Variance in within-pair reproductive success drives the opportunity for sexual selection annually and over the lifetimes of males in a multi-brooded songbird

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Abstract

In pair-bonding species, male reproductive success consists of 'within-pair' offspring produced with their socially-paired mate(s), and 'extra-pair' offspring produced with additional females throughout the population. Both reproductive pathways offer distinct opportunities for sexual selection to operate in wild populations, as each are composed of sub-components of mate attraction, female fecundity, and paternity allocation. Identifying key sources of variance and covariance among these components is a crucial step towards understanding the reproductive strategies that males use to maximize fitness both annually and over their lifetimes. We use 16 years of complete reproductive data from a population of black-throated blue warblers (*Setophaga caerulescens*) to decompose variance in male annual and lifetime reproductive success and thereby identify if the opportunity for sexual selection acts consistently over the lifetimes of individual males and what reproductive strategies likely favor maximum lifetime fitness. The majority of variance in male reproduction was attributable to within-pair sources of variance, but the specific effects of individual components of variance differed annually versus over the lifetimes of individual males. Positive lifetime covariance between within-pair and extra-pair success indicates that males able to maximize within-pair success likely achieve higher overall lifetime fitness via both the within-pair and extra-pair reproductive pathways.

Introduction

Sexual selection represents the evolutionary processes that result from differences in mating or fertilization success within a population (Andersson 1994). The opportunity, or potential, for sexual selection to operate is proportional to the population-wide variance in mating and/or reproductive success; if variance is low (e.g. all individuals have similar numbers of mates and offspring) then sexual selection will be weak, whereas if variance in reproductive output is high (e.g. few individuals monopolize mating opportunities and produce many offspring), selection can potentially be strong (Crow 1958, 1991; Emlen and Oring 1977; Wade and Arnold 1980; Shuster 2009). However, an individual's total reproductive success (T_{RS}) is itself composed of several component sources, each of which may have different population-wide variances and hence represent distinct avenues through which sexual selection may operate (Webster et al. 1995; Whittingham and Dunn 2004; Freeman-Gallant et al. 2005; Dolan et al. 2007; Lawler 2007; Lebigre et al. 2012). Determining where the greatest sources of variance and covariance exist among these components can help identify the mechanisms that lead to the greatest opportunities for sexual selection to operate, as well the reproductive strategies that may enable individuals to maximize fitness annually and over their lifetimes.

Sexual selection tends to operate more strongly among males than among females in many animal populations (Bateman 1948; Wade 1979; Arnold and Duvall 1994; Shuster 2009; but see Clutton-Brock 2007). Females are often the choosier sex because they are energetically limited in the number of broods and/or offspring they can produce (i.e. fecundity) and show relatively little among-individual variation in reproductive success compared to males (e.g. Hoogland and Foltz 1982; Freeman-Gallant et al. 2005; Lebigre et al. 2012). In contrast, male reproductive success is often limited by the number of potential mates they can attract and by the

number of offspring that they sire throughout the population, leading to greater variance in T_{RS} as some males attract numerous females and/or sire many offspring while others have low mating or siring success (e.g. Freeman-Gallant et al. 2005; Webster et al. 2007; Lebigre et al. 2012). Male T_{RS} stems from two pathways in socially monogamous and other species that form pair-bonds: 'within-pair' offspring produced by their social mate(s) and additional, 'extra-pair' offspring produced throughout the population by females socially paired to other males (Birkhead and Møller 1995; Webster et al. 1995; Whittingham et al. 2006). Both pathways are themselves comprised of multiplicative components of mate attraction (i.e. pre-copulatory) and paternity (i.e. post-copulatory) success, as well as by the fecundity of a male's within-pair and extra-pair mates (Figure 1). Each constituent component of within-pair and extra-pair reproductive success (W_{RS}, E_{RS}) may have different genetic, among-individual, and environmental sources of variation (Webster et al. 2007; Losdat et al. 2015; Evans and Garcia-Gonzalez 2016) and hence represent separate opportunities for sexual selection to operate.

Several studies have sought to identify sources of variance among mate attraction and paternity success (e.g. Vedder et al. 2011; Losdat et al. 2015; Evans and Garcia-Gonzalez 2016), but less emphasis has been placed on the importance of female fecundity in driving variation in male T_{RS}. In particular, the ability of some females in a population to produce multiple broods has the potential to drastically increase overall variance in male W_{RS} by doubling the number of within-pair offspring they can potentially sire (e.g. Nagy and Holmes 2005; Kaiser et al. 2017). Alternatively, if extra-pair routes are of primary importance for driving the opportunity for sexual selection in such populations, multi-brooding should not affect variance in W_{RS}, but rather allow some males to capitalize on additional opportunities to gain extra-pair success with multi-brooding females throughout the population, leading to greater variance in E_{RS} than in W_{RS} (e.g. Webster et al. 2007; Lebigre et al. 2012; Losdat et al. 2015). Thus, quantifying the relative

influence of sub-component sources of within-pair and extra-pair female fecundity (i.e. number of broods, number of offspring per brood) on male T_{RS} has the potential to identify independent opportunities for sexual selection to operate and thus potential targets of selection in wild populations.

Much work has focused on the role that E_{RS} can play in driving the opportunity for sexual selection in socially monogamous species. The advent of molecular paternity assignment has revealed previously cryptic sources of variance in individual reproductive success (Coltman et al. 1999; Griffith et al. 2002; Uller and Olsson 2008) that often increases the overall opportunity for sexual selection to operate (e.g. Yezerinac et al. 1995; Dolan et al. 2007; Webster et al. 2007; Balenger et al. 2009; Vedder et al. 2011; Lebigre et al. 2013). However, some authors suggest that many of the purported effects of E_{RS} on the opportunity for selection may be inflated by incomplete sampling of extra-pair sires in the population (Whittingham and Dunn 2004; Freeman-Gallant et al. 2005; Albrecht et al. 2007), or may vary with annual variation in social-environmental factors such as population density (Møller and Birkhead 1993; Taff et al. 2013). Others have noted that W_{RS} is the major source of variance in male T_{RS} in populations with both frequent and relatively rare extra-pair mating (Whittingham and Dunn 2004; Albrecht et al. 2007), suggesting that variation in E_{RS} may not necessarily be the driving force behind the opportunity for sexual selection to operate. However, the majority of studies investigating the opportunity for sexual selection are conducted over relatively short timescales and are thus limited to decomposing variance in annual reproductive success only. Given within-individual heterogeneity in annual reproduction due to delayed maturation of sexual signals (e.g. Germain et al. 2012; Hawkins et al. 2012), social status-dependent access to mates (e.g. Le Boeuf and Peterson 1969; DuVal 2012), and terminal investment due to senescence (Pianka and Parker 1975; Clutton-Brock 1984; Martin and Festa-Bianchet 2011; Froy et al. 2013; Tarwater and

Arcese 2017; Piper et al. 2018), individual strategies to maximize annual or lifetime reproductive success may differ, depending on socio-environmental context or individual phenotype. If drivers of sexual selection acted consistently over the lifetimes of individuals, we would observe little variation among years in the effects of individual components of W_{RS} and E_{RS} on total variance in annual reproductive success (T_{ARS}). Similarly, individual components of W_{RS} and E_{RS} would exhibit consistent effects on T_{ARS} and total variance in lifetime (T_{LRS}) reproductive success, as well as realized mean annual and lifetime reproductive success in the population ($\overline{ARS}$ and $\overline{LRS}$, respectively). If, however, individual males trade off shorter- versus longer-term reproductive success, the effects of individual components of variance in W_{RS} and E_{RS} would exhibit opposing patterns between annual and lifetime reproductive success. Thus, evaluating how components of reproduction that affect overall variance in T_{ARS} and T_{LRS} may differ, and quantifying how such components actually affect realized $\overline{ARS}$ and $\overline{LRS}$, are crucial to our understanding of how the opportunity for sexual selection operates in wild populations.

For males of many species, particularly those that engage in bi-parental care, reproductive gains through extra-pair mating may be offset by losses in within-pair paternity, resulting in a negative covariance (and hence a reproductive trade-off) between W_{RS} and E_{RS}. For instance, seeking extra-pair copulations may come at the expense of losing within-pair paternity through reduced mate-guarding (Westneat and Stewart 2003; Kokko and Morrell 2005; Dias et al. 2009; Harts et al. 2016; Reitsma et al. 2017). In contrast, some studies find positive overall covariance between W_{RS} and E_{RS}, indicating that males with a higher propensity for acquiring extra-pair mates and/or siring extra-pair young are also more likely to have higher within-pair success (Yezerinac et al. 1995; Albrecht et al. 2007; Ferree and Dickinson 2014; Reid et al. 2014). We currently have a poor understanding of where potential sources of such trade-offs

exist in wild populations, in part due to the data requirements needed to accurately quantify covariance among individual components of W_{RS} and E_{RS}. Co-variances have the potential to dramatically shape the evolutionary dynamics of reproductive systems (Lebigre et al. 2013; Reid et al. 2014). Evaluating sources of covariance among individual components of W_{RS} and E_{RS} is therefore a key facet of identifying potential sources of reproductive trade-offs and thus quantifying the overall opportunity for sexual selection to operate.

Accurately identifying which individual components of (co)variance drive the opportunity for sexual selection to operate, as well as realized reproductive success in the population, annually and over the lifetime of individuals requires comprehensive breeding data which encompasses pairing, female fecundity, and genetic paternity for a large sample of individual males over their lifetimes. Here, we use 16 years of detailed breeding observations and genetic paternity data from a longitudinal study of black-throated blue warblers (*Setophaga caerulescens*) to identify the contributions of components of W_{RS} and E_{RS}, as well as their covariances, to the opportunity for sexual selection in this socially monogamous, multi-brooded songbird. We decompose T_{ARS} and T_{LRS} to their component sources of (co)variance to identify which sources represent the greatest overall opportunity for sexual selection to operate in this system, both annually and over the lifetimes of individual males. If within-pair reproductive success consistently drives the opportunity for sexual selection in this multi-brooded species, we predict that components of W_{RS} will a) explain more of the total variance in both annual and lifetime reproductive success, b) exhibit relatively stable effects on variance in reproductive success over time, and c) be positively correlated with higher realized annual and lifetime reproductive success in the population. Secondly, we test for the presence of reproductive trade-offs between components of W_{RS} and E_{RS}. If strong sources of negative covariance exist among components of W_{RS} and E_{RS}, it would suggest that selection favors males trading off one

reproductive pathway for the other. If, however, there is non-negative covariance between W_{RS} and E_{RS}, it would suggest that males which employ reproductive strategies that achieve higher success in one pathway experience higher overall fitness on average, and that selection favors males which capitalize on multiple facets of reproductive success.

