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RESEARCH ARTICLE

Temporal variation in the effects of individual and environmental factors on nest success

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ABSTRACT

Factors that affect the survival of nestling birds can drive the dynamics of populations and the evolution of life histories. Such factors may include a variety of intrinsic, biotic, or abiotic factors that vary in magnitude or effect over ecological time scales. Consequently, estimates of the influence of such factors on nest success may differ when estimated from short- vs. long-term studies. We tested this possibility by estimating the influence of 2 intrinsic factors (female age and inbreeding coefficient), 2 abiotic factors (rainfall and temperature), and 3 biotic factors (breeding density, parasitism rate, and brood parasitism) previously found to predict success (≥ 1 fledged young) in a 39 yr study of a Song Sparrow (*Melospiza melodia*) population on Mandarte Island, British Columbia, Canada. We then compared those estimates to others obtained from parallel models based on the the first 13 yr, middle 13 yr, and last 13 yr of the study. Over the entire study, nest success increased in females from ages 1 to 3 yr but declined thereafter. Nest success also declined as female inbreeding, rainfall during nesting, and breeding density increased. We further observed that nests parasitized by Brown-headed Cowbirds (*Molothrus ater*) or located in areas subject to high parasitism rates failed more often than unparasitized nests or those in areas with fewer parasitized nests. By contrast, the only factors identified as influencing nest success in all three 13 yr study periods examined were female age and population density, whereas the effects of inbreeding, brood parasitism, and rainfall varied temporally. Our results indicate that precise estimates of the effects of intrinsic, abiotic, and biotic drivers on nest success may require long-term studies, particularly for influential factors that occur episodically.

Keywords: demography, long-term study, *Melospiza melodia*, *Molothrus ater*, nest success

Variación temporal en los efectos de rasgos individuales y ambientales sobre el éxito de anidación

RESUMEN

Los factores que afectan la supervivencia de los polluelos pueden determinar las dinámicas de las poblaciones y la evolución de las historias de vida, pero pueden incluir una variedad de factores intrínsecos, bióticos y abióticos que varían en magnitud o efecto a lo largo de escalas de tiempo ecológicas. Consecuentemente, las estimaciones de la influencia de estos factores sobre el éxito de anidación pueden diferir cuando son estimadas a partir de estudios de corto vs. largo plazo. Evaluamos esta posibilidad mediante la estimación de la influencia de dos factores intrínsecos (edad de la hembra, coeficiente de endogamia), dos factores abióticos (precipitación, temperatura) y tres factores bióticos (densidad reproductiva, parasitismo de *Molothrus* y parasitismo de nidada) que previamente habían sido señalados como capaces de predecir el éxito (≥ 1 joven emplumado) en un estudio de 39 años de una población insular de *Melospiza melodia*. Luego comparamos esas estimaciones con otras obtenidas a partir de modelos paralelos basados en los 13 años iniciales, medios y finales del estudio. A lo largo de todo el estudio, el éxito de anidación aumentó en las hembras desde la edad de 1 a 3 años pero disminuyó a partir de allí. El éxito de anidación también disminuyó a medida que la endogamia femenina, la precipitación durante la anidación y la densidad reproductiva aumentaron. También observamos que los nidos parasitados por *Molothrus ater*, o ubicados en áreas sujetas a altas tasas de parasitismo, fallaron más a menudo que los nidos no parasitados o aquellos en áreas con menos nidos parasitados. En contraste, los únicos factores identificados como influyentes del éxito de anidación en los tres períodos de 13 años de estudio examinados fueron la edad de la hembra y la densidad poblacional, mientras que los efectos de la endogamia, el parasitismo de nidada y la precipitación variaron temporalmente. Nuestros resultados indican que las estimaciones precisas del efecto de las variables intrínsecas, bióticas y abióticas en el éxito de anidación pueden requerir estudios de largo plazo, particularmente para factores influyentes que ocurren esporádicamente.

Palabras clave: demografía, estudio de largo plazo, éxito de anidación, *Melospiza melodia*, *Molothrus ater*

INTRODUCTION

Nest success is a key factor in the dynamics and evolution of avian populations (Martin 2015). Because nest success can vary with traits of individuals, with the composition of populations, and with changes in the biotic and abiotic environment (Lebreton et al. 1992, Dinsmore et al. 2002, Arcese 2003, Germain et al. 2015), short-term studies of nest success may yield biased estimates of variable influence when population size or composition, or biotic and abiotic environmental factors, vary at temporal scales that exceed the study's duration (Wiens 1977, Franklin 1989, Norris et al. 2007, Clutton-Brock and Sheldon 2010, Martínez-Padilla et al. 2014, Blight et al. 2015). In such cases, long-term studies may be needed to reliably identify management actions most likely to influence nest success, population growth, or evolutionary response in the future (Arcese 2003,

Benton et al. 2006, Lovett et al. 2007, Clutton-Brock and Sheldon 2010). We explored these possibilities by estimating the influence of 2 intrinsic factors (female age and inbreeding coefficient), 2 abiotic factors (rainfall and temperature), and 3 biotic factors (breeding densities, parasitism rates, and brood parasitism) on nest success (≥ 1 fledgling) in a 39 yr study of an island Song Sparrow (*Melospiza melodia*) population subject to marked environmental variation (Table 1). We then compared those estimates to results from 3 parallel models based on three 13 yr periods—representing the first, middle, and last thirds of the overall study—to test for temporal change in variable influence.

Hypotheses and Predictions

Published studies of avian nest success provide a rich suite of factors hypothesized to drive success, which can be classed as intrinsic, abiotic, or biotic in origin (Table 1). We

TABLE 1. Factor classes, associated variables, usage rationale, and the expected relationships of each variable in predicting nest success in our study population of Song Sparrows on Mandarte Island, British Columbia, Canada, 1975–2014.

| Factor class | Variable | Rationale | References | Prediction |
|--------------|-------------------------------------|--|--|--|
| Intrinsic | Female age | Prior nesting experience improves reproductive performance until senescence | Nol and Smith 1987, Sæther 1990, Forslund and Pärt 1995, Smith et al. 2006c, Horie and Takagi 2012 | Nest success rates increase and then decrease with female age |
| | Inbreeding coefficient (<i>f</i>) | Inbred birds suffer higher rates of hatching failure and may be more likely to abandon nests during periods of inclement weather | Keller 1998, Marr et al. 2006 | Nest success rates decrease with increased inbreeding coefficients |
| Abiotic | Cumulative rainfall (mm) | Influences level of environmental stress through various mechanisms and correlated with nest abandonment | Wingfield et al. 1983, Wingfield 1985, Radford et al. 2001, Öberg et al. 2015 | Nest success rates decrease with high cumulative rainfall during the nest period |
| | Minimum temperature (°C) | Influences energy required for thermoregulation of nest female and eggs or nestlings and correlated with nest abandonment | Wingfield et al. 1983, Syroechkovsky et al. 2002, MacDonald et al. 2013 | Nest success rates decrease with low minimum temperatures during the nest period |
| Biotic | Local breeding density | Influences level of male parental care, food availability, and likelihood of predation/parasitism | Arcese and Smith 1988, Wingfield et al. 1990, Arcese et al. 1992, Sofaer et al. 2014 | Nest success rates decrease with increasing breeding population densities |
| | Local brood parasitism rate | Local parasitism rates influence likelihood of being parasitized and/or nest failure | Arcese et al. 1996, Hauber 2000, Smith et al. 2006c | Nest success rates decrease with increasing rates of local brood parasitism |
| | Brood parasitism | Influences host fledgling survival and can influence energy expenditure of nest parents due to increased brood costs | Woodworth 1997, Elliott 1999, Hauber 2003, Ludlow et al. 2014 | Nests parasitized by Brown-headed Cowbirds are less successful |

review some of these factors below as background to those explored here.

Intrinsic factors. The intrinsic traits of individuals arise via experience, development, and inheritance and are often used to define “individual quality” (Arcese 2003, Wilson and Nussey 2010, Germain and Arcese 2014). In Song Sparrows, intrinsic traits such as age (yr) and inbreeding (f) are known to influence various traits affecting annual and lifetime success (Keller 1998, Taylor et al. 2010, Tarwater and Arcese 2017a, 2017c). In other species, age-related increases in reproductive success are widely observed (Forslund and Pärt 1995, Decker et al. 2012, Duckworth et al. 2012, Horie and Takagi 2012) and often followed by declines indicative of senescence (Keller et al. 2008, Balbontín and Møller 2015) that may be exacerbated by environmental stress (Kristensen et al. 2005, Marr et al. 2006). We therefore expected females of “prime age” (2–3 yr old) and relatively outbred females in our study population to experience the highest nest success on average (Table 1).

Abiotic factors. Abiotic factors such as severe weather also affect reproductive success (McDonald et al. 2004, Reichert et al. 2012), often by affecting energetic costs (Wingfield et al. 1990, Reid et al. 2000, MacDonald et al. 2013). For example, high rainfall, wind, or cold temperatures can reduce nest success by reducing the ability of adults to feed themselves or nestlings (Wingfield 1985, Radford et al. 2001, Syroechkovsky et al. 2002, MacDonald et al. 2013, Öberg et al. 2015), leading to abandonment of eggs or young, or by dislodging nests (McClure 1942, Best and Stauffer 1980, Wingfield 1985, McDonald et al. 2004). We therefore expected that nest success would decline in periods of high cumulative rainfall and low minimum temperatures (Table 1).

