

Direct and indirect genetic and fine-scale location effects on breeding date in song sparrows

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Summary

1. Quantifying direct and indirect genetic effects of interacting females and males on variation in jointly expressed life-history traits is central to predicting microevolutionary dynamics. However, accurately estimating sex-specific additive genetic variances in such traits remains difficult in wild populations, especially if related individuals inhabit similar fine-scale environments.

2. Breeding date is a key life-history trait that responds to environmental phenology and mediates individual and population responses to environmental change. However, no studies have estimated female (direct) and male (indirect) additive genetic and inbreeding effects on breeding date, and estimated the cross-sex genetic correlation, while simultaneously accounting for fine-scale environmental effects of breeding locations, impeding prediction of microevolutionary dynamics.

3. We fitted animal models to 38 years of song sparrow (*Melospiza melodia*) phenology and pedigree data to estimate sex-specific additive genetic variances in breeding date, and the cross-sex genetic correlation, thereby estimating the total additive genetic variance while simultaneously estimating sex-specific inbreeding depression. We further fitted three forms of spatial animal model to explicitly estimate variance in breeding date attributable to breeding location, overlap among breeding locations and spatial autocorrelation. We thereby quantified fine-scale location variances in breeding date and quantified the degree to which estimating such variances affected the estimated additive genetic variances.

4. The non-spatial animal model estimated nonzero female and male additive genetic variances in breeding date (sex-specific heritabilities: 0.07 and 0.02, respectively) and a strong, positive cross-sex genetic correlation (0.99), creating substantial total additive genetic variance (0.18). Breeding date varied with female, but not male inbreeding coefficient, revealing direct, but not indirect, inbreeding depression. All three spatial animal models estimated small location variance in breeding date, but because relatedness and breeding location were virtually uncorrelated, modelling location variance did not alter the estimated additive genetic variances.

5. Our results show that sex-specific additive genetic effects on breeding date can be strongly positively correlated, which would affect any predicted rates of microevolutionary change in response to sexually antagonistic or congruent selection. Further, we show that inbreeding effects on breeding date can also be sex specific and that genetic effects can exceed phenotypic variation stemming from fine-scale location-based variation within a wild population.

Key-words: associative genetic effects, breeding habitat, emergent trait, lay date, nest location, quantitative genetics, reproduction, sexual conflict

Introduction

Quantifying genetic contributions to population-wide variation in life-history traits is fundamental to predicting

evolutionary responses to selection (Réale *et al.* 2003b; Charmantier & Garant 2005; Kruuk, Charmantier & Garant 2014). However, partitioning variance in life-history traits in wild populations remains challenging, despite advances in data quality and analytical methods (Kruuk, Charmantier & Garant 2014). Challenges remain in part because phenotypic variation can reflect indirect

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(associative) genetic effects of interacting individuals as well as direct genetic effects of individuals that primarily express traits of interest (Moore, Brodie & Wolf 1997; Wolf *et al.* 1998; Wolf 2003; Wilson 2014). Furthermore, if related individuals are clustered within local environments, genetic effects may be indistinguishable from correlated environmental effects (Kruuk & Hadfield 2007; Shaw & Shaw 2014). Reliable evolutionary predictions consequently require studies that partition variance in life-history traits into direct and indirect genetic as well as local environmental components, and hence require studies where known relatives are distributed across local environmental variation.

Annual breeding date (e.g. egg laying or parturition date) is a key life-history trait that commonly links reproductive and environmental phenology and substantially affects individual fitness in many species across diverse taxa, including reptiles (e.g. Sinervo & Doughty 1996; Olsson & Shine 1997), mammals (e.g. Green & Rothstein 1993; Réale *et al.* 2003a) and birds (e.g. Sheldon, Kruuk & Merilä 2003). Specifically, breeding earlier often increases annual reproductive success or adult survival (Sheldon, Kruuk & Merilä 2003; Wilson & Arcese 2003; Charmantier *et al.* 2008), or offspring survival and recruitment (Festa-Bianchet 1988; Hochachka 1990; Naef-Daenzer, Widmer & Nuber 2001). However, despite resulting selection for earlier breeding (e.g. Réale *et al.* 2003a, b; Brommer & Rattiste 2008; Teplitsky *et al.* 2010; Porlier *et al.* 2012), predicted microevolutionary changes towards earlier breeding are not always observed (Charmantier & Gienapp 2014; Gienapp & Brommer 2014). Such discrepancies might arise because the total additive genetic variance in breeding date is not adequately estimated (Liedvogel, Cornwallis & Sheldon 2012). Specifically, evolutionary predictions might be biased because indirect effects of males on female breeding date are not quantified (Brommer & Rattiste 2008; Teplitsky *et al.* 2010; Brommer *et al.* 2015), and/or because correlated local environmental effects affecting relatives bias estimates of additive genetic variances (e.g. van der Jeugd & McCleery 2002; Kruuk & Hadfield 2007; Stopher *et al.* 2012).

Recent studies indicate that direct and indirect genetic effects can contribute to variance in diverse mating and reproductive traits expressed by interacting females and males in insects (e.g. Wolf 2003; Hall, Lailvaux & Brooks 2013; Edward *et al.* 2014) and birds (e.g. Brommer & Rattiste 2008; Reid *et al.* 2014a). Well-established theory shows that the rate and direction of any microevolutionary change depends on both direct and indirect genetic effects and on the cross-sex genetic correlation between the two, as well as on the magnitude and direction of sex-specific selection. Resulting microevolution might then diverge from predictions based on estimates of genetic variation in and selection on one sex only (e.g. Wolf *et al.* 1998; Wolf 2003; Bijma, Muir & Van Arendonk 2007a; Bijma *et al.* 2007b; Edward *et al.* 2014). For breeding

date, direct and indirect effects might, respectively, arise via the female, who conceives the offspring, and via her mate, who may influence the timing of conception (e.g. through timing of mating or resource provision, Brommer *et al.* 2015). However, few studies have rigorously estimated the direct (i.e. female) and indirect (i.e. male) genetic effects on breeding date and the cross-sex genetic correlation. Nonzero direct and indirect additive genetic variances and a negative genetic correlation were estimated for common gulls (*Larus canus*, Brommer & Rattiste 2008), but other studies estimated that direct and/or indirect genetic variances were close to zero (e.g. red-billed gulls, *Larus novaehollandiae scopulinus*, Teplitsky *et al.* 2010; blue tits, *Cyanistes caeruleus*, Caro *et al.* 2009; great tits, *Parus major*, Liedvogel, Cornwallis & Sheldon 2012), precluding the estimation of cross-sex genetic correlations.