Material and Methods

Population monitoring

We monitored an individually marked population of black-throated blue warblers over 16 years (1999-2015) at the Hubbard Brook Experimental Forest (3,160ha) in New Hampshire, USA (43˚56′N, 71˚45′W). The breeding ecology of this long-term study population is described in detail elsewhere (e.g. Rodenhouse et al. 2003; Sillett et al. 2004; Holmes 2011; Kaiser et al. 2017). In brief, black-throated blue warblers are migratory, territorial songbirds found in relatively high densities at our study site. Arrival and the onset of breeding typically occurs in early May (Holmes et al. 2017), and males defend 1-4 ha territories until breeding ends in August (Sillett et al. 2004). Each season, adult males and females are captured in mist nets, marked with a unique combination of three colored leg bands and one aluminium U.S. Geological Survey (USGS) leg band, and blood sampled (~70 µl) from the brachial vein. All nesting attempts by socially-paired mates (i.e. pairs that jointly defend territories and provision offspring) are monitored on three study plots (35-85 ha). Nestlings are banded with one USGS leg band and blood sampled (~30 µl) on day 6 after hatching, and then monitored daily until fledge date (approx. 9 days after hatching, Holmes et al. 2017).

Genetic paternity assignment and calculation of annual/lifetime reproductive success

Detailed methods regarding genetic paternity assignment for this system are described by Kaiser et al. (2017). Briefly, we genotyped 4097 offspring and >95% of all adults in the study area (including candidate males adjacent to plot boundaries) at six highly polymorphic microsatellite loci using Genemapper v.4.1 (Applied Biosystems). We conducted parentage analyses for each year and study plot separately using CERVUS v3.0 (Kalinowski et al. 2007), which uses a maximum likelihood-based approach to infer parentage.

We define a male's annual reproductive success as the number of fledglings that he sired in a given year. Within-pair success represents the number of sired offspring fledged from his social female(s) nests on his territory, while extra-pair success represents all other fledged offspring that he sired within the population that year. Lifetime reproductive success is defined as a male's summed annual reproductive success over his lifetime as a breeder in the population. Genetic paternity data were not available before 1999 and after 2016 at the time of analysis; therefore we excluded n = 11 males that were breeders before 1999 and n = 21 males that survived beyond 2016 from analyses of lifetime reproductive success to avoid underestimating this metric for males that may have produced offspring outside of the study period.

Statistical analyses

All analyses were performed in R 3.5.1 (R Development Core Team 2018). Our initial dataset consisted of 1108 observations of male annual reproductive success from 1999-2015. For all analyses, we excluded observations from male territories that were part of brood manipulation (n = 50) or food supplementation (n = 79) experiments. To ensure that our analyses included the most accurate information possible on extra-pair reproductive success, we also excluded males that had a higher likelihood of siring unsampled extra-pair offspring outside of the study area (n

= 210 males with territories located within 210m [the equivalent of ~3 territory lengths] of the plot boundaries, Kaiser et al. 2017). Results remained qualitatively similar between the reduced and full dataset (e.g. variance decomposition results changed by <1% for total annual reproductive success).

We first decomposed population-wide variance in T_{ARS} and T_{LRS} over the entire study period to identify the components of variance in annual and lifetime reproductive success that present the greatest opportunity for sexual selection to operate. Variance in total reproductive success (T_{RS}, here representing either total annual [T_{ARS}] or lifetime [T_{LRS}] reproductive success) is the sum of variances of a male's within-pair reproductive success (W_{RS}) and extra-pair reproductive success (E_{RS}) success, as well as 2× their associated covariance:

$$\mathrm{Var}(T_{RS}) = \mathrm{Var}(W_{RS}) + \mathrm{Var}(E_{RS}) + 2\ \mathrm{Cov}(W_{RS}, E_{RS}).$$

Following Webster et al. (1995), each of these components of variance in T_{RS} can be further partitioned into separate subcomponents of pairing success (i.e. number of mates, M), female fecundity, and paternity (P) allocation (and their associated covariances), which act multiplicatively to equal either W_{RS} or E_{RS} for an individual male (Figure 1). However, our variance decomposition differs from Webster et al. (1995) in that here we further partition female fecundity into two parts: the number of broods (B) produced per female, given that some females in our population will double-brood under favorable environmental conditions (Nagy and Holmes 2005a; Kaiser et al. 2015), and female fecundity per brood (i.e. the number of offspring produced per brood, F). For ease of interpretation, we present each component of variance or covariance as the population wide (co)variance of the component itself (e.g. M_w represents variance in within-pair pairing success, and $\mathrm{Cov}(M_w,M_e)$ represents the covariance between within-pair and extra-pair pairing success), but see Supporting Information S1 for full

descriptions of how each variance component was calculated. Males that had zero success in one component of W_{RS} or E_{RS} were not included in analyses of downstream components of variance decomposition to avoid conflating variance estimates (following Webster et al. 1995; Freeman-Gallant et al. 2005). Note that this method of variance decomposition also estimates remainder terms, where the total remainder (D_T) is equal to $D_w + D_e + D_{we}$. These remainder terms capture multivariate skewness expressed in the higher order moments of the distributions of each subcomponent of reproductive success, such that total variance in T_{ARS} and T_{LRS} is not a simple sum of the component variances and covariances (Bohrnstedt and Goldberger 1969; Webster et al. 1995; Dolan et al. 2007; Lawler 2007).

We identified components of (co)variance in both T_{ARS} and T_{LRS} that constituted a substantial percentage (arbitrary cut-off of ≥10%) of the total variance across the full study period. For T_{ARS}, we further conducted time-series analyses to evaluate whether these key components in annual reproductive success consistently provided the greatest opportunity for sexual selection in each year of study (i.e. under varying socio-environmental conditions such as population density or population age-structure). To do so, we replicated our variance decomposition (above) for each individual year in the study period, extracted the percent of total variance in T_{ARS} attributed to each key component, as well as overall (co)variance in W_{RS} and E_{RS}, and both visually inspected time series plots for presence of lags and conducted Kwiatkowki-Phillips-Schmidt-Shin (KPSS) tests to determine if each time series was trend stationary (i.e. lack of overall positive/negative trend over the study period).

Lastly, we determined the relative effect of each key component of W_{RS} and E_{RS} on mean annual and lifetime reproductive success ($\overline{ARS}$ and $\overline{LRS}$) in the population using generalized mixed effects models and a model averaging approach. For $\overline{ARS}$, we constructed a global mixed

model (Poisson distribution) which included male identity and year as random effects, and M_w, B_w, P_w, M_e, B_e as fixed effects (see Table 1 for justification) as well as the interaction between B_w and B_e, to represent the covariance between these two components that explain a substantial portion of variance in T_{ARS} (Table 1). All fixed effects were standardized to mean = 0, SD = 1 to reduce any influence of measurement scale on model results (White and Burnham 1999). We ran all possible combinations of these fixed effects (n = 40 models total) and selected a subset with a difference in Akaike Information Criterion (ΔAIC) ≤ 7 from the top model. We chose a cutoff of ΔAIC ≤ 7 to ensure that estimates of the relative influences of each predictor on $\overline{ARS}$ were as conservative and inclusive as possible (Burnham and Anderson 2002). We then recalculated relative AIC weights from this subset of models, assessed the relative support for each predictor by summing the AIC weight of each model in which it was included. Averaged parameter estimates for each predictor were weighted by the cumulative AIC weight of each model in which it was included to create one representative estimate of the relative effects of each component on $\overline{ARS}$ (Burnham and Anderson 2002; Germain and Arcese 2014; Germain et al. 2015, 2018). Statistical significance for each fixed effect was assessed by whether 95% confidence intervals (CIs) overlapped zero.

We repeated this approach for $\overline{LRS}$, constructing a global mixed model (Poisson distribution) which included male identity and male longevity (years breeding in the population) as random effects, and M_w, B_w, Fw, P_w, M_e, B_e, F_e, and P_e as fixed effects, as well as the interactions between $M_w \times F_w$, $M_e \times F_e$, $M_w \times M_e$, $M_w \times F_e$, $M_w \times P_e$, $B_w \times B_e$, $B_w \times P_e$, $F_w \times M_e$, and $F_e \times F_w$ to represent covariances among these key components of variance in T_{LRS} (see Table 2 for justification). We again ran all possible combinations of these fixed effects (n = 4458

models), selected those within ΔAIC ≤ 7 of the top model, and constructed an average model based on relative AIC weights (as above).

Results

Male black-throated blue warblers exhibited considerable variation in both within-pair (mean = 1.7 young sired ±1.9SD, range = 0–9) and extra-pair (mean = 1.1 young sired ±1.5SD, range = 0–9) annual reproductive success, leading to substantial variation in the total number of offspring produced annually (mean = 2.8 ±2.3SD, range = 0–14; Figure 2a). Similarly, males varied in the number of within-pair (mean = 2.76 ±3.2SD, range = 0–23) and extra-pair (mean = 1.77±2.4SD, range = 0–14) offspring produced over their lifetimes. Hence, the Hubbard Brook population had relatively large variance in lifetime reproductive success (mean = 4.54 ± 4.7SD, range = 0–28; Figure 2b) indicating that most males produced few offspring and a small proportion produced many.

The opportunity for sexual selection in Annual Reproductive Success

Decomposition of the total opportunity for sexual selection in annual reproductive success revealed that the majority of variance (~64%) in T_{ARS} was attributable to variance in within-pair reproductive success, of which within-pair paternity success (P_w) constituted the greatest proportion (26.4%, Table 1). Despite this, both the number of within-pair mates (M_w) and number of broods produced by within-pair mates (B_w) also each accounted for roughly 10% of T_{ARS}, suggesting multiple distinct opportunities for sexual selection to operate within the W_{RS} pathway of annual reproductive success (Table 1). In contrast, the ~42% of variance in T_{ARS}

attributable to the extra-pair pathway (E_{RS}) was almost entirely accounted for by the number of extra-pair mates the male acquired (M_e, 39.6%; Table 1). Overall covariance between W_{RS} and E_{RS} was slightly negative (-6.2% of total variance in T_{ARS}), with only the positive covariance between the number of broods by within-pair and extra-pair females (Cov[B_w, B_e]) accounting for a substantial proportion of variance in T_{ARS} (10.6%, Table 1).

