Research

Cite this article: Germain RR, Wolak ME, Reid JM. 2018 Individual repeatability and heritability of divorce in a wild population. *Biol. Lett.* **14**: 20180061.
<http://dx.doi.org/10.1098/rsbl.2018.0061>

Received: 27 January 2018
Accepted: 16 May 2018

Subject Areas:

behaviour, evolution, ecology

Keywords:

indirect genetic effects, mating system
evolution, social monogamy, quantitative
genetics

Authors for correspondence:

Ryan R. Germain
e-mail: ryan.r.germain@gmail.com
Matthew E. Wolak
e-mail: matthew.wolak@auburn.edu

[†]Present address: Lab of Ornithology, Cornell University, Ithaca, NY, USA.

^{*}Present address: Department of Biological Sciences, Auburn University, Auburn, AL, USA.

[¶]These authors contributed equally to this work.

Electronic supplementary material is available online at <http://dx.doi.org/10.6084/m9.figshare.c.4111487>.

Evolutionary biology

Individual repeatability and heritability of divorce in a wild population

Ryan R. Germain^{†,¶}, Matthew E. Wolak^{*,¶} and Jane M. Reid

School of Biological Sciences, University of Aberdeen, Aberdeen, UK

^{id} RRG, 0000-0002-2473-0070; MEW, 0000-0002-7962-0071; JMR, 0000-0002-5007-7343

Understanding micro-evolutionary responses of mating systems to contemporary selection requires estimating sex-specific additive genetic variances and cross-sex genetic covariances in key reproductive strategy traits. One key trait comprises the occurrence of divorce versus mate fidelity across sequential reproductive attempts. If divorce represents an evolving behavioural strategy that responds to selection it must have non-zero individual repeatability and heritability, but quantitative estimates from wild populations are scarce. We used 39 years of individual breeding records and pedigree data from free-living song sparrows (*Melospiza melodia*) to quantify sex-specific permanent individual and additive genetic variances, and hence estimate repeatability and heritability, in liability for divorce. We estimated moderate repeatability among females, but little repeatability among males. Estimates of additive genetic variance were small in both sexes, and the cross-sex genetic covariance was close to zero. Consequently, the total heritability was small but likely non-zero, indicating low potential for micro-evolutionary response to selection. Rapid micro-evolutionary change of divorce rate, therefore, appears unlikely, even if there were substantial fitness benefits of divorce and resulting selection.

1. 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), is a key feature of animal mating systems and outcome of sexual selection [1,2]. Such resilience can fundamentally influence the distribution of offspring across parents and resulting population-wide variance in fitness.

Divorce occurs in numerous socially monogamous taxa and may increase individual fitness by counteracting constraints on initial mate choice, and hence be adaptive [2,3]. However, for there to be ongoing micro-evolution of divorce rate in response to selection [2,4–6], liability for divorce must have non-zero heritability and hence vary consistently among individuals (i.e. have non-zero repeatability).

In general, repeatable expression of mating and reproductive traits implies that selection could act consistently on individuals, and typically defines the maximum possible heritability [7,8]. Decomposing total phenotypic variance into permanent (i.e. repeatable) individual variance (V_I), additive genetic variance (V_A) and environmental variance allows estimation of heritability and indicates the potential for micro-evolutionary responses to contemporary selection [9]. However, divorce represents an interesting jointly expressed (i.e. 'emergent') trait that results from female–male interactions and can be simultaneously influenced by genetic and non-genetic effects of both pair members. Further, correlated effects of genotypes, when expressed in females versus males, create non-zero cross-sex genetic covariance ($COV_{A\phi\sigma}$) and can generate evolutionary sexual conflict over divorce [10]. Such non-zero $COV_{A\phi\sigma}$ alters

the contributions of sex-specific genetic effects to the phenotypic and total additive genetic variances in divorce rate, and alters the potential for evolutionary responses to sex-specific selection resulting from the fitness consequences of divorce [11]. Understanding the evolutionary dynamics of divorce, and the implications for other co-evolving reproductive behaviours contributing to mating systems, therefore requires explicit estimation of sex-specific V_I ($V_{I\varnothing}$ and $V_{I\sigma}$), V_A ($V_{A\varnothing}$ and $V_{A\sigma}$) and $\text{COV}_{A\varnothing\sigma}$, in divorce in populations experiencing un-manipulated natural and sexual selection environments.