Meanwhile, numerous ecological studies have quantified broad-scale (i.e. regional) environmental effects on breeding date, including climate, temperature and food phenology (e.g. Winkler, Dunn & McCulloch 2002; Réale *et al.* 2003b; Wilson & Arcese 2003; Visser, Holleman & Gienapp 2006; Dunn *et al.* 2011; Burger *et al.* 2012). Fine-scale effects of individuals' local breeding environments on breeding date have also been documented, for example, reflecting breeding location or territory quality (e.g. Lambrechts *et al.* 2004; Wilkin, Perrins & Sheldon 2007; Germain *et al.* 2015). Consequently, quantitative genetic studies aiming to estimate genetic variance in breeding date have accounted for the effects of breeding location (e.g. Liedvogel, Cornwallis & Sheldon 2012; Saunders & Cuthbert 2014), or assume that phenotypic variance stemming from location is encompassed in 'permanent individual' variance (e.g. Auld, Perrins & Charmantier 2013). However, explicit decompositions of phenotypic variance in breeding date to direct and indirect genetic effects vs. fine-scale environmental effects stemming from individual breeding locations are still rare, potentially impeding accurate prediction of the microevolutionary dynamics of this key life-history trait.

Although the quantitative genetic 'animal models' that are increasingly used to estimate genetic and environmental components of variance in life-history traits expressed in wild populations can reduce bias in estimated additive genetic variances stemming from shared environments among relatives (Kruuk & Hadfield 2007), such models can still yield inflated estimates if phenotypic resemblance stemming from shared locations and hence fine-scale environmental effects are not explicitly accounted for (Stopher *et al.* 2012). Additionally, the method by which such location-based variance is estimated, and the spatial scale considered, can affect the estimates of both environmental and additive genetic variance (Stopher *et al.* 2012). However, when genetic and fine-scale location effects covary (e.g. due to social structure or shared habitat use by parents and offspring), accounting for fine-scale location effects may cause additive genetic variance to be

underestimated (Shaw & Shaw 2014). Therefore, in the absence of experimental interventions, accurately estimating additive genetic variance in key life-history traits such as breeding date in wild populations requires systems where genetic and local environmental sources of variance are not intrinsically confounded. This in turn requires comprehensive pedigree data from systems where relatives are not spatially clustered within microenvironments.

Compilation of the complete, spatially referenced pedigrees that are required to accurately partition variance in life-history traits into additive genetic and fine-scale location-based components is often most feasible in relatively small populations, but such populations commonly experience inbreeding. Inbred individuals commonly show inbreeding depression in multiple life-history traits (Kruuk, Sheldon & Merilä 2002; Szulkin *et al.* 2007; Keller, Reid & Arcese 2008; Grueber *et al.* 2010). Since unmodelled inbreeding depression can bias estimates of additive genetic variances, inbreeding effects need to be incorporated into quantitative genetic analyses (Reid & Keller 2010). Furthermore, inbred individuals can affect the reproductive behaviour of their outbred mates, for example, affecting parental care in burying beetles (*Nicrophorus vespilloides*, Matthey & Smiseth 2015). However, because few wild population studies possess sufficiently comprehensive genotypic data to quantify the inbreeding coefficients (f) of paired females and males, estimates of direct and indirect inbreeding depression on fitness-related traits jointly expressed by breeding pairs (as opposed to traits expressed by each sex independently) are lacking.

We fitted animal models to 38 years of pedigree and breeding data from song sparrows (*Melospiza melodia*) inhabiting Mandarte Island, British Columbia, Canada, to quantify female and male additive genetic variances in breeding date and the cross-sex genetic correlation, female and male inbreeding depression, and the variance in breeding date attributable to breeding location (i.e. fine-scale environmental effects). We implemented and compared three different methods of modelling location effects, and quantify the degree to which accounting for location effects altered the estimated additive genetic variances. To aid interpretation, we additionally directly quantified the degree of spatial autocorrelation (SAC) in breeding date within the study system, and quantified the correlation between relatedness and breeding location, and hence the degree to which the breeding locations of relatives were spatially clustered.

Materials and methods

STUDY POPULATION

Mandarte Island (~6 ha) holds a resident song sparrow population that has been monitored intensively since 1975. Song sparrows typically form socially monogamous breeding pairs, where males and females cooperate to defend territories and rear chicks.

Females lay first clutches in March–May and pairs typically rear 2–3 broods per year (Smith, Marr & Hochachka 2006). Although extrapair paternity is common (Sardell *et al.* 2010), all chicks are exclusively reared on their natal territory by their mother and her socially paired male.

Each year since 1975 (except 1980, when fieldwork was reduced), song sparrow nests on Mandarte were located by systematically observing all breeding pairs. Nest locations (hereafter ‘breeding locations’) were recorded to ± 2.5 m on maps drawn from aerial photographs and then converted to Universal Transverse Mercator (UTM) coordinates. Nests were visited every 3–5 days, and chicks were uniquely colour-ringed 5–6 days post-hatch. Immigrants to Mandarte (mean = 1.1/year) were mist-netted and uniquely colour-ringed soon after arriving. The identities of the socially paired female and male attending each nest were subsequently recorded. Breeding date was recorded as the Julian date (days since January 1) on which the first egg of each female’s first clutch was laid in each year. Breeding date was observed directly for nests found before or during laying or back-calculated from observed hatch date or chick age for nests found subsequently (Appendix S1, Supporting Information). Overall, the location, breeding date and identities of paired females and males are known for $\geq 99\%$ of all 3350 nests initiated during 1975–2014. Previous analyses suggest that breeding location affects several aspects of reproductive success (Germain *et al.* 2015), but that specific breeding locations are not systematically monopolized by prime-age or ‘higher-quality’ females (Germain & Arcese 2014). The relatively short life span of individual song sparrows (mean 2.2 years, Smith, Marr & Hochachka 2006) relative to the long-term study allows the contributions of breeding location to life-history traits to be estimated largely independently of the effects of any individual females or males that occupied each location.

PEDIGREE AND PATERNITY

A full pedigree including all song sparrows ringed on Mandarte during 1975–2014 was compiled by assigning all chicks to the male and female attending each nest (Keller 1998; Reid *et al.* 2014b, 2015). Since 1993, all ringed chicks were blood-sampled and genotyped at ~160 highly polymorphic microsatellite loci to assign genetic parentage (Nietlisbach *et al.* 2015). All genetic mothers matched those assigned from observed behaviour. Sires were assigned to $>99\%$ of sampled chicks with $\geq 99\%$ individual-level statistical confidence, revealing 28% extrapair paternity (Sardell *et al.* 2010; Reid *et al.* 2014b, 2015). Paternity of song sparrows hatched before 1993 that survived to breed subsequently was also genetically verified where possible. All genetic paternity assignments were used to correct the pedigree for extrapair paternity so far as feasible (Sardell *et al.* 2010; Reid *et al.* 2014b, 2015).

