Sources of (co)variation in alternative siring routes available to male great tits (*Parus major*)

Yimen G. Araya-Ajoy[1,2,3*], Sylvia Kuhn[2], Kimberley J. Mathot[1,4], Alexia Mouchet[1], Ariane Mutzel[1,5], Marion Nicolaus[1,6], Jan J. Wijmenga[1], Bart Kempenaers[2], Niels J. Dingemanse[1,7]

[1]Research Group Evolutionary Ecology of Variation, Max Planck Institute for Ornithology, Seewiesen, Germany

[2]Department of Behavioral Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Seewiesen, Germany

[3]Current address: Center for Biodiversity Dynamics, Norwegian University of Science and Technology, Trondheim, Norway

[4]Current address: Royal Netherlands Institute for Sea Research (NIOZ), Department of Coastal Studies (COS) and Utrecht University, Den Burg, Texel, the Netherlands

[5]Current address: Department of Biology, University of Kentucky, Lexington, Kentucky, United States

[6]Current address: Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, the Netherlands

[7]Behavioural Ecology, Department of Biology, Ludwig-Maximilians University of Munich, Planegg-Martinsried, Germany

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***Corresponding author**: email: yimencr@gmail.com ; Tel: 4948506487

Males of socially monogamous species can increase their siring success via within-pair and extra-pair fertilizations. In this study, we focused on the different sources of (co)variation between these siring routes, and asked how each contributes to total siring success. We quantified the fertilization routes to siring success, as well as behaviors that have been hypothesized to affect siring success, over a five-year period for a wild population of great tits *Parus major*. We considered siring success and its fertilization routes as “interactive phenotypes” arising from phenotypic contributions of both members of the social pair. We show that siring success is strongly affected by the fecundity of the social (female) partner. We also demonstrate that a strong positive correlation between extra-pair fertilization success and paternity loss likely constrains the evolution of these two routes. Moreover, we show that more explorative and aggressive males had less extra-pair fertilizations, whereas more explorative females laid larger clutches. This study thus demonstrates that (co)variation in siring routes is caused by multiple factors not necessarily related to characteristics of males. We thereby highlight the importance of acknowledging the multi-level structure of male fertilization routes when studying the evolution of male mating strategies.

INTRODUCTION

Most mating systems offer multiple ways by which males can maximize their siring success (Gross 1996). In socially monogamous animals, extra-pair and within-pair fertilizations represent such alternative pathways (Webster et al. 1995; Griffith et al. 2002). Therefore, a male's total siring success will be determined by variation in, and covariation among, these different routes (Webster et al. 1995; Lebigre et al. 2013). This (co)variation is in turn determined by the joint effects of the phenotypic characteristics of the male and its social (female) mate, and the influence of environmental effects (Petrie and Kempenaers 1998; Westneat and Stewart 2003). For example, if higher resource holding potential increases a male's ability to gain within-pair fertilizations while simultaneously increasing its chances to gain extra-pair paternity, differences between males in siring success will exist due to among-male variation in ability to monopolize resources. In such cases, directional selection is expected to deplete genetic variation in both resource-holding potential and any route to siring success, unless trade-offs or other processes constrain their adaptive evolution (Merilä et al. 2001). For instance, investment in avoidance of paternity loss might trade-off with investment in obtaining extra-pair copulations in instances where males face limitations in the time or energy available for these activities (Westneat and Stewart 2003; Kokko 2005). Such trade-offs between fertilization routes (whether environmental or genetic in nature) may result in a situation where traits increasing fertilization success through one route will decrease success through another. These trade-offs may be mediated by a male's behavioral strategy and determine the relative contribution of the different fertilization routes in an individual's annual siring success (Westneat and Stewart 2003; Kokko 2005). Hence, the sources of variation in, and covariation between, siring routes will represent an important determinant of the evolutionary trajectories of male reproductive strategies.

Several studies quantifying the covariance between the different routes to siring success find that males that are successful in avoiding paternity loss are also more likely to gain extra-pair fertilizations (Webster et al. 1995; Kempenaers et al. 1997; Schlicht and Kempenaers 2013; Reid et al. 2014b). As detailed above, such patterns can result from among-male variation in resource-holding potential, but they can also emerge because of spatiotemporal variation in the availability of resources. Such patterns are not mutually exclusive and, notably, do not imply the absence of trade-offs between siring routes (van Noordwijk and Jong 1986). This is because covariances between life-history traits are often simultaneously affected by multiple processes (Stearns 1989). For instance, in addition to the (co)variation between fertilization routes generated by variation in resource availability, investment in avoiding paternity loss might still trade-off with the amount of time and/or resources available for investment in extra-pair fertilization behaviors. The overall pattern of correlation between fertilization routes is therefore influenced simultaneously by variation in male attributes (e.g. resource-holding potential), spatiotemporal variation in environmental conditions, and trade-offs between fertilization routes. Importantly, in cases where associations between fertilization routes are opposite across hierarchical levels, fertilization routes may seem completely unrelated if effects cancel each other out in unpartitioned (i.e., ‘raw’) datasets. The potential existence of multiple processes contributing to the overall patterns of covariance between traits and siring routes thus warrants the decomposition of the sources of variation and covariation.

