Song Sparrow nestling, just after banding and measuring. Photo credit: K. E. Dybala.

variables to Ref_7 to account for this trend while identifying the variables that could explain the variation in survival around the trend.

The model set included linear and quadratic effects of each variable, with either a single overall effect of each variable, or separate effects on survival during each of the dependent, transitional, and independent fledgling stages. We quantified support for each model by comparing its fit to Ref_i and by calculating the fraction of the total annual variation in juvenile survival accounted for by each variable (R_{Dev}^2 ; Skalski 1996, Grosbois et al. 2008). We considered models that improved on the fit of Ref_i (reduction in Akaike information criterion for small sample size, $\Delta AIC_c < 0$) and with $R_{Dev}^2 > 0.20$ to have strong support (Grosbois et al. 2008).

Individual variation in survival.—Finally, we separately examined how well body mass and fledge date accounted for the additional variation in survival among individuals. By definition, these individual variables could not account for the annual variation in survival, so we added effects of individual body mass and fledge date to Ref_i , the primary reference model that best accounted for this annual variation. The model set included linear and quadratic effects of each variable, with either a single overall effect of each variable, or separate effects on survival during each fledgling stage. However, for this model set, we expected all variables to improve on the fit of Ref_i if they accounted for at least some of the

variation in survival among individuals, so we did not consider this to be evidence of strong support for these variables. Instead, we considered variables in the models with the lowest AIC_c scores ($\Delta AIC_c < 2$) to have strong support.

RESULTS

Juvenile survival.—The data set included 1795 marked Song Sparrows fledged at Palomarin from 1980 through 2010, with none marked in 1986 when nest-searching effort was greatly reduced. A total of 691 (38.5%) of the marked Song Sparrow fledglings were recaptured or recognized by their unique color band combinations by 31 December of the year following fledging, but most of these (490; 70.9%) were recaptured in the mist-nets within the first 13 weeks after fledging.

The top model describing variation in survival and recapture probability had very strong support (Akaike weight, $w = 0.999$; Table 1a) and became the primary reference model (Ref_i) to which models including effects of candidate variables were compared. This model included effects of fledgling stage and year on survival probability. However, there was also evidence for a long-term trend in survival underlying the annual variability, since the nested model with a long-term trend in survival by year (Ref_7) had much stronger support than the model with no effect of year (Ref_i ; $\Delta AIC_c > 10$; Table 1a). Furthermore, this long-term trend accounted for a considerable proportion of the

TABLE 1. Model-selection results for the analysis of juvenile survival.

Survival (ϕ)	k	AIC _c	Δ AIC _c	w	Dev	R^2_{Dev}	
						Var	T,Var
a) Reference models, including effects of age and year							
Ref _i = $w_1 + w_{2-3} + w_{4-5} + w_{6-12} + t$	76	7326.66	0.00	0.999	1615.05		
Ref _T = $w_1 + w_{2-3} + w_{4-5} + w_{6-12} + T$	48	7348.60	21.94	0.000	1695.85		0.38
Ref _i = $w_1 + w_{2-3} + w_{4-5} + w_{6-12}$	47	7396.10	69.44	0.000	1745.42		
b) Effects of variables contributing to annual variation in juvenile survival							
Ref _T + Stage \times Rain	51	7325.58	0.00	0.440	1666.58	0.36	0.60
Ref _i	76	7326.66	1.08	0.257	1615.05		
Ref _T + Rain	49	7327.91	2.33	0.138	1673.08	0.28	0.55
Ref _T + Stage \times Rain ²	54	7328.79	3.21	0.089	1663.53	0.40	0.63
Ref _T + Rain ²	50	7329.08	3.49	0.077	1672.16	0.29	0.56
c) Effects of variables contributing to individual variation in juvenile survival							
Ref _i + Mass	77	7312.89	0.00	0.505	7154.03		
Ref _i + Stage \times Date	79	7314.68	1.79	0.206	7151.57		
Ref _i + Mass ²	78	7314.99	2.10	0.177	7154.00		
Ref _i + Stage \times Mass	79	7316.64	3.75	0.077	7153.53		