Standard algorithms were used to calculate individual f relative to the 1975 pedigree baseline (Keller 1998; Lynch & Walsh 1998; Reid *et al.* 2014b). New immigrants to Mandarte were assumed to be unrelated to each other and to all existing residents at arrival (Wolak & Reid 2016). Offspring of immigrant-resident pairings were therefore defined as outbred ($f = 0$). Immigrants were themselves assumed to be outbred relative to the 1975 Mandarte pedigree baseline ($f = 0$), but results remained qualitatively similar after excluding phenotypic data from immigrants, thereby eliminating the need to specify immigrant f (Appendix S2).

Unobserved extrapair paternity before 1993 presumably introduces error into the 1975–1992 pedigree, potentially affecting estimates of additive genetic variance and inbreeding depression in breeding date. However, approximately 90% of all pedigree links are likely to be correct (100% of 1975–2014 maternal links with no missing data, ~100% of 1993–2014 paternal links and ~72% of 1975–1992 paternal links assuming an extrapair paternity rate similar to that observed subsequently). Such small pedigree error is likely to cause relatively little bias in estimates of additive genetic variance (Charmantier & Réale 2005; Firth *et al.* 2015). Furthermore, analyses restricted to the period covered by the fully corrected genetic pedigree (1993–2014) returned qualitatively similar estimates, although with less precision due to reduced sample size and hence statistical power (Appendix S2).

QUANTITATIVE GENETIC ANALYSES

A series of univariate animal models was fitted to partition phenotypic variance in breeding date into direct and indirect genetic and fine-scale environmental components, and to simultaneously estimate direct and indirect inbreeding depression. The initial (hereafter ‘non-spatial’) univariate animal model was as follows:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{a}_\varnothing + \mathbf{Z}_2\mathbf{a}_\sigma + \mathbf{Z}_3\mathbf{PI}_\varnothing + \mathbf{Z}_4\mathbf{PI}_\sigma + \mathbf{Z}_5\mathbf{Y} + \mathbf{e}, \quad \text{eqn 1}$$

where \mathbf{y} is a vector of observed breeding dates, \mathbf{X} and \mathbf{Z} are design matrices relating observations to fixed or random effects, $\boldsymbol{\beta}$ is a vector of fixed effects, and \mathbf{a} , \mathbf{PI} , \mathbf{Y} and \mathbf{e} are vectors of random additive genetic, permanent individual, year and residual effects. This model estimated female and male additive genetic variances ($V_{A\varnothing}$ and $V_{A\sigma}$), female and male permanent individual variances ($V_{PI\varnothing}$ and $V_{PI\sigma}$) and overall year (V_Y) and residual (V_e) variances in breeding date. Here, $V_{PI\varnothing}$ and $V_{PI\sigma}$ comprise permanent environmental and non-additive genetic variances, and V_e comprises non-permanent non-genetic female, male and environment effects. Female and male additive genetic effects were assumed to be jointly distributed following a multivariate normal distribution (MVN): $\mathbf{a} = [\mathbf{a}'_\varnothing, \mathbf{a}'_\sigma] \sim \text{MVN}(\mathbf{0}, \mathbf{G} \otimes \mathbf{A})$, where prime denotes a vector transpose and \otimes denotes the Kronecker product. Here, \mathbf{A} represents the additive genetic relationship matrix between all individuals calculated from the pedigree (Kruuk 2004), and \mathbf{G} represents the variance–correlation matrix to be estimated by the model:

$$\mathbf{G} = \begin{bmatrix} V_{A\varnothing} & \\ \text{Corr}_{A\varnothing,\sigma} & V_{A\sigma} \end{bmatrix}, \quad \text{eqn 2}$$

where $\text{Corr}_{A\varnothing,\sigma}$ represents the cross-sex additive genetic correlation in breeding date. The univariate model was formulated to directly estimate the cross-sex genetic correlation in breeding date rather than the additive genetic covariance ($\text{Cov}_{A\varnothing,\sigma}$), to facilitate direct and comparable estimations of uncertainty in the genetic correlation and variance components. The genetic correlation rather than the covariance was therefore specified in expressions for total phenotypic and total additive genetic variance, but these terms are easily interchanged (eqn S1 in Appendix S2).

Estimation of $V_{A\varnothing}$, $V_{A\sigma}$ and $\text{Corr}_{A\varnothing,\sigma}$ requires observations of breeding date from numerous related females and males, but does not necessarily require multiple observations of breeding date per individual, or require individuals to breed with multiple mates (e.g. Reid *et al.* 2014a; Wolak & Reid 2016). Indeed,

simulations confirmed that there were no substantial biases in estimates of sex-specific additive genetic or permanent individual variances given our pedigree and data structure (Appendix S3). Further non-spatial animal models were also fitted to confirm that estimates of sex-specific additive genetic variances and the cross-sex genetic correlation were not biased by exclusive or repeat pairings between mates, by parental environmental effects or by the restricted maximum-likelihood (REML) algorithm (Appendix S2).

SPATIAL ANIMAL MODELS

The non-spatial animal model (eqn 1) was extended to explicitly estimate the variance in breeding date associated with breeding location, thereby estimating variance arising from fine-scale environmental effects acting within the study area and testing whether failing to model such effects biased estimates of $V_{A\varnothing}$ or $V_{A\sigma}$. In seasonally breeding birds, among-individual variation in breeding date may be substantially affected by local environmental cues acting at the spatial scale that individuals experience during their daily movements (Caro *et al.* 2009; Thomas *et al.* 2010). Individual breeding locations may therefore represent a more biologically meaningful scale for heterogeneity than generic habitat classifications (Wilkin, Perrins & Sheldon 2007). We therefore estimated the variance in breeding date associated with breeding location (defined at a range of spatial scales, see below), which is assumed to capture multidimensional fine-scale environmental effects, rather than modelling effects of vegetation, topography or any other specific habitat or environmental attribute individually (e.g. Liedvogel, Cornwallis & Sheldon 2012; Saunders & Cuthbert 2014). The underlying assumption that fine-scale environmental effects associated with breeding locations have not changed greatly during 1975–2014 is justified because repeated vegetation maps indicate minor temporal change and topographical characteristics have remained constant.

Three different spatial models, hereafter ‘grid’, ‘overlap’ and ‘SAC’, were constructed to estimate different aspects of fine-scale location effects on breeding date and to compare the estimates of $V_{A\varnothing}$ and $V_{A\sigma}$ from each spatial model with those from the non-spatial model. Each spatial model formed an independent extension of the non-spatial model by adding a vector of random location effects (\mathbf{Loc}) and associated design matrix \mathbf{Z}_6 :

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{a}_\varnothing + \mathbf{Z}_2\mathbf{a}_\sigma + \mathbf{Z}_3\mathbf{PI}_\varnothing + \mathbf{Z}_4\mathbf{PI}_\sigma + \mathbf{Z}_5\mathbf{Y} + \mathbf{Z}_6\mathbf{Loc} + \mathbf{e}. \quad \text{eqn 3a}$$

Since each spatial model used a different method, the additional component $\mathbf{Z}_6\mathbf{Loc}$ differs among them. However, for simplicity, a common notation is used to denote location-based variance.