Quantifying (co)variation among siring routes in socially monogamous species is challenging because each of the routes is difficult to define as the property of a single individual. For example, paternity loss is often treated as a male trait, although it depends both on the male’s characteristics in relation to the neighboring males, and the promiscuity level of its social mate (Petrie and Kempenaers 1998; Westneat and Stewart 2003; Reid et al. 2014a). Moreover, female fecundity can affect male paternity loss because highly fecund females produce more eggs to be fertilized, resulting in an increased probability for their social (male) partner to lose paternity. It follows that the evolutionary dynamics of siring routes will not only depend on the sources of (co)variation within the sexes but also across them (Reid et al. 2014a). Female phenotypic characteristics causing variation in, and covariation among, siring routes can be viewed as environmental effects on siring routes, notably these environmental components have genes and can thus evolve. In the quantitative genetics literature, traits that are affected by the phenotype of other individuals are sometimes called 'interactive phenotypes' (Moore et al. 1997). This type of interaction may generate (co)variation in pathways to male fertilization success and affect their response to selection (Wolf et al. 1998; Wolf 2003). Variance partitioning approaches (detailed below) have proven insightful in the study of the sources of variation and covariation of this type of interacting phenotype (McGlothlin and Brodie 2009; Dingemanse and Araya-Ajoy 2015).

Using a variance partitioning approach, we quantified the sources of (co)variation between behavioral traits and siring routes to determine their contribution to the annual siring success of great tits (*Parus major*). Great tits are socially monogamous and commonly engage in extra-pair reproduction (Brommer et al. 2007; van Oers et al. 2008; Patrick et al. 2012; Araya-Ajoy et al. 2016). During five consecutive years (2010-2014), we monitored the breeding ecology of a Bavarian population breeding in 12 nest box plots, and measured annual siring success (defined as the total number of eggs sired by a male in a focal year). We had two main objectives: i) determine the contribution of each of the fertilization routes to overall siring success and ii) estimate the extent to which the (co)variation between fertilization routes is determined by characteristics of both members of the social pair and by their response to spatiotemporal variation in environmental conditions. To achieve these goals, we first decomposed male annual siring success into its underlying components: extra-pair fertilization success (the number of eggs that a focal male sired that were laid by females other than its social mate) and within-pair fertilization success (the number of eggs that a focal male sired that were laid by its social mate), which is in turn determined by clutch size (the number of eggs produced by the focal male's social mate) and paternity loss (number of eggs laid by the focal male's social mate that were sired by extra-pair males) (Fig. 1). We then used a variance-partitioning approach to quantify the relative contributions of male and female identity effects, spatiotemporal effects, and within-male-cross-year (i.e., residual) effects on an individual's siring success (both for total annual success and for each of the underlying siring routes). We refer to "identity" effects as the phenotypic characteristics that vary among-individuals (due to genes and/or permanent environmental effects) and cause variation in any of the fertilization routes. Residual variation captures within-male-cross-year variation; this distinct level of variation reflects important biological processes (Westneat et al. 2015) including patterns of within-individual plasticity in response to unmeasured environmental variables, however, we acknowledge that variation at this level is also caused by stochastic events and/or measurement error. We then extended this variance partitioning approach and estimated the (co)variation between the alternative siring routes and annual siring success caused by the above-mentioned sources.

This variance partitioning approach does not provide information about the specific individual-level phenotypes of males or females affecting an individual's annual siring success, but can be used to quantify the overall importance of phenotypic traits specific to females and males that are not attributable to (within-individual) short-term responses to the environment (Griffing 1967). We therefore proceeded to determine whether specific male behavioral traits were associated with a male's fertilization strategy and whether behavioral traits of both sexes explained variation captured by the male and female identity effects described above. We focused on the effects of male and female exploration behavior and male aggressiveness. Exploration behavior has previously been shown to affect various aspects of extra-pair reproduction in great tits. Studies conducted in a British population found that a male's exploration behavior was positively associated with its extra-pair fertilization success, but negatively associated to its ability to avoid paternity loss (Patrick et al. 2012). Studies conducted in a Dutch population, furthermore, found that males paired to females of similar exploration type lost more paternity (van Oers et al. 2008). Moreover, in our German population there is evidence suggesting that exploratory behavior is related to female reproductive investment (Nicolaus et al. 2015). With respect to aggressiveness, we hypothesized that increased aggressiveness towards male intruders reduces paternity loss (Araya-Ajoy and Dingemanse 2014; Duckworth 2006). If investment in securing within-pair fertilizations would trade-off with the expression of behaviors that enables males to gain extra-pair copulations, we also expected that aggressive males would gain less extra-pair paternity.