Biotic factors. Biotic effects on reproductive success can arise via the direct or indirect effects of predation, brood parasitism, or competition (Lack 1966, Ricklefs 1969, Martin 1992). For example, predators can reduce nest success by reducing parental feeding rate (Martin 2011, Zanette et al. 2011) or consuming eggs or young (Schmidt and Ostfeld 2003, Borgmann et al. 2013). Brood parasites can reduce success by destroying host nests (Arcese et al. 1996, Elliott 1999, Hauber 2000), removing host eggs prior to laying their own (Sealy 1992, Smith and Arcese 1994), and increasing the energetic costs of brood rearing (Woodworth 1997, Hauber 2003, Hoover 2003, Ludlow et al. 2014). Previous studies in Song Sparrows had found that nest failure increased with the number of Brown-headed Cowbird eggs laid in the population annually and that parasitized nests produced ~ 0.5 fewer young than nonparasitized nests on average (Smith and Arcese 1994, Arcese et al. 1996). We therefore predicted that parasitized nests, and those in areas experiencing relatively high parasitism by

Brown-headed Cowbirds, would be less successful (Table 1).

High breeding density can also reduce reproductive performance by influencing parental care, per capita food availability, and predator or parasite activity (e.g., Ball and Wingfield 1987, Arcese and Smith 1988, Wingfield et al. 1990, Smith and Arcese 1994, McKellar et al. 2014). We therefore expected nest success to decline at high breeding densities (Table 1).

METHODS

Study System

The Song Sparrow population resident on Mandarte Island, British Columbia, Canada (6 ha; 48°38'N, 123°17'W), was monitored in detail every year from 1975 to 2014 (except 1980). Mandarte Island experiences a mild maritime climate averaging 12.5°C from March to August, and 7°C from September to February, but receives about twice as much rain in fall–winter as in spring–summer (mean = 100 mm and 40 mm, respectively; Victoria International Airport weather station; <http://climate.weather.gc.ca>). Song Sparrows in this region average 24 g in mass and are socially monogamous, open-cup nesters. Females incubate 1–5 eggs in 1–4 nests yr⁻¹, with both social parents caring for young (Arcese et al. 2002, Smith et al. 2006a).

Territories were monitored every 2–5 days after the initiation of breeding (March–April) to record ownership and breeding status. Most nests (95% of 3,274) were found during incubation, and their locations were recorded to ± 2 m resolution using maps based on air photos. All nestlings were individually marked and followed to independence from parental care (24–30 days). Immigrants were banded soon after settling on the island, and all birds after 1990 were genotyped at multiple microsatellite loci (e.g., Nietlisbach et al. 2017; for detailed methods, see Smith 2006). Population size, structure, and reproductive rate were thus precisely known.

Factor Definitions

We explored 2 intrinsic, 2 abiotic, and 3 biotic factors that potentially affected nest success (≥ 1 fledgling) from a total of 2,895 nests over a 39 yr period. Intrinsic factors included the age and f of nesting females. Female age was unknown in 1975 but was known for 97% of total nest records by 1979, and for nearly 100% of records thereafter (Appendix Figure 4). Because females may breed for ≤ 9 yr (median = 2; Table 2 and Appendix Figure 5), we included age and age² as fixed effects in models to accommodate quadratic fits between female age and performance (e.g., Tarwater and Arcese 2017a, 2017c). We didn't include male age in our analyses because males contribute to parental care only after young hatch and because prior results had

indicated small average effects of male age on reproductive rate (Keller et al. 2008, M. D. Crombie and P. Arcese personal observation).

Inbreeding (f) was estimated by merging a social (1975–1990) and genetic (1991–2014) pedigree to obtain precise estimates for >75% of birds hatched after 1993, based on the identity of all 4 social and/or genetic grandparents (Sardell et al. 2010, Reid et al. 2014). Prior to 1994, f was estimated for 0–88% of birds annually, based mainly on the social pedigree but with reduced precision due to extrapair paternity (Reid et al. 2014). Females with precise estimates of f initiated 1,819 nests (63% of 2,895 nests), mainly in the last half of the study (Appendix Figure 6). To include all females in analyses, we imputed the mean value (\pm SE) of f over the study (0.06 ± 0.001 , $n = 1,076$; Table 2) for all birds that did not have precise estimates of f . Doing so allowed us to compare factors potentially influencing success over all years without excluding the earliest years, when populations were larger and fluctuations more extreme. The consequences of imputation were explored by comparing models with and without imputed data included, but we report imputed model estimates here because those results were similar to estimates from models based only on females with precise estimates of f (see Appendix Table 4 and Appendix Figure 7).

Abiotic factors included cumulative rainfall (mm) and the minimum temperature ($^{\circ}$ C) experienced during the nesting period, defined as the 31-day window from the initiation of nesting to fledging (e.g., Arcese et al. 2002). The earliest nest was built during the last week of February, and the latest during the third week of July. Weather was recorded 11 km west of Mandarte Island (Victoria International Airport; <http://climate.weather.gc.ca>).

Biotic factors included local breeding density and brood parasitism rate in the vicinity of nests, and the parasitism of individual nests (presence–absence of one or more Brown-headed Cowbird eggs). Local density was estimated for each nest as the number of nests within a 50 m radius that were initiated by other females in the same year, irrespective of timing (an area of 7,854 m², representing 2–8 territories on average; Smith et al. 2006b; see also Germain and Arcese 2014). We estimated local parasitism similarly, but as the fraction of nests within the 50 m radius that were parasitized. Brood parasitism was recorded as presence or absence of one or more Brown-headed Cowbird eggs and treated as a binary variable to estimate direct effects of parasitism from the potential effects of parasite activity (Smith and Arcese 1994, Arcese et al. 1996). Other potential nest predators on the island include Northwestern Crows (*Corvus caurinus*), deer mice (*Mus musculus*), Glaucous-winged Gulls (*Larus glaucescens*), river otters (*Lontra canadensis*), Red-winged Blackbirds (*Agelaius phoeniceus*), and European Starlings (*Sturnus*

vulgaris). However, in the absence of Brown-headed Cowbirds, nest depredation averages <20% annually and is relatively constant (Arcese and Marr 2006).

The Julian date of the first egg laid in each nest (“lay date”) was used as a covariate in models to account for seasonal variation in nest success (e.g., Appendix Figure 8) and was known by observing clutches or by backdating nestling age. Lay date was unknown for 149 nests (5% of 2,895 nests) that were found after young fledged, found after failing, or never found but known to exist on the basis of female behavior. We estimated lay date for these 149 nests as the mean lay date of nests active in the same part of the breeding season annually, and we report the consequences of doing so in Appendix Table 4 and Appendix Figure 7. Results reported below include imputed lay dates.

Female identity (female ID) and year of study were included as random effects in models. Female ID helped account for uneven sampling across females, and year of study accounted for annual variation in models not attributed to our main factors of interest (Table 1).

Temporal Analysis

We tested for temporal variation in the influence of the above factors on nest success by running parallel models (see below) based on three 13 yr periods selected sequentially from the 39 yr dataset, representing the early (1975–1988), middle (1989–2001), and late (2002–2014) study periods. However, because these periods may also have differed systematically with respect to the factors of interest, we explore those potential differences in Appendix Table 5.

Statistical Analysis

All analyses were performed in R 3.0.2 (R Development Core Team 2013). We estimated the influence of 7 factors of interest on nest success (Table 1) using records from 39 yr and 2,895 nests, and generalized linear mixed models (R package lme4 v1.1–7; Bates et al. 2015) with a logit link and binomial error distribution to estimate the probability of success (success = 1, failure = 0). Logistic regression was a suitable statistical method in the present study because >95% of nests were found during incubation and their outcomes were known. Thus, we didn’t incorporate bias from not including nests with unknown outcomes. All models were run with and without nests including imputed values for f and lay date, but only those including imputed data are reported here because imputation improved model estimates but had little influence on their magnitude (see Appendix Table 4 and Appendix Figure 7).

To estimate factor influence, we first ran univariate models of each intrinsic, abiotic, and biotic factor of interest to estimate its effect on nest success (7 models). We then modeled all possible combinations of factors,

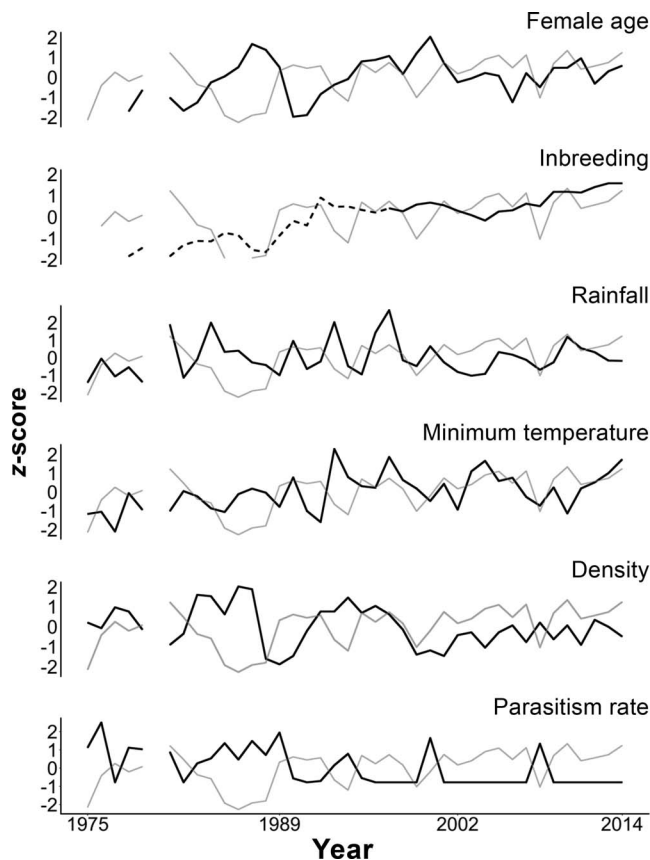


FIGURE 1. Temporal variation in nest success (gray lines) and 6 potential drivers of success (solid black lines) on Mandarte Island, British Columbia, Canada, 1975–2014. The black dashed line represents inbreeding (f) estimates largely based on social pedigree, which reduces the precision of those estimates via extrapair paternity (~27% of young; Reid et al. 2014); the precision of f increased through time as genetic data were accumulated and lineages refined. Detailed monitoring did not occur in 1980.