The ‘grid’ model quantified the variance in breeding date attributable to discrete, spatially independent clusters of breeding locations using a predefined grid system (Germain & Arcese 2014; Germain *et al.* 2015). Using ArcGIS 10.1 (ESRI, Redlands, CA, USA), a fixed grid of tessellating hexagons was overlaid and a unique identifier was assigned to each grid cell (Appendix S4). Random effects of the identity of the cell that contained each breeding (i.e. nest) location were then fitted. Cell identity effects were assumed to be univariate normally distributed as $\mathbf{Loc} \sim N(\mathbf{0}, V_{\text{Loc}} \times \mathbf{I})$, where the identity matrix (\mathbf{I}) defines location effects as independently and identically distributed. To identify the most

appropriate cell size, and thus the spatial scale at which location-based variance in breeding date was greatest, 14 grid models with cell diameters spanning 4–30 m (areas ~10–585 m²) were compared (Appendix S4). The model with cell diameter 16 m (area 166.3 m²) was best supported, estimated the greatest variance in breeding date due to breeding location and is therefore reported. In practice, cell diameter had little influence on estimates of $V_{A\sigma}$ and $V_{A\sigma}$ (Appendix S4).

The spatial ‘overlap’ model estimated the degree to which breeding attempts made at adjacent breeding locations commenced on similar dates. ArcGIS was used to construct circular spatial buffers around each breeding location (Germain & Arcese 2014; Germain *et al.* 2015). A matrix describing the area of buffer overlap for all pairwise combinations of breeding locations was calculated (\mathcal{S}), then scaled so that each breeding location had a ‘spatial relatedness’ of 1 with itself and 0 with all non-overlapping locations (e.g. Stopher *et al.* 2012). Thus, \mathcal{S} describes the covariances among breeding locations based on their area of buffer overlap, analogous to how \mathbf{A} describes genetic covariances among individuals based on their shared genes. Random location effects were assumed to be univariate normally distributed as $\text{Loc} \sim \text{N}(\mathbf{0}, V_{\text{Loc}} \times \mathcal{S})$. This model estimated the variance in breeding date attributable to shared space, given that covariance in breeding dates between overlapping locations is expected to be greater than between non-overlapping locations (Stopher *et al.* 2012; Wilson 2014). Effects of spatial scale were investigated by sequentially increasing buffer area from 50 to 2000 m² and recalculating \mathcal{S} , thereby spanning a range of areas within the study system (Appendix S5). Results using a 100-m² buffer (radius = 5.6 m) are presented (following Germain & Arcese 2014; Germain *et al.* 2015); however, estimated variance components were similar across all buffer areas (Appendix S5).

The ‘SAC’ model included an explicit spatial autocovariate estimating the distance (m) between breeding locations at which differences in breeding date were expected to be zero (Fortin & Dale 2005). It thereby directly estimated the spatial scale of phenotypic covariance in breeding date within Mandarte. Coordinates of all breeding locations were rounded to the nearest 1 m, then jittered by $d/5$, where d was the smallest distance between unique nest locations (1 m). This ensured that no two observations had identical coordinates, which may impede the estimation of SAC (Fortin & Dale 2005). A two-dimensional spherical spatial correlation structure was fitted to the animal model residual effect structure, where V_{Loc} quantifies the spatial range over which phenotypic observations are non-independent (Appendix S6).

The degree of phenotypic SAC in breeding date was additionally quantified outside the animal model framework, by calculating Moran’s I . This metric (bounded at –1 and 1, where 0 indicates zero SAC) estimates the summed covariation in breeding date among breeding locations at a given distance, divided by the number of pairwise comparisons (Fortin & Dale 2005). Observed breeding dates were year-standardized to remove the variation due to among-year environmental effects. Spatial covariance in breeding date was resampled in increments of 25 m [a distance slightly larger than the width of two overlapping 100-m² spatial buffers (diameter = 11.28 m, overlap model)] for 1000 permutations, and considered statistically significant at an adjusted alpha value of 0.002 to account for spatial dependence among resampling increments (Appendix S6).

Finally, to quantify the degree to which related song sparrows bred closer together (or further apart) than less closely related

individuals of either sex, and thereby examine the data set’s ability to distinguish genetic and fine-scale environmental effects, matrices were constructed describing the relatedness among all females and males and the Euclidean distance among all breeding locations across all years. Canonical correlation analysis was used to quantify the correlations between the distance and relatedness matrices for each sex (Legendre & Fortin 2010).

IMPLEMENTATION

All animal models included separate fixed regressions of breeding date on female f and male f , thereby estimating sex-specific inbreeding depression in breeding date and facilitating accurate estimation of additive genetic variance (Reid & Keller 2010). All animal models also included sex-specific fixed effects of three age groups (1, 2–4 and 5+) since previous analyses show that middle-aged song sparrows breed earlier than yearlings or older individuals (Smith, Marr & Hochachka 2006). Immigrants were assumed to be 1 year old at arrival because song sparrows disperse solely as juveniles (Arcese 1989a; Wilson & Arcese 2008). Overall, 109 observations of breeding date where one or both adults were of unknown identity or age (primarily from 1975 and 1980) were excluded from analyses.

Since breeding date was modelled as a joint (‘emergent’) trait stemming from the direct effects of the breeding female and indirect effects of her socially paired male, the total phenotypic variance (V_{P}) for breeding date, conditioned on the fitted fixed effects, is approximated as follows:

$$V_{\text{P}} = V_{A\sigma} + V_{A\delta} + 2([\text{Corr}_{A\sigma\delta} \times \sqrt{V_{A\sigma} \times V_{A\delta}}] \times 2k_{\text{mean}}) + V_{\text{PI}\sigma} + V_{\text{PI}\delta} + V_{\text{Y}} + V_{\text{Loc}} + V_{\text{e}} \quad \text{eqn 3b}$$

where the spatial variance component V_{Loc} is zero for the non-spatial model. Here, $2k_{\text{mean}}$ is the mean female–male relatedness across all observed breeding pairs, calculated from the pedigree as twice the mean pairwise coefficient of kinship (k_{mean} , Bijma, Muir & Van Arendonk 2007a; Bijma *et al.* 2007b; Bouwman *et al.* 2010). The female- and male-specific narrow-sense heritabilities (h_{σ}^2 and h_{δ}^2) of breeding date can then be, respectively, calculated as:

$$h_{\sigma}^2 = \frac{V_{A\sigma}}{V_{\text{P}}} \quad \text{and} \quad h_{\delta}^2 = \frac{V_{A\delta}}{V_{\text{P}}} \quad \text{eqn 4}$$