As a final step we synthesized the above-mentioned analyses using a path diagram (Fig. 1). We aimed to model the contribution of each fertilization route to annual siring success, as well as the relationships between the alternative fertilization routes. We also quantified the variance in each fertilization route attributable to aggression and exploration behavior. First, we estimated how much variation in male annual siring success was caused by within-pair fertilization success and how much by extra-pair fertilization success. By definition, these two routes account for all variation in male annual siring success. In a similar fashion, we then quantified the variance in within-pair fertilization success caused by clutch size and paternity loss. Importantly, these two routes can only affect annual siring success through their effect on within-pair fertilization success. We then proceeded to determine the effects of the two behavioral traits on each fertilization route, appreciating that these behaviors can only influence annual siring success by affecting clutch size, paternity loss, and/or extra-pair fertilization success. By combining the information concerning the relationships within and among fertilization routes, we were able to quantify how much of the variance in annual siring success at each hierarchical level (i.e., among-males, among-females, among-plot-years or within-male-cross-years) was attributable to each fertilization route and their correlations, while determining the mediating roles of aggressive and explorative behavior.

METHODS

Study site

We studied a population of great tits breeding in nest boxes in Southern Germany (Bavarian Landkreis Starnberg; 47º 58' N, 11º 14' E). The nest boxes were located in 12 plots established in 2009; each plot was approximately 9 hectares in size and consisted of a regular grid of 50 nest boxes with 50 meters between adjacent boxes. From April onwards, nest boxes were checked twice per week to determine lay date (back-calculated assuming that one egg was laid per day), onset of incubation and clutch size. Nestlings were blood sampled and marked with an aluminum ring when they were 6 days old; any unhatched eggs or deceased nestlings were collected. Parents were caught with a spring trap in the nest box the next day, measured, bled, and marked with a unique combination of rings if not ringed previously.

Male variation in siring success

We recorded a total of 8182 eggs in our population distributed over 990 first clutches (defined as nests starting within 30 days after the first egg of the focal year in a focal plot was found) between 2010 and 2014. Because we were interested in siring success and aimed to avoid bias in our measure due to variation in hatching success or early survival of within- or extra-pair offspring (García-González 2008), we attempted to genotype all successfully fertilized eggs (i.e., hatched nestlings, unhatched eggs and nestlings deceased prior to blood sampling). We were able to genotype 7109 (81%) of the 8182 recorded eggs. We performed genetic parentage assignments for these 7109 fertilized eggs using genetic and spatial information incorporated in Bayesian full probability models (R package MasterBayes; Hadfield et al. 2006). We excluded all breeding attempts where maternity was uncertain (i.e., where the genetic mother was not sampled) and used a 90% confidence cut-off to take a paternity assignment forward to further analyses (for further details see Araya-Ajoy et al 2016). This resulted in 6441 offspring (90% of the 7109 genotyped offspring) with assigned paternity from 558 males and 567 female parents over 862 breeding attempts. We detected 621 extra-pair offspring and managed to determine the identity of the genetic father for 438 (71%) of them. The unassigned extra-pair offspring may have been sired by males in our plots that were not blood sampled or by males breeding in natural cavities within or adjacent to our study plots. Given current debates on the pros and cons of alternative paternity assignment methods (Walling et al. 2010), we also performed the paternity assignment in another commonly used package (Cervus 3.0.6); this produced very similar findings (Araya-Ajoy et al. 2016). We estimated male paternity loss as the number of eggs produced by the social female of a focal clutch that were not sired by the social male, and male extra-pair paternity gain as the number of eggs that a focal male sired with females other than its social mate. Within-pair fertilization success was calculated as the clutch size minus the number of extra-pair offspring in the focal male's brood, and male annual siring success was approximated as the sum of within- and extra-pair fertilization success.

Male aggressiveness assay

We measured male aggressive responses to standardized simulated territorial intrusions for each first brood. Each male was subjected to two aggression tests during the laying phase of its social mate (one and three days after the first egg was found) and two during her incubation phase (one and three days after the onset of incubation). The behavioral test started when a taxidermic mount of a male great tit with a playback song was presented one meter away from the subject's nest box on a 1.2 meter wooden pole. We subsequently recorded the behavior of the focal male for a period of three minutes after it had entered a 15-meter radius around the nest box. Details of the experimental setup, and assayed behaviors, are given in Araya-Ajoy and Dingemanse (2014). As a measure of the intensity of the aggressive response of a male during a focal breeding attempt (i.e., unique combination of male and year identity), we mean-centered the minimum approach distance for each breeding stage and averaged the breeding attempt measures during the four assays. We obtained measures of male aggressiveness for 811 (94% of the 862) breeding attempts of 541 (96% of the 558) males. In 30 % of the tests males did not respond to a simulated territorial intrusion (i.e. the male was not observed within 15 min of the start of the simulated territorial intrusion; for details see Araya and Dingemanse 2014), therefore not all the values for each breeding attempt were calculated using the same number of observations. Importantly, the probability that a male responded to an aggression test was positively related to the intensity of its response when responding (mean r =0.75, 95% CI=0.08, 1.00). This suggests that the response towards a simulated territorial intrusion is a measure of how much a male invests in territory defense.

