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Authors: Crombie, Merle D., and Arcese, Peter

RESEARCH ARTICLE

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

Merle D. Crombie and Peter Arcese*

Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, Canada
* Corresponding author: peter.arcese@ubc.ca

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 ($\geq$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 (*f*)	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 age^2 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 (± 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 (°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,
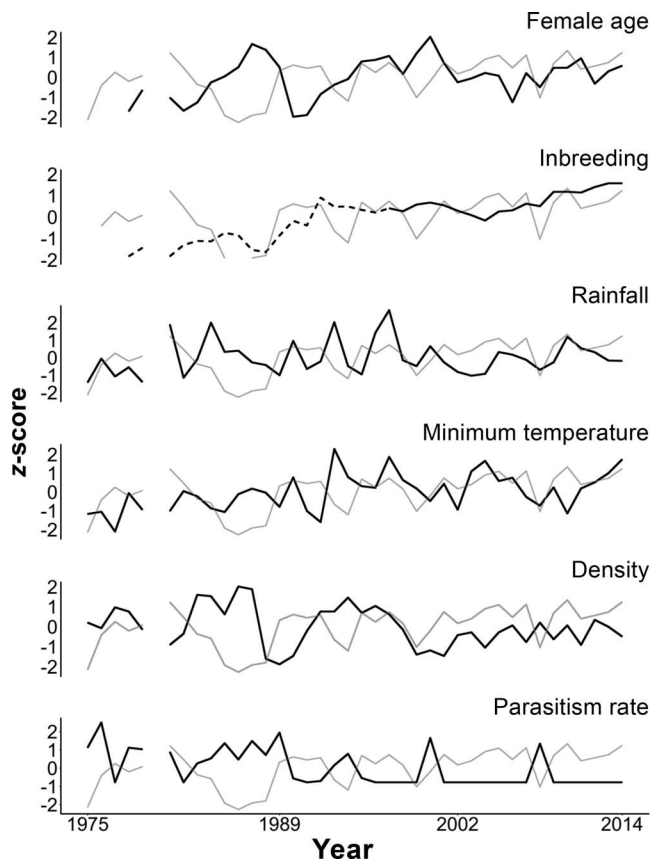
FIGURE 1. Temporal variation in nest success (gray lines) and 6 potential drivers of success (solid black lines) on Mandarte Island, British Columbia, Canada, 1975–2014. The black dashed line represents inbreeding (*f*) estimates largely based on social pedigree, which reduces the precision of those 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 (ΔAIC $<$ 2 from the top model; Burnham and Anderson 2002). Female age and age^2 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 date^2 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 age^2 (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 (β) $\pm$ 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
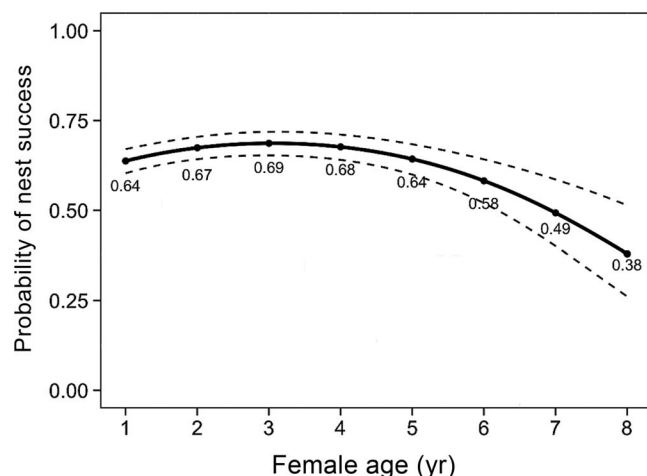
FIGURE 2. Probability of nest success in relation to the age of female Song Sparrows (solid line; dashed lines indicate 95% confidence intervals) on Mandarte Island, British Columbia, Canada, 1975–2014. Values are logit back-transformed partial effects of female age and female age^2 from the averaged model to predict nest success over the 39 yr of the study, while keeping all other intrinsic, abiotic, and biotic factors at their mean.

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).

(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 (β = 0.76, 95% CI: 0.11–1.41, n = 2,706), then declined later in life (female age^2; β = −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 (β = −0.23, 95% CI: −0.43 to −0.03, n = 2,895) and those exposed to more rainfall (β = −0.37, 95% CI: −0.60 to −0.13, n = 2,895), high local breeding density (β = −0.55, 95% CI: −0.83 to −0.27, n = 2,818), and high local parasitism rates (β = −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 (β = 0.25, 95% CI: −0.20 to 0.69, n = 2,895 and β = −0.08, 95% CI: −0.36 to 0.21, n = 2,893, respectively).