Variance in T_{ARS} varied across the 16 year study, indicating that the overall opportunity for sexual selection differed among years (Figure 3a). Despite this, variance in T_{ARS} was trend stationary (KPSS trend = 0.13, p = 0.08), indicating no overall positive/negative trend in the change in variance over the study period. The percent of T_{ARS} attributable to variance in W_{RS} likewise varied considerably, but also remained trend stationary (KPSS trend = 0.13, p = 0.07) and accounted for more total variance than E_{RS} in each year of study (Figure 3b). Among components of variance in within-pair reproductive success (Figure 3b), both number of within-pair mates (M_w) and number of within-pair broods (B_w) alternated above and below 10% of variance in T_{ARS}, and while M_w exhibited no obvious trend (KPSS trend = 0.11, p = 0.1), variance in B_w bordered on a significant negative trend over the study period (KPSS trend = 0.15, p = 0.05, Figure 3b). Similarly, the proportion of within-pair offspring sired (P_w), which consistently accounted for the largest percentage of T_{ARS} among within-pair components, also bordered on a significant negative trend (KPSS trend = 0.14, p = 0.05), due to high within-pair variance during the early portion of the study. Both E_{RS} and its main component, the number of extra-pair mates acquired, consistently accounted for ~40% of T_{ARS} and both were trend stationary (E_{RS} – KPSS trend = 0.05, p = 0.1; M_e – KPSS trend = 0.10, p = 0.1). In contrast, the overall covariance between W_{RS} and E_{RS} varied from -73% to 28% of total variance in T_{ARS} over the study period, where negative values indicate a trade-off between within-pair and extra-pair reproductive success (Figure 3d). Despite this wide range of variance in T_{RS} attributed to $Cov(W_{RS}, E_{RS})$, the

overall covariance between within-pair and extra-pair reproductive success remained trend stationary (KPSS trend = 0.07, p = 0.1), as did its main constituent component, the covariance between within-pair and extra-pair number of broods (KPSS test = 0.08, p = 0.1).

Our global model of the effects of each key component on $\overline{ARS}$ was a good fit to the data (R^2 = 0.43). Our model subset included six models with ΔAIC ≤ 7 from the top model; the cumulative AIC weight of this model subset was <0.98. All five fixed effects and the interaction between B_w and B_e were included in our final averaged model. Of these, M_w, B_w, P_w, and M_e had significant, positive effects on $\overline{ARS}$ (Figure 4), indicating that males at Hubbard Brook achieved the highest annual reproductive success by pairing with multiple double-brooded females, securing within-pair paternity, and mating with multiple extra-pair females (See Supporting Information S2 for full parameter estimates from final averaged model and all models in top subset).

The opportunity for selection in Lifetime Reproductive Success

Decomposition of the opportunity for sexual selection in lifetime reproductive success revealed that, similar to T_{ARS}, substantially more variance in T_{LRS} was attributable to variance in within-pair reproductive success than to variance in extra-pair success (46.7% versus 26.7%, respectively, Table 2). Indeed, every individual component of W_{RS} contributed a substantial (>10%) proportion of total variance in T_{LRS}, and the covariance between M_w and F_w accounted for over 50%. Similarly, although M_e again contributed the most of any single component to variance in E_{RS}, F_e and P_e also accounted for ≥10% of total variance. The covariance between M_e and F_e contributed to almost 100% of variance in T_{LRS}, indicating that the interaction between

these two components is a strong driver of variance in male lifetime reproductive success (Table 2). Several components of within-pair/extra-pair covariances contributed to more than 10% of the total positive or negative variance in T_{LRS}, suggesting the potential for both synergistic and trade-off effects between individual components of each pathway. However, overall covariance between W_{RS} and E_{RS} was positive and accounted for as much total variance in T_{LRS} as E_{RS} itself (~27%), indicating that there is no overall trade-off between the within-pair and extra-pair pathways in terms of male lifetime reproductive success in this system. Despite the strong potential for these listed sources of (co)variance to affect overall population-wide variance in male T_{LRS}, large, negative sources of (co)variance (D_w, D_e, D_{we}, D_T, Table 2) were unaccounted for in our decomposition. Although the biological significance of such remainder terms is difficult to interpret without knowledge of how higher-order moments of the distribution of each within-pair and extra-pair component affect lifetime reproductive success (e.g. multivariate skewness: Bohrnstedt and Goldberger 1969; Lawler 2007), their relatively large, negative values suggest that some amount of realized variation in T_{LRS} is not captured by decomposing variance to its within-pair and extra-pair components and their associated covariances.

Our global model of the effects of each key component on mean lifetime reproductive success was an extremely good fit to the data ($R^2 = 0.86$). A total of 147 models were included in the subset of models within $\Delta AIC \leq 7$ from the top model, which included all fixed effects and all interaction terms; the cumulative AIC weight of this model subset was <0.99. We detected significant, positive effects of B_w, F_w, P_w, B_e, F_e, P_e on $\overline{LRS}$, and significant negative effects from the interactions between M_w x F_w, and M_e x F_e, indicating that males in this population achieve the highest lifetime reproductive success by pairing with fewer double-brooded females that produced more offspring per brood and allocated more within-pair paternity to the focal male, and by mating with fewer double-brooding extra-pair females that likewise produced more

offspring per brood and allocated more paternity towards the focal male. All other terms had CIs that overlapped zero (Figure 5), and were not considered to have statistically significant effects on $\overline{LRS}$ (see Supporting Information S3 for full parameter estimates from final averaged model and all models in top subset).

Discussion

Quantifying the opportunity for sexual selection among different components of individual reproductive success is a key parameter for determining the evolutionary dynamics of mating systems within wild populations (Webster et al. 1995; Reid et al. 2014; Losdat et al. 2015). By identifying sources of the opportunity for sexual selection, and determining how the effects of these sources may change annually or over the lifetimes of individual males, we can elucidate the reproductive strategies that males employ to maximize reproductive success as well as determine how such strategies may change over time. In a free living, multi-brooded songbird population, we found that among-individual variation in within-pair components of reproductive success consistently accounted for more of the total overall variance in both annual and lifetime reproductive success than did extra-pair components of variance (Table 1, Table 2, Figure 3). Several of these within-pair components were likewise associated with higher mean annual (Figure 4) and lifetime (Figure 5) reproductive success, and generally exhibited non-negative covariance with extra-pair components, suggesting that allocating resources towards attracting and defending access to socially-paired mates is likely a key tactic for maximizing annual and lifetime fitness in species which exhibit environmentally-mediated multiple brooding.

The majority of variance in total annual reproductive success (T_{ARS}) was accounted for by four individual components of variance and one component of covariance which each explained ≥10% (Table 1). Of these individual components, the number of extra-pair mates that a male acquired (M_e) accounted for the single largest amount of total variance in T_{ARS}. However, the number of within-pair mates that a male socially paired with (M_w), as well as the number of broods these females produced (B_w) and the proportion of within-pair offspring sired by the male (P_w) accounted for more total variance than M_e and the remaining components of extra-pair reproduction combined (Table 1). Although the percentage of T_{ARS} accounted for by W_{RS} did vary somewhat from year-to-year in our study (Figure 3b), the influences of each individual component of W_{RS} were relatively stable over the longer-term, indicating that individual behavioral strategies aimed at maximizing annual reproductive success should be under consistent selection in this population. This finding contrasts with previous work indicating that the influence of particular variance components on the opportunity for selection can co-vary with socio-environmental factors like annual breeding density over shorter time periods (e.g. Møller and Birkhead 1993; Taff et al. 2013; Evans and Garcia-Gonzalez 2016). Total variance in annual reproductive success was also substantially influenced by one component of covariance, that between the number of broods produced by a male's socially-paired mate(s) and his extra-pair mate(s) (Cov[B_w, B_e], Table 1). The overall covariance between W_{RS} and E_{RS} was slightly negative for T_{ARS} (~ -6%, Table 1) and tended to be negative in most years (Figure 3d); however, this positive covariance between B_w and B_e was relatively consistent in accounting for ≥10% of total variance in T_{ARS}, and was never negative over the 16 year study (Figure 3d). This indicates that while the opportunity for sexual selection to operate on synergistic effects of multiple brooding among within-pair and extra-pair mates can vary somewhat annually, males never experienced a trade-off between the number of broods their socially-paired and extra-pair mates

produced. While future studies will need to pinpoint the precise spatial and/or environmental variables which drive the positive covariance between within-pair and extra-pair double brooding, our results indicate that this covariance makes a relatively small but important contribution towards driving the opportunity for sexual selection in this system.

In practice, all four key individual components of variance in T_{ARS} (i.e. M_w, B_w, P_w, and M_e) had significant, positive effects on mean annual reproductive success ($\overline{ARS}$) in black-throated blue warblers (Figure 4). Previous work from this population likewise indicates that greater investment in aspects of within-pair reproduction results in a higher reproductive net-gain for individual males, and that males on high-quality, food-rich territories tend to invest in behaviors that enhance W_{RS} (e.g. increased mate-guarding and territorial defense) over those that enhance E_{RS} (e.g. extra-territorial forays; Kaiser et al. 2015, 2017). Food limitation appears to be the proximate mechanism behind such territorially-driven variation in mating strategies at Hubbard Brook, as females nesting in food-rich territories are more likely to double brood than those occupying food-limited habitat (Holmes et al. 1996; Nagy and Holmes 2005a; Kaiser et al. 2015, 2017). Taken together, our results indicate that securing a high-quality breeding territory is the key strategy for male black-throated blue warblers to maximize annual reproductive success via the within-pair pathway, and that doing so does not necessarily limit their ability to also achieve some E_{RS} through mating with multiple extra-pair females. Indeed, doing so may occasionally result in a higher reproductive net gain via the positive covariance between within-pair and extra-pair female brooding (Table 1, Figure 3). For instance, males on food-rich territories with double-brooding females may have neighboring females that likewise double-brood given greater food resources (Holmes et al. 1996; Nagy and Holmes 2005b), increasing the availability of extra-pair offspring for the focal male to sire. With warming temperatures, earlier springs and longer breeding seasons increase the frequency of double-brooding in black-throated

blue warblers and other passerines (Townsend et al. 2013; Both et al. 2019), which may explain the near-negative trend in B_w over our study (i.e. more double-brooding females will decrease overall variance in B_w; Figure 3). Increased growing season length with earlier leaf-out date and later leaf senescence, documented at Hubbard Brook (Richardson et al. 2006) and elsewhere (Ibáñez Inés et al. 2010; Fridley 2012) could therefore translate to higher realized annual reproductive success for males able to capitalize on both maximizing W_{RS} among their double-brooding socially-paired mate(s) and gaining additional E_{RS} with extra-pair females throughout the population.