Exploratory behavior assay

We assayed exploration behavior of males and females when their nestlings were 7 days old. We recorded exploration behavior using a cage test adapted from the "novel environment test" used to score exploration behavior in winter (for more details see Stuber et al. 2013). Exploration behavior was filmed during a 2-min recording period. Individual movements between perches, walls, and floor were scored from the video recordings. Locations included 3 sections of the floor and 6 sections of the cage area (see Figure 1 in Stuber et al. 2013). The total number of movements between sections was used as a proxy of exploration behavior, similar to how it is scored in laboratory-based assays conducted in winter (e.g., Dingemanse et al. 2002). We obtained data on exploration behavior for 511 (90% of 558) males and 738 (85% of 862) breeding attempts, and for 521 (91% of 567) females and 747 (86% of 862) breeding attempts.

Statistical analyses

Variance partitioning of routes to siring success

We first quantified the sources of variation in male annual siring success and its underlying components, clutch size, paternity loss, within-pair fertilization success, and extra-pair fertilization success. We used mixed-effects models to determine variance attributable to male identity (n=558 individual males), female identity (n=567 individual females), spatiotemporal environmental effects (by fitting n=60 unique combinations of plot and year identities; elsewhere in the manuscript referred to as “plot-year”) and unidentified exogenous variables and measurement error causing residual variation (i.e., residual variance; 862 observations). Our ability to disentangle male versus female-identity effects hinged on the availability of repeated measures collected across years, which we had for (i) 201 out of 558 (36%) males (no. of individuals (no. of years): 357 (1), 125 (2), 53 (3), 19 (4), 4(5)), (ii) 189 out of 567 (33%) females (378 (1), 114 (2), 53 (3), 13 (4), 9 (5)), and, importantly, (iii) 201 out of 558 (24%) males breeding with different females across years (424 (1), 103 (2), 27 (3), 3 (4), 1 (5)).

To achieve the partitioning of variance, we used mixed-effects models with random intercepts for male and female identity (see Appendix S1 for model equations). We also included random intercepts for each combination of plot and year (plot-year; 60 levels) to quantify any (interacting) spatial and/or temporal effect on male fertilization routes and siring success. For these and all subsequent models, annual siring success, within-pair fertilization success, and clutch size were modeled with a Gaussian error distribution. Paternity loss and extra-pair fertilization success were modeled assuming an over-dispersed Poisson distribution. We acknowledge that zero inflation may be a concern not fully dealt with by modeling over-dispersion in this way and we therefore also fitted models with these variables coded as a binary trait and assuming a binomial error distribution (Table S2, Appendix S2).

Covariation between fertilization routes and siring success

We used a series of bivariate mixed-effects models to quantify the relationships between the fertilization routes and annual siring success at the different levels (i.e., among-males, among-social females, among-plot-years, and within-individuals). These models always consisted of two response variables with a random effect structure analogous to the univariate models (see Appendix S1 for a detailed description). We used these models to quantify i) the effect of each fertilization route on annual siring success, and ii) the relationships between alternative fertilization routes. First, we quantified the covariation between annual siring success and within-pair fertilizations (bivariate model 1), and between annual siring success and extra-pair fertilizations (bivariate model 2). We then studied the paths contributing to within-pair fertilization success: we quantified the covariation between within-pair fertilizations and clutch size (bivariate model 3), and between within-pair fertilizations with paternity loss (bivariate model 4). As a next step, we quantified the relationships between the alternative fertilization routes: we assessed the correlation between within- and extra-pair fertilizations (bivariate model 5), paternity loss and clutch size (bivariate model 6), extra-pair fertilizations and clutch size (bivariate model 7), and extra-pair fertilizations with paternity loss (bivariate model 8). Annual siring success, clutch size and within-pair fertilizations were modeled on the data scale (i.e., using a Gaussian error distribution) and paternity loss and extra-pair fertilizations on a log scale (using a Poisson error distribution). We also constructed these multivariate models with paternity loss and extra-pair fertilizations fitted as Gaussian and binomial responses to ensure that the interpretation of the results were robust to the chosen error distributions (see Appendix S2, Table S3 and S4).

Correlations between behavioral traits and fertilization routes.