excluding interactions, to identify models that best explained success from the entire set of candidate models using Akaike's Information Criterion ($\Delta AIC < 2$ from the top model; Burnham and Anderson 2002). Female age and age² were always modeled together, and all models included female ID and year as random effects, with lay date as a covariate ($n = 128$ candidate models). Exploratory analyses indicated that including lay date² neither reduced model deviance nor improved the precision of model estimates, and it was therefore not included in the results presented here. Variance inflation factors (VIFs) were calculated for each factor in the global model (including all 7 factors) using the “corvif” function provided in Zuur et al. (2010: appendix S1). Most factors were not strongly correlated (VIFs < 2.5), except for minimum temperature with lay date (VIFs ~ 5) and female age with age² (VIFs ~ 12.5). Continuous variables were standardized to mean = 0 and SD = 0.5 following Gelman (2008) to allow the direct comparison of model coefficients, including untransformed binary predictors (e.g., brood parasitism; for applications of this scaling approach, see Schielzeth 2010, Grueber et al. 2011). Candidate models were averaged, and variables were considered influential if model coefficients ($\beta \pm 95\%$ confidence intervals (CI) did not overlap zero (hereafter “averaged model”).

To test whether variables comprising the averaged model varied over time, we repeated the steps above for the first 13 yr, middle 13 yr, and last 13 yr of the study. We then compared the magnitude of each factor in each period and over the entire 39 yr study to evaluate the consistency with which each factor influenced nest success.

RESULTS

Of 2,895 nest attempts examined, 64% were successful (Appendix Figure 9). Annual variation in the 7 factors hypothesized to affect nest success was substantial (Figure 1 and Table 2). Female age and f varied from 1 yr to 9 yr

TABLE 2. Range, median, and first and third quartiles ($Q_1:Q_3$) of the intrinsic, abiotic, and biotic variables used to predict nest success in our study population of Song Sparrows on Mandarte Island, British Columbia, Canada, 1975–2014. Annual rates of brood parasitism are reported here to show variation in the likelihood of parasitism but are modeled as a binary variable associated with each nest (see text).

| Factor | Unit | Range | Median | $Q_1:Q_3$ |
|--------------------------------|-------------------------------|--------------|--------|-----------|
| Female age | yr | 1 to 9 | 2.00 | 1:3 |
| Inbreeding coefficient | – | 0 to 0.28 | 0.05 | 0.01:0.09 |
| Imputed inbreeding coefficient | – | 0 to 0.28 | 0.06 | 0.04:0.06 |
| Cumulative rainfall | mm | 0 to 128 | 31.4 | 20.2:49.6 |
| Minimum temperature | °C | –3.2 to 10.2 | 2.7 | 0.4:5.7 |
| Local parasitism rate | Parasitized nests/50 m buffer | 0 to 12 | 0 | 0:3 |
| Local breeding density | Nests/50 m buffer | 0 to 46 | 12 | 7:17 |
| Brood parasitism rate | Annual proportion | 0 to 0.44 | 0 | 0:0.22 |
| Lay date | Julian day | 57 to 202 | 131 | 109:151 |
| Imputed lay date | Julian day | 57 to 202 | 132 | 110:151 |

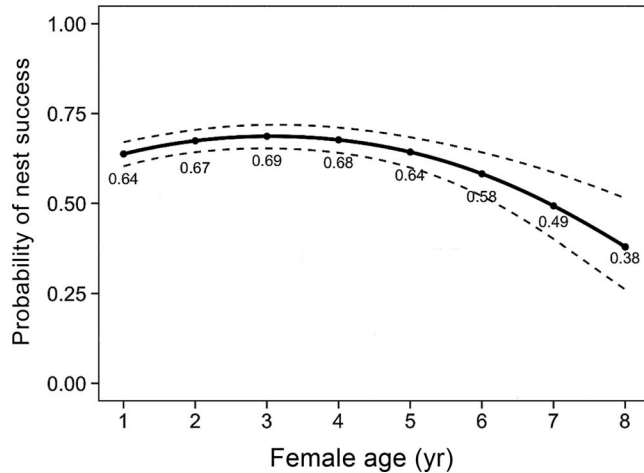


FIGURE 2. Probability of nest success in relation to the age of female Song Sparrows (solid line; dashed lines indicate 95% confidence intervals) on Mandarte Island, British Columbia, Canada, 1975–2014. Values are logit back-transformed partial effects of female age and female age² from the averaged model to predict nest success over the 39 yr of the study, while keeping all other intrinsic, abiotic, and biotic factors at their mean.

(coefficient of variation [CV] = 0.62) and from 0 yr to 0.28 yr (CV = 0.91), respectively (Table 2). Cumulative rainfall and minimum temperature during nesting varied from 0 mm to 128 mm (CV = 0.59) and from -3.2°C to 10.2°C (CV = 0.91), respectively (Table 2). Local density, local parasitism, and the annual proportion of nests parasitized varied from zero nests to 46 nests (CV = 0.60), from zero nests to 12 nests (CV = 1.37), and from 0% to 44% (CV = 2.78) across years, respectively (Table 2).

Five of 7 hypotheses in Table 1 were supported in univariate tests of the 7 factors of interest. Nest success initially increased with female age ($\beta = 0.76$, 95% CI: 0.11–1.41, $n = 2,706$), then declined later in life (female age²; $\beta = -0.82$, 95% CI: -1.48 to -0.17 , $n = 2,706$), revealing a quadratic relationship between nest success and female age overall (Figure 2). In addition, nests initiated by more inbred females ($\beta = -0.23$, 95% CI: -0.43 to -0.03 , $n = 2,895$) and those exposed to more rainfall ($\beta = -0.37$, 95% CI: -0.60 to -0.13 , $n = 2,895$), high local breeding density ($\beta = -0.55$, 95% CI: -0.83 to -0.27 , $n = 2,818$), and high local parasitism rates ($\beta = -0.57$, 95% CI: -0.90 to -0.25 , $n = 2,812$) were also less likely to succeed. By contrast, neither the minimum temperature during nesting nor an act of brood parasitism predicted nest success in single-factor models ($\beta = 0.25$, 95% CI: -0.20 to 0.69 , $n = 2,895$ and $\beta = -0.08$, 95% CI: -0.36 to 0.21 , $n = 2,893$, respectively).

Of 128 possible models, 4 were within $\Delta\text{AIC} < 2$ of the best model (hereafter “top-ranked models”; Table 3). The average of these top-ranked models included all 7 factors of interest, with a cumulative Akaike weight of 0.40

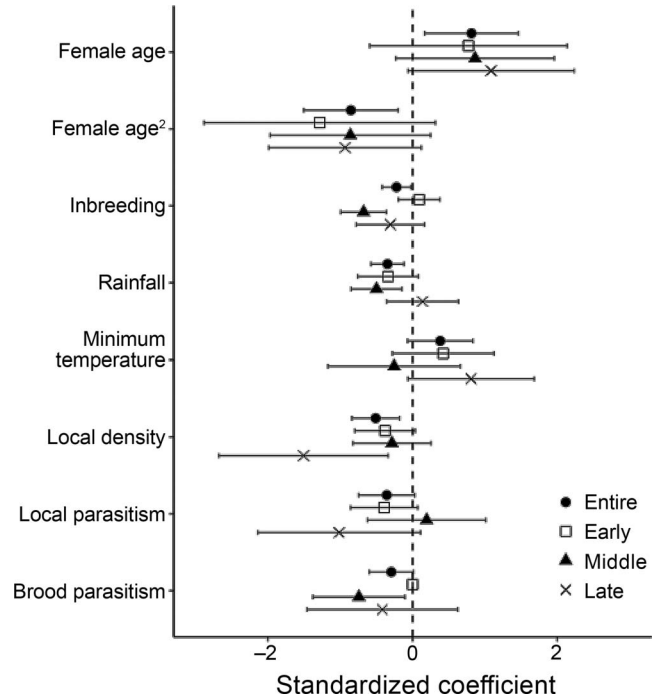


FIGURE 3. Standardized coefficients (with 95% confidence intervals) of the averaged models to predict nest success from the entire (1975–2014), early (1975–1988), middle (1989–2001), and late (2002–2014) study periods on Mandarte Island, British Columbia, Canada (see Appendix Table 6).