Of 128 possible models, 4 were within ΔAIC < 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
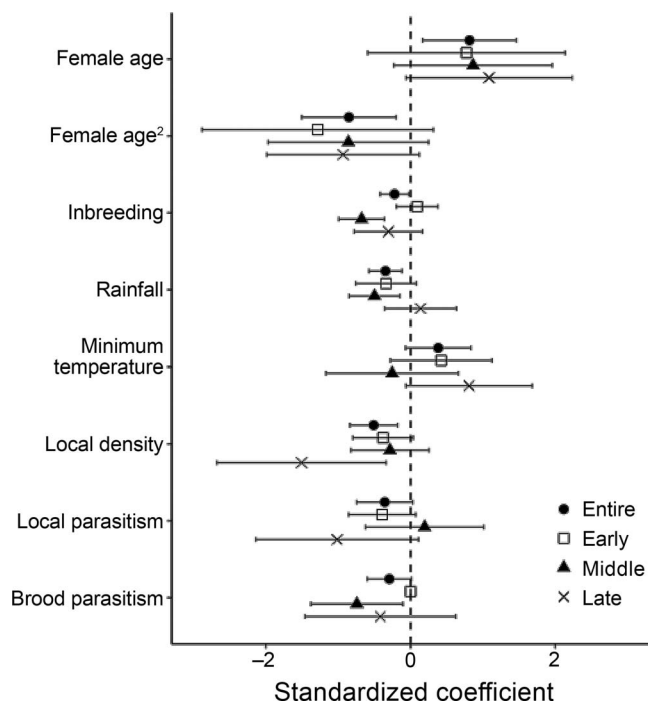
(hereafter "averaged model"; Table 3). In the averaged model (n = 2,639), brood parasitism tended to be a negative predictor of success (95% CI: −0.6 to 0.01; Table 3), whereas local parasitism became less influential on success (95% CI: −0.74 to 0.03; Table 3) compared to univariate models. Overall, 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 age^2 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 (ΔAIC < 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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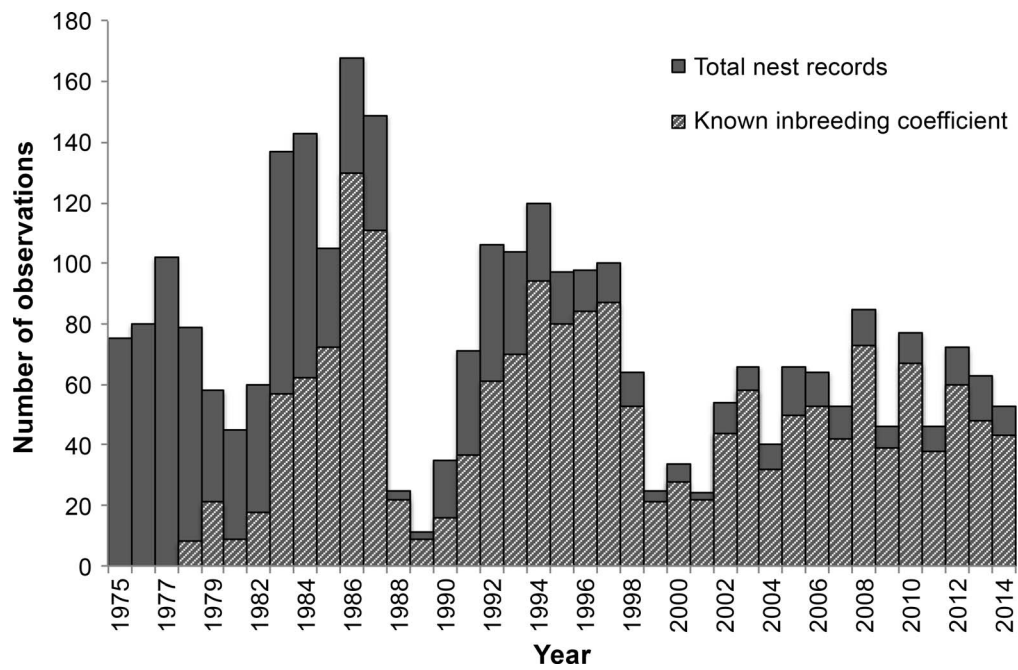