Within-pair components of variance also accounted for the majority of variance in total lifetime reproductive success (T_{LRS}), as we found for T_{ARS}, but the relative influences of within-pair and extra-pair sources of (co)variance on the opportunity for sexual selection differed somewhat between annual and lifetime reproduction. In total, W_{RS} components accounted for ~47% of variance in T_{LRS}, whereas components of E_{RS} components accounted for ~27% of variance (Table 2). Further, more individual components of T_{LRS} accounted for ≥10% of variance than those of T_{ARS}. Several of these individual components accounted for over half (to almost all) of the total variance in T_{LRS} before taking negative covariance terms and remainder (D) terms into account (Table 2). Indeed, a striking feature of our variance decomposition of T_{LRS} is that several covariance terms, most notably between individual within-pair and extra-pair components, accounted for substantial proportions of variance, with the overall covariance between W_{RS} and E_{RS} accounting for as much of the total variance as overall extra-pair variance (~27%; Table 2). This highlights that potential synergies and tradeoffs among individual reproductive components may play a much larger role in influencing reproductive success over a male's lifetime than within a single breeding season. In particular, the largest components of such covariance were positive and involved the number of within-pair and/or extra-pair mates

and the fecundity per brood of within-pair and/or extra-pair females (i.e. Cov[M_w, M_e], Cov[M_w, F_e], Cov[F_w, M_e], Cov[F_w, F_e]; Table 2). Substantial, positive within-pair/extra-pair covariances in the opportunity for sexual selection, as observed here, indicate that there are large potential lifetime fitness benefits for males able to capitalize on mating with extra-pair females while still investing in behaviors that enhance W_{RS} with their socially-paired mate(s). Previous research from this and other systems indicate that local breeding synchrony likely plays a role in the ability of males to copulate with extra-pair female neighbours while maintaining their own within-pair reproductive success (Stutchbury and Neudorf 1998; Chuang et al. 1999; Webster et al. 2001; Stewart et al. 2010). By mating with synchronously fertile females on nearby adjacent territories, males of some species can reduce the risk of losing within-pair paternity of their own offspring via reduced mate guarding while seeking potential extra-pair mates over greater distances throughout the population (Kempenaers 1997; Weatherhead 1997). Future work investigating environmental drivers of the opportunity for sexual selection should thus consider the role of local breeding synchrony as it relates to positive covariances between the W_{RS} and E_{RS} pathways.

Of the components of (co)variance found to have a substantial influence on the opportunity for sexual selection in lifetime reproductive success, six had significant, positive effects on $\overline{LRS}$in the population (Figure 5). Surprisingly, neither the number of within-pair nor number of extra-pair mates had any significant effect on $\overline{LRS}$, contrary to our results for $\overline{ARS}$ (Figure 4). Instead, all individual components of variance related to female fecundity (B_w, F_w, B_e, F_e) and male siring success (P_w, P_e) had significant positive effects on $\overline{LRS}$, indicating that realized male reproductive success is more strongly influenced by female breeding quality and paternity allocation than aspects of male mate attraction. Indeed, the interaction between number

of within-pair mates and their fecundity per brood, as well as the interaction between number of extra-pair mates and fecundity per brood of those mates were found to have significant negative effects on $\overline{LRS}$ (Figure 5), indicating that male black-throated blue warblers experience a lifetime trade-off in terms of the number and the quality of their mates through both the W_{RS} and E_{RS} pathways. These results are consistent with the hypothesis that males with multiple within-pair and/or extra-pair mates suffer reproductive loses annually compared to monogamous males (e.g. Dunn and Robertson 1993; Poirier et al. 2004). However, such patterns of negative covariance and lower reproductive success are not widely reported over the lifetimes of breeding males, in particular when contrasted with the apparent positive effects of more within-pair and extra-pair mates within a single breeding season. Taken together, our results suggest that males in this population may sacrifice short-term reproductive gains (i.e. higher $\overline{ARS}$ via more within-pair and/or extra-pair mates) for longer-term fitness benefits (represented by higher $\overline{LRS}$).

Overall, our results suggest that variance in within-pair reproductive success clearly drives the opportunity for sexual selection in this multiple-brooded population. While the components of (co)variance which most strongly affect both the opportunity for sexual selection and realized reproductive success differed somewhat between short (i.e. annual) and longer (i.e. lifetime) timescales, components of W_{RS} consistently accounted for more total variance in T_{ARS} and T_{LRS}, and had more contributions to higher mean annual and lifetime reproductive success, than did components of E_{RS}. The potential for annual reproductive tradeoffs between within-pair and extra-pair components of variance were outweighed by the overall positive covariance among these reproductive pathways. Thus, males able to maximize W_{RS} likely achieve higher overall lifetime fitness via both the within-pair and extra-pair reproductive pathways. Minimal observed effects of annual variation in socio-environmental factors on the influences of

components of W_{RS} indicate that consistent selection pressures may offer some males (e.g. those on food-rich territories, Kaiser et al. 2015, 2017) the opportunity to capitalize on long-term reproductive benefits (e.g. double-brooding by their socially-paired female), even if such benefits result in short term losses in annual reproductive success via reduced effort in seeking additional mates. In contrast, males on food-poor territories may experience more selective pressure to allocate resources towards extra-pair reproduction given their lower probability of within-pair success (Kaiser et al. 2015, 2017), leading to greater variance in components of E_{RS} in this subset of males. Future studies should seek to determine if and how the opportunity for sexual selection differs between such high vs. low-quality territories, particularly as changing climate conditions alter breeding-season length and potentially reduce population-wide variance in key components of reproduction such as the ability of females to initiate multiple broods. Such studies will not only provide unique insight into how habitat type can influence sexual selection and the lifetime fitness of individual males, but also advance our understanding of how changing socio-environmental conditions can ultimately alter the mating systems of wild populations in seasonal environments.

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Author contributions

R.R.G. and M.S.W. conceived the study, and R.R.G. conducted statistical analyses and wrote the manuscript with input from all authors. M.T.H, S.A.K, T.S.S. and M.S.W. collected data, and S.A.K. conducted parentage assignment.

Literature Cited

Albrecht, T., J. Schnitzer, J. Kreisinger, A. Exnerová, J. Bryja, and P. Munclinger. 2007. Extrapair paternity and the opportunity for sexual selection in long-distant migratory passerines. Behav. Ecol. 18:477–486.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, NJ.

Arnold, S. J., and D. Duvall. 1994. Animal mating systems: a synthesis based on selection theory. Am. Nat. 143:317–348.

Balenger, S. L., L. Scott Johnson, H. L. Mays Jr, and B. S. Masters. 2009. Extra-pair paternity in the socially monogamous mountain bluebird *Sialia currucoides* and its effect on the potential for sexual selection. J. Avian Biol. 40:173–180.

Bateman, A. J. 1948. Intra-sexual selection in Drosophila. Heredity 2:349–368.

Birkhead, T. R., and A. P. Møller. 1995. Extra-pair copulation and extra-pair paternity in birds. Anim. Behav.49:843–848.

Bohrnstedt, G. W., and A. S. Goldberger. 1969. On the exact covariance of products of random variables. J. Am. Stat. Assoc. 64:1439–1442.

Both, C., R. Ubels, and P.-A. Ravussin. 2019. Life-history innovation to climate change: can single-brooded migrant birds become multiple breeders? J. Avian Biol. 50:e01951.

Burnham, K., and D. Anderson. 2002. Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. Springer, New York, NY.

Chuang, H. C., M. S. Webster, and R. T. Holmes. 1999. Extrapair Paternity and Local Synchrony in the Black-Throated Blue Warbler. Auk 116:726–736.

Clutton-Brock, T. 2007. Sexual selection in males and females. Science 318:1882–1885.

Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. Am. Nat. 123:212–229.

Coltman, D. W., D. R. Bancroft, A. Robertson, J. A. Smith, T. H. Clutton-brock, and J. M. Pemberton. 1999. Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. Mol. Ecol. 8:1199–1209.

Crow, J. F. 1991. Fitness variation on natural populations. Pp. 91–97 *in* Evolution and Animal Breeding Systems. C.A.B. International, Wallingford.

Crow, J. F. 1958. Some possibilities for measuring selection intensities in man. Hum. Biol. 30:1–13.

Dias, R. I., P. Salles, and R. H. Macedo. 2009. Mate guarding and searching for extra-pair copulations: Decision-making when interests diverge. Ecol. Inform.4:405–412.

Dolan, A. C., M. T. Murphy, L. J. Redmond, K. Sexton, and D. Duffield. 2007. Extrapair paternity and the opportunity for sexual selection in a socially monogamous passerine. Behav. Ecol. 18:985–993.

Dunn, P. O., and R. J. Robertson. 1993. Extra-pair paternity in polygynous tree swallows. Anim. Behav. 45:231–239.

DuVal, E. H. 2012. Variation in annual and lifetime reproductive success of lance-tailed manakins: alpha experience mitigates effects of senescence on siring success. Proc. R. Soc. B 279:1551–1559.

Emlen, S. T., and L. W. Oring. 1977. Ecology, Sexual Selection, and the Evolution of Mating Systems. Science 197:215–223.

Evans, J. P., and F. Garcia-Gonzalez. 2016. The total opportunity for sexual selection and the integration of pre-and post-mating episodes of sexual selection in a complex world. J. Evol. Biol. 29:2338–2361.