(hereafter “averaged model”; Table 3). In the averaged model ($n = 2,639$), brood parasitism tended to be a negative predictor of success (95% CI: -0.6 to 0.01 ; Table 3), whereas local parasitism became less influential on success (95% CI: -0.74 to 0.03 ; Table 3) compared to univariate models. Overall, based on the averaged model coefficients, nests were less likely to succeed when initiated by inbred females (95% CI: -0.42 to -0.03 ; Table 3), when subjected to high rainfall during the nesting period (95% CI: -0.57 to -0.12 ; Table 3), in years with high breeding densities (95% CI: -0.84 to -0.18 ; Table 3), and if they were parasitized by Brown-headed Cowbirds (95% CI: -0.6 to 0.01 ; Table 3). As in our univariate tests, nest success first increased (95% CI: 0.17 – 1.46 ; Table 3) then declined with female age (95% CI: -1.5 to -0.2 ; Table 3).

By contrast, none of the 7 factors we tested predicted nest success in all three 13 yr periods (Figure 3 and Appendix Table 6). Female age and female age² were included only in models based on the entire 39 yr study, but the direction and magnitude of their estimated effects on nest success were consistent across periods (Figure 3 and Appendix Table 6). Local density behaved similarly, predicting reduced nest success over the entire study but varying in magnitude across periods (Figure 3 and Appendix Table 6). By contrast, despite detecting negative effects of inbreeding, rainfall, and parasitism on nest

TABLE 3. Parameter estimates for factors identified as predictors of nest success in top-ranked models for our Song Sparrow dataset from Mandarte Island, British Columbia, Canada, 1975–2014.

| Model rank | Female age | Female age ² | Inbreeding | Rainfall | Minimum temperature | Local density | Local parasitism | Brood parasitism | Akaike weight (w_i) |
|----------------|------------|-------------------------|------------|----------|---------------------|---------------|------------------|------------------|-------------------------|
| 1 | 0.81 | −0.85 | −0.22 | −0.34 | 0.38 | −0.48 | −0.35 | −0.30 | 0.15 |
| 2 | 0.82 | −0.85 | −0.22 | −0.33 | – | −0.47 | −0.37 | −0.29 | 0.11 |
| 3 | 0.82 | −0.86 | −0.22 | −0.36 | 0.40 | −0.62 | – | −0.28 | 0.09 |
| 4 | 0.80 | −0.84 | −0.22 | −0.36 | 0.37 | −0.48 | −0.33 | – | 0.06 |
| | | | | | | | | | Cumulative w_i |
| Averaged model | 0.81 | −0.85 | −0.22 | −0.35 | 0.38 | −0.51 | −0.35 | −0.29 | 0.40 |
| SE | 0.33 | 0.33 | 0.10 | 0.12 | 0.23 | 0.17 | 0.20 | 0.16 | |

Notes: Top-ranked models ($\Delta AIC < 2$) are a subset of 128 possible models. Averaged model parameter estimates are calculated using Akaike weights (w_i ; see Burnham and Anderson 2002).

success over the entire study, we found these effects to be highly variable in magnitude and direction across periods (Figure 3).

DISCUSSION

We found strong support for the influence of 7 intrinsic, abiotic, and biotic factors previously found to affect nest success in birds in a 39 yr study of a single Song Sparrow population, but we also found that the magnitude and significance of those effects varied temporally (Table 1 and Figure 3). Such variation might arise because the factors we considered are linked to other latent variables not included in our models, or because reducing sample size (from 39 yr to 13 yr) also reduced the precision of estimates based on small or inconsistent effects. Below, we first explore potential causes of temporal variation in our estimates and then discuss their implications.

Nest success was similar in 1-yr-old and 5-yr-old female Song Sparrows, 5–8% higher in 3-yr-olds, but 9–38% lower in females ≥ 6 yr old (Figure 2). This pattern mirrors age-related changes in annual reproductive success reported from this population (Keller et al. 2008, Tarwater and Arcese 2017a, 2017c), indicating that variation in nest success contributes to that pattern. Age-related variation in reproductive success is widely reported in birds (Sæther 1990, Forslund and Pärt 1995, Martin 1995) and is typically attributed to initial increases in food acquisition and predator avoidance skills, followed by senescence in one or more traits (e.g., Desrochers and Magrath 1993, Robertson and Rendell 2001, Smith et al. 2006a, Keller et al. 2008). However, age-related variation in reproductive effort, performance, and survival also reflects individual life history (Reznick et al. 2000, Roach and Carey 2014). Thus, variation in nest success may also reflect a female's allocation of resources to her own survival vs. reproduction in the current year, which trade off strongly in the Mandarte Song Sparrow population (Tarwater and Arcese 2017a, 2017c). The fact that female age was retained in

models based on the first, middle, and last 13 yr of the study (Table 1 and Figure 3), despite an expected increase in associated prediction intervals (Figure 3 and Appendix Table 6), indicates that age-related variation in nest success is a persistent feature of this population. By contrast, because few females reach senescent age classes in species with high average mortality (Nussey et al. 2008), the age-related declines in success that we documented will have very limited effects on demography overall (Brommer et al. 2007, Roach and Carey 2014).

Nest success also declined as inbreeding (f) increased in female Song Sparrows (Tables 1 and Figure 3), supporting Keller's (1998) finding that hatch success and nestling survival were lower in the nests of inbred females, and Taylor et al.'s (2010) finding that the survival of Song Sparrow embryos declined as homozygosity and f increased. However, the estimated effect of f on nest success was modest, being 16% lower in the most inbred vs. outbred females ($f = 0.28$ vs. 0.00, respectively; Table 2). In addition, f was retained as a predictor of success in only the middle third of our study, which coincided with a rapid increase in mean f (Figures 1 and 3). Temporal variation in the magnitude of inbreeding depression is expected, given interactions with episodic stressors such as extreme weather events (Table 1), and the potentially large effects are unlikely to be detected in short-term studies (Keller et al. 1994, Coltman et al. 1999, Meagher et al. 2000, Kristensen et al. 2005).

Nest success declined as rainfall increased during the nesting period over the entire study (Figure 3 and Table 1), but those effects varied temporally (Figure 3 and Appendix Table 6). Rainfall is a well-known stressor during nesting and a proximate cause of nest failure, with the potential for tonic and interactive effects (Ricklefs 1969, Frederick and Collopy 1989, Aguilar et al. 2000, McDonald et al. 2004, Sillett et al. 2004, Ouyang et al. 2012). In Great Tits (*Parsus major*), stress-induced increases in plasma corticosterone preceded nest failure and occurred more often during inclement weather (Ouyang et al. 2012). In Black-throated

Blue Warblers (*Setophaga caerulescens*), reproductive success declined as breeding density increased, but more so in years with high rainfall (Sillett et al. 2004). The existence of such interactions and the irregularity of weather and climatic extremes emphasize the value of long-term studies, especially when combined in meta-analyses (Sæther and Bakke 2000, Sæther and Engen 2002). In contrast to rainfall, temperature during nesting was unrelated to nest success (Figure 3), despite the fact that temperature can affect the energetic costs of breeding (Bryan and Bryant 1999, Pérez et al. 2008, Ardia et al. 2009) and nest-site preference (Germain et al. 2015). Interestingly, Song Sparrows in coastal California produced more broods and more young in years with higher cumulative rainfall (Chase et al. 2005). Tarwater and Arcese (2017b) also reported that higher rainfall in late winter and summer led to longer breeding seasons on average. Future studies might therefore consider both cumulative and episodic rainfall, given that higher rainfall is expected to increase reproductive output but may also reduce nest success.

Nest success also declined as population density increased (Table 1 and Figure 3), with a similar effect in all periods examined, but with prediction intervals that included zero in the last 13-year period, when sample size was least ($n = 778$; Figure 3 and Appendix Table 6). Two potential mechanisms for this decline are (1) that Brown-headed Cowbirds visit the island more often and depredate more nests at higher host densities or (2) that high population density reduces nest success by increasing intraspecific strife or by reducing per capita food abundance (Table 1). Using 16 yr of data in which Brown-headed Cowbirds were present on Mandarte Island and 23 yr when they were absent, we found that nest success declined significantly with increasing density in years with Brown-headed Cowbirds present ($\beta = -0.46$, 95% CI: -0.77 to -0.14) but not in years when they were absent ($\beta = -0.40$, 95% CI: -0.91 to 0.11). This result confirms that Brown-headed Cowbirds have the potential to regulate host population growth at population and regional scales (Arcese et al. 1996, Jewell and Arcese 2008). The rate of brood parasitism near a focal nest also reduced its success, as did being parasitized (Figure 3). But these effects varied across periods because Brown-headed Cowbirds were absent in many years and rare later in our study, when Song Sparrow density was also low on average (Figure 1).

We detected the effects of several factors hypothesized previously to influence nest success in birds but found that their occurrence and magnitude varied greatly over 4 decades. In Song Sparrows, age-related variation in nest success and the negative effects of high breeding density were consistent predictors of success, whereas those linked to inbreeding, Brown-headed Cowbirds, and weather were

episodic but sometimes large. These findings reemphasize the value of long-term studies, given that rare events can have large but uncertain effects on populations (Ludwig 1999) and may also interact with population structure and the biotic or abiotic environment to influence abundance and distribution (Wiens 1987, Franklin 1989, Norris et al. 2007, Clutton-Brock and Sheldon 2010, Martínez-Padilla et al. 2014, Blight et al. 2015). Meta-analyses of other long-term studies, especially those aimed at identifying factors with large and persistent effects on populations (e.g., Sæther and Engen 2002, Sutherland et al. 2017), could help managers prioritize actions and anticipate temporal variation in success as a consequence of co-occurring trends in climate, population structure, or community composition.