Advances in quantitative genetic methods mean that $V_{A\varnothing}$, $V_{A\sigma}$ and $\text{COV}_{A\varnothing\sigma}$ underlying emergent traits can be estimated given complex relatedness structures arising in wild populations [9]. Since divorce versus mate fidelity represent alternative phenotypic outcomes of pairing decisions across consecutive breeding attempts, divorce is appropriately modelled as a ‘threshold trait’, where breeding pairs’ underlying continuous joint liabilities for divorce translate into expression at some threshold (e.g. [12]). Such models also permit estimation of ‘total heritability’ of divorce, resulting from the combination of $V_{A\varnothing}$, $V_{A\sigma}$ and $\text{COV}_{A\varnothing\sigma}$ [13], which represents the overall potential for micro-evolutionary responses to selection on the population-wide distribution of liabilities [11]. Such analyses require phenotypic observations of divorce versus mate fidelity, conditional on survival between consecutive breeding attempts, from diverse relatives [14]. We use 39 years of comprehensive observations of free-living song sparrows (*Melospiza melodia*) to estimate (i) population-level divorce rate, (ii) $V_{I\varnothing}$, $V_{I\sigma}$, $V_{A\varnothing}$, $V_{A\sigma}$ and $\text{COV}_{A\varnothing\sigma}$ in divorce and (iii) individual repeatability and the sex-specific and total heritability, thereby assessing the potential for ongoing evolution of divorce as a key reproductive strategy.

2. Material and methods

A resident population of individually colour-ringed song sparrows on Mandarte Island, Canada has been intensively studied since 1975. Each year, all individuals alive in late April (typical start of breeding [15]) are recorded in a comprehensive census to determine over-winter survival and pairing status (re-sighting probability greater than 0.99 [16]), and all breeding attempts are closely monitored (electronic supplementary material, S1). Females and males form socially persistent pairings and jointly rear offspring (1–4 broods per year), but can form new pairings within and between breeding seasons following divorce or mate death.

To identify cases of divorce versus mate fidelity, we extracted each female’s lifetime sequence of breeding events (one or more eggs laid) where re-pairing could have occurred (i.e. she initiated a subsequent breeding event) and categorized these events as divorce (i.e. paired with a different mate for her subsequent breeding event when mate death did not occur), mate fidelity or mate death according to the pair-bond’s fate (electronic supplementary material, S1). Instances of mate death were identified from daily field observations and April censuses and excluded from our dataset.

We fitted two generalized linear mixed models to decompose total variance in pair liability for divorce. Model 1 estimated variances attributable to $V_{I\varnothing}$, $V_{I\sigma}$ and of unique female–male social pairings (V_S), and the year when a focal breeding event occurred (V_Y). Model 2 additionally estimated $V_{A\varnothing}$, $V_{A\sigma}$ and $\text{COV}_{A\varnothing\sigma}$ in pair liability for divorce, using comprehensive pedigree data to quantify relatedness (i.e. an ‘animal

model’ [9]; electronic supplementary material, S2). $\text{COV}_{A\varnothing\sigma}$ is the covariance between additive genetic effects of alleles expressed in all females versus all males, not the genetic covariance between a female and her socially paired mate (e.g. [15,17]; electronic supplementary material, S3). Thus, both models treat divorce as an emergent trait of the breeding pair and do not specify sex-specific effects as ‘direct’ or ‘indirect’ (electronic supplementary material, S3). Our current aim was to partition the total naturally occurring variation in liability for divorce and thereby appropriately estimate heritability, not to explain variation in the occurrence of divorce. Fixed effects were consequently restricted to a two-level factor that defined whether an observation of divorce versus mate fidelity spanned breeding events separated by the non-breeding season (between-season) versus consecutive events within the same season (‘within-season’; electronic supplementary material, S1) and separate regressions on female and male individual coefficients of inbreeding (f , model 2 only), thereby estimating inbreeding depression in liability for divorce and minimizing any associated bias in estimated V_A [18].

Sex-specific repeatabilities in liability for divorce were estimated from model 1 as

$$\text{Repeatability}_{\varnothing} = \frac{V_{I\varnothing}}{V_{P,\text{Model1}}} \quad \text{and} \quad \text{Repeatability}_{\sigma} = \frac{V_{I\sigma}}{V_{P,\text{Model1}}}.$$

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

$$h_{\varnothing}^2 = \frac{V_{A\varnothing}}{V_{P,\text{Model2}}} \quad \text{and} \quad h_{\sigma}^2 = \frac{V_{A\sigma}}{V_{P,\text{Model2}}}.$$

The ‘total heritability’ (T^2) was calculated from model 2 as:

$$T^2 = \frac{V_{A\varnothing} + V_{A\sigma} + 2(\text{COV}_{A\varnothing\sigma})}{V_{P,\text{Model2}}}.$$