The total additive genetic variance in breeding date is estimated as:

$$V_{\text{ATot}} = V_{A\sigma} + V_{A\delta} + 2([\text{Corr}_{A\sigma\delta} \times \sqrt{V_{A\sigma} \times V_{A\delta}}]), \quad \text{eqn 5}$$

(Bijma, Muir & Van Arendonk 2007a; Bijma *et al.* 2007b; Bouwman *et al.* 2010). The ratio of total additive genetic variance to total phenotypic variance (T^2), which represents the total amount of additive genetic variance in breeding date upon which selection may act and hence underpins any predicted evolutionary response to selection, is as follows:

$$T^2 = \frac{V_{\text{ATot}}}{V_{\text{P}}} \quad \text{eqn 6}$$

Standard errors for female and male heritabilities, T^2 , and all fixed effects estimates were calculated. However, standard errors

provide less reliable estimates of uncertainty for variance component estimates employing REML and the average information algorithm, because several key assumptions utilized to compute approximate standard errors are commonly violated (Meyer 2008; Wolak & Reid 2016). Therefore, profile likelihoods were used to estimate 95% confidence intervals (95% CIs) for each variance component, and the cross-sex genetic correlation, and thereby test their statistical significance in multidimensional parameter space (Meyer 2008). Likelihood ratio tests supported the conclusions drawn from profile likelihoods and were also used to determine whether the three spatial animal models fitted the data better than the non-spatial model.

All analyses were conducted using R 3.02 (R Development Core Team 2013). Animal models were fitted using ASREML-R (Butler *et al.* 2009), facilitated by the MASTERBAYES and NADIV packages (Hadfield, Richardson & Burke 2006; Wolak 2012). Moran's I was calculated using package NCF (Bjørnstad 2009). Raw means are presented ± 1 SD.

Results

The final data set comprised 1040 breeding dates in 38 years (1976–1979, 1981–2014) from a mean of 28.5 ± 15.3 breeding pairs per year. Breeding date varied substantially among years (Fig. 1a), with an overall mean Julian date of 107 ± 13 (April 17th, Appendix S1). The 1040 breeding attempts were made by 518 individual

female and 483 male song sparrows, comprising 782 unique social pairings (Appendix S2). There were means of 2.1 ± 1.3 (range 1–7) observations per individual female and 2.2 ± 1.4 (range 1–9) observations per individual male; 247 (48%) females and 205 (42%) males contributed one observation.

The pruned pedigree comprised 1088 individuals. Mean relatedness ($2k_{\text{mean}}$) across the 782 pairings that contributed phenotypic data was 0.117 ± 0.125 . Mean pairwise kinship (k) across all females that contributed phenotypic data was 0.029 ± 0.04 (range = 0.00–0.393), and mean female f was 0.041 ± 0.051 (range 0.00–0.277). Mean k across all males that contributed phenotypic data was 0.030 ± 0.04 (range = 0.00–0.399), and mean male f was 0.037 ± 0.05 (range 0.00–0.274). Mean cross-sex k among all possible combinations of females and males that contributed phenotypic data was 0.029 ± 0.04 (range = 0.00–0.424, Appendix S3).

NON-SPATIAL ANIMAL MODEL

The non-spatial model estimated moderate female ($V_{A\phi} = 12.3$) and small male ($V_{A\sigma} = 3.6$) additive genetic variance for breeding date, with 95% CIs that did not converge to zero (Table 1). The cross-sex genetic correlation was estimated to be approximately equal to one

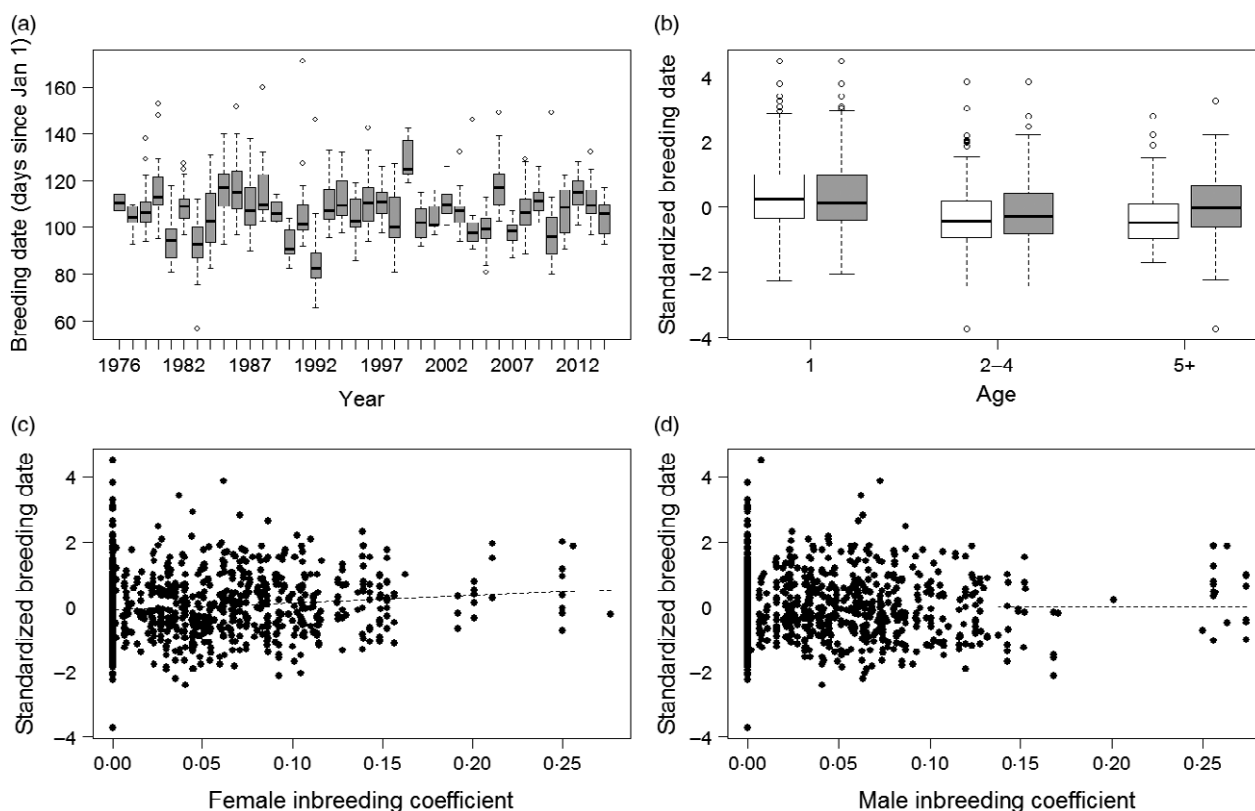


Fig. 1. Summaries of variation in song sparrow breeding date (a) among years, and with (b) female (white boxes) and male (grey boxes) age and (c) female and (d) male inbreeding coefficient. In b–d, breeding date is z-standardised within years to facilitate visualisation. Box lines in (a) and (b) represent the median, upper and lower quartiles, while whiskers extend to 1.5 \times the interquartile range. Dashed lines in (c) and (d) represent linear regressions.