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REFERENCES

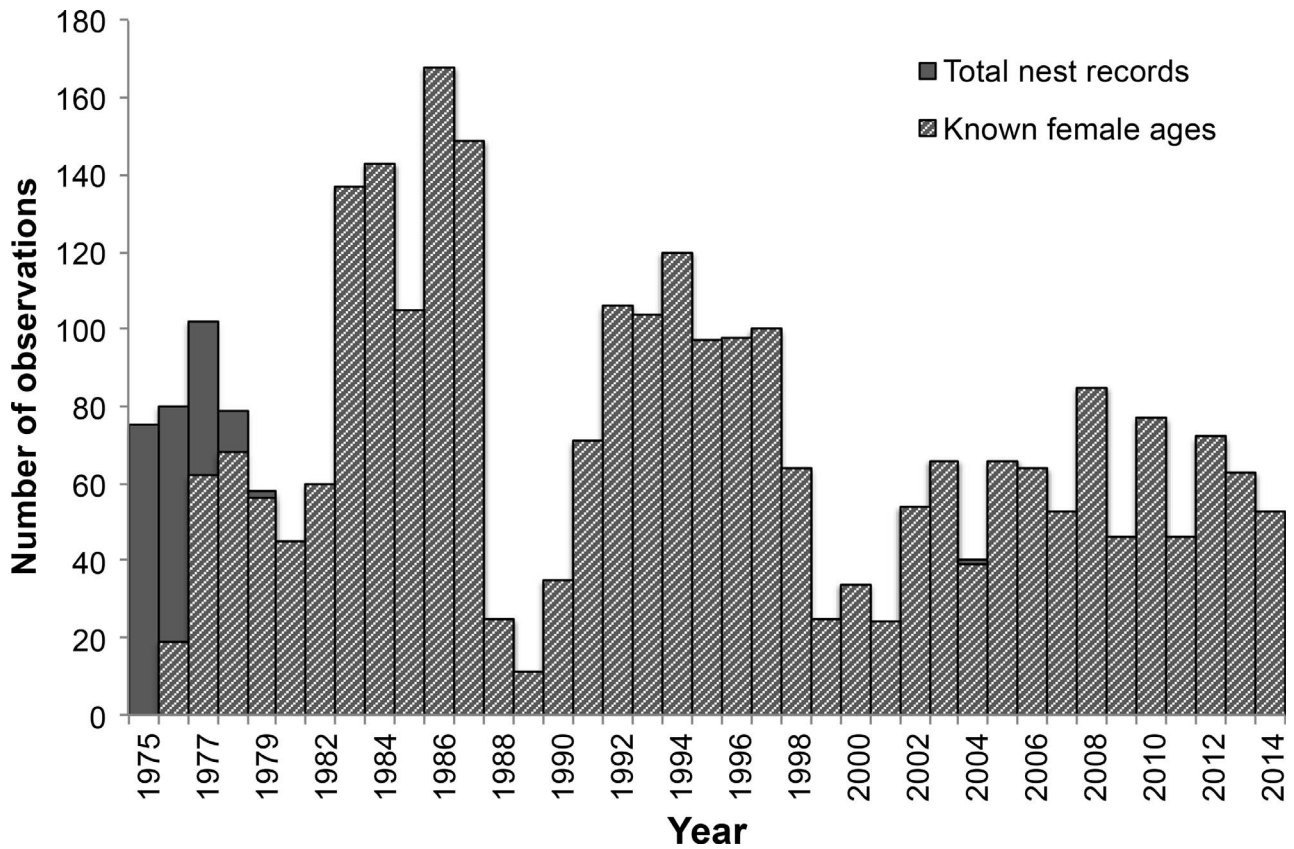
- Aguilar, T. M., M. Maldonado-Coelho, and M. Â. Marini (2000). Nesting biology of the Gray-Hooded Flycatcher (*Mionectes rufiventris*). *Ornitologia Neotropical* 11:223–230.
- Arcese, P. (2003). Individual quality, environment, and conservation. In *Animal Behavior and Wildlife Conservation* (M. Festa-Bianchet and M. Apollonio, Editors). Island Press, Washington, DC, USA. pp. 271–296.
- Arcese, P., and A. Marr (2006). Population viability in the presence and absence of cowbirds, catastrophic mortality, and immigration. In *Conservation and Biology of Small Populations: The Song Sparrows of Mandarte Island* (J. N. M. Smith, L. F. Keller, A. B. Marr, and P. Arcese, Editors). Oxford University Press, New York, NY, USA. pp. 175–192.
- Arcese, P., and J. N. M. Smith (1988). Effects of population density and supplemental food on reproduction in Song Sparrows. *Journal of Animal Ecology* 57:119–136.
- Arcese, P., J. N. M. Smith, and M. I. Hatch (1996). Nest predation by cowbirds and its consequences for passerine demography. *Proceedings of the National Academy of Sciences USA* 93:4608–4611.

- Arcese, P., J. N. M. Smith, W. M. Hochachka, C. M. Rogers, and D. Ludwig (1992). Stability, regulation, and the determination of abundance in an insular Song Sparrow population. *Ecology* 73:805–822.
- Arcese, P., M. K. Sogge, A. B. Marr, and M. A. Patten (2002). Song Sparrow (*Melospiza melodia*). In *Birds of North America Online* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.
- Ardia, D. R., J. H. Pérez, E. K. Chad, M. A. Voss, and E. D. Clotfelter (2009). Temperature and life history: Experimental heating leads female Tree Swallows to modulate egg temperature and incubation behaviour. *Journal of Animal Ecology* 78:4–13.
- Balbontín, J., and A. P. Møller (2015). Environmental conditions during early life accelerate the rate of senescence in a short-lived passerine bird. *Ecology* 96:948–959.
- Ball, G. F., and J. C. Wingfield (1987). Changes in plasma levels of luteinizing hormone and sex steroid hormones in relation to multiple-broodedness and nest-site density in male starlings. *Physiological and Biochemical Zoology* 60:191–199.
- Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Stat. Softw.* 67:1–48.
- Benton, T. G., S. J. Plaistow, and T. N. Coulson (2006). Complex population dynamics and complex causation: Devils, details and demography. *Proceedings of the Royal Society B* 273: 1173–1181.
- Best, L. B., and F. Stauffer (1980). Factors affecting nesting success in riparian bird communities. *The Condor* 82:149–158.
- Blight, L. K., K. A. Hobson, T. K. Kyser, and P. Arcese (2015). Changing gull diet in a changing world: A 150-year stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) record from feathers collected in the Pacific Northwest of North America. *Global Change Biology* 21:1497–1507.
- Borgmann, K. L., C. J. Conway, and M. L. Morrison (2013). Breeding phenology of birds: Mechanisms underlying seasonal declines in the risk of nest predation. *PLOS One* 8: e65909.
- Brommer, J. E., A. J. Wilson, and L. Gustafsson (2007). Exploring the genetics of aging in a wild passerine bird. *The American Naturalist* 170:643–650.
- Bryan, S. M., and D. M. Bryant (1999). Heating nest-boxes reveals an energetic constraint on incubation behaviour in Great Tits, *Parus major*. *Proceedings of the Royal Society of London, Series B* 266:157.
- Burnham, K. P., and D. R. Anderson (2002). *Model Selection and Multimodel Inference: An Information-Theoretic Approach*, second edition. Springer, New York, NY, USA.
- Chase, M. K., N. Nur, and G. R. Geupel (2005). Effects of weather and population density on reproductive success and population dynamics in a Song Sparrow (*Melospiza melodia*) population: A long-term study. *The Auk* 122:571–592.
- Clutton-Brock, T., and B. C. Sheldon (2010). Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* 25:562–573.
- Coltman, D. W., J. G. Pilkington, J. A. Smith, and J. M. Pemberton (1999). Parasite-mediated selection against inbred soay sheep in a free-living, island population. *Evolution* 53:1259–1267.
- Decker, K. L., C. J. Conway, and J. J. Fontaine (2012). Nest predation, food, and female age explain seasonal declines in clutch size. *Evolutionary Ecology* 26:683–699.
- Desrochers, A., and R. D. Magrath (1993). Age-specific fecundity in European Blackbirds (*Turdus merula*): Individual and population trends. *The Auk* 110:255–263.
- Dinsmore, S. J., G. C. White, and F. L. Knopf (2002). Advanced techniques for modeling avian nest survival. *Ecology* 83: 3476–3488.
- Duckworth, G. D., R. Altwegg, and D. M. Harebottle (2012). Demography and population ecology of the Hadedda Ibis (*Bostrychia hagedash*) at its expanding range edge in South Africa. *Journal of Ornithology* 153:421–430.
- Elliott, P. F. (1999). Killing of host nestlings by the Brown-headed Cowbird. *Journal of Field Ornithology* 70:55–57.
- Forslund, P., and T. Pärt (1995). Age and reproduction in birds—hypotheses and tests. *Trends in Ecology & Evolution* 10:374–378.
- Franklin, J. F. (1989). Importance and justification of long-term studies in ecology. In *Long-Term Studies in Ecology* (G. E. Likens, Editor). Springer, New York, NY, USA. pp. 3–19.
- Frederick, P. C., and M. W. Collopy (1989). Nesting success of five ciconiiform species in relation to water conditions in the Florida Everglades. *The Auk* 106:625–634.
- Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine* 27:2865–2873.
- Germain, R. R., and P. Arcese (2014). Distinguishing individual quality from habitat preference and quality in a territorial passerine. *Ecology* 95:436–445.
- Germain, R. R., R. Schuster, K. E. Delmore, and P. Arcese (2015). Habitat preference facilitates successful early breeding in an open-cup nesting songbird. *Functional Ecology* 29:1522–1532.
- Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology* 24:699–711.
- Hauber, M. E. (2000). Nest predation and cowbird parasitism in Song Sparrows. *Journal of Field Ornithology* 71:389–398.
- Hauber, M. E. (2003). Hatching asynchrony, nestling competition, and the cost of interspecific brood parasitism. *Behavioral Ecology* 14:227–235.
- Hoover, J. P. (2003). Multiple effects of brood parasitism reduce the reproductive success of Prothonotary Warblers, *Protonotaria citrea*. *Animal Behaviour* 65:923–934.
- Horie, S., and M. Takagi (2012). Nest positioning by male Daito White-eyes *Zosterops japonicus daitoensis* improves with age to reduce nest predation risk. *Ibis* 154:285–295.
- Jewell, K. J., and P. Arcese (2008). Consequences of parasite invasion and land use on the spatial dynamics of host populations. *Journal of Applied Ecology* 45:1180–1188.
- Keller, L. F. (1998). Inbreeding and its fitness effects in an insular population of Song Sparrows (*Melospiza melodia*). *Evolution* 52:240–250.
- Keller, L. F., P. Arcese, J. N. M. Smith, W. M. Hochachka, and S. C. Stearns (1994). Selection against inbred Song Sparrows during a natural population bottleneck. *Nature* 372:356–357.
- Keller, L. F., J. M. Reid, and P. Arcese (2008). Testing evolutionary models of senescence in a natural population: Age and inbreeding effects on fitness components in Song Sparrows. *Proceedings of the Royal Society B* 275:597–604.