The total variance in liability ($V_{P,\text{Model1}}$, $V_{P,\text{Model2}}$) was calculated separately for each model (electronic supplementary material, S3). Models were fitted using Bayesian inference in R [19] with relatively uninformative priors (electronic supplementary material, S5). Posterior distributions of repeatabilities, heritabilities and T^2 were calculated from marginal posterior distributions of underlying variance components. We report liability-scale posterior modes, means and 95% credible intervals (CI) from 5000 posterior samples, and present prior distributions alongside posteriors to facilitate inference. Estimates and conclusions were robust to alternative model specifications (electronic supplementary material, S5).

3. Results

There were 1419 breeding events where divorce could have occurred, involving 566 unique social pairings among 358 females and 341 males. Divorce occurred on 166 (11.7%) occasions (details in electronic supplementary material, S1).

Model 1 revealed that the largest component of variance in overall liability for divorce was $V_{I\varnothing}$, while $V_{I\sigma}$ was comparatively small (table 1; electronic supplementary material, S4). Because V_S and V_Y were also small, female repeatability for divorce was moderate (approx. 16%; table 1). The lower 95% CI limit converged towards zero, but 98% of posterior samples exceeded 0.01, departing from the prior distribution (figure 1a) and indicating that female repeatability is most likely greater than zero. By contrast, male repeatability was smaller (table 1); only 76% of posterior samples exceeded 0.01 (figure 1b). Divorce was less likely to occur within a breeding season than between seasons (table 1).

Figure 1. Marginal posterior samples (bars), density (solid black line), mean (red dotted line) and 95% CI limits (dashed lines) of sex-specific repeatabilities for divorce in (a) female and (b) male song sparrows. Blue lines illustrate prior distributions (electronic supplementary material, S5). Areas where the posterior density exceeds the prior density highlight parameter values that are likely supported by the data.

Table 1. Marginal posterior modes, means and 95% CIs from models decomposing total variance in liability for divorce. V_I and V_A represent permanent individual and additive genetic variances for females (♀) and males (♂). $\text{COV}_{A\text{♀}\text{♂}}$ is the cross-sex genetic covariance. V_S and V_Y are the social pair and year variances, respectively. Posterior statistics for sex-specific repeatabilities and heritabilities (h^2), 'total heritability' (T^2), fixed effects of within-season versus between-season (intercept) and regressions on individual female or male coefficient of inbreeding (f) are also shown.

	model 1		model 2	
	mode, mean	95% CI	mode, mean	95% CI
variance components				
$V_{I\text{♀}}$	0.24, 0.28	4×10^{-6} , 0.53	0.003, 0.22	6×10^{-7} , 0.48
$V_{I\text{♂}}$	0.001, 0.09	5×10^{-8} , 0.26	0.002, 0.08	4×10^{-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
$V_{A\text{♀}}$			0.001, 0.07	5×10^{-9} , 0.25
$V_{A\text{♂}}$			0.001, 0.08	4×10^{-8} , 0.21
$\text{COV}_{A\text{♀}\text{♂}}$			−0.0002, −0.003	−0.08, 0.06
variance ratios				
repeatability $_{\text{♀}}$	0.16, 0.17	3×10^{-6} , 0.30		
repeatability $_{\text{♂}}$	0.001, 0.05	3×10^{-8} , 0.15		
$h^2_{\text{♀}}$			0.001, 0.04	2×10^{-9} , 0.14
$h^2_{\text{♂}}$			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
$f_{\text{♀}}$			1.92, 1.98	−0.66, 4.45
$f_{\text{♂}}$			0.59, 0.94	−1.72, 3.61

Model 2 showed that $V_{A\text{♀}}$ and $V_{A\text{♂}}$ in liability for divorce were both small, and $\text{COV}_{A\text{♀}\text{♂}}$ was estimated as close to zero (table 1; electronic supplementary material, S4). Sex-specific heritabilities were, therefore, small for both females and males. However, posterior distributions departed from the priors, with higher density at higher values (e.g. at the posterior means, figure 2a,b) implying that heritabilities, and underlying $V_{A\text{♀}}$ and $V_{A\text{♂}}$, exceed zero. Indeed, $V_{A\text{♀}}$, $V_{A\text{♂}}$ and $\text{COV}_{A\text{♀}\text{♂}}$

combined to generate a small but likely non-zero total heritability (T^2) for divorce (table 1); 92% of posterior samples exceeded 0.01. This again deviates from the prior distribution (figure 2c), and from the posterior distribution that would have resulted given zero $V_{A\text{♀}}$, $V_{A\text{♂}}$ and hence T^2 (electronic supplementary material, S5). Liability for divorce tended to increase with increasing individual coefficient of inbreeding (f), especially in females, but the 95% CIs overlapped zero (table 1).

