1   **Individual repeatability and heritability of divorce in a wild population**

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24 **ABSTRACT**

25 Understanding micro-evolutionary responses of mating systems to contemporary selection

26 requires estimating sex-specific additive genetic variances and cross-sex genetic covariances in

27 key reproductive strategy traits. One key trait comprises the occurrence of divorce versus mate-

28 fidelity across sequential reproductive attempts. If divorce represents an evolving behavioural

29 strategy it must have non-zero individual repeatability and heritability, but quantitative estimates

30 from wild populations are scarce. We used 39 years of individual breeding records and pedigree

31 data from free-living song sparrows (*Melospiza melodia*) to quantify sex-specific permanent

32 individual and additive genetic variances, and hence estimate repeatability and heritability, in

33 liability for divorce. We estimated moderate repeatability in females, but little repeatability in

34 males. Estimates of additive genetic variance were small in both sexes, and the cross-sex genetic

35 covariance was close to zero. The total heritability was likely non-zero but small, indicating low

36 potential for micro-evolutionary response to selection. Rapid micro-evolution of divorce rate

37 therefore appears unlikely, even if there were substantial fitness benefits of divorce and resulting

38 selection.

INTRODUCTION

Pair-bond resilience, resulting from mate-fidelity (i.e. maintaining pair-bonds over multiple breeding attempts) versus divorce (i.e. dissolving pair-bonds to re-pair with a new mate) [1,2], is a key feature of animal mating systems [3] that results from sexual selection and can fundamentally influence the distribution of offspring across parents and the resulting population-wide distribution of fitness. Divorce occurs in numerous taxa and may increase individual fitness by counter-acting constraints on initial mate choice, and hence be adaptive [2,4]. However, if there is to be ongoing adaptive micro-evolution of divorce rate [2,5–7], then individual liability for divorce must vary consistently among individuals (i.e., have non-zero individual repeatability) and have non-zero heritability.

In general, repeatable expression of mating and reproductive traits implies that selection may act consistently on individuals over their lifetimes, and defines the maximum possible heritability [8,9]. Decomposing phenotypic variance into repeatable individual variance (V_I), additive genetic variance (V_A), and environmental variance allows estimation of heritability and, in principle, indicates the potential for micro-evolutionary responses to selection [10]. However, divorce represents an interesting class of jointly-expressed traits that require female-male interactions, and hence can be influenced by genetic effects of both sexes. Further, correlated expression of sex-specific genetic effects, leading to non-zero cross-sex genetic covariance ($COV_{A\female\male}$), can generate evolutionary sexual conflict (e.g. [11]). Understanding the evolutionary causes and consequences of divorce therefore requires explicit estimation of sex-specific V_A ($V_{A\female}$ and $V_{A\male}$), and $COV_{A\female\male}$, in populations experiencing un-manipulated natural and sexual selection environments.

61   Analytical advances mean that $V_{A\female}$, $V_{A\male}$, and $COV_{A\female\male}$ underlying jointly-expressed

62   traits can be estimated from complex relatedness structures arising in wild populations (e.g.[10]).

63   Since divorce versus mate-fidelity represent alternative outcomes of pairing decisions across

64   consecutive breeding attempts, divorce is appropriately modelled as a 'threshold trait', where

65   breeding pairs' underlying continuous liabilities for divorce translate into expression at some

66   threshold (e.g. [12]). Such models also permit estimation of 'total heritability' of divorce, which

67   represents the overall potential for micro-evolutionary responses to selection on the population-

68   wide distribution of liabilities [13]. Such analyses require phenotypic observations of divorce

69   versus mate-fidelity, conditional on survival between consecutive breeding attempts, from

70   diverse relatives [14]. We use 39 years of comprehensive observations of free-living song

71   sparrows (*Melospiza melodia*) to estimate (*i*) population-level divorce rate, (*ii*) $V_{A\female}$, $V_{A\male}$ and

72    $COV_{A\female\male}$ in divorce, and (*iii*) individual repeatability and the sex-specific and total heritability,

73   thereby assessing the potential for ongoing evolution of this reproductive strategy.