Notes: Only reference models and models with Δ AIC_c < 4 are shown. See Appendices A–C for the full tables of results. Recapture probability for all models shown included effects of age, in weeks after fledging, and year (week + t). Survival model notation includes effects of age, in groups of weeks after fledging ($w_1 + w_{2-3} + w_{4-5} + w_{6-12}$), year (t), and trend in year (T). Variables include linear and quadratic effects of precipitation during the previous rainy season (October–March; Rain), nestling body mass (Mass), and fledge date (Date). Models included either a single overall effect of each variable or effects that varied by fledging stage (Stage). R^2_{Dev} is the fraction of temporal variation around the trend in survival that is accounted for by the annual variable alone (Var), or the total temporal variation in survival accounted for by the trend and variable together (T,Var). Akaike weights (w) and number of estimated parameters (k) are also given.

total annual variation in survival ($R^2_{\text{Dev}} = 0.38$). Accordingly, the cumulative probability of surviving the first 12 weeks after fledging varied by year with a declining trend (Fig. 1a). Estimates ranged from a high of 0.51 (95% confidence interval: 0.42–0.60) in 1982 to a low of 0.02 (0.004–0.17) in 1990, and averaged 0.22 (0.16–0.28).

Within each year, model-averaged weekly survival was lowest during the first week after fledging (Fig. 1b), averaging 0.60 (0.58–0.63). The weekly survival rate during the second and third week after fledging averaged 0.94 (0.91–0.96), so that the probability of surviving the entire dependent stage (weeks 1–3 after fledging) averaged 0.53 (0.49–0.57). Weekly survival during the transitional stage (weeks 4–5) averaged 0.78 (0.76–0.80), and weekly survival during the independent stage (weeks 6–12) averaged 0.94 (0.92–0.96). Recapture probabilities also varied by week, increasing from a low of 0.013 (0.012–0.015) during the second week after fledging, to a peak of 0.27 (0.25–0.28) during the fifth week after fledging, before declining again (Fig. 1c).

Candidate explanatory variables.—Precipitation during the previous winter rainy season (October–March) ranged from 0.38 to 1.39 m, with a mean of 0.78 m (Fig. 2). The mean fledge date for each cohort ranged from 16 May to 30 June, and the mean standardized nestling body mass for each cohort ranged from 13.8 g to 15.3 g. There was no evidence for linear or quadratic trends in any of these three variables ($P > 0.1$). Song Sparrow territory density declined steadily by 0.03 territories·ha⁻¹·yr⁻¹ ($P < 0.001$), but there was no trend in relative territory density, which ranged from 0.42

territories/ha fewer to 0.36 territories/ha more than expected from the long-term trend. None of these four candidate variables were strongly correlated (Pearson's $r < 0.25$).

Annual variation in survival.—Of the four candidate variables hypothesized to affect annual variation in survival during the first 12 weeks after fledging, prior rainy season precipitation had the strongest support, with the combined Akaike weights of all models representing this effect totaling 0.744 (Table 1b). Of these models, support was strongest for the model including linear effects of prior rainy season precipitation that varied by stage (Δ AIC_c > 2). The estimated effect (β) on the survival of independent juveniles was strong and positive ($\beta = 0.66$, 95% CI 0.19–1.14; Fig. 3), but there was no evidence for an effect during the dependent stage ($\beta = 0.06$, 95% CI –0.14–0.25) or the transitional stage ($\beta = 0.08$, 95% CI –0.21–0.37). Despite the striking differences in the effect of prior rainy season precipitation during each stage, if we had only estimated a single, overall effect during all three stages, the estimated effect would have been weakly positive ($\beta = 0.16$, 95% CI 0.09–0.23; Fig. 3).

The effect of prior rainy season precipitation on independent juveniles accounted for 36% of the variation around the overall declining trend in juvenile survival, and this effect and the trend together accounted for 60% of the total annual variation in juvenile survival (Table 1b). In contrast, models including effects of relative territory density, cohort mean fledge date, or cohort mean body mass had very little support. Each of these effects accounted for less than 20% of the variation

around the declining trend in juvenile survival (Appendix B).