Figure 2. Marginal posterior distributions for (a) female and (b) male heritabilities (h^2), and (c) the total heritability (T^2) for divorce in song sparrows. See figure 1 for plot description.

4. Discussion

The approximately 12% divorce rate observed in song sparrows is relatively low compared to other temperate-breeding passerine birds (approx. 20–50%; [14,20,21]). However, there was evidence of moderate $V_{1\varnothing}$ and hence female repeatability, but lower $V_{1\sigma}$ and male repeatability, in liability for divorce (figure 1a,b; electronic supplementary material, S4). These estimates imply that sex-specific h^2 is not *a priori* zero (i.e. given zero repeatability). However, in practice, h^2 was estimated to be small in both sexes.

Most previous quantitative genetic analyses of divorce come from human twin studies and show relatively high heritabilities with divorce defined as a sex-specific trait (e.g. 0.3–0.6 [22,23]). However, such estimates may be inflated by shared environmental and cultural effects [9], and often only consider whether individuals ever divorced over their lifetime. Our focus on sequential breeding events,

considering among-individual variances across repeat observations, allows estimation of individual repeatability as well as pair and year variances, which encompass variances stemming from ecological and/or social environmental effects that could influence the occurrence of divorce. The only previous quantitative genetic analysis of divorce in a wild (non-human) population also estimated low female heritability in savannah sparrows (*Passerculus sandwichensis*) [14]. Because Wheelwright & Teplitsky's [14] estimate of male repeatability for divorce was not distinguishable from zero, heritability estimates were restricted to females and did not consider potential contributions of $V_{A\sigma}$ or $COV_{A\varnothing\sigma}$. Our results suggest that sex-specific genetic effects expressed in both sexes contribute to the total additive genetic variance, and hence to the total heritability for divorce (T^2) in song sparrows. Indeed small, potentially undetectable, effects in each sex can combine to generate detectable total T^2 [13]. Thus, the overall apparent potential for micro-evolutionary responses to selection on divorce is greater when considering the interactive effects of the sexes jointly (i.e. considering divorce as an emergent trait) than when considering either sex alone.

Many studies have investigated the potential costs and benefits of divorce in wild populations, particularly in socially monogamous birds (for reviews, see [2,3,5]). Divorce is generally considered to be adaptive, and increases an individual's subsequent breeding success and hence fitness under certain conditions [2,3]. However, ongoing micro-evolutionary responses to such contemporary selection require V_A . Our results indicate that such V_A , and consequent potential for evolutionary response to selection, while probably non-zero, is smaller than is often implicitly assumed [2,4–6]. Further, relatively low divorce rates, such as observed in song sparrows, will intrinsically limit the intensity of selection [12]. Overall, rapid and marked micro-evolutionary changes in the frequency of divorce appear unlikely, even if divorce was beneficial for one or both sexes. Consequently, there is also limited potential for genetic covariance between liability for divorce and other key reproductive strategy traits, such as female extra-pair reproduction (EPR), negating the suggestion that divorce and EPR both represent manifestations of an underlying 'weak-pair' syndrome [24] and limiting the potential for indirect selection.

Ethics. All field procedures are approved by the University of British Columbia Animal Care Committee ethical review (certificates UBCACC A12-0229 and A14-0336).

Data accessibility. Data and code are available as the electronic supporting information.

Authors' contributions. R.R.G. and M.E.W. designed the study and conducted analyses with input from J.M.R. All authors contributed to writing, agree to be held accountable for all aspects of the work and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

Funding. All authors were supported by a European Research Council grant to J.M.R. Fieldwork was supported by the Natural Sciences and Engineering Research Council of Canada and the University of British Columbia.

Acknowledgements. We thank the Tsawout and Tseycum First Nation bands for access to Mandarte, Peter Arcese, Lukas Keller, Pirmin Nietlisbach and the University of Aberdeen Maxwell High Performance Computing cluster.