We also quantified relationships between behaviors and fertilization routes. As above, we used a series of bivariate mixed-effects models to quantify hypothesized relationships between behaviors and the fertilization routes at each specified level (i.e., among-males, among-social females, among-plot-years and within-individuals-cross-years). Specifically, we quantified the covariation at the different levels between a male's aggressive or exploration behavior and its extra-pair fertilization success (bivariate models 9 & 10). We also performed bivariate models to quantify the relationship between paternity loss and male aggression (bivariate model 11), male exploration (bivariate model 12) and female exploration (bivariate model 13). Finally we studied the effects of female exploration on clutch size (bivariate model 14). We also constructed these multivariate models with paternity loss and extra-pair fertilizations fitted as Gaussian and binomial responses, to ensure that the interpretation of the results were robust to the chosen error distributions (see Appendix S2, Table S5).

Pathways to annual siring success

We summarized the results from the above-mentioned bivariate models to study the relationships between behavior, siring routes and siring success using the path diagram depicted in Figure 1 (see table S1 for a summary of these models). We aimed to model the hypothesized causal relationships of behavior affecting each fertilization route, and the fertilization routes affecting overall siring success.

From the bivariate mixed-effects models (1-2), we estimated the causal effect of within- and extra-pair fertilizations on male annual siring success. These relationships are causal because annual siring success is by definition fully determined by within- and extra-pair fertilizations. Therefore, we used the covariances between each fertilization route and annual siring success estimated with the bivariate models to calculate a slope (β) that represents the effect of each siring route on annual siring success at each of the studied levels. A focal slope (β) was calculated as the covariance between the two variables divided by the variance of the focal route. Using the estimated covariances, we also calculated the amount of variance explained (R^2) in annual siring success by each of the fertilization routes. Variance explained was calculated simply as the squared correlation, but note that when the effects size (β) was not significant, the proportion of variance explained is not readily interpretable. Similarly, we estimated the effects of, and variance explained by, paternity loss and clutch size in within-pair fertilizations (bivariate models 3 & 4). We then proceeded to estimate bivariate correlations between within- and extra-pair fertilizations, clutch size and paternity loss, extra-pair fertilizations and clutch size, and extra-pair fertilizations and paternity loss (bivariate models 5-8). We estimated these relationships as correlations, as both variables could arguably be viewed both as a predictor (i.e., causal effect) and as a response. For instance, the relationship between extra-pair fertilization success and within-pair fertilization success could be caused by a factor affecting both of these traits simultaneously, like resource abundance. When focusing on the behaviors and their relationships with the fertilization routes, we present their associations as slopes, because we hypothesized that behaviors causally affected the fertilization routes (bivariate models 9-14). As a final step, we estimated the total effects of clutch size, paternity loss, and the behavioral traits on annual siring success (β), as well as the respective proportion of variance explained (R^2) by each trait in annual siring success. The total effects and variance explained were calculated using Wright path rules (Wright 1934), multiplying the effect sizes of the different steps in the path of each trait to annual siring success (see table 5).

General modeling procedures

We fitted mixed-effects models (detailed above) using a Bayesian framework implemented in the R-package (R Core Team 2015) MCMCglmm (Hadfield 2010). Uni- and multi-variate models were run for 3,050,000 iterations per model, from which we discarded the initial 50000 (burn-in period). Each chain was sampled at an interval of 3000 iterations, which resulted in a low autocorrelation among thinned samples (<0.05). Posterior means and 95% credible intervals were estimated across the thinned samples for the mean effects (fixed effects) and (co)variances. Fixed effect priors were normally distributed and diffuse with a mean of zero and a large variance (100). Different priors were used for the variance-covariance matrices; the results presented in the paper correspond to parameter-expanded priors for univariate models and inverse-gamma priors for bivariate models. Posterior distributions were robust to reasonable prior variation and were used to estimate derived quantities (e.g. proportion of variance explained, correlations and slopes). We considered covariance, correlation and slope estimates statistically significant in the frequentist's sense, when it's estimated 95% credible intervals did not overlap zero.

RESULTS

Male paternity: descriptive statistics

Clutch size ranged from 2-17 eggs with a mean of 8.3. Mean paternity loss was 0.7 offspring (range 0-8), with 40% of males losing at least one offspring and ~10% of all the offspring being extra-pair. When a clutch contained extra-pair offspring, on average there were 1.8 offspring sired by an extra-pair male. Mean extra-pair fertilization success was 0.5 offspring (range: 0-11), with 24% of males siring at least one extra-pair offspring. Mean siring success was 8.1 offspring (range: 2-17). In a closed population the average amount of extra-pair paternity gain and paternity loss should be the same, but our population was not closed and we could not assign extra-pair fathers to all offspring (because some extra-pair sires were not breeding in our nest boxes or were not sampled). Thus, the population-average estimates of extra-pair gain and within-pair loss were somewhat different.