Individual variation in survival.—Although there was no evidence for an effect of cohort mean body mass or fledge date on annual variation in survival, there was support for effects of both variables on individual variation in survival (Table 1c). As expected, all of the models including individual variables improved on the fit of Ref_i, but the top models ($\Delta AIC_c < 2$) included both variables (Appendix C). Of the models including an effect of body mass, support was strongest for the model constraining the effect to be the same during all three fledging stages ($\Delta AIC_c > 2$), and support for this model was strongest in this model set (Akaike $w = 0.505$). The estimated effect was linear and positive ($\beta = 0.14$, 95% CI 0.07–0.21; Fig. 3), but this result was driven by the strong, positive effects during the dependent ($\beta = 0.21$, 95% CI 0.02–0.40) and independent ($\beta = 0.26$, 95% CI 0.01–0.51) stages, while the effect was not detectable during the transitional stage ($\beta = -0.03$, 95% CI 0.34–0.27).

Of the models including an effect of fledge date, support was strongest for the model that allowed the effect to vary by stage ($\Delta AIC_c > 2$), and support for this model was the second-strongest in this model set (Akaike $w = 0.206$; Table 1c). The effect was positive for dependent juveniles ($\beta = 0.21$, 95% CI 0.02–0.40), and negative for transitional juveniles ($\beta = -0.46$, 95% CI -0.83 – 0.09). The effect also trended negative for independent juveniles, but with confidence intervals overlapping zero ($\beta = -0.25$, 95% CI -0.58 – 0.07). Once again, despite the striking differences in the estimated effect of fledge date during each stage, if we had only estimated a single, overall effect during all three stages, the estimated effect would have been weakly negative ($\beta = -0.09$, 95% CI -0.17 to -0.02).

DISCUSSION

We hypothesized that parental care buffers the survival of dependent juveniles from variation in environmental conditions, so that the survival of independent juveniles is more sensitive to this variation and contributes more to total variation in annual juvenile survival. Our results supported this hypothesis. First, prior rainy season precipitation had a strong, positive effect on the apparent survival of independent juveniles, consistent with an influence on food availability, but had no effect on the survival of dependent juveniles (Fig. 3). Newly independent juveniles are inefficient foragers, and even small reductions in food availability may greatly increase the proportion of the day spent foraging, making them more vulnerable to both starvation and predation (Weathers and Sullivan 1989). We also cannot exclude the possibility that precipitation affected the dispersal probability of independent juveniles, thereby affecting their apparent survival rates. Nevertheless, dependent juveniles were not affected, echoing the results of the previous study