- Black JM. 1996 *Partnerships in birds—the study of monogamy*. Oxford, UK: Oxford University Press.
- Culina A, Radersma R, Sheldon BC. 2015 Trading up: the fitness consequences of divorce in monogamous birds. *Biol. Rev.* **90**, 1015–1034. (doi:10.1111/brv.12143)
- Dubois F, Cézilly F. 2002 Breeding success and mate retention in birds: a meta-analysis. *Behav. Ecol. Sociobiol.* **52**, 357–364. (doi:10.1007/s00265-002-0521-z)
- Diamond JM. 1987 A Darwinian theory of divorce. *Nature* **329**, 765–766. (doi:10.1038/329765a0)
- Choudhury S. 1995 Divorce in birds: a review of the hypotheses. *Anim. Behav.* **50**, 413–429. (doi:10.1006/anbe.1995.0256)
- McNamara JM, Forslund P. 1996 Divorce rates in birds: predictions from an optimization model. *Am. Nat.* **147**, 609–640. (doi:10.1086/285869)
- Boake CRB. 1989 Repeatability: its role in evolutionary studies of mating behavior. *Evol. Ecol.* **3**, 173–182. (doi:10.1007/BF02270919)
- Dingemanse NJ, Dochtermann NA. 2013 Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J. Anim. Ecol.* **82**, 39–54. (doi:10.1111/1365-2656.12013)
- Kruuk LEB. 2004 Estimating genetic parameters in natural populations using the 'animal model'. *Phil. Trans. R. Soc. Lond. B* **359**, 873–890. (doi:10.1098/rstb.2003.1437)
- Bonduriansky R, Chenoweth SF. 2009 Intralocus sexual conflict. *Trends Ecol. Evol.* **24**, 280–288. (doi:10.1016/J.TREE.2008.12.005)
- Bijma P. 2011 A general definition of the heritable variation that determines the potential of a population to respond to selection. *Genetics* **189**, 1347–1359. (doi:10.1534/genetics.111.130617)
- Roff DA. 1996 The evolution of threshold traits in animals. *Q. Rev. Biol.* **71**, 3–35. (doi:10.1086/419266)
- Bijma P, Muir WM, Van Arendonk JAM. 2007 Multilevel selection 1: quantitative genetics of inheritance and response to selection. *Genetics* **175**, 277–288. (doi:10.1534/genetics.106.062711)
- Wheelwright NT, Teplitsky C. 2017 Divorce in an island bird population: causes, consequences, and lack of inheritance. *Am. Nat.* **190**, 557–569. (doi:10.1086/693387)
- Germain RR, Wolak ME, Arcese P, Losdat S, Reid JM. 2016 Direct and indirect genetic and fine-scale location effects on breeding date in song sparrows. *J. Anim. Ecol.* **85**, 1613–1624. (doi:10.1111/1365-2656.12575)
- Wilson S, Norris DR, Wilson AG, Arcese P. 2007 Breeding experience and population density affect the ability of a songbird to respond to future climate variation. *Proc. R. Soc. B* **274**, 2539–2545. (doi:10.1098/rspb.2007.0643)
- Wolak ME, Reid JM. 2016 Is pairing with a relative heritable? Estimating female and male genetic contributions to the degree of biparental inbreeding in song sparrows (*Melospiza melodia*). *Am. Nat.* **187**, 736–752. (doi:10.1086/686198)
- Reid JM, Keller LF. 2010 Correlated inbreeding among relatives: occurrence, magnitude, and implications. *Evolution* **64**, 973–985. (doi:10.1111/j.1558-5646.2009.00865.x)
- R Development Core Team. 2015 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Lindén M. 1991 Divorce in great tits—chance or choice? An experimental approach. *Am. Nat.* **138**, 1039–1048. (doi:10.1086/285267)
- Ramsay SM, Otter KA, Mennill DJ, Ratcliffe LM, Boag PT. 2000 Divorce and extrapair mating in female black-capped chickadees (*Parus atricapillus*): separate strategies with a common target. *Behav. Ecol. Sociobiol.* **49**, 18–23. (doi:10.1007/s002650000270)
- Jocklin V, McGue M, Lykken DT. 1996 Personality and divorce: a genetic analysis. *J. Pers. Soc. Psychol.* **71**, 288–299. (doi:10.1037//0022-3514.71.2.288)
- Jerskey BA, Panizzon MS, Jacobson KC, Neale MC, Grant MD, Schultz M, Eisen SA, Tsuang MT, Lyons MJ. 2010 Marriage and divorce: a genetic perspective. *Pers. Individ. Dif.* **49**, 473–478. (doi:10.1016/j.paid.2010.05.007)
- Forstmeier W, Nakagawa S, Griffith SC, Kempenaers B. 2014 Female extra-pair mating: adaptation or genetic constraint? *Trends Ecol. Evol.* **29**, 456–464. (doi:10.1016/j.tree.2014.05.005)