Variance components of annual siring success and its routes

Analysis of the sources of variation in siring success demonstrated that (unidentified) individual-specific traits of females contributed more strongly to siring success than individual-specific traits of males (as the variance attributable to female versus male identity was 22% versus 8%). While 3% of the variation was explained by spatiotemporal environmental variation across unique combinations of plot and year (plot-year effects; Table 1), most of the variation was unexplained (67%, Table 1). The relative contribution of different variance components differed between siring routes (Table 1; Fig. 1): individual-specific traits of females explained significantly more variation than individual-specific traits of males in within-pair reproduction (35% versus 6%) and clutch size (49% versus 4%). However, both male and female identity explained similar amounts of variance (6-8%) in paternity loss and extra-pair fertilization success.

Relative contribution of each siring route on overall siring success

We found that variation in siring success mostly derived from within-pair fertilizations (72%) rather than from extra-pair fertilizations (27%) (R^2_{Total}; Model 1 vs. 2 in Table 2). Variation in within-pair siring success was in turn largely attributable to the social mate’s clutch size rather than to paternity loss (R^2_{Total} Model 3 vs. 4). We further found that extra-pair fertilizations only explained variation in annual siring success associated to residual variation, representing the combined effects of unmeasured environmental variables, stochasticity, and measurement error ($R^2_{Observations}$; Model 2). The same was true for paternity loss explaining variation in within-pair fertilization success ($R^2_{Observations}$; Model 4), implying that the variance in annual siring success caused by paternity loss and gain was mostly of environmental nature (or attributable to measurement error). In agreement with our finding that male identity effects on clutch size and paternity loss were very relatively small, we found that within-pair fertilizations did not explain significant variation in annual siring success at the male identity level.

Correlations between alternative siring routes

We found a positive relationship between clutch size and paternity loss (Model 6; Table 3). This correlation was largely determined by a significant residual (i.e., within-male-cross-year) correlation ($Cor_{among\text{-}observations}$, Model 6; Table 3): breeding attempts with larger clutches contained more extra-pair offspring. We also found a tight positive correlation at the plot-year level between paternity loss and gain ($Cor_{among\text{-}plot\text{-}years}$; Model 8; Table 3): as expected, plot-years with more extra-pair fertilizations also had more paternity loss.

Behavioral traits and siring routes

More aggressive (Model 9) and more explorative (Model 10) behavior in males were associated with lower numbers of extra-pair fertilizations (Table 4). The link between male exploration behavior and extra-pair paternity gain was, notably, at the among-male level. In other words, males that were on average highly explorative across years were also on average gaining less extra-pair paternity. The overall effect of male aggression on extra-pair paternity gain was “significant”, although none of the level-specific effects were “significant” (Table 4). The overall effect of aggression on extra-pair fertilization success, however, should mostly be influenced by the residual (i.e., within-male-cross-year) level because of the low values of male repeatability in extra-pair fertilization success. This implies that in a year where a focal male was relatively aggressive it also had a lower extra-pair fertilization success compared to years where it was less aggressive. Finally, exploration behavior in females was positively associated with clutch size (Model 13), although none of the level-specific effects was significant. Nevertheless, both the among-female and the within-individual-cross-year effects were positive, suggesting that these two levels drive the overall effect. Overall, behavioral traits explained a small percentage (1.2%) of the variance in annual siring success (Table 5).

DISCUSSION

In this study, we quantified the sources of variation in siring success in a wild population of great tits during five consecutive years. We found that most of the variation in siring success was determined by within-pair fertilization success. Within-pair fertilization success was in turn substantially influenced by female identity effects (Fig. 1, Table 1), mostly due to repeatable variation in female fecundity (i.e., clutch size; Table 1, 5). Male and female identity effects on male paternity loss and extra-pair paternity gain were very small (Table 1), and had a negligible influence on annual siring success (Table 2, 5). Instead, the effects of extra-pair fertilizations and paternity loss on male annual siring success were mostly linked to within-individual-cross-year (i.e., residual) variation (Table 2, 5). In general, a high proportion of variation in, and covariation between, the alternative fertilization routes was associated with such residual variation, suggesting that within-individual plasticity in response to environmental variation and/or stochastic processes largely determined variation in siring success. Finally, our results suggest that more exploratory and aggressive male behavior was associated with lower extra-pair fertilization success, whereas more exploratory female behavior was associated with a larger clutch size. While all of these behaviors were associated with male siring success, their net effects on annual siring success were small (Table 5).

Female phenotype strongly affected siring success

Female identity explained two times more variance in siring success compared to male identity (Table 1). Our analyses suggest that female effects acted particularly through within-pair fertilization success mediated by clutch size, which implies that a male's siring success was largely mediated by its social mate's average level of fecundity. In contrast, male identity explained only a minor portion of the variation in within-pair fertilization success and clutch size. This suggests that differential female investment in response to repeatable among-male variation in phenotypic attributes plays a minor role, which is consistent with another study on great tits (Browne and McCleery 2007). Our results do not support the "differential allocation hypothesis", which predicts that females should invest more in reproduction when mated with attractive males (Burley 1986; Sheldon 2010), because 'attractiveness' is viewed as an individual-level character (e.g., mediated by 'genetic quality'). The results from our study and Browne and McCleery (2007) imply that either female great tits do not strategically modify investment in reproduction as a function of characteristics of their mate, or that the differential investment occurs at a different stage of the reproductive season (e.g. nestling provisioning phase).