APPENDIX
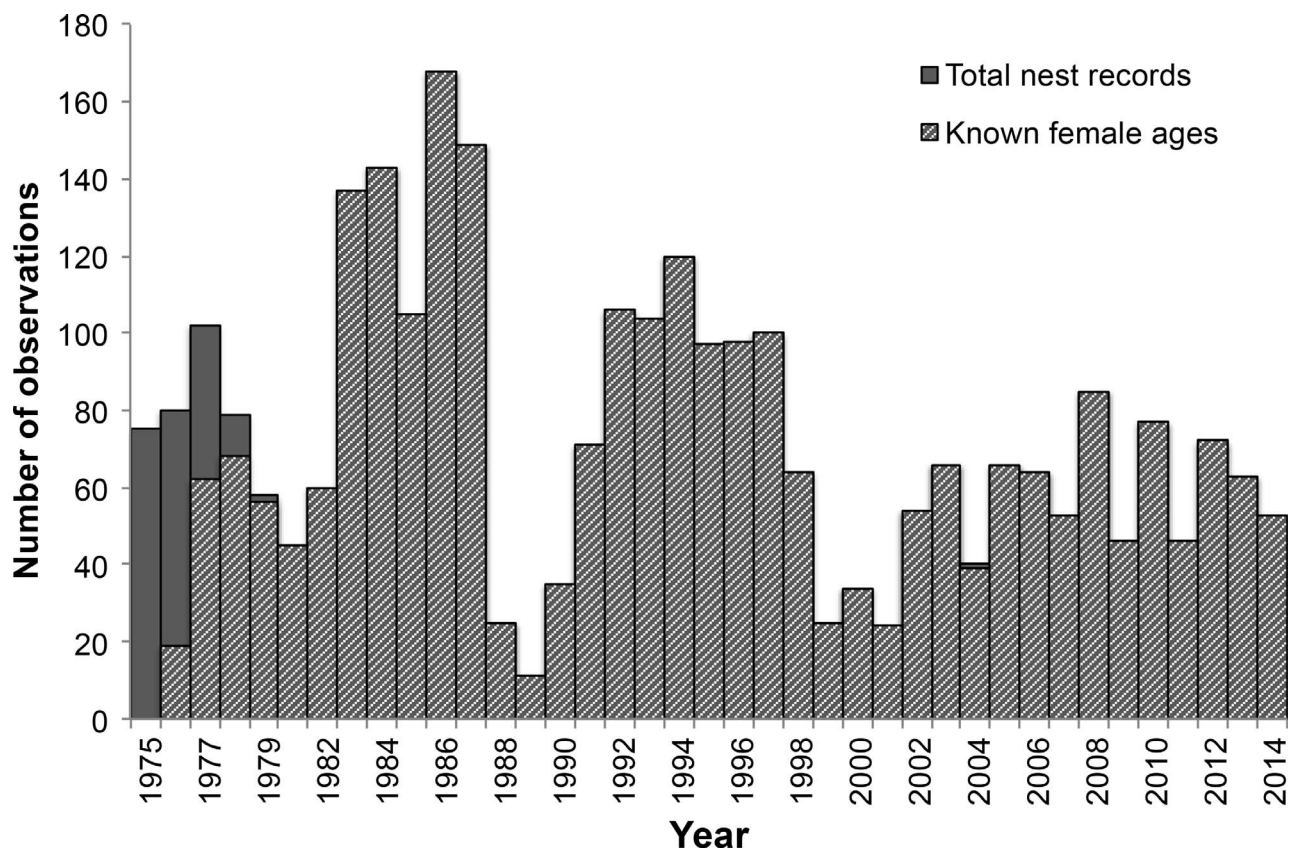
APPENDIX FIGURE 4. Proportion of females of known age in our Song Sparrow dataset from Mandarte Island, British Columbia, Canada, 1975–2014. Lighter bars represent the total number of nests for which female age was known, and darker bars the total number of nest records in the dataset; the former completely overlap the latter in years where female ages were known for all nest records.
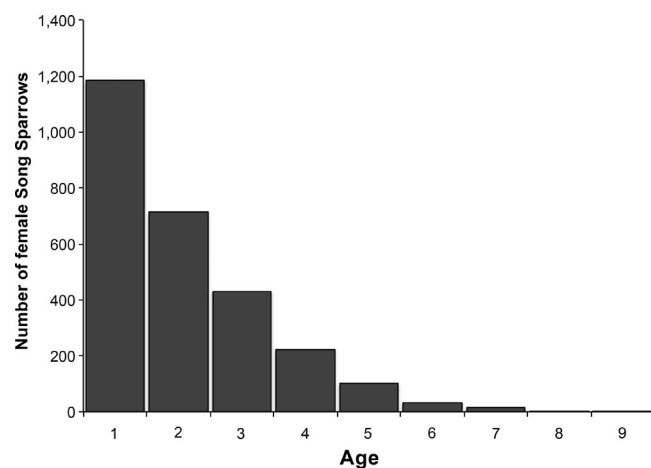
APPENDIX FIGURE 5. Cumulative age distribution of breeding female Song Sparrows on Mandarte Island, British Columbia, Canada, 1975–2014 ($n = 2,710$).