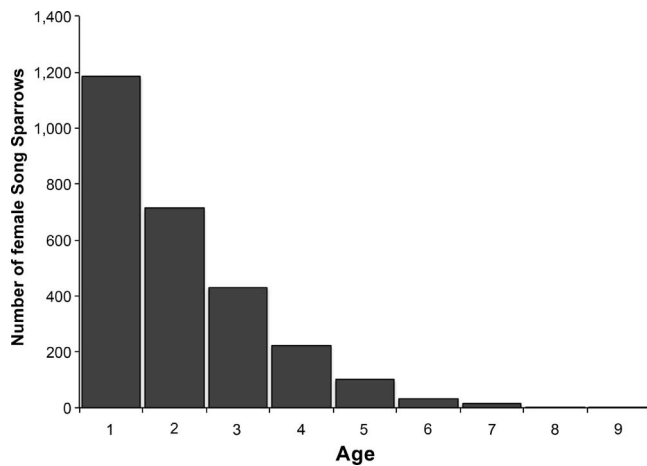
- Kristensen, T. N., P. Sørensen, M. Kruhøffer, K. S. Pedersen, and V. Loeschcke (2005). Genome-wide analysis on inbreeding effects on gene expression in *Drosophila melanogaster*. *Genetics* 171:157–167.
- Lack, D. (1966). *Population Studies of Birds*. Oxford University Press, New York, NY, USA.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lovett, G. M., D. A. Burns, C. T. Driscoll, J. C. Jenkins, M. J. Mitchell, L. Rustad, J. B. Shanley, G. E. Likens, and R. Haeuber (2007). Who needs environmental monitoring? *Frontiers in Ecology and the Environment* 5:253–260.
- Ludlow, S. M., R. M. Brigham, and S. K. Davis (2014). Nesting ecology of grassland songbirds: Effects of predation, parasitism, and weather. *The Wilson Journal of Ornithology* 126:686–699.
- Ludwig, D. (1999). Is it meaningful to estimate a probability of extinction? *Ecology* 80:298–310.
- MacDonald, E. C., A. F. Camfield, J. E. Jankowski, and K. Martin (2013). Extended incubation recesses by alpine-breeding Horned Larks: A strategy for dealing with inclement weather? *Journal of Field Ornithology* 84:58–68.
- Marr, A. B., P. Arcese, W. M. Hochachka, J. M. Reid, and L. F. Keller (2006). Interactive effects of environmental stress and inbreeding on reproductive traits in a wild bird population. *Journal of Animal Ecology* 75:1406–1415.
- Martin, K. (1995). Patterns and mechanisms for age-dependent reproduction and survival in birds. *American Zoologist* 35: 340–348.
- Martin, T. E. (1992). Interaction of nest predation and food limitation in reproductive strategies. *Current Ornithology* 9: 163–197.
- Martin, T. E. (2011). The cost of fear. *Science* 334:1353–1354.
- Martin, T. E. (2015). Age-related mortality explains life history strategies of tropical and temperate songbirds. *Science* 349: 966–970.
- Martínez-Padilla, J., S. M. Redpath, M. Zeineddine, and F. Mougeot (2014). Insights into population ecology from long-term studies of red grouse *Lagopus lagopus scoticus*. *Journal of Animal Ecology* 83:85–98.
- McClure, H. E. (1942). Mourning dove production in southwestern Iowa. *The Auk* 59:64–75.
- McDonald, P. G., P. D. Olsen, and A. Cockburn (2004). Weather dictates reproductive success and survival in the Australian Brown Falcon *Falco berigora*. *Journal of Animal Ecology* 73: 683–692.
- McKellar, A. E., P. P. Marra, P. T. Boag, and L. M. Ratcliffe (2014). Form, function and consequences of density dependence in a long-distance migratory bird. *Oikos* 123:356–364.
- Meagher, S., D. J. Penn, and W. K. Potts (2000). Male–male competition magnifies inbreeding depression in wild house mice. *Proceedings of the National Academy of Sciences USA* 97:3324–3329.
- Nietlisbach, P., L. F. Keller, G. Camenisch, F. Guillaume, P. Arcese, J. M. Reid, and E. Postma (2017). Pedigree-based inbreeding coefficient explains more variation in fitness than heterozygosity at 160 microsatellites in a wild bird population. *Proceedings of the Royal Society B* 284:20162763.
- Nol, E., and J. N. M. Smith (1987). Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. *Journal of Animal Ecology* 56:301–313.
- Norris, D. R., P. Arcese, D. Preikshot, D. F. Bertram, and T. K. Kyser (2007). Diet reconstruction and historic population dynamics in a threatened seabird. *Journal of Applied Ecology* 44:875–884.
- Nussey, D. H., T. Coulson, M. Festa-Bianchet, and J.-M. Gaillard (2008). Measuring senescence in wild animal populations: Towards a longitudinal approach. *Functional Ecology* 22:393–406.
- Öberg, M., D. Arlt, T. Pärt, A. T. Laugen, S. Eggers, and M. Low (2015). Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. *Ecology and Evolution* 5:345–356.
- Ouyang, J. Q., M. Quetting, and M. Hau (2012). Corticosterone and brood abandonment in a passerine bird. *Animal Behaviour* 84:261–268.
- Pérez, J. H., D. R. Ardia, E. K. Chad, and E. D. Clotfelter (2008). Experimental heating reveals nest temperature affects nestling condition in Tree Swallows (*Tachycineta bicolor*). *Biology Letters* 4:468–471.
- Radford, A. N., R. H. McCleery, R. J. W. Woodburn, and M. D. Morecroft (2001). Activity patterns of parent Great Tits *Parus major* feeding their young during rainfall. *Bird Study* 48:214–220.
- R Development Core Team (2013). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reichert, B. E., C. E. Cattau, R. J. Fletcher, Jr., W. L. Kendall, and W. M. Kitchens (2012). Extreme weather and experience influence reproduction in an endangered bird. *Ecology* 93: 2580–2589.
- Reid, J. M., L. F. Keller, A. B. Marr, P. Nietlisbach, R. J. Sardell, and P. Arcese (2014). Pedigree error due to extra-pair reproduction substantially biases estimates of inbreeding depression. *Evolution* 68:802–815.
- Reid, J. M., P. Monaghan, and G. D. Ruxton (2000). Resource allocation between reproductive phases: The importance of thermal conditions in determining the cost of incubation. *Proceedings of the Royal Society of London, Series B* 267:37–41.
- Reznick, D., L. Nunney, and A. Tessier (2000). Big houses, big cars, superfleas and the costs of reproduction. *Trends in Ecology & Evolution* 15:421–425.
- Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9.
- Roach, D. A., and J. R. Carey (2014). Population biology of aging in the wild. *Annual Review of Ecology, Evolution, and Systematics* 45:421–443.
- Robertson, R. J., and W. B. Rendell (2001). A long-term study of reproductive performance in Tree Swallows: The influence of age and senescence on output. *Journal of Animal Ecology* 70: 1014–1031.
- Sæther, B.-E. (1990). Age-specific variation in reproductive performance of birds. *Current Ornithology* 7:251–283.
- Sæther, B.-E., and Ø. Bakke (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653.