Ferree, E. D., and J. L. Dickinson. 2014. Male western bluebirds that sire extrapair young are also successful within-pair mates. Anim. Behav. 90: 11–19

Freeman-Gallant, C. R., N. T. Wheelwright, K. E. Meiklejohn, S. L. States, and S. V. Sollecito. 2005. Little effect of extrapair paternity on the opportunity for sexual selection in savannah sparrows (*Passerculus sandwichensis*). Evolution 59:422–430.

Fridley, J. D. 2012. Extended leaf phenology and the autumn niche in deciduous forest invasions. Nature 485:359–362.

Froy, H., R. A. Phillips, A. G. Wood, D. H. Nussey, and S. Lewis. 2013. Age-related variation in reproductive traits in the wandering albatross: evidence for terminal improvement following senescence. Ecol. Lett. 16:642–649.

Germain, R. R., and P. Arcese. 2014. Distinguishing individual quality from habitat preference and quality in a territorial passerine. Ecology 95:436–445.

Germain, R. R., M. W. Reudink, P. P. Marra, P. T. Boag, and L. M. Ratcliffe. 2012. Delayed maturation of multiple signals in a migratory songbird. Behav. Ecol. Sociobiol. 66:419–431.

Germain, R. R., R. Schuster, K. E. Delmore, and P. Arcese. 2015. Habitat preference facilitates successful early breeding in an open-cup nesting songbird. Funct. Ecol. 29:1522–1532.

Germain, R. R., R. Schuster, C. E. Tarwater, W. M. Hochachka, and P. Arcese. 2018. Adult survival and reproductive rate are linked to habitat preference in territorial, year-round resident Song Sparrows *Melospiza melodia*. Ibis 160:568–581.

Griffith, S. C., I. P. Owens, and K. A. Thuman. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol. Ecol. 11:2195–2212.

Harts, A. M. F., I. Booksmythe, and M. D. Jennions. 2016. Mate guarding and frequent copulation in birds: A meta-analysis of their relationship to paternity and male phenotype. Evolution 70:2789–2808.

Hawkins, G. L., G. E. Hill, and A. Mercadante. 2012. Delayed plumage maturation and delayed reproductive investment in birds. Biol. Rev. 87:257–274.

Holmes, R. T. 2011. Avian population and community processes in forest ecosystems: Long-term research in the Hubbard Brook Experimental Forest. Forest Ecol. Manag. 262:20–32.

Holmes, R. T., S. A. Kaiser, N. L. Rodenhouse, T. S. Sillett, M. S. Webster. 2017. Black-throated Blue Warbler (*Setophaga caerulescens*), version 3.0. In: Birds of North America (P. Pyle, and M. A. Patten, eds). Cornell Lab of Ornithology, Ithaca, NY, USA.

Holmes, R. T., P. P. Marra, and T. W. Sherry. 1996. Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. J. Anim. Ecol. 65:183–195.

Hoogland, J. L., and D. W. Foltz. 1982. Variance in male and female reproductive success in a harem-polygynous mammal, the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). Behav. Ecol. Sociobiol. 11:155–163.

Ibáñez Inés, Primack Richard B., Miller-Rushing Abraham J., Ellwood Elizabeth, Higuchi Hiroyoshi, Lee Sang Don, Kobori Hiromi, and Silander John A. 2010. Forecasting phenology under global warming. Philos. T. Roy. Soc. B. 365:3247–3260.

Kaiser, S. A., B. B. Risk, T. S. Sillett, and M. S. Webster. 2017. Ecological and social factors constrain spatial and temporal opportunities for mating in a migratory songbird. Am. Nat. 189:283–296.

Kaiser, S. A., T. S. Sillett, B. B. Risk, and M. S. Webster. 2015. Experimental food supplementation reveals habitat-dependent male reproductive investment in a migratory bird. Proc. R. Soc. B. 282:20142523.

Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol. Ecol. 16:1099–1106.

Kempenaers, B. 1997. Does Reproductive Synchrony Limit Male Opportunities or Enhance Female Choice for Extra-Pair Paternity? Behaviour 134:551–562.

Kokko, H., and L. J. Morrell. 2005. Mate guarding, male attractiveness, and paternity under social monogamy. Behav Ecol 16:724–731.

Lawler, R. R. 2007. Fitness and extra-group reproduction in male Verreaux's sifaka: An analysis of reproductive success from 1989–1999. Am. J. Phys. Anthropol. 132:267–277.

Le Boeuf, B. J., and R. S. Peterson. 1969. Social status and mating activity in elephant seals. Science 163:91–93.

Lebigre, C., P. Arcese, and J. M. Reid. 2013. Decomposing variation in male reproductive success: age-specific variances and covariances through extra-pair and within-pair reproduction. J. Anim. Ecol. 82:872–883.

Lebigre, C., P. Arcese, R. J. Sardell, L. F. Keller, and J. M. Reid. 2012. Extra-pair paternity and the variance in male fitness in song sparrows (*Melospiza melodia*). Evolution 66:3111–3129.

Losdat, S., P. Arcese, and J. M. Reid. 2015. Double decomposition: decomposing the variance in subcomponents of male extra-pair reproductive success. J. Anim. Ecol. 84:1384–1395.

Martin, J. G. A., and M. Festa-Bianchet. 2011. Age-independent and age-dependent decreases in reproduction of females. Ecol. Lett. 14:576–581.

Møller, A. P., and T. R. Birkhead. 1993. Cuckoldry and sociality: a comparative study of birds. Am. Nat. 142:118–140.

Nagy, L. R., and R. T. Holmes. 2005a. Food limits annual fecundity of a migratory songbird: an experimental study. Ecology 86:675–681.

Nagy, L. R., and R. T. Holmes. 2005b. To double-brood or not? Individual variation in the reproductive effort in Black-Throated Blue Warblers (*Dendroica Caerulescens*). Auk 122:902–914.

Pianka, E. R., and W. S. Parker. 1975. Age-specific reproductive tactics. Am. Nat. 109:453–464.

Piper, W. H., K. M. Brunk, G. L. Jukkala, E. A. Andrews, S. R. Yund, and N. G. Gould. 2018. Aging male loons make a terminal investment in territory defense. Behav Ecol Sociobiol 72:95.

Poirier, N. E., L. A. Whittingham, and P. O. Dunn. 2004. Males achieve greater reproductive success through multiple broods than through extrapair mating in house wrens. Anim. Behav. 67:1109–1116.

R Development Core Team. 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reid, J., P. Arcese, L. Keller, and S. Losdat. 2014. Female and male genetic effects on offspring paternity: additive genetic (co)variances in female extra-pair reproduction. Evolution 68:3357–2370.

Reitsma, L. R., J. A. Jukosky, A. J. Kimiatek, M. L. Goodnow, and M. T. Hallworth. 2017. Extra-pair paternity in a long-distance migratory songbird beyond neighbors' borders and across male age classes. Can. J. Zool. 96:49–54.

Richardson, A. D., A. S. Bailey, E. G. Denny, C. W. Martin, and J. O'keefe. 2006. Phenology of a northern hardwood forest canopy. Glob. Change Biol. 12:1174–1188.

Rodenhouse, N., T. Sillett, P. Doran, and R. Holmes. 2003. Multiple density–dependence mechanisms regulate a migratory bird population during the breeding season. Proc. R. Soc. B. 270:2105–2110.

Shuster, S. M. 2009. Sexual selection and mating systems. PNAS 106 Suppl 1:10009–16.

Sillett, T. S., N. L. Rodenhouse, and R. T. Holmes. 2004. Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. Ecology 85:2467–2477.

Stewart, S. L. M., D. F. Westneat, and G. Ritchison. 2010. Extra-pair paternity in eastern bluebirds: effects of manipulated density and natural patterns of breeding synchrony. Behav Ecol Sociobiol 64:463–473.

Stutchbury, B. J. M., and D. L. Neudorf. 1998. Female control, breeding synchrony, and the evolution of extra-pair mating systems. Ornithol. Mono. 103–121.

Taff, C. C., C. R. Freeman-Gallant, P. O. Dunn, and L. A. Whittingham. 2013. Spatial distribution of nests constrains the strength of sexual selection in a warbler. J. Evol. Biol. 26:1392–1405.

Tarwater, C. E., and P. Arcese. 2017. Age and years to death disparately influence reproductive allocation in a short-lived bird. Ecology 98:2248–2254.

Townsend, A. K., T. S. Sillett, N. K. Lany, S. A. Kaiser, N. L. Rodenhouse, M. S. Webster, and R. T. Holmes. 2013. Warm springs, early lay dates, and double brooding in a North American migratory songbird, the black-throated blue warbler. PLOS ONE 8:e59467.

Uller, T., and M. Olsson. 2008. Multiple paternity in reptiles: patterns and processes. Mol. Ecol. 17:2566–2580.

Vedder, O., J. Komdeur, M. van der Velde, E. Schut, and M. J. L. Magrath. 2011. Polygyny and extra-pair paternity enhance the opportunity for sexual selection in blue tits. Behav Ecol Sociobiol 65:741–752.

Wade, M. J. 1979. Sexual selection and variance in reproductive success. Am. Nat. 114:742–747.

Wade, M. J., and S. J. Arnold. 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. Anim. Behav. 28:446–461.

Weatherhead, P. J. 1997. Breeding synchrony and extra-pair mating in red-winged blackbirds. Behav Ecol Sociobiol 40:151–158.

Webster, M. S., H. C. Chuang-Dobbs, and R. T. Holmes. 2001. Microsatellite identification of extrapair sires in a socially monogamous warbler. Behav Ecol 12:439–446.

Webster, M. S., S. Pruett-Jones, D. F. Westneat, and S. J. Arnold. 1995. Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. Evolution 49:1147–1157.

Webster, M. S., K. A. Tarvin, E. M. Tuttle, and S. Pruett-Jones. 2007. Promiscuity drives sexual selection in a socially monogamous bird. Evolution 61:2205–2211.

Westneat, D. F., and I. R. K. Stewart. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. Annu. Rev. Ecol. Syst. 34:365–396.

White, G., and K. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

Whittingham, L. A., and P. O. Dunn. 2004. Effects of extra-pair and within-pair reproductive success on the opportunity for selection in birds. Behav. Ecol. 16:138–144.