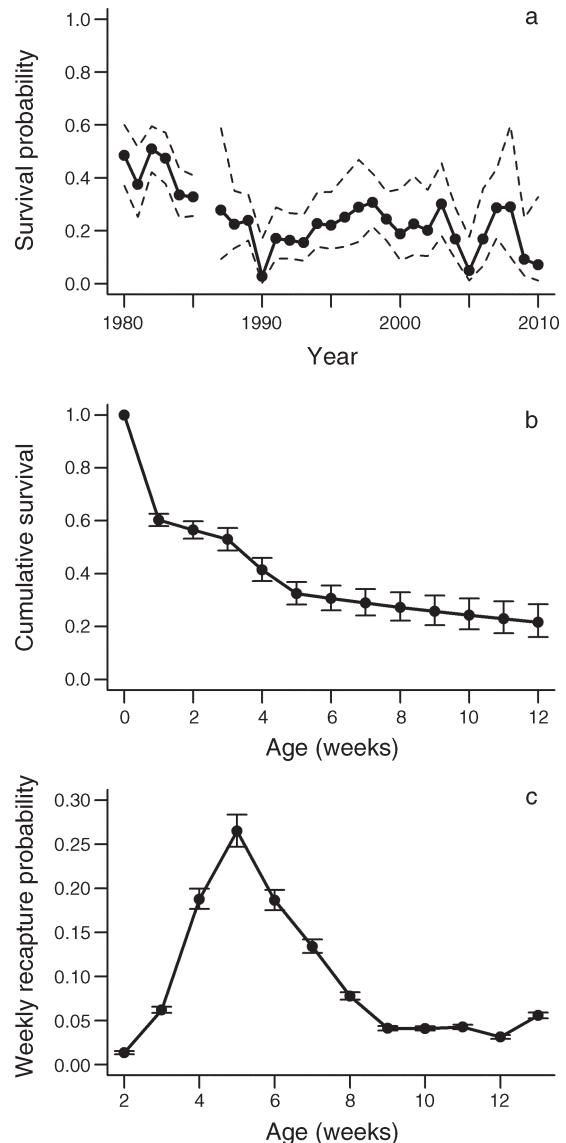


FIG. 1. Survival and recapture probabilities of juvenile Song Sparrows at Palomarin, California, USA. (a) Model-averaged annual probability of surviving the first 12 weeks after fledging. (b) Average cumulative survival by week after fledging, where age 0 is fledge day. (c) Average recapture probability by week after fledging, where week 2 is defined as the first week during which recaptures were possible. All are shown with 95% confidence intervals.

that found no effect of prior rainy season precipitation on adult survival in this population (Dyballa 2012). These results suggest that adults were able to compensate for the changes in environmental conditions following dry rainy seasons, minimizing the effects on themselves as well as on their dependent young.

Second, the effect of prior winter precipitation on the survival of independent juveniles accounted for more of the total variation in juvenile survival during the first 12 weeks after fledging than any other variable we

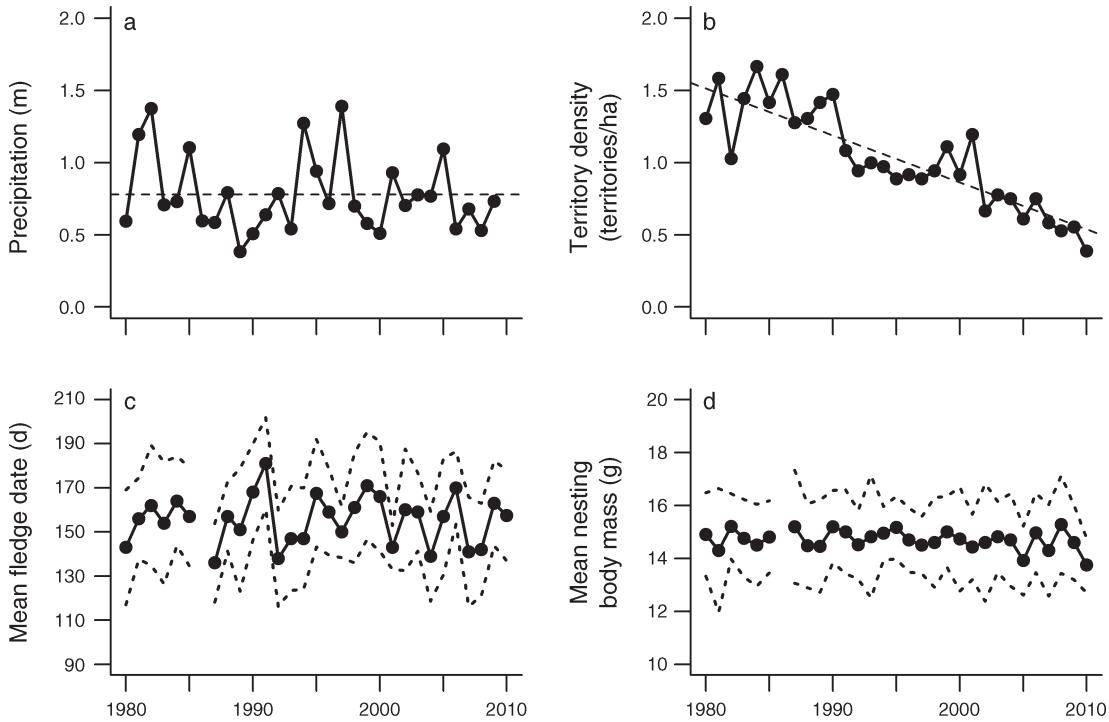


FIG. 2. Annual variation in precipitation, density, and cohort mean fledge date and nestling body mass at Palomarin, 1980–2010. (a) Total precipitation in the previous rainy season (October–March), shown with the 30-year average (dashed line). (b) Annual Song Sparrow territory density in the 36-ha study area, shown with the long-term trend line (dashed line). (c) Mean fledge date of each cohort, where 31 March = day 90. (d) Mean body mass (g) of each cohort, standardized to a 7-day-old nestling. Both panels (c) and (d) show the annual standard deviation (dashed lines).