Table 1. Estimates (Est) of variance components (and associated 95% confidence intervals [95% CI]), fixed effect coefficients (± 1 standard error [SE]) and heritabilities (± 1 SE) from four separate univariate animal models of song sparrow breeding date

Model	Non-spatial		Grid		Overlap		Spatial autocorrelation (SAC)	
	Est	95% CI	Est	95% CI	Est	95% CI	Est	95% CI
$V_{A\varphi}$	12.3***	6.1–20.7	12.2***	6.0–20.6	12.4***	6.2–20.9	12.5***	6.3–20.9
$V_{A\sigma}$	3.6**	1.4–6.9	3.2**	1.1–6.3	3.4**	1.2–6.7	3.4**	1.3–6.6
$V_{PI\varphi}$	12.3**	5.7–19.3	10.8*	4.2–17.8	11.7*	5.0–18.9	10.6*	4.1–17.5
$V_{PI\sigma}$	<0.001	<0.001–0.4	<0.001	<0.001–0.4	<0.001	<0.001–0.4	<0.001	<0.001–0.4
V_Y	76.4***	54.9–109.6	76.4***	54.9–109.5	76.2***	54.7–109.3	77.1***	55.4–110.5
V_{Loc}	–	–	3.6*	1.2–6.7	1.6	0.1–5.7	0.03	0.01–0.05
V_e	60.9	55.8–66.5	58.8	53.7–64.5	59.8	54.2–65.9	62.4	57.2–68.2
$Corr_{A\varphi\sigma}$	0.99	0.70–0.99	0.99	0.70–0.99	0.99	0.70–0.99	0.99	0.70–0.99
Fixed effects	Est	SE	Est	SE	Est	SE	Est	SE
Intercept	114.4	1.9	114.5	1.9	114.4	1.9	114.3	1.9
♀ Age								
2–4 years	–6.6	0.6	–6.5	0.6	–6.6	0.6	–6.6	0.6
5+ years	–6.1	1.3	–6.1	1.3	–6.1	1.3	–6.3	1.3
♀ $\beta - f$	29.6	8.4	28.5	8.3	29.3	8.3	29.2	8.3
♂ Age								
2–4 years	–2.9	0.7	–3.1	0.7	–2.9	0.7	–3.0	0.7
5+ years	–1.5	1.1	–1.5	1.1	–1.4	1.1	–1.3	1.1
♂ $\beta - f$	–2.4	7.5	–3.0	7.5	–2.5	7.5	–2.5	7.4
Heritability								
h^2_{φ}	0.07	0.03	0.07	0.03	0.07	0.03	0.07	0.03
h^2_{σ}	0.02	0.01	0.02	0.01	0.02	0.01	0.02	0.01
T^2	0.18	0.06	0.17	0.06	0.17	0.06	0.17	0.06
Loglik	–2857.2		–2854.8	$\Lambda = 4.9$ $P = 0.03$	–2857.1	$\Lambda = 0.4$ $P = 0.55$	–2856.0	$\Lambda = 2.6$ $P = 0.11$

V_A and V_{PI} represent additive genetic and permanent individual variances for females (♀) and males (♂). V_Y , V_{Loc} and V_e are the year, breeding location and residual variances. $Corr_{A\varphi\sigma}$ is the cross-sex genetic correlation, and $\beta - f$ is the regression on individual inbreeding coefficient. h^2 is the sex-specific heritability, and T^2 is the ratio of total additive genetic variance to phenotypic variance.

Asterisks denote significant variance components (excluding residual variance) for each model at $P \leq 0.05$ (*), 0.01 (**) and 0.001 (***), as assessed by likelihood ratio tests. The test statistic (Λ) and P values are from likelihood ratio tests comparing each spatial model (grid, overlap, SAC) to the initial non-spatial model.

(Table 1). There was also moderate permanent individual variance for females ($V_{PI\varphi} = 12.3$), but not for males ($V_{PI\sigma} \approx 0$, Table 1). The year and residual variances were substantial, comprising the largest proportions of total phenotypic variance (Table 1). Sex-specific heritabilities were estimated as 0.07 ± 0.03 SE and 0.02 ± 0.01 SE for females and males, respectively, and T^2 was 0.18 ± 0.06 SE.

Breeding date increased with increasing female f , showing that more inbred females bred substantially and significantly later (Table 1, Fig. 1c). In contrast, breeding date did not vary significantly with male f , as the estimated effect size was small and the associated SE was large (Table 1, Fig. 1d). Middle-aged females bred earliest on average, followed by older females and then first-year females (Table 1, Fig. 1b). This pattern was similar but less pronounced in males (Table 1, Fig. 1b).

SPATIAL VARIATION

Observed breeding locations spanned the extent of available habitat on Mandarte (Fig. 2). Visual inspection

showed considerable heterogeneity in breeding date at a very small spatial scale (Fig. 2). Indeed, Moran's I showed no evidence of significant SAC beyond the starting distance of 25 m (Fig. 3, Appendix S6).

Correlation coefficients (r) between the relatedness and distance matrices were very small, but negative for both females ($r = -0.035$, 95% CI = -0.034 , -0.037) and males ($r = -0.030$, 95% CI = -0.029 , -0.032). This indicates that closer relatives tended to breed slightly further apart than expected by chance, but that the proportion of variation in distance explained by relatedness was very small ($\sim 0.1\%$).

In the grid model, the 1040 breeding dates were allocated to 212 discrete cells (mean = 5.1 ± 3.9 observations per cell, range 1–21), with means of 4.4 ± 3.1 (range 1–16) individual females and 4.2 ± 3.0 (range 1–15) males per cell, and means of 1.8 ± 1.0 (range 1–6) unique cells per female and 1.8 ± 1.0 (range 1–7) unique cells per male over their lifetimes. A small but significant proportion of variance in breeding date was attributed to cell identity (Table 1). The grid model fitted the data better

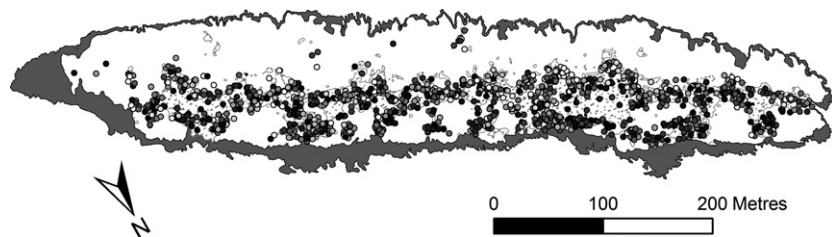


Fig. 2. Visual representation of 1040 breeding locations (points) spanning 38 years on Mandarte Island. Grey outline represents the rocky intertidal area, white represents grass meadow, and light-grey stipples represent the current extent of shrub cover by which most nests are located. Shading of breeding locations represents their relative breeding date, z -standardized by year, where white to grey to black points represent the earliest to latest relative breeding dates, with $N_{\text{obs}} \approx 40$ breeding locations per shade. The heterogeneity of shading across adjacent locations illustrates that there is little spatial structure in breeding date within Mandarte at scales exceeding individual locations.