- Sæther, B.-E., and S. Engen (2002). Pattern of variation in avian population growth rates. *Philosophical Transactions of the Royal Society of London, Series B* 357:1185–1195.
- Sardell, R. J., L. F. Keller, P. Arcese, T. Bucher, and J. M. Reid (2010). Comprehensive paternity assignment: Genotype, spatial location and social status in Song Sparrows, *Melospiza melodia*. *Molecular Ecology* 19:4352–4364.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1:103–113.
- Schmidt, K. A., and R. S. Ostfeld (2003). Songbird populations in fluctuating environments: Predator responses to pulsed resources. *Ecology* 84:406–415.
- Sealy, S. G. (1992). Removal of Yellow Warbler eggs in association with cowbird parasitism. *The Condor* 94:40–54.
- Sillett, T. S., N. L. Rodenhouse, and R. T. Holmes (2004). Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. *Ecology* 85:2467–2477.
- Smith, J. N. M. (2006). Song Sparrows, Mandarte Island, and methods. In J. N. M. Smith, L. F. Keller, A. B. Marr, and P. Arcese (Editors), *Conservation and Biology of Small Populations: The Song Sparrows of Mandarte Island*. Oxford University Press, New York, NY, USA. pp. 17–30.
- Smith, J. N. M., and P. Arcese (1994). Brown-headed Cowbirds and an island population of Song Sparrows: A 16-year study. *The Condor* 96:916–934.
- Smith, J. N. M., P. Arcese, K. O'Connor, and J. Reid (2006b). Social mechanisms: Dominance, territoriality, song, and the mating system. In *Conservation and Biology of Small Populations: The Song Sparrows of Mandarte Island* (J. N. M. Smith, L. F. Keller, A. B. Marr, and P. Arcese, Editors). Oxford University Press, New York, NY, USA. pp. 89–112.
- Smith, J. N. M., A. B. Marr, P. Arcese, and L. F. Keller (2006c). The Song Sparrow and the Brown-headed Cowbird. In *Conservation and Biology of Small Populations: The Song Sparrows of Mandarte Island* (J. N. M. Smith, L. F. Keller, A. B. Marr, and P. Arcese, Editors). Oxford University Press, New York, NY, USA. pp. 65–87.
- Smith, J. N. M., A. B. Marr, and W. M. Hochachka (2006a). Life history: Patterns of reproduction and survival. In *Conservation and Biology of Small Populations: The Song Sparrows of Mandarte Island* (J. N. M. Smith, L. F. Keller, A. B. Marr, and P. Arcese, Editors). Oxford University Press, New York, NY, USA. pp. 31–42.
- Sofaer, H. R., T. S. Sillett, K. M. Langin, S. A. Morrison, and C. K. Ghalambor (2014). Partitioning the sources of demographic variation reveals density-dependent nest predation in an island bird population. *Ecology and Evolution* 4:2738–2748.
- Sutherland, W. J., L. V. Dicks, N. Ockendon, and R. K. Smith (Editors) (2017). *What Works in Conservation 2017*. Open Book, Cambridge, UK.
- Syroechkovsky, E. V., K. E. Litvin, and E. N. Gurtovaya (2002). Nesting ecology of Bewick's Swans on Vaygach Island, Russia. *Waterbirds* 25:221–226.
- Tarwater, C. E., and P. Arcese (2017a). Age and years to death disparately influence reproductive allocation in a short-lived bird. *Ecology* 98:2248–2254.
- Tarwater, C. E., and P. Arcese (2017b). Individual fitness and the effects of a changing climate on the cessation and length of the breeding period using a 34-year study of a temperate songbird. *Global Change Biology* 24. In press.
- Tarwater, C. E., and P. Arcese (2017c). Young females pay higher costs of reproduction in a short-lived bird. *Behavioral Ecology and Sociobiology* 71(5):84.
- Taylor, S. S., R. J. Sardell, J. M. Reid, T. Bucher, N. G. Taylor, P. A. Arcese, and L. K. Keller (2010). Inbreeding coefficient and heterozygosity–fitness correlations in unhatched and hatched Song Sparrow nestmates. *Molecular Ecology* 19:4454–4461.
- Tompa, F. (1971). Catastrophic mortality and its population consequences. *The Auk* 88:753–759.
- Wiens, J. A. (1977). On competition and variable environments. *American Scientist* 65:590–597.
- Wilson, A. J., and D. H. Nussey (2010). What is individual quality? An evolutionary perspective. *Trends in Ecology & Evolution* 25:207–214.
- Wingfield, J. C. (1985). Influences of weather on reproduction in male Song Sparrows, *Melospiza melodia*. *Journal of Zoology (London)* 205:525–544.
- Wingfield, J. C., R. E. Hegner, A. M. Dufty, Jr., and G. F. Ball (1990). The “challenge hypothesis”: Theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist* 136:829.
- Wingfield, J. C., M. C. Moore, and D. S. Farner (1983). Endocrine responses to inclement weather in naturally breeding populations of White-crowned Sparrows (*Zonotrichia leucophrys pugetensis*). *The Auk* 100:56–62.
- Woodworth, B. L. (1997). Brood parasitism, nest predation, and season-long reproductive success of a tropical island endemic. *The Condor* 99:605–621.
- Zanette, L. Y., A. F. White, M. C. Allen, and M. Clinchy (2011). Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* 334:1398–1401.
- Zuur, A. F., E. N. Ieno, and C. S. Elphick (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14.

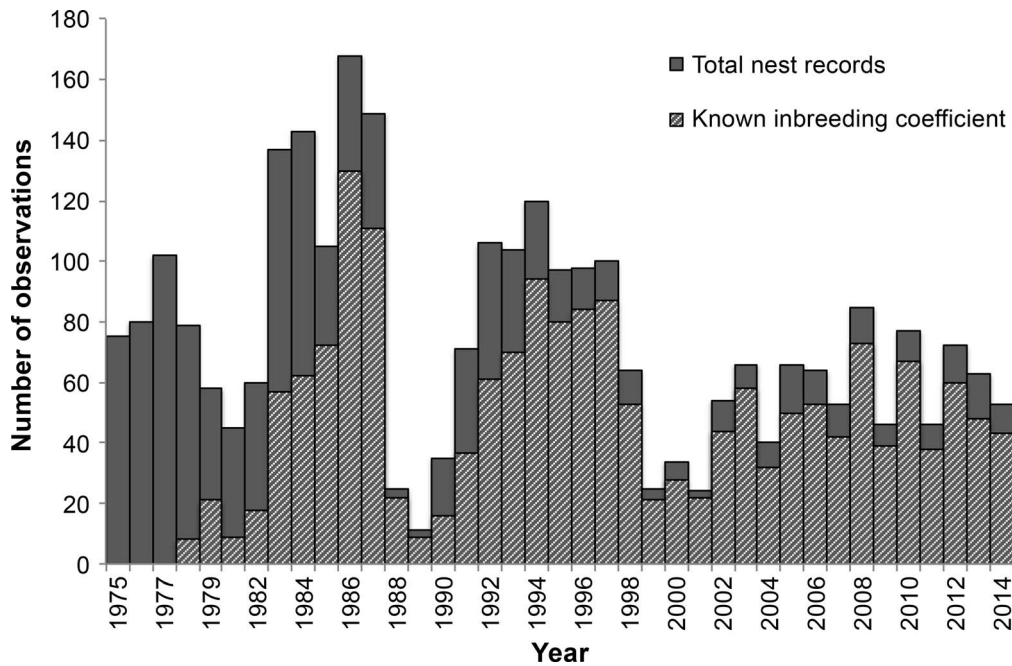
APPENDIX



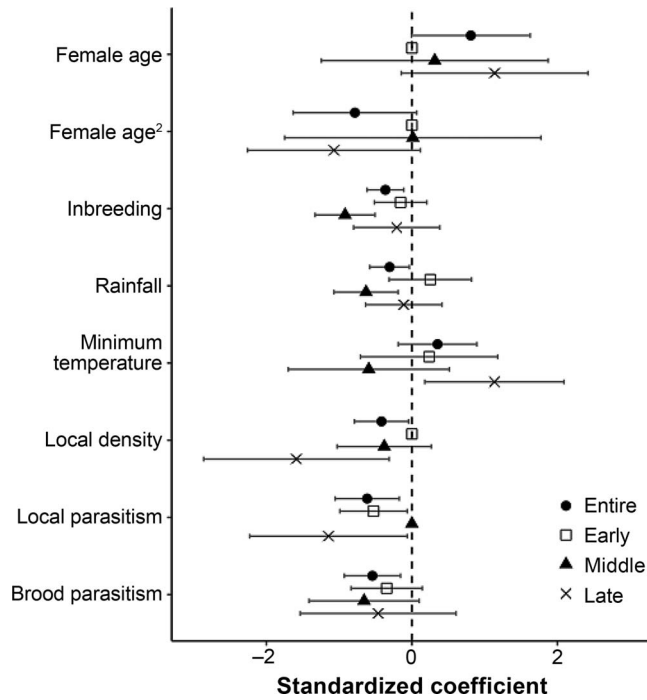
APPENDIX FIGURE 4. Proportion of females of known age in our Song Sparrow dataset from Mandarte Island, British Columbia, Canada, 1975–2014. Lighter bars represent the total number of nests for which female age was known, and darker bars the total number of nest records in the dataset; the former completely overlap the latter in years where female ages were known for all nest records.



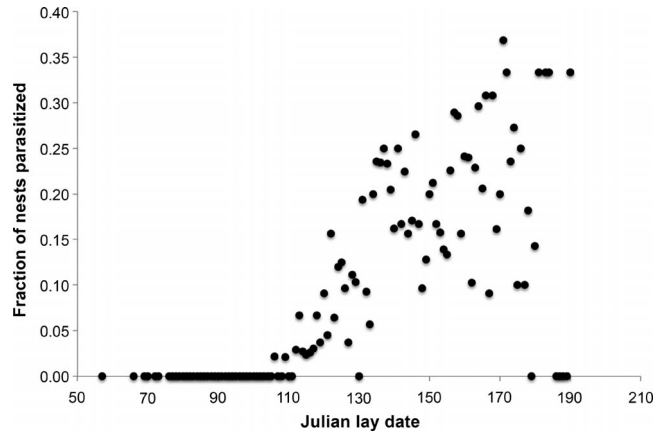
APPENDIX FIGURE 5. Cumulative age distribution of breeding female Song Sparrows on Mandarte Island, British Columbia, Canada, 1975–2014 ($n = 2,710$).