Whittingham, L. A., P. O. Dunn, and M. K. Stapleton. 2006. Repeatability of extra-pair mating in tree swallows. Mol. Ecol. 15:841–849.

Yezerinac, S. M., P. J. Weatherhead, and P. T. Boag. 1995. Extra-pair paternity and the opportunity for sexual selection in a socially monogamous bird (*Dendroica petechia*). Behav Ecol Sociobiol 37:179–188.

Table 1: Decomposition of variance in total annual reproductive success (T_{ARS}) of black-throated blue warblers across 16 years of study. For each row, variance terms (see Figure 1 for definitions) represent the focal component of (co)variance in T_{ARS}, but note that actual calculation of each term involves population-wide means for additional components (see Supporting Information S1 and Webster et al. 1995 for further details). D denotes remainder terms for within-pair, extra-pair, and covariance pathways, where $D_T = D_w + D_e + D_{we}$. Values depict the absolute variance in each component, as well as their relative variance (i.e. divided by population mean $T_{ARS}^2 = 8.713$), and the percentage of total variance in T_{ARS} attributable to each term. Crosses (†) denote variance terms which fall above our cutoff of >10% total variance in T_{ARS}.

Source	Variance term	Absolute variance	Relative variance	% total variance
Total variance in ARS	$\boldsymbol{T_{ARS}}$	**5.467**	**0.677**	**100**
Within-pair terms	M_w	0.544	0.067	10.0†
	B_w	0.591	0.073	10.8†
	F_w	0.426	0.053	7.8
	P_w	1.443	0.179	26.4†
	$Cov(M_w, B_w)$	0.018	0.002	0.3
	$Cov(M_w, F_w)$	-0.030	-0.004	-0.5
	$Cov(M_w, P_w)$	-0.035	-0.004	-0.6
	$Cov(B_w, F_w)$	-0.027	-0.004	-0.5
	$Cov(B_w, P_w)$	-0.059	-0.007	-1.1
	$Cov(F_w, P_w)$	0.191	0.024	3.5
Total within-pair variance	$\boldsymbol{W_{RS}}$	**3.487**	**0.432**	**63.8**
	$\boldsymbol{D_W}$	**0.425**	**0.053**	**7.7**
Extra-pair terms	M_e	2.166	0.269	39.6†
	B_e	0.180	0.022	3.3
	F_e	0.130	0.016	2.4
	P_e	0.482	0.060	8.8
	$Cov(M_e, B_e)$	0.014	0.002	0.3
	$Cov(M_e, F_e)$	0.025	0.003	0.5
	$Cov(M_e, P_e)$	-0.075	-0.009	-1.4
	$Cov(B_e, F_e)$	0.005	0.001	0.1
	$Cov(B_e, P_e)$	-0.242	-0.030	-4.4
	$Cov(F_e, P_e)$	-0.196	-0.024	-3.6
Total extra-pair variance	$\boldsymbol{E_{RS}}$	**2.319**	**0.288**	**42.4**
	$\boldsymbol{D_E}$	**-0.17**	**-0.022**	**-4.5**
Within-pair and extra-pair covariances	$Cov(M_w, M_e)$	-0.419	-0.052	-7.7
	$Cov(M_w, B_e)$	0.099	0.012	1.8
	$Cov(M_w, F_e)$	-0.009	-0.001	-0.2
	$Cov(M_w, P_e)$	-0.484	-0.060	-8.9
	$Cov(B_w, M_e)$	0.023	0.003	4.2
	$Cov(B_w, B_e)$	0.579	0.072	10.6†
	$Cov(B_w, F_e)$	0.008	0.001	0.2
	$Cov(B_w, P_e)$	-0.389	-0.048	-7.1
	$Cov(F_w, M_e)$	0.121	0.015	2.2
	$Cov(F_w, B_e)$	-0.044	-0.005	-0.8
	$Cov(F_w, F_e)$	0.063	0.008	1.2
	$Cov(F_w, P_e)$	-0.096	-0.012	-1.8
	$Cov(P_w, M_e)$	0.090	0.011	1.6
	$Cov(P_w, B_e)$	0.071	0.009	1.3
	$Cov(P_w, F_e)$	-0.025	-0.003	-0.4

	$Cov(P_w, P_e)$	-0.097	-0.012	-1.8
Total WP and EP covariance	$\boldsymbol{Cov(W_{RS}, E_{RS})}$	**-0.339**	**-0.042**	**-6.2**
	$\boldsymbol{D_{WE}}$	**0.170**	**0.020**	**-0.6**
Remainder	$\boldsymbol{D_T}$	**0.425**	**0.051**	**3.9**

Table 2: Decomposition of variance in total lifetime reproductive success (T_{LRS}) of black-throated blue warblers across 16 years of study. For each row, variance terms (see Figure 1 for definitions) represent the focal component of (co)variance in T_{LRS}, but note that actual calculation of each term involves population-wide means for additional components (see Supporting Information S1 and Webster et al. 1995 for further details). *D* denotes remainder terms for within-pair, extra-pair, and covariance pathways, where $D_T = D_w + D_e + D_{we}$. Values depict the absolute variance in each component, as well as their relative variance (i.e. divided by population mean $T_{LRS}^2 = 20.57$), and the percentage of total variance in T_{LRS} attributable to each term. Crosses (†) denote variance terms which fall above our cutoff of >10% total variance in T_{LRS}.

Source	Variance term	Absolute value	Standardized value*	% total variance
Total Variance	$\boldsymbol{T_{LRS}}$	**21.77**	**1.058**	**100**
Within-pair terms	M_w	5.766	0.280	26.5†
	B_w	5.331	0.259	24.5†
	F_w	7.672	0.373	35.2†
	P_w	6.140	0.299	28.2†
	$Cov(M_w, B_w)$	1.718	0.084	7.8
	$Cov(M_w, F_w)$	12.383	0.602	56.9†
	$Cov(M_w, P_w)$	0.539	0.026	2.5
	$Cov(B_w, F_w)$	-0.213	-0.010	-1.0
	$Cov(B_w, P_w)$	-0.165	-0.008	-0.8
	$Cov(F_w, P_w)$	0.908	0.044	4.2
Total within-pair variance	$\boldsymbol{W_{RS}}$	**10.171**	**0.494**	**46.7**
	$\boldsymbol{D_W}$	**-29.908**	**-1.455**	**-137.3**
Extra-pair terms	M_e	19.627	0.954	90.1†
	B_e	1.216	0.059	5.6
	F_e	7.345	0.357	33.7†
	P_e	3.336	0.162	15.3†
	$Cov(M_e, B_e)$	0.318	0.016	1.5
	$Cov(M_e, F_e)$	21.767	1.047	99.9†
	$Cov(M_e, P_e)$	-1.491	-0.072	-6.8
	$Cov(B_e, F_e)$	0.259	0.013	1.2
	$Cov(B_e, P_e)$	-1.752	-0.085	-8.1
	$Cov(F_e, P_e)$	-1.773	-0.086	-8.1
Total extra-pair variance	$\boldsymbol{E_{RS}}$	**5.806**	**0.282**	**26.7**
	$\boldsymbol{D_E}$	**-43.046**	**-2.083**	**-197.6**
Within-pair and extra-pair covariances	$Cov(M_w, M_e)$	12.860	0.625	59.1†
	$Cov(M_w, B_e)$	0.394	0.019	1.8
	$Cov(M_w, F_e)$	8.264	0.402	37.9†
	$Cov(M_w, P_e)$	-3.141	-0.145	-14.4†
	$Cov(B_w, M_e)$	0.478	0.023	2.2
	$Cov(B_w, B_e)$	3.648	0.177	16.8†
	$Cov(B_w, F_e)$	0.389	0.019	1.8
	$Cov(B_w, P_e)$	-2.627	-0.128	-12.1†
	$Cov(F_w, M_e)$	15.835	0.770	72.7†
	$Cov(F_w, B_e)$	-0.432	-0.021	-2.0
	$Cov(F_w, F_e)$	10.395	0.505	47.7†
	$Cov(F_w, P_e)$	-0.319	-0.015	-1.5
	$Cov(P_w, M_e)$	1.101	0.053	5.1

	$Cov(P_w, B_e)$	-0.166	-0.008	-0.8
	$Cov(P_w, F_e)$	0.379	0.018	1.7
	$Cov(P_w, P_e)$	-0.484	-0.024	-2.2
Total WP and EP covariance	$\boldsymbol{Cov(W_{RS}, E_{RS})}$	**5.792**	**0.278**	**26.6**
	$\boldsymbol{D_{WE}}$	**-40.782**	**-1.991**	**-187.2**
Remainder	$\boldsymbol{D_T}$	**-113.0736**	**-5.529**	**-522.1**