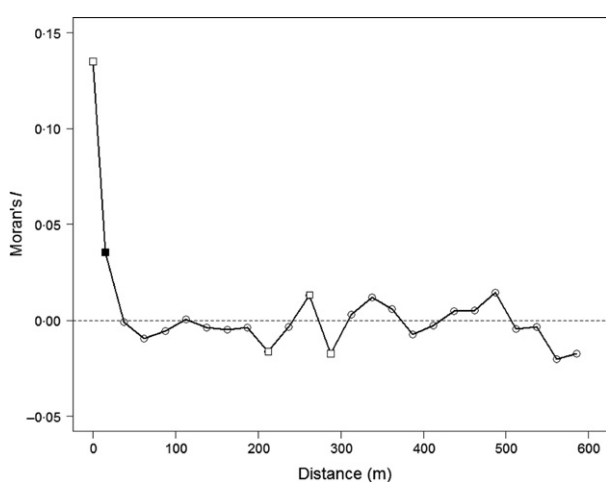


Fig. 3. Moran's I correlogram of spatial dependence in breeding date at discrete distance increments of 25 m across Mandarte (total length ~ 600 m, Fig. 2). Open circles denote resampling increments where no spatial autocorrelation (SAC) was detected, open squares denote SAC at an uncorrected α level of 0.05, filled square denotes significant SAC at α level corrected for spatial dependence of data among distance classes ($\alpha' = 0.002$, Appendix S6).

than the non-spatial model (likelihood ratio test, $P = 0.03$), providing evidence of persistent fine-scale location effects on breeding date. However, estimates of $V_{A\sigma}$, $V_{A\sigma}$, V_Y and $\text{Corr}_{A\sigma}$ were quantitatively similar to those estimated by the non-spatial model, and h_{σ}^2 , h_{σ}^2 and T^2 were consequently unchanged (Table 1). Estimates of $V_{PI\sigma}$ and V_R were slightly smaller than those estimated by the non-spatial model, as was the estimated slope of the regression on female f , but age effects for both sexes were similar in both models (Table 1).

The mean overlap among 100-m² buffers around all 1040 breeding locations was 570 ± 280 m² (range 0–1298). When the resulting S matrix was fitted in the animal model, V_{Loc} was greater than zero, but smaller than that estimated by the grid model (Table 1). Consequently, the overlap model did not fit the data better than the non-spatial model (Table 1). All other variance components, $\text{Corr}_{A\sigma}$, h_{σ}^2 , h_{σ}^2 , T^2 and the sex-specific effects of

f and age were very similar to those estimated by the non-spatial model (Table 1).

The SAC model produced the lowest estimate of V_{Loc} , which was only marginally greater than zero (Table 1). This indicates that there is very little SAC in breeding date across Mandarte, consistent with Moran's I calculated from the raw phenotypic data (Fig. 3). The SAC model did not fit the data better than the non-spatial animal model (Table 1), and all other variance components, $\text{Corr}_{A\sigma}$, h_{σ}^2 , h_{σ}^2 , T^2 and sex-specific f and age effects were again very similar to those estimated by the non-spatial model (Table 1).

Discussion

Predicting microevolutionary change in life-history traits that are jointly expressed by interacting females and males requires estimation of female and male additive genetic variances, and the cross-sex genetic correlation, independent of environmental effects. However, these quantities have rarely been estimated for key life-history traits such as breeding date. We used long-term pedigree and phenology data from song sparrows to partition variance in breeding date into female (direct) and male (indirect) additive genetic variances and inbreeding effects, and fine-scale environmental variance associated with breeding location. We estimated significant female and male additive genetic variances, a strong positive cross-sex genetic correlation and inbreeding depression attributable to females, but not males. Variance associated with breeding location was small and, since location and relatedness were very weakly correlated, explicitly modelling location effects did not alter the estimated sex-specific additive genetic variances.

ADDITIVE GENETIC VARIANCES

While indirect genetic and environmental effects of parents on offspring are widely recognized (e.g. maternal effects), examples of indirect genetic effects operating among unrelated or distantly related individuals are rarer (Moore, Brodie & Wolf 1997; Wolf 2003; Hall, Lailvaux

& Brooks 2013; Edward *et al.* 2014; Reid *et al.* 2014a; Wolak & Reid 2016). Indeed, several studies estimating additive genetic variance in breeding date in wild vertebrate populations assume, either implicitly or explicitly, that breeding date is a sex-limited female trait (e.g. Réale *et al.* 2003a; Sheldon, Kruuk & Merilä 2003; Kruuk & Hadfield 2007; Caro *et al.* 2009; Saunders & Cuthbert 2014). Few studies have simultaneously estimated the indirect genetic effects of a females' mate on breeding date (Brommer & Rattiste 2008; Caro *et al.* 2009; Teplitsky *et al.* 2010; Liedvogel, Cornwallis & Sheldon 2012). Moreover, nonzero estimates of $V_{A\sigma}$ have only been reported in long-lived, monogamous species where male courtship feeding can advance female breeding date (Brommer & Rattiste 2008; Teplitsky *et al.* 2010). While our estimate of $V_{A\sigma}$ was lower than $V_{A\phi}$, it exceeded zero, showing that indirect genetic effects of socially paired males influenced female breeding date in a species without courtship feeding. Since both male and female song sparrows contribute to territory defence (Arcese 1989b) and breeding locations with better shelter and food resources can advance breeding date (Germain *et al.* 2015), males may affect breeding date by helping to defend a female's access to high-quality breeding locations.

Our estimate of a strong, positive cross-sex genetic correlation for breeding date also suggests that underlying alleles have congruent pleiotropic effects in both sexes and/or that sex-specific causal loci are tightly linked. Quantitative genetic theory consequently predicts that if there were selection for earlier breeding in both sexes, breeding date might initially evolve more rapidly than given a weaker or negative cross-sex genetic correlation, but genetic variation might be rapidly depleted (Moore, Brodie & Wolf 1997; Wolf *et al.* 1998). In contrast, Brommer & Rattiste (2008) estimated a strong negative cross-sex genetic correlation for breeding date and suggested that this potentially antagonistic genetic relationship might maintain genetic variation in similar natural populations. Other studies estimating female and male genetic variances in breeding date were unable to estimate meaningful cross-sex genetic correlations because one or both sex-specific variances did not differ from zero (Caro *et al.* 2009; Teplitsky *et al.* 2010; Liedvogel, Cornwallis & Sheldon 2012). Consequently, general conclusions regarding the patterns of sex-specific genetic variance in breeding date in natural populations, or the cross-sex genetic correlation, cannot yet be drawn. Our estimate of a strong, positive cross-sex genetic correlation for breeding date also contrasts with previous work suggesting that cross-sex correlations will be smaller or more negative for fitness components than for physiological or behavioural traits (Poissant, Wilson & Coltman 2010).