considered (Table 1b). These results are consistent with the previous study that identified prior rainy season precipitation as a major driver of variation in overall annual juvenile survival in this population (Dybala 2012), but further clarify that it only affected the

survival of independent juveniles. Therefore, variation in apparent juvenile survival was driven by variation in the survival of independent juveniles, not dependent juveniles. There has been a recent surge in the number of studies investigating survival during the dependent,

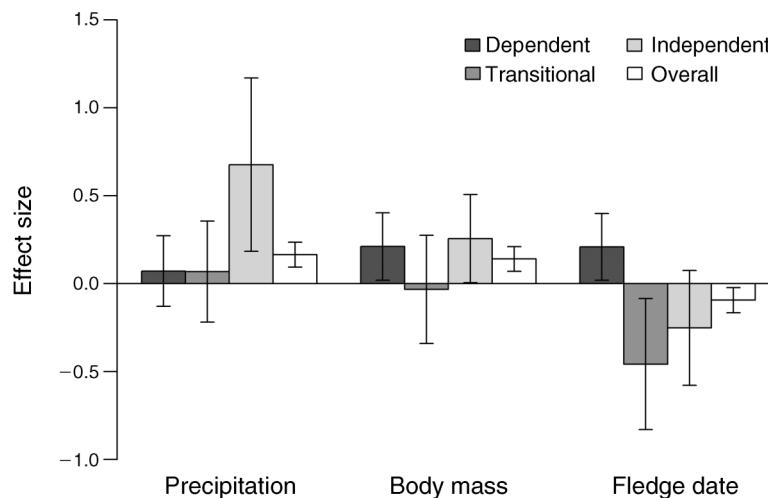


FIG. 3. Estimated effects of candidate variables on weekly survival during the dependent (weeks 1–3), transitional (weeks 4–5), and independent (weeks 6–12) stages, as well as the estimated overall effect (weeks 1–12). Effect sizes are shown on the logit scale, with 95% confidence intervals. Shown are the effects of prior rainy season precipitation on annual survival, and effects of body mass and fledge date on individual survival probabilities.

“post-fledging” stage in passerines, when mortality is highest (e.g., Adams et al. 2006, Fisher and Davis 2011, Streby and Andersen 2011). However, our results indicate a need for further study of survival and dispersal during the independent stage, and demonstrate that the primary drivers of variation in annual juvenile survival may not be detectable during the dependent stage due to the buffering effect of parental care.

Because we expected this buffering effect of parental care to reduce the overall influence of environmental variability on dependent juveniles, we did not expect strong effects of any variable on survival during this stage. In accordance with this hypothesis, there was no support for an effect of any of the annual variables on dependent juveniles. However, there was strong support for effects of fledge date and nestling body mass on individual variation in survival during the dependent stage (Fig. 3). These effects are commonly attributed to seasonal variation in food availability and the need for body fat to withstand temporary food shortages, respectively (Naef-Daenzer et al. 2001, Fisher and Davis 2011), and would seem to indicate a failure in the parental care buffer to minimize these effects. Alternatively, our results may indicate individual and seasonal variation in the quality of the parental care buffer itself. For example, rather than representing a direct effect of body fat on survival, nestling body mass may instead be regarded as an index of the quality of parental care received (Martin 1987), which has its own effects on survival probability. Similarly, rather than representing seasonal variation in food availability, an effect of fledge date may instead reflect seasonal variation in the quality or duration of parental care, such as if the dependent stage is cut short for first broods in preparation for subsequent nest attempts (Wheelwright and Templeton 2003, Gruebler and Naef-Daenzer 2008). Parent quality (in terms of age, experience, and effort) has been shown to influence juvenile growth, development, recruitment, and survival rates (Nol and Smith 1987, Saino et al. 1997, Rush and Stutchbury 2008, Proffitt et al. 2010, Lee et al. 2012). Further research in this area would help disentangle the direct and indirect relationships between parent quality, parental care, timing, food availability, and nestling body mass, and their effects on juvenile survival.