Male and female identity effects explained a similar amount of variation (~7%) in male paternity loss. Repeatable among-female variation in promiscuity will inherently lead to such female identity effects. A male's paternity loss is the same trait as its social mate's extra-pair paternity reproduction. Extra-pair paternity has also been referred to as a “meta-trait” (Westneat & Stewart 2003) given that it is determined by at least three players: the cuckolded male, the extra-pair father and the female (Petrie and Kempenaers 1998). Female effects on siring routes can thus be viewed as a social environment effect on siring success (Forstmeier et al. 2011; Reid et al. 2014a). Indirect genetic effects theory developed in the field of quantitative genetics suggests that such social environment effects may impose major evolutionary constraints (Wolf et al. 1998; McGlothlin et al. 2010; see also Brommer & Rattiste (2008) for an empirical example). From the female’s perspective, benefits of extra-pair reproduction remain unclear (Arnqvist and Kirkpatrick 2005; Forstmeier et al. 2014). If females engage in extra-pair reproduction to reap genetic benefits (Jennions and Petrie 2000), this would cause an inter-sexual conflict between the male’s efforts to reduce paternity loss and the female’s benefits arising from extra-pair reproduction. Although researchers have been aware that female phenotype affects siring success, our study empirically quantified the multiple routes by which females may affect the evolution of male within- and extra-pair reproductive tactics.

Patterns of (co)variance in male fertilization routes

Males showed low among-year repeatability in annual siring success and in any of the fertilization routes (Table 1). This implies that there is little consistency in a male’s “preferred” fertilization route and that most of the observed variation is environmental in nature (i.e., varying within-male-cross-years) or caused by stochastic processes and measurement error. The low variance attributed to plot-year effects suggests that the environmental factors causing variation in male fertilization routes vary at a local scale, as the plot-year effects should capture variation across years at a larger spatial scale. For instance, the immediate social environment of an individual (i.e., mediated by traits of neighboring males and females; e.g. Schlicht et al. 2015) might impact paternity loss and probability to gain extra-pair paternity, provided that this social environment varies within males across-years, thereby causing the observed variation in fertilization routes. Another factor that could cause residual variation in the fertilization routes is male age. Older males typically sire more extra-pair offspring (e.g. Schlicht et al. 2015), and this is also the case in our population (see Appendix S2, Table S6). As documented in other studies (Cleasby and Nakagawa 2012) age did not affect paternity loss in our population.

We did not find significant among-male correlations between any of the fertilization routes. Thus, males that consistently had a higher number of extra-pair fertilizations did not necessarily have a higher number of within-pair fertilizations (Table 3), implying that there were no “super” males that were able to consistently monopolize both within- and extra-pair fertilizations. Furthermore, males that gained more extra-pair fertilizations did not necessarily suffer more paternity loss (Table 3). Thus, there is no evidence for a trade-off between investing in behaviors that increase extra-pair fertilizations and investing in securing within-pair fertilizations. Note, however, that the estimates of these correlations had broad confidence intervals, despite relatively high sample sizes. Our interpretations about the significance and biological meaning therefore need to be considered with care.

We found that within-pair paternity loss was highly positively correlated at the plot-year level. This means that in areas and years where more extra-pair fertilizations occur there is on average more paternity loss. This is an expected result that comes with interesting evolutionary implications. Specifically, it implies that, at the population level, within-pair paternity loss and extra-pair paternity gain cannot evolve independently, because they are essentially auto-correlated. In other words, this is a zero-sum game: when someone gains, somebody else has to lose. Therefore, an increase in the frequency of individuals that are successful in gaining extra-pair fertilizations has to be linked to an increase of individuals that lose within-paternity. This is a clear example where competition must result in an evolutionary constraint (Wilson 2014). We also found that more eggs were fertilized by an extra-pair male in larger clutches. Inspecting the level-specificity of this relation, we assume that it is caused by a simple probabilistic process. This could occur (a) when there is a fixed probability that an egg is sired by an extra-pair male, or (b) when more promiscuous females are more fecund. The latter is not supported by our study, because the association between clutch size and paternity loss at the female identity level was weak and non-significant.