Phenotypic selection gradients suggest that there is consistent selection for earlier breeding in female song sparrows, because females that breed earlier have higher annual reproductive success (Wilson & Arcese 2003; Essak 2013) and because early-hatched offspring are more likely

to recruit to the breeding population (Hochachka 1990). However, in song sparrows and many other species, selection on male breeding date has yet to be estimated explicitly (but see Brommer & Rattiste 2008; Teplitsky *et al.* 2010). Unbiased male selection gradients are particularly hard to estimate in species where not all males breed, such as socially polygynous species or those with strongly male-biased adult sex ratios, because many males that do not express an observable breeding date also have low fitness (e.g. Hadfield 2008). Future studies of the microevolutionary dynamics of breeding date should therefore directly estimate additive genetic covariances between breeding date and components of female and male fitness, and hence directly predict the evolutionary responses to selection.

LOCATION VARIANCE

The degree to which variation in breeding date and other life-history traits stems from fine-scale (i.e. local) vs. broad-scale (i.e. regional) environmental variation is of intrinsic interest and must be modelled to minimize bias in estimated additive genetic variances (van der Jeugd & McCleery 2002; Kruuk & Hadfield 2007; Stopher *et al.* 2012). However, estimates of fine-scale environmental variance associated with individual location (V_{Loc}) can vary substantially with the method used and the spatial scale considered (Stopher *et al.* 2012). Different methods quantify different aspects of fine-scale environmental variation, meaning that there is no single ubiquitously best approach. We used three complimentary methods ('grid', 'overlap' and 'SAC') implemented across a range of ecologically relevant fine spatial scales spanning the study area, to estimate V_{Loc} in breeding date in song sparrows. Our results suggest that breeding location affected breeding date ('grid model'), that breeding attempts in immediately adjacent locations tended to commence on somewhat similar dates ('overlap model'), but that the overall SAC in breeding date was weak ('SAC' model). Figure 2 supports these results, showing that there is no clear island-wide pattern of spatial variation in breeding date. Indeed, all estimates of V_{Loc} were much smaller than the estimated among-year variance, which likely primarily reflects regional-scale environmental variation such as annual climate. Specifically, among-year variation in song sparrow breeding date is correlated with temperature and rainfall associated with the El Niño Southern Oscillation (Wilson & Arcese 2003). Overall, our analyses suggest that variance in breeding date due to fine-scale environmental effects associated with breeding location, and ultimately underlying habitat quality within the study system, is relatively small compared to female and male additive genetic variances and the total additive genetic variance measured by T^2 , and substantially smaller than broad-scale annual environmental variance. Unsurprisingly, therefore, our estimate of relatively small V_{Loc} contrasts with location effects estimated over larger geographic

areas or across more heterogeneous habitat. For instance, breeding location explained a large proportion of phenotypic variance in breeding date in piping plovers (*Charadrius melodus*) across the North American Great Lakes, with little additive genetic variance evident (Saunders & Cuthbert 2014). However, because dispersal distances in plovers ranged up to ~ 450 km (mean ~ 80 km), the estimated location variance may reflect geographic variation in temperature rather than the inherent properties of the breeding locations themselves (Saunders & Cuthbert 2014).

Our results further show that there is little correlation between breeding location and relatedness across Mandarte. In fact, the correlation was weakly negative, implying that across all generations combined, more closely related song sparrows bred very slightly further apart than less closely related individuals. This finding concurs with existing evidence that the kinship between female song sparrows and males on neighbouring territories does not differ markedly from that with males on more distant territories (Reid *et al.* 2015). Further, natal and breeding locations of song sparrows hatched on Mandarte are independent, showing that dispersal distance is approximately random with respect to relatedness within the study area (Arcese 1989a, b). Consequently, the additive genetic and location variances in breeding date were not confounded, and modelling location effects did not alter estimates of $V_{A\sigma}$ or $V_{A\sigma}$, the associated heritabilities or T^2 compared to the non-spatial model (Table 1). In contrast, other studies suggest that failing to model spatial covariances can cause additive genetic variances and heritabilities to be substantially overestimated, for example, in great tits (*P. major*, van der Jeugd & McCleery 2002) and red deer (*Cervus elaphus*, Stopher *et al.* 2012), where relatives tend to cluster within habitats, meaning that genetic and fine-scale environmental effects covary. However, Shaw & Shaw (2014) suggest that modelling such correlated effects might cause V_A to be underestimated. The song sparrow data set is therefore very well suited for distinguishing additive genetic and fine-scale spatial components of variance in breeding date (and other traits).

INBREEDING DEPRESSION

Direct inbreeding depression in female life-history traits is widely documented (e.g. Kruuk, Sheldon & Merilä 2002; Szulkin *et al.* 2007; Keller, Reid & Arcese 2008; Grueber *et al.* 2010), but indirect effects of male f on jointly expressed traits are rarely explicitly estimated in wild populations. In song sparrows, breeding date increased with female f , equating to a delay of about 7 days in females whose parents were first-order relatives ($f = 0.25$). However, females did not breed later when socially paired to an inbred male. This contrasts with experimental evidence that inbred social mates reduced the fitness of their outbred partners in burying beetles (Matthey & Smiseth 2015), suggesting that more studies are required to elucidate

general patterns. Meanwhile, the absence of an indirect effect of male f on female breeding date does not necessarily mean that there is no inbreeding depression in male breeding date. For example, on Mandarte, the typically male-biased adult sex ratio means that not all males can be socially paired for females' first annual breeding attempts (Sardell *et al.* 2010). Some of these males become socially paired for females' subsequent attempts, following within-season divorce or territory takeovers (Arcese 1989a), meaning that they have a very late breeding date. The total variation in male breeding date, spanning males that were and were not initially socially paired, may vary with male f and hence show inbreeding depression. However, because female breeding date substantially affects the population's total annual reproductive output (Wilson & Arcese 2003), the absence of an indirect effect of male f on female breeding date may reduce the overall effect of inbreeding on population growth rate and persistence.

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Data accessibility

Data deposited in the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.n0513> (Germain *et al.* 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Observation details of breeding date.

Appendix S2. Alternative versions of the ‘non-spatial’ model.

Appendix S3. Assessment of bias in additive genetic variance estimates.

Appendix S4. Alternative versions of the ‘grid’ model.

Appendix S5. Alternative versions of the ‘overlap’ model.

Appendix S6. Details of the ‘spatial autocorrelation’ model.