74

MATERIAL AND METHODS

76   A resident population of individually colour-ringed song sparrows on Mandarte Island, Canada

77   has been intensively studied since 1975. All individuals alive in late April (typical start of

78   breeding [15]) are recorded in a comprehensive census to determine over-winter survival and

79   pairing status (re-sighting probability >0.99 [16]), and all breeding attempts are closely

80   monitored (Electronic Supplemental Material S1). Females and males form socially persistent

81   pairings that cooperate to rear offspring (1–4 broods per year), but can form new pairings within

82   and between breeding seasons following divorce or mate-death.

83   To identify cases of divorce versus mate-fidelity, we extracted each female's lifetime

84   sequence of breeding events (≥1 egg laid) where re-pairing could have occurred (i.e. she initiated

85   a subsequent breeding event) and categorized these events as divorce, mate-fidelity or mate-

86   death according to the fate of the pair-bond and whether her current mate was still alive during

87   her subsequent event (ESMS1). Instances of mate-death were identified from daily field

88   observations and the April census, and excluded from our dataset.

89   We fitted two generalized linear mixed models to decompose total variance in liability for

90   divorce into permanent individual and additive genetic components. Model 1 estimated variances

91   attributable to permanent effects of individual females ($V_{I♀}$), males ($V_{I♂}$), social pairs (V_S), and

92   the year when a focal breeding event occurred (V_Y). Model 2 utilised comprehensive pedigree

93   information (ESMS2) to additionally estimate $V_{A♀}$, $V_{A♂}$, and $COV_{A♀♂}$ in liability for divorce

94   (i.e. an 'animal model' [10]). $COV_{A♀♂}$ is the covariance between additive genetic effects of

95   alleles expressed in all females versus all males, not the genetic covariance between a female and

96   her socially-paired mate (e.g. [15,17]; ESMS3). Fixed effects were restricted to a two-level

97   factor that defined whether an observation spanned breeding events separated by the non-

98   breeding season ('between-season') versus consecutive events within the same season ('within-

99   season', ESMS1) and separate regressions on female and male individual coefficients of

100   inbreeding (*f*) (Model 2 only), thereby estimating inbreeding depression in liability for divorce

101   and minimising any associated bias in estimated V_A [18]. Phenotypic observations were

102   restricted to individuals with known grandparents to minimise under-estimation of *f* (ESMS3).

103   Sex-specific repeatabilities in liability for divorce were estimated from Model 1 as:

104
$$Repeatability = \frac{V_I}{V_{P\_Model1}}$$

105   Sex-specific heritabilities (h^2) were estimated from Model 2 as:

106
$$h^2 = \frac{V_A}{V_{P\_Model2}}$$

107   The 'total heritability' (T^2) was calculated from Model 2 as:

108
$$T^2 = \frac{V_{A♀} + V_{A♂} + 2(COV_{A♀♂})}{V_{P\_Model2}}$$

109   Total variance in liability ($V_{P\_Model\ 1}$, $V_{P\_Model\ 2}$) was calculated separately for each model

110   (ESMS3). Models were fitted using Bayesian inference in R. Posterior distributions of

111   repeatabilities, heritabilities, and T^2 were calculated from marginal posterior distributions of

112   underlying variance components. We report liability-scale posterior modes, means and 95%

113   credible intervals (95%CI) from 5000 posterior samples. Estimates were obtained using

114   uninformative priors and were robust to alternative model specifications (ESMS5).

115

RESULTS

117   There were 1,419 breeding events where divorce could have occurred, involving 566 unique

118   social pairings among 358 females and 341 males. Divorce occurred on 166 (11.7%) occasions

119   (details in ESMS1).