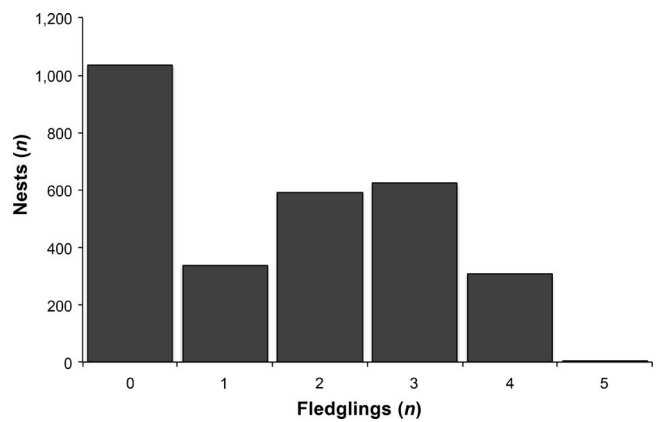
APPENDIX FIGURE 6. Proportion of inbreeding coefficients known in our Song Sparrow dataset from Mandarte Island, British Columbia, Canada, 1975–2014. Lighter bars represent the total number of observations for which the inbreeding coefficient of the female associated with each nest was known (based on knowing all 4 social and/or genetic grandparents), and darker bars represent the total number of nest records in the dataset; the former completely overlap the latter in years for which all female inbreeding coefficients could be estimated.



APPENDIX FIGURE 7. Standardized coefficients (with 95% CI) of the averaged models to predict nest success of breeding female Song Sparrows on Mandarte Island, British Columbia, Canada, during the entire (1975–2014), early (1975–1988), middle (1989–2001), and late (2002–2014) study periods using non-imputed data for lay date and inbreeding (see text).



APPENDIX FIGURE 8. Fraction of Song Sparrow nests parasitized by Brown-headed Cowbirds on Mandarte Island, British Columbia, Canada, throughout the breeding season, 1975–2014. Points show the proportions of parasitized nests with the same lay date ($n = 2,895$ nests).



APPENDIX FIGURE 9. Distribution of numbers of young fledged from 2,895 Song Sparrow nests on Mandarte Island, British Columbia, Canada, 1975–2014.

APPENDIX TABLE 4. Parameter estimates for factors identified as predictors of Song Sparrow nest success in top-ranked models using non-imputed data (see text) from our study population on Mandarte Island, British Columbia, Canada, 1975–2014.

| Model rank | Female age | Female age ² | Inbreeding | Rainfall | Minimum temperature | Local density | Local parasitism | Brood parasitism | Akaike weight (w_i) |
|----------------|------------|-------------------------|------------|----------|---------------------|---------------|------------------|------------------|-------------------------|
| 1 | – | – | –0.36 | –0.30 | – | –0.41 | –0.63 | –0.54 | 0.16 |
| 2 | 0.81 | –0.78 | –0.36 | –0.31 | – | –0.42 | –0.62 | –0.55 | 0.14 |
| 3 | – | – | –0.37 | –0.31 | 0.35 | –0.42 | –0.61 | –0.54 | 0.13 |
| 4 | 0.81 | –0.78 | –0.37 | –0.31 | 0.35 | –0.43 | –0.60 | –0.55 | 0.12 |
| | | | | | | | | | Cumulative w_i |
| Averaged model | 0.81 | –0.78 | –0.36 | –0.31 | 0.35 | –0.42 | –0.61 | –0.54 | 0.55 |
| SE | 0.42 | 0.43 | 0.13 | 0.14 | 0.28 | 0.19 | 0.22 | 0.20 | |

Notes: Top-ranked models ($\Delta AIC < 2$) are a subset of 128 possible models. Averaged model parameter estimates are calculated using Akaike weights (w_i ; see Burnham and Anderson 2002).

APPENDIX TABLE 5. Range, median, and first and third quartiles ($Q_1:Q_3$) of the intrinsic, abiotic, and biotic variables used to predict Song Sparrow nest success and fledgling numbers in the early (1975–1988), middle (1989–2001), and late (2002–2014) study periods on Mandarte Island, British Columbia, Canada.

| Factor | Unit | Range | Median | $Q_1:Q_3$ |
|--------------------------------|-------------------------------|--------------|--------|-----------|
| Early period | | | | |
| Female age | yr | 1 to 6 | 2.0 | 1.0:3.0 |
| Inbreeding coefficient | – | 0 to 0.25 | 0.00 | 0.00:0.01 |
| Imputed inbreeding coefficient | – | 0 to 0.25 | 0.06 | 0.00:0.06 |
| Cumulative rainfall | mm | 0.2 to 99.3 | 30.0 | 19.4:47.0 |
| Minimum temperature | °C | –1.9 to 8.5 | 2.7 | –0.2:4.8 |
| Local parasitism rate | Parasitized nests/50 m buffer | 0 to 12 | 3 | 1:5 |
| Local breeding density | Nests/50 m buffer | 0 to 46 | 16 | 11:23 |
| Brood parasitism rate | Annual proportion | 0 to 0.44 | 0.22 | 0.17:0.25 |
| Lay date | Julian day | 57 to 194 | 131 | 110:151 |
| Imputed lay date | Julian day | 57 to 194 | 132 | 110:151 |
| Middle period | | | | |
| Female age | yr | 1 to 7 | 2.0 | 1.0:3.0 |
| Inbreeding coefficient | – | 0 to 0.28 | 0.05 | 0.03:0.09 |
| Imputed inbreeding coefficient | – | 0 to 0.28 | 0.06 | 0.03:0.07 |
| Cumulative rainfall | mm | 0 to 115.8 | 33.0 | 21.8:59.8 |
| Minimum temperature | °C | –3.2 to 9.6 | 2.9 | 2.0:6.1 |
| Local parasitism rate | Parasitized nests/50 m buffer | 0 to 7 | 0 | 0:1 |
| Local breeding density | Nests/50 m buffer | 0 to 26 | 12 | 8:16 |
| Brood parasitism rate | Annual proportion | 0 to 0.36 | 0.01 | 0:0.13 |
| Lay date | Julian day | 66 to 200 | 132 | 109:151 |
| Imputed lay date | Julian day | 66 to 200 | 131 | 109:151 |
| Late period | | | | |
| Female age | yr | 1 to 9 | 2.0 | 1.0:3.0 |
| Inbreeding coefficient | – | 0 to 0.2 | 0.07 | 0.05:0.10 |
| Imputed inbreeding coefficient | – | 0 to 0.2 | 0.06 | 0.05:0.09 |
| Cumulative rainfall | mm | 1.2 to 128 | 31.2 | 19.2:46.3 |
| Minimum temperature | °C | –2.9 to 10.2 | 3.0 | 1.2:6.0 |
| Local parasitism rate | Parasitized nests/50 m buffer | 0 to 6 | 0 | 0:0 |
| Local breeding density | Nests/50 m buffer | 1 to 17 | 7 | 5:10 |
| Brood parasitism rate | Annual proportion | 0 to 0.28 | 0 | 0:0 |
| Lay date | Julian day | 80 to 202 | 132 | 109:151 |
| Imputed lay date | Julian day | 80 to 202 | 132 | 110:151 |

APPENDIX TABLE 6. Averaged, standardized parameter estimates (β , with SE) and relative importance of variables from top-ranked models within $\Delta\text{AIC} < 2$ of the averaged model explaining Song Sparrow nest success in the early (1975–1988), middle (1989–2001), and late (2002–2014) study periods on Mandarte Island, British Columbia, Canada. Models included year and female ID as random effects, with lay date as a covariate.

| Study period | Factor | β | SE |
|---------------------|-------------------------|---------|------|
| Early ^a | Female age | 0.77 | 0.70 |
| | Female age ² | -1.28 | 0.82 |
| | Inbreeding | 0.09 | 0.15 |
| | Rainfall | -0.34 | 0.21 |
| | Minimum temperature | 0.42 | 0.36 |
| | Local density | -0.38 | 0.21 |
| | Local parasitism | -0.39 | 0.24 |
| | Brood parasitism | - | - |
| | Lay date | -0.35 | 0.32 |
| Middle ^b | Female age | 0.86 | 0.56 |
| | Female age ² | -0.86 | 0.57 |
| | Inbreeding | -0.68 | 0.16 |
| | Rainfall | -0.50 | 0.18 |
| | Minimum temperature | -0.26 | 0.47 |
| | Local density | -0.28 | 0.28 |
| | Local parasitism | 0.19 | 0.42 |
| | Brood parasitism | -0.74 | 0.32 |
| | Lay date | -0.05 | 0.23 |
| Late ^c | Female age | 1.09 | 0.59 |
| | Female age ² | -0.93 | 0.54 |
| | Inbreeding | -0.31 | 0.24 |
| | Rainfall | 0.14 | 0.25 |
| | Minimum temperature | 0.81 | 0.45 |
| | Local density | -1.51 | 0.60 |
| | Local parasitism | -1.01 | 0.57 |
| | Brood parasitism | -0.42 | 0.53 |
| | Lay date | -0.84 | 0.53 |

^a 20 models with $\Delta\text{AIC} < 2$; $n = 999$ nests.

^b 5 models with $\Delta\text{AIC} < 2$; $n = 862$ nests.

^c 15 models with $\Delta\text{AIC} < 2$; $n = 778$ nests.