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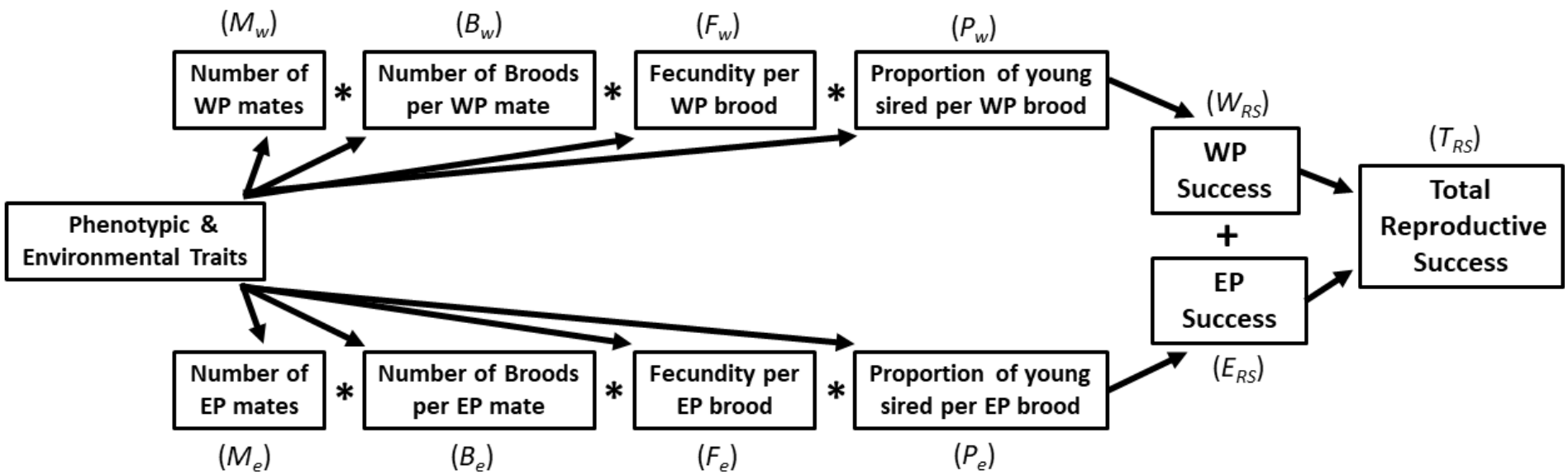
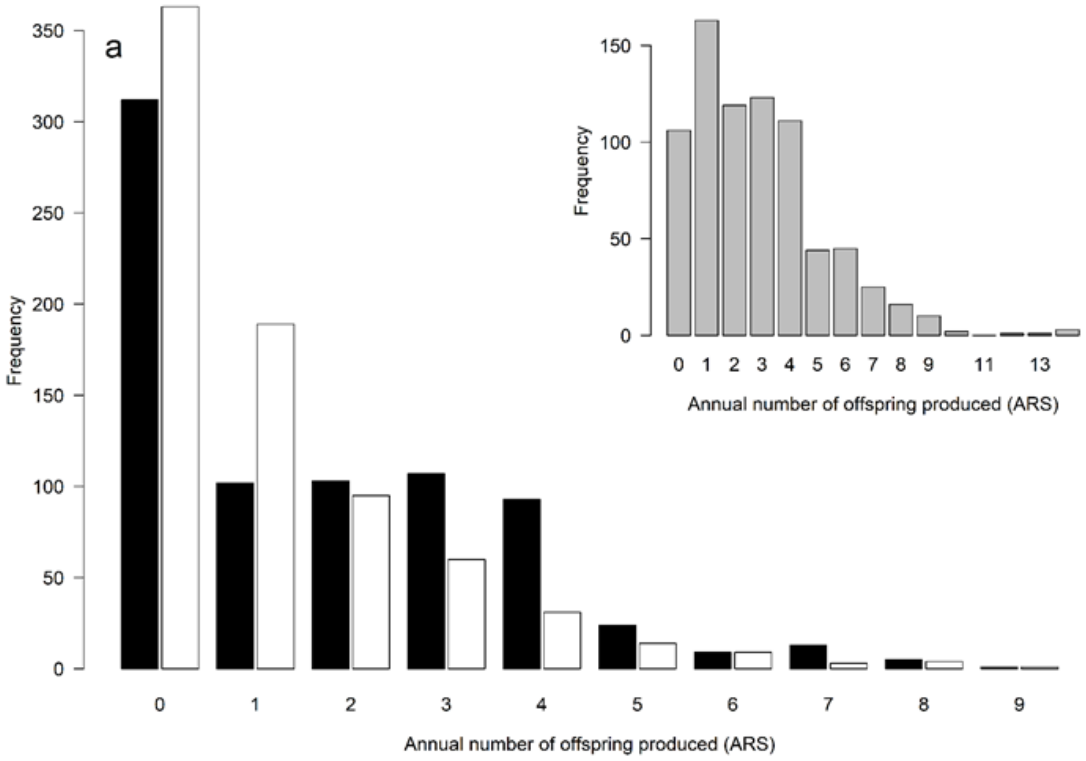


Figure 1: Flow chart depicting the components of within-pair (WP) and extra-pair (EP) reproductive success, which combine to determine an individual's total reproductive success. Arrows indicate the effects that environmental and phenotypic traits can have on WP and EP components, and hence on total reproductive success. Italic terms (in parentheses) denote abbreviations used for each component of variance. Note that components of within-pair and extra-pair pathways are multiplicative, whereas WP and EP success themselves are additive components of total annual reproductive success (adapted from Webster et al. 1995).


a
Frequency
Annual number of offspring produced (ARS)
Frequency
Annual number of offspring produced (ARS)

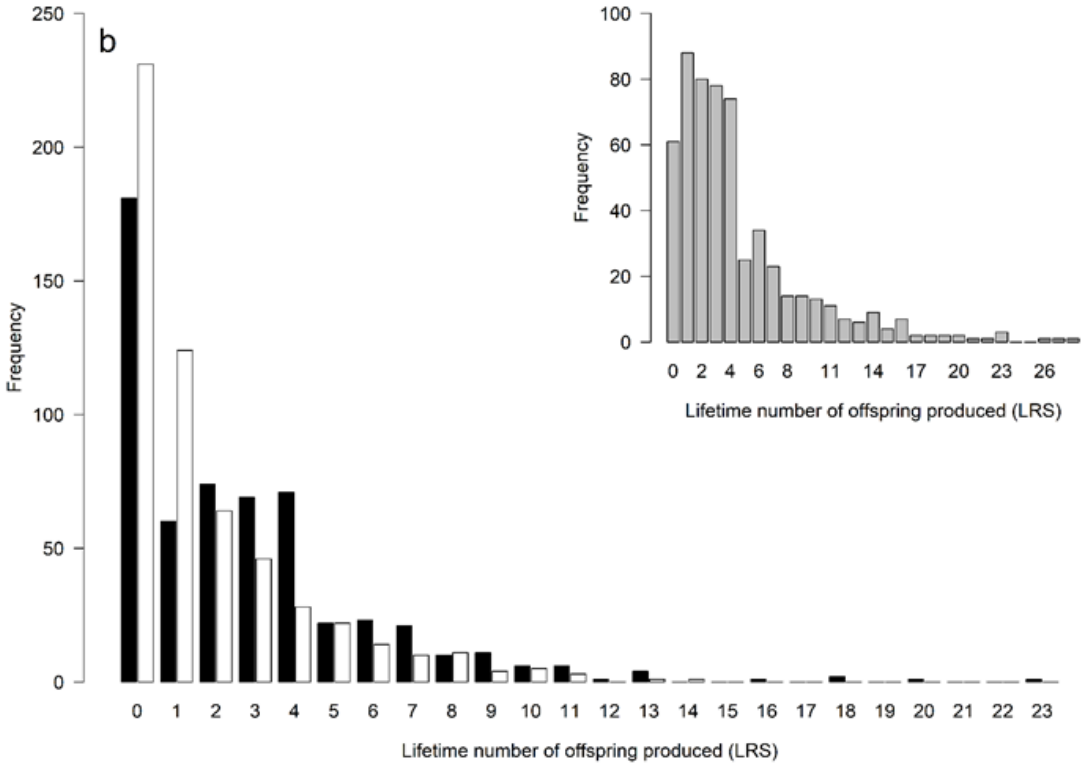

b
Frequency
Lifetime number of offspring produced (LRS)
Frequency
Lifetime number of offspring produced (LRS)

Figure 2: Total number of within-pair (black bars) and extra-pair (white bars) offspring produced by male black-throated blue warblers a) annually (n = 769 male-years) and b) over their complete breeding lifetime (n = 572 males). In each panel, insert (grey bars) depicts total number of offspring (within-pair and extra-pair) produced by these same males.

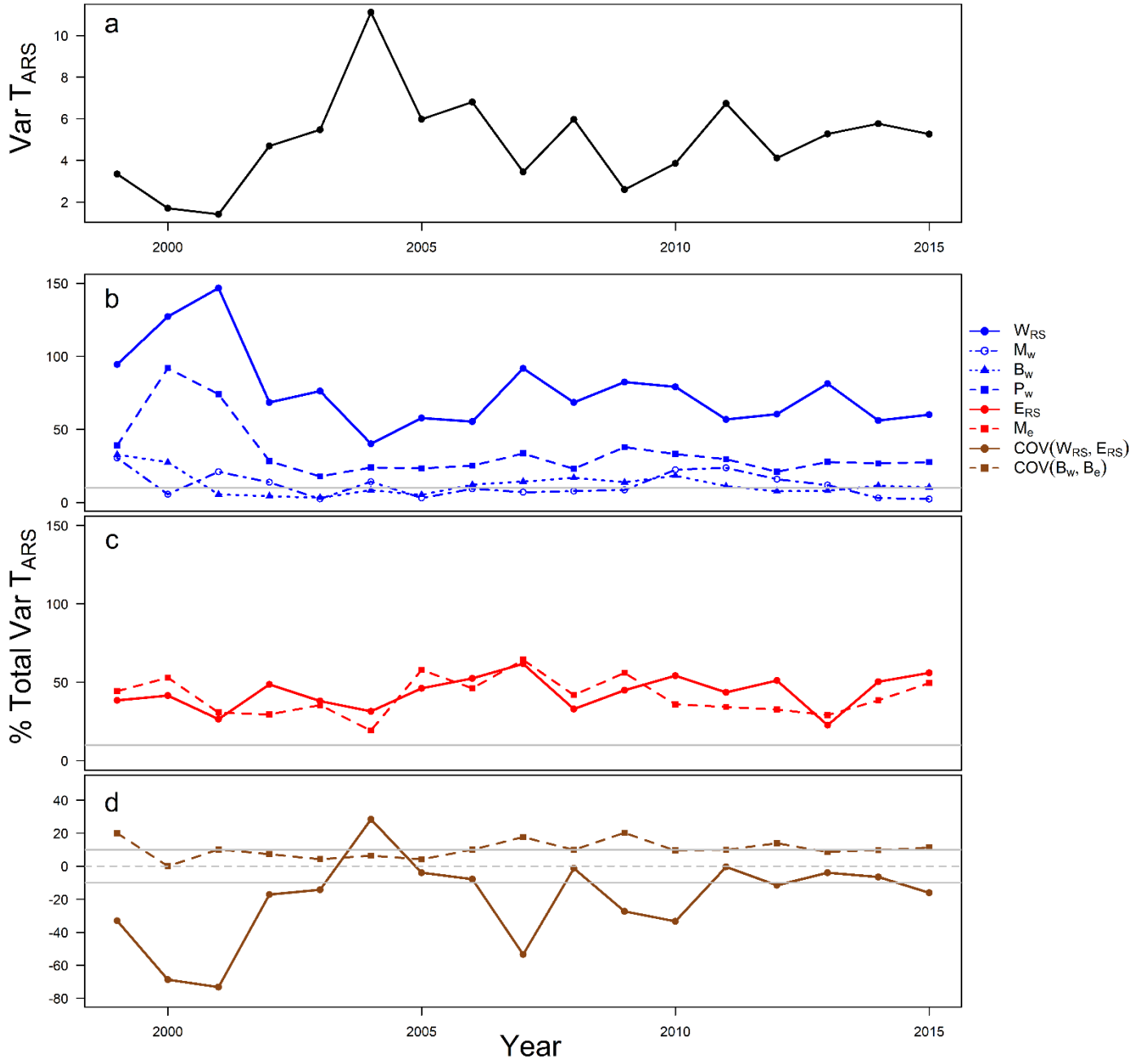

a
Var T_{ARS}
b
c
d
% Total Var T_{ARS}
Year
W_{RS}
M_w
B_w
P_w
E_{RS}
M_e
COV(W_{RS}, E_{RS})
COV(B_w, B_e)