120   Model 1 revealed that the largest component of variance in liability for divorce was

121     $V_{I♀}$, while $V_{I♂}$ was comparatively small (table 1, ESMS4). Because V_S and V_Y were also small,

122   female repeatability for divorce was moderate (~16%; table 1). The lower 95%CI limit

123   converged towards zero, but 98% of the posterior distribution exceeded 0.01, departing from the

124   prior distribution (figure 1a), and indicating that female repeatability is most likely greater than

125   zero. In contrast, male repeatability was smaller (table 1); only 76% of the posterior distribution

126   exceeded 0.01 (figure 1b). Divorce was less likely to occur within- than between-seasons (table

127   1).

128   Model 2 showed that $V_{A\female}$ and $V_{A\male}$ in liability for divorce were both small, and

129    $COV_{A\female\male}$ was estimated as close to zero (table 1, ESMS4). Sex-specific heritabilities were

130   therefore small for both females and males, yet noticeably different from the prior distributions

131   (particularly at the posterior means, figure 2a,b). However, $V_{A\female}$, $V_{A\male}$, and $COV_{A\female\male}$ still

132   combine to generate a small but likely non-zero total heritability (T^2) for divorce (table 1); 92%

133   of the posterior distribution exceeded 0.01 (ESMS5), again deviating from the prior distribution

134   (figure 2c). Liability for divorce tended to increase with increasing f, especially in females, but

135   the 95%CIs overlapped zero (table 1).

136

137   **DISCUSSION**

138   The ~12% divorce rate observed in song sparrows is relatively low compared to other temperate-

139   breeding passerine birds (~20–50%; [14,19,20]). However, there was evidence of moderate $V_{I\female}$

140   and hence female repeatability, but lower $V_{I\male}$ and male repeatability, in liability for divorce

141   (figure 1a,b, ESMS4). These estimates imply that sex-specific h^2 is not *a priori* zero. However,

142   h^2 was estimated to be small in both sexes.

143   Most previous quantitative genetic analyses of divorce come from human twin-studies,

144   and show relatively high heritabilities when divorce is defined as a sex-specific trait (e.g. 0.3–0.6

145   [21,22]). However, such estimates may be inflated by shared environmental and cultural effects

146   [10], and often only consider whether individuals ever divorced over their lifetime. Our focus on

147   sequential breeding events, considering among-individual variances across repeat observations,

148   allows estimation of individual repeatability as well as pair and year variances, which account

149   for population or environmental changes that could otherwise bias heritability estimates. The

150   only previous quantitative genetic analysis of divorce in a wild (non-human) population,

151   similarly estimated low female heritability in savannah sparrows (*Passerculus sandwichensis*)

152   [14]. Because [14] could not distinguish their estimate of repeatability for divorce in males from

153   zero, heritability estimates were restricted to females and did not consider potential contributions

154   of $V_{A\male}$ or $COV_{A\female\male}$. Our results suggest that both song sparrow sexes contribute to the total

155   additive genetic variance, and hence to the total heritability for divorce (T^2). Thus the overall

156   potential for micro-evolutionary responses to selection in this reproductive strategy is greater

157   when considering the interactive effects of the sexes jointly than when considering a single sex

158   alone.

159   Many studies have investigated the potential costs and benefits of divorce in wild

160   populations, particularly in socially-monogamous birds (reviews: [2,4,6]). While divorce is

161   generally considered adaptive in terms of improving an individual's subsequent breeding success

162   under certain conditions [2,4], responses to selection and hence ongoing micro-evolution require

163   contemporary V_A. Our results indicate that such V_A, and consequent potential for evolutionary

164   response to selection, may be smaller than is often implicitly assumed [2,5–7]. Further, low

165   divorce rates will intrinsically limit the intensity of selection [12]. Overall, rapid and marked

166   micro-evolutionary changes in the frequency of divorce appear unlikely, even if divorce were

167   beneficial for one or both members of a breeding pair.

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Ethics

171 All field procedures approved by the University of British Columbia Animal Care Committee

172 ethical review (certificates UBCACC A12-0229 and A14-0336).