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.
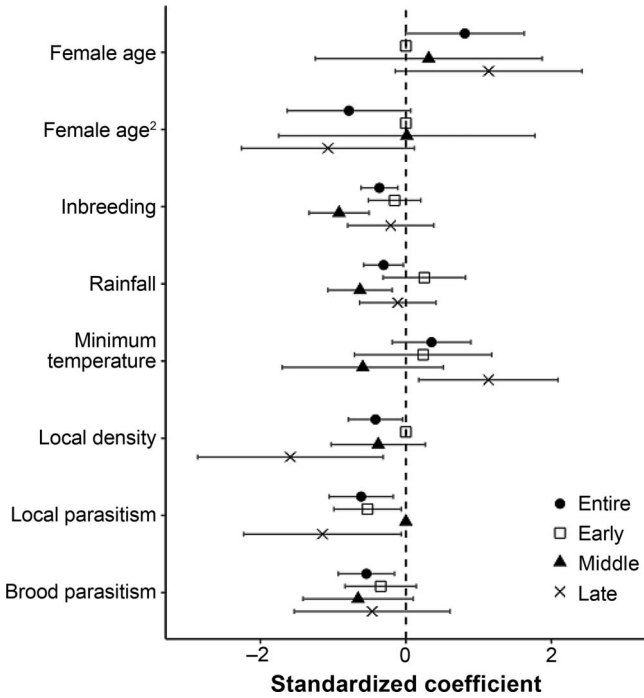
APPENDIX FIGURE 7. Standardized coefficients (with 95% CI) of the averaged models to predict nest success of breeding female Song Sparrows on Mandarte Island, British Columbia, Canada, during the entire (1975–2014), early (1975–1988), middle (1989–2001), and late (2002–2014) study periods using non-imputed data for lay date and inbreeding (see text).
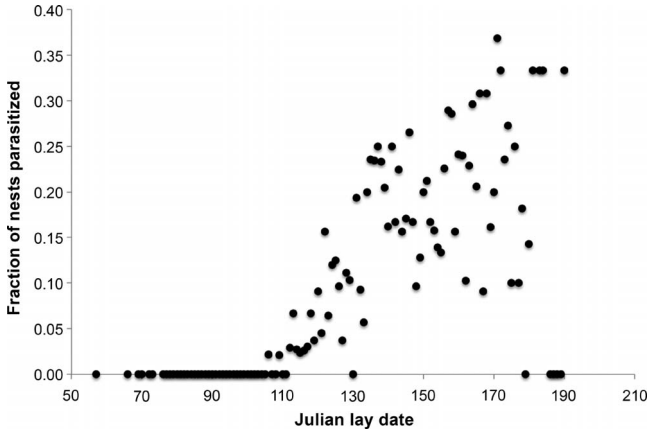
APPENDIX FIGURE 8. Fraction of Song Sparrow nests parasitized by Brown-headed Cowbirds on Mandarte Island, British Columbia, Canada, throughout the breeding season, 1975–2014. Points show the proportions of parasitized nests with the same lay date ($n = 2,895$ nests).
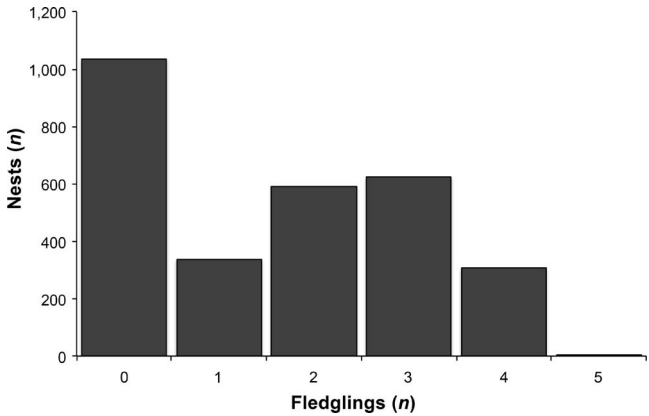
APPENDIX FIGURE 9. Distribution of numbers of young fledged from 2,895 Song Sparrow nests on Mandarte Island, British Columbia, Canada, 1975–2014.

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 (ΔAIC < 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 ΔAIC <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 ΔAIC < 2; $n = 999$ nests.
[b] 5 models with ΔAIC < 2; $n = 862$ nests.
[c] 15 models with ΔAIC < 2; $n = 778$ nests.