Figure 3: Time series plots depicting a) yearly variance in total annual reproductive success (T_{ARS}) across a population of black-throated blue warblers, and yearly decompositions of the percent of total variance in T_{ARS} attributable to b) within-pair reproductive success (W_{RS}), c) extra-pair reproductive success (E_{RS}), and d) the covariance between within-pair and extra-pair reproductive success [$Cov(W_{RS}, E_{RS})$]. For panels b, c, and d, colored dashed, dotted, and dot-dashed lines represent the yearly percentage of total variance in T_{ARS} attributable to constituent components of W_{RS}, E_{RS}, and $Cov(W_{RS}, E_{RS})$ found to represent 'substantial variance' (≥ 10%) across the study period (see Table 1), depicted as solid grey lines. For panel d, dashed gray line represents the transition from positive to negative covariance. Note different y-axis scales for panels a) and d).

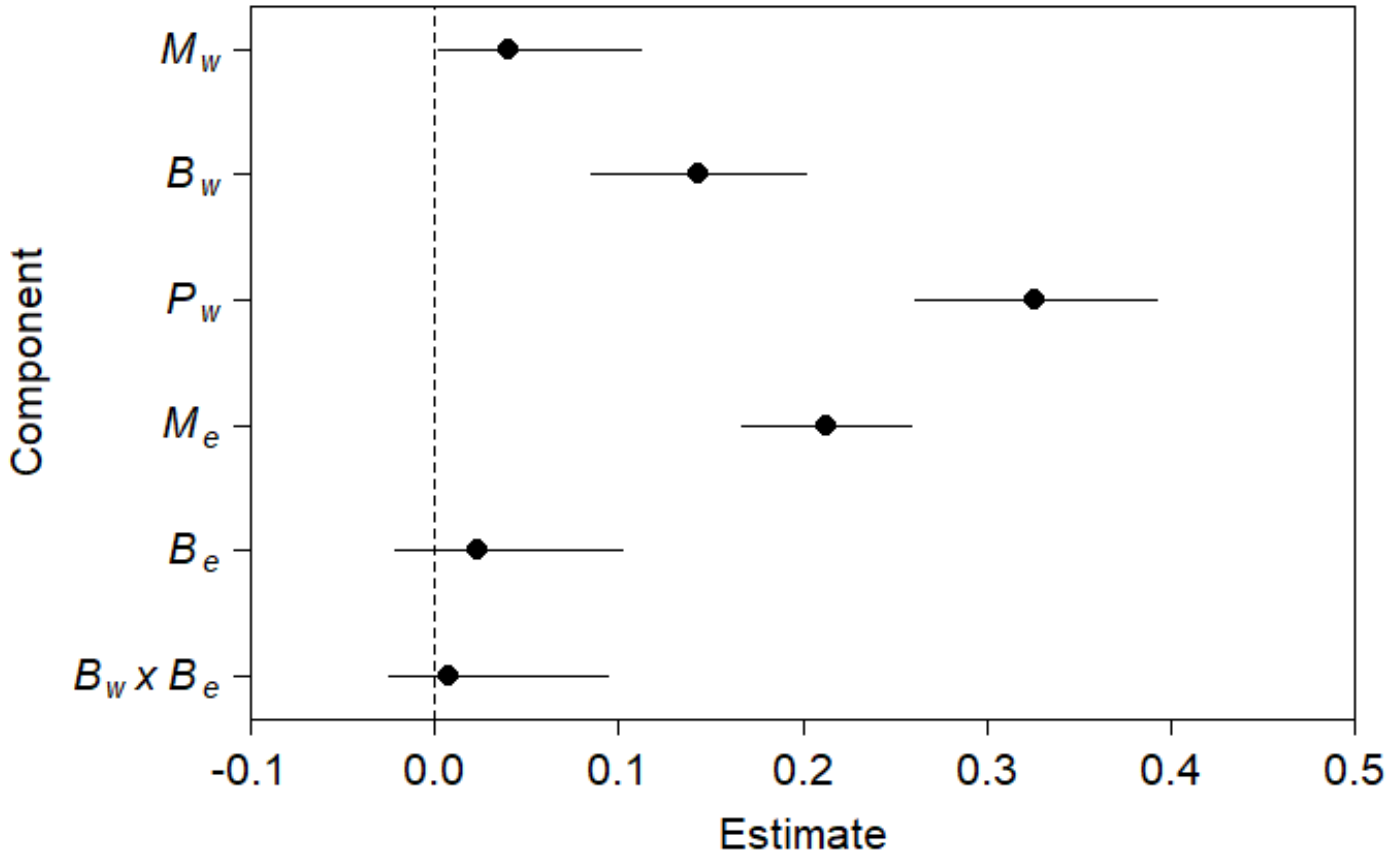


Figure 4: Effects plots from averaged generalized mixed-effects models testing the relative influence of each key component of (co)variance on mean annual reproductive success ($\overline{ARS}$). Points represent parameter estimates from final averaged model while whiskers depict 95% CIs. Dotted line represents 0, and parameter are considered significant if CIs do not overlap zero. Full results from averaged model and all models in top subset are provided in Supporting Information S2.

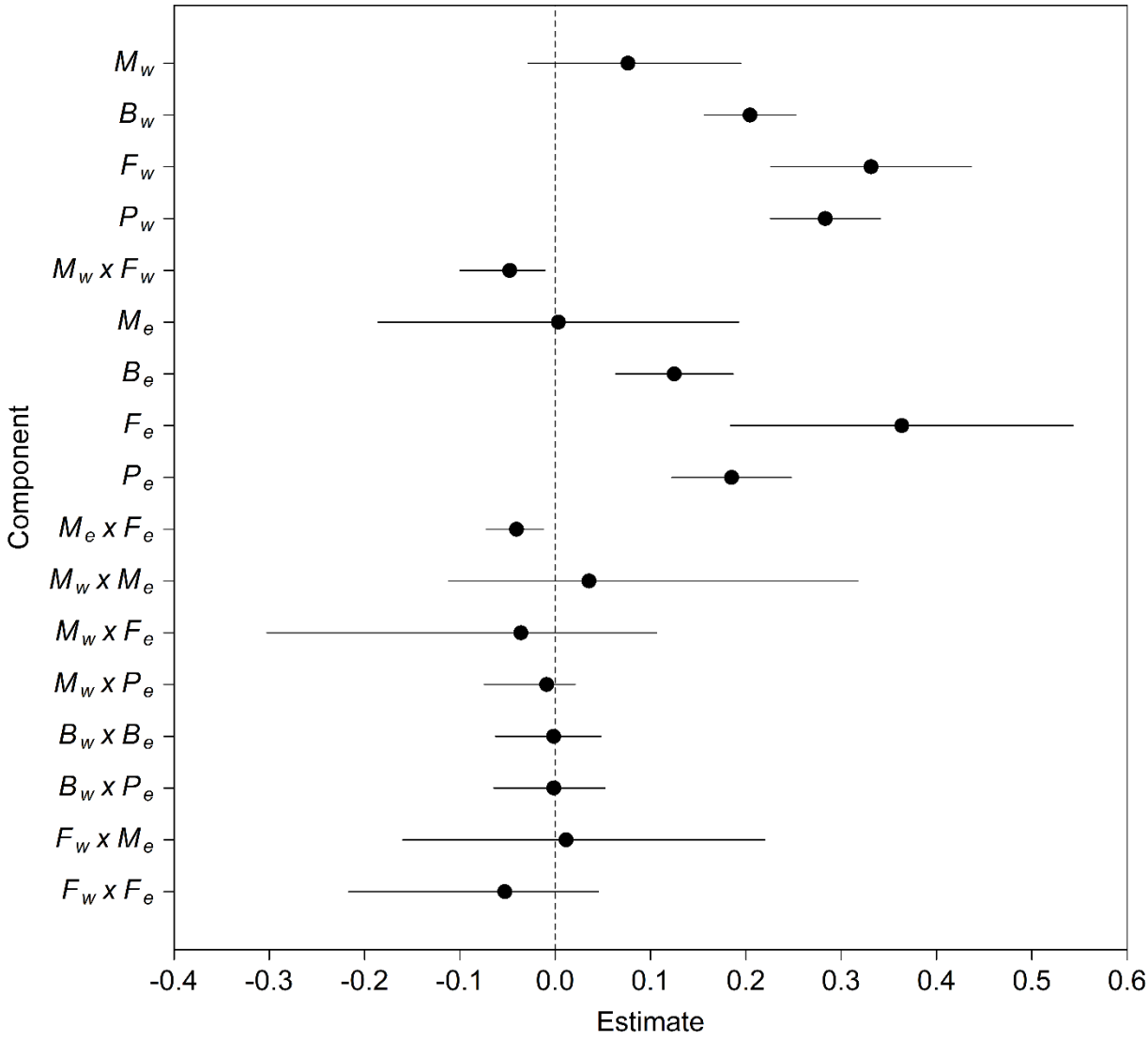


Figure 5: Effects plots from averaged generalized mixed-effects models testing the relative influence of each key component of (co)variance on mean lifetime reproductive success ($\overline{LRS}$). Points represent parameter estimates from final averaged model while whiskers depict 95% CIs. Dotted line represents 0, and parameters are considered significant if CIs do not overlap zero. Full results from averaged model and all models in top subset are provided in Supporting Information S3.