The overall declining trend in apparent juvenile survival during the first three months after fledging was independent of the effects of the four variables under consideration. Although other factors not considered here could be responsible for this decline, there was also a strong declining trend in absolute territory density (Fig. 2b), which is likely related to the long-term habitat change in the study area. We suspect that the Song Sparrow carrying capacity in the study area has declined, leading to larger territory sizes, lower territory density, and increased natal dispersal of juvenile Song Sparrows outside the study area. Because emigration is confounded with mortality in mark-recapture analyses

(Lebreton et al. 1992), increased natal dispersal would result in the observed long-term decline in their apparent survival. Variation in territory density around the long-term trend had little effect on apparent survival (Fig. 2), but relative territory density deviated from the trend by less than 0.5 territories/ha (Fig. 1), far less than the variability in the population density on Mandarte Island, where density-dependent reproductive success and recruitment in Song Sparrows has been demonstrated (Arcese et al. 1992). The Song Sparrow population density at Palomarin appears to be closely tracking the changing habitat in the study area, and not reaching densities that would strongly influence juvenile survival.

Finally, few studies of juvenile survival have examined whether the drivers of variation change as juveniles become independent (but see Portier et al. 1998, Tarwater et al. 2011), but the results of our study provide evidence that they can change, and in unexpected ways. For example, the strong, opposite effects of fledge date on the survival of dependent and transitional juveniles were unanticipated (Fig. 3), and indicated that different mechanisms were operating during each stage. A likely candidate for the difference between these stages is natal dispersal, which begins during the transitional stage (Dybala 2012), and is detectable in the steeper drop in cumulative apparent survival during weeks 4 and 5 (Fig. 1b). The negative effect of fledge date on the survival of transitional juveniles may reflect an increase in dispersal probability over the course of the breeding season, separate from the effect of fledge date on the survival of dependent juveniles (as we have discussed here), but further research would be required to identify the specific mechanisms responsible. Nevertheless, if we had not allowed the effect of fledge date to vary by stage, only the weak overall negative relationship would have been detected, obscuring both the complexity and the strength of the effect during each stage.

Through examining the contributions of different life stages to population growth rates, many studies have found that variation in juvenile survival can be a major source of the variation in population growth rates (Gaillard et al. 2000, Raithel et al. 2007, Reid et al. 2011, Jeppsson and Forslund 2012). Others have found evidence that the sensitivity of juvenile survival to environmental conditions may have contributed to population declines (Peach et al. 1999, Robinson et al. 2004), and projected differences in responses of adult and juvenile survival to climate change (Dybala 2012). By further subdividing the juvenile life stage into its distinct developmental stages, we found evidence for a buffering effect of parental care on the survival of dependent juveniles, such that the survival of independent juveniles is more sensitive to environmental conditions and contributes more to variation in juvenile survival. Therefore, we expect the survival of independent juveniles to be a major driver of population responses to environmental change, including climate

change. We recommend that future efforts to understand or project the population-level effects of environmental change not only examine the effects on juvenile survival, but specifically consider the survival of independent juveniles, as well as how the drivers of variation in juvenile survival may vary by stage.

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SUPPLEMENTAL MATERIAL

Appendix A

Model-selection results for the effects of age and year on juvenile survival ([Ecological Archives E094-143-A1](#)).

Appendix B

Model-selection results for the effects of the candidate variables on annual variation in juvenile survival ([Ecological Archives E094-143-A2](#)).

Appendix C

Model-selection results for the effects of body mass and fledge date on individual variation in juvenile survival ([Ecological Archives E094-143-A3](#)).