173

Data accessibility

175 Data are available from Dryad (doi: upon acceptance).

176

Authors' contributions

178 RRG and MEW designed the study and conducted analyses with input from JMR, all authors

179 contributed to writing.

180

Competing interests

182 We declare no competing interests.

183

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245

246   **Table 1**: Marginal posterior modes, means and 95%CIs from models decomposing the liability

247   for divorce. V_I and V_A represent permanent individual and additive genetic variances for females

248   (♀) and males (♂). $COV_{A♀♂}$ is the cross-sex genetic covariance. V_S and V_Y are the social pair

249   and year variances, respectively. Posterior statistics for sex-specific repeatabilities and

250   heritabilities (h^2), 'total heritability' (T^2), fixed effects of within- versus between-season and

251   regressions on individual female or male coefficient of inbreeding (f) are also shown.

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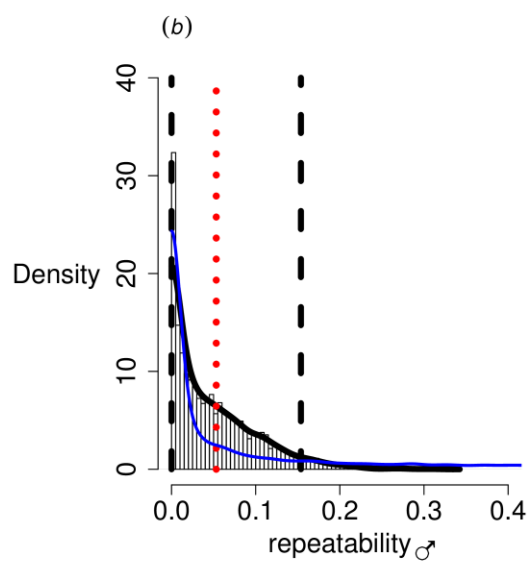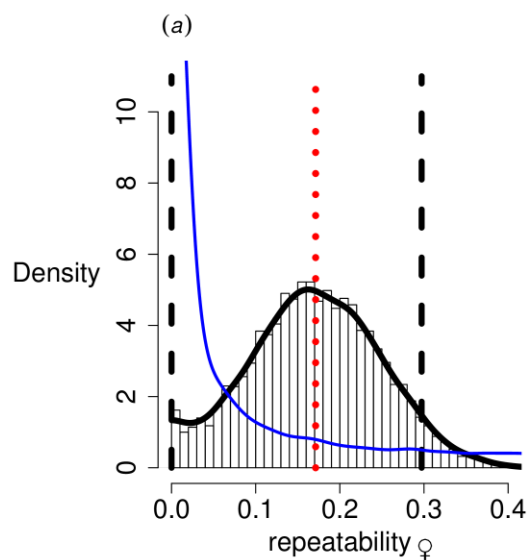|	Model 1		Model 2	
	mode, mean	95%CI	mode, mean	95%CI
variance components				
$V_{I♀}$	0.24, 0.28	4×10^{-6}, 0.53	0.003, 0.22	6×10^{-7}, 0.48
$V_{I♂}$	0.001, 0.09	5×10^{-8}, 0.26	0.002, 0.08	$4.\times10^{-8}$, 0.25
V_S	0.001, 0.14	2×10^{-9}, 0.46	0.003, 0.15	4×10^{-8}, 0.48
V_Y	0.001, 0.07	4×10^{-7}, 0.19	0.001, 0.07	8×10^{-9}, 0.19
$V_{A♀}$			0.001, 0.07	5×10^{-9}, 0.25
$V_{A♂}$			0.001, 0.08	4×10^{-8}, 0.21
$COV_{A♀♂}$			-0.0002, -0.003	-0.08, 0.06
variance ratios				
repeatability♀	0.16, 0.17	3×10^{-6}, 0.30		
repeatability♂	0.001, 0.05	3×10^{-8}, 0.15		
$h^2_♀$			0.001, 0.04	2×10^{-9}, 0.14
$h^2_♂$			0.001, 0.04	3×10^{-8}, 0.12
T^2			0.02, 0.08	1×10^{-4}, 0.20
fixed effects				
intercept	-0.64, -0.66	-0.89, -0.44	-0.81, -0.90	-1.28, -0.59
within-season	-1.08, -1.10	-1.34, -0.85	-1.11, -1.12	-1.37, -0.87
$f_♀$			1.92, 1.98	-0.66, 4.45
$f_♂$			0.59, 0.94	-1.72, 3.61