Correlations between alternative fertilization routes will affect their contribution to annual siring success. Variation in annual siring success can be calculated as the sum of the variance in within-pair fertilizations and extra-pair fertilizations plus two times their covariance (Webster et al. 2005). Similarly, the variance in within-pair fertilizations is determined by the (co)variation between within-pair paternity loss and clutch size. Therefore, the correlation between clutch size and paternity loss causes that variation in within-pair fertilizations is lower compared to expectations based on a separate contribution of clutch size and paternity loss. The covariation between paternity loss and extra-pair paternity gain at the plot-year level represents an extreme example of this issue, because the tight correlation (0.93) between these routes cancels out any contribution of each of these traits to the variation in annual siring success at the plot-year level. Our study shows how correlations between siring routes determine the relative contribution of each of the fertilization routes to annual siring success (see Table 2 for the correlations and Table S6 for the variance explained by the correlations between routes). Note that the amount of variance associated with the correlation between the fertilization routes, if underpinned by genetic variation, will determine the degree to which these correlations accelerate or slow down the evolutionary responses to selection on each fertilization route and on its associated traits.

The role of behavior in mediating siring success

We expected that male and female identity effects on siring routes would be explained to some extent by behavioral attributes of the members of the social pair. We hypothesized that a male's investment in aggressive behavior would reduce his paternity loss and simultaneously constrain his ability to gain extra-pair paternity (due to time and/or energy allocation trade-offs). However, we found no support for such dual effects. Although there was an overall negative association between male aggression and extra-pair gain, it remains unclear at which level this effect occurs (Table 4). The overall effect seems to be driven by a within-male-cross-year effect, i.e. in years where males were more aggressive, they also gained less extra-pair paternity, which suggests that investment in aggressive behavior may indeed constrain a male's ability to gain paternity. However, investment in aggressive behavior was not associated with paternity loss (Table 3). This does not necessarily imply that aggressiveness does not prevent paternity loss: the observed correlation could be the result of a "best-of-a-bad-job" (Kempenaers et al. 1995), such that paternity loss would have been even higher if males would not have been aggressive. For example, an increased threat of cuckoldry by neighboring males could make individuals behave more aggressively, but they might still lose more paternity because their increased aggressiveness did not fully secure against paternity loss in such social environments. Moreover, the effect of male aggressive behavior on male extra-pair fertilization success may not be causal, but could result from an unknown environmental factor affecting both traits simultaneously.

Our results further suggest that more exploratory males had a lower extra-pair fertilization success. Because this effect was at the among-male level, it should lead to negative directional selection favoring slow-exploring males. However, given that repeatable differences in paternity loss were small and did not translate into repeatable differences in annual siring success (Table 2), there may be no selection on exploration behavior in our population. Our results contradict a study that found that male exploration behavior is positively linked to extra-pair fertilization success (Patrick et al. 2012). The different outcomes of these studies may be explained by the use of different measures of exploration behavior, or because Patrick et al. (2012) did not partition the association between behavior and paternity in among- versus within-individual levels. Assuming the latter, it would be difficult to distinguish between a causal relationship where behavior affects siring success or a situation where environmental factors simultaneously affect siring success and behavior (Dingemanse et al. 2012). We also studied the effect of female exploration behavior on male fertilization routes. Females with higher exploratory tendencies laid larger clutches, which seemed mostly due to within-female-cross-year effects (although the confidence interval slightly overlapped zero, Table 4). Previous work also suggested that the probability of paternity loss depends on the interaction between exploration behavior of the two pair members (van Oers et al. 2008). We explored this in our population by testing whether the interaction between male and female exploratory behavior explained variation in paternity loss, but did not find any evidence in support of this idea (results not shown).

Multi-level (co)variation and evolutionary responses

Partitioning the sources of covariation between behavior and traits closely related to fitness is key to understanding responses to selection (Roff 1992). Such covariation between behaviors and e.g. within- and extra-pair fertilization success may be caused by environmental pleiotropy, i.e., by a correlated plastic response of multiple traits to the same environmental gradient. Importantly, this type of covariation would not result in phenotypic evolution due to selection (Kruuk et al. 2003). Responses to selection are only expected if the covariance between behaviors and fitness are at the among-individual level and underpinned by an additive genetic covariance (Lynch and Walsh 1998). Given that behaviors have an average repeatability of ~0.4 (Bell et al. 2009) and on average only 50% of this variation is due to additive genetic effects (Dochtermann et al. 2015), phenotypic correlations between behaviors are only partly expected to result in an adaptive evolutionary response to selection. Moreover, given the modest repeatabilities of paternity loss and extra-pair paternity gain, the reported (non-partitioned) correlations between these traits and behaviors (Duckworth 2006; Patrick et al. 2012; van Oers et al. 2008), must largely represent within-individual effects (Dingemanse et al. 2012). Indeed, in our study, the significant correlation between aggressiveness and extra-pair paternity gain seems to be driven by environmental effects. Had we not partitioned this correlation into among- versus within-individual effects, we could have erroneously concluded that aggressive "personalities" were selected against in our population.

Concluding remarks

This study shows that multiple sources of variation affected male routes to siring success in a species with a socially monogamous mating system. Our study highlights that different biological mechanisms act at different hierarchical levels and that the social environment is an important source of variation in siring success. We show that, at the among-individual level, male exploration behavior is negatively associated with paternity gain and that female exploration behavior is positively associated with clutch size. Our study also highlights that