253

254 **Figure 1.** Marginal posterior samples (bars), density (solid black line), mean (red dotted line)

255 and 95%CI limits (dashed lines) of sex-specific repeatabilities for divorce in (*a*) female and (*b*)

256 male song sparrows. Blue lines illustrate prior distributions (ESMS5).

257 **Figure 2.** Marginal posterior distributions for (*a*) female and (*b*) male heritabilities (h^2), and (*c*)

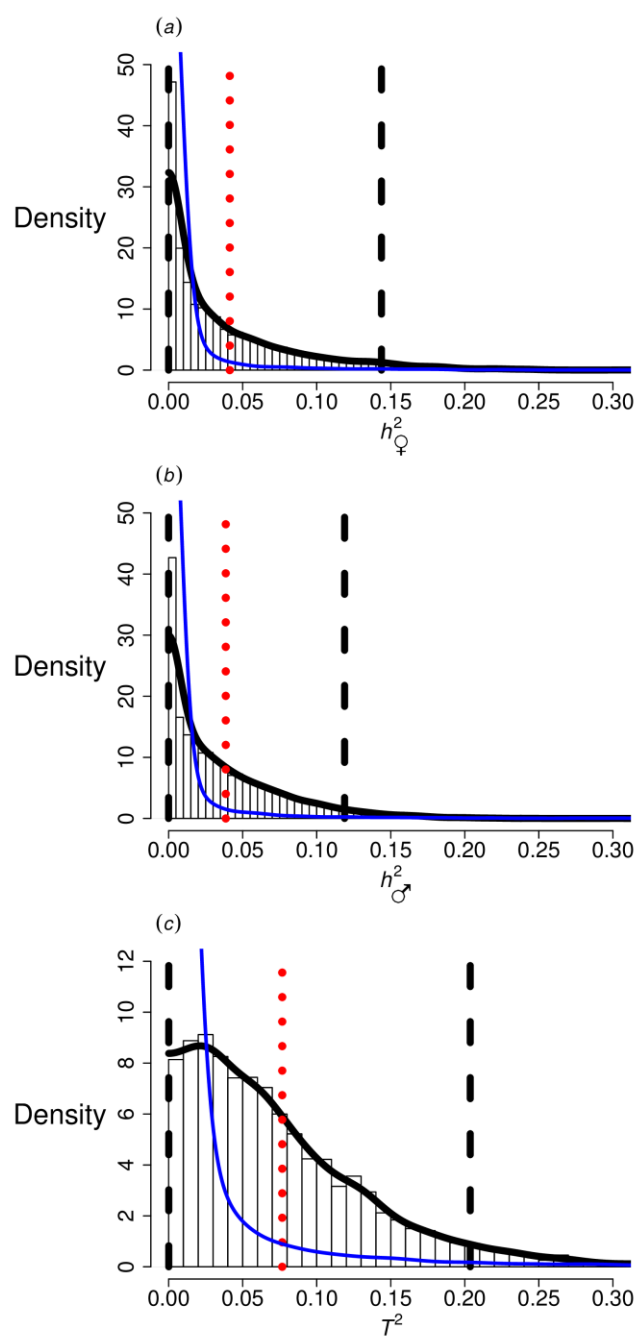258 the total heritability (T^2) for divorce in song sparrows. See figure 1 for plot description.

259

260   Figure 1

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264   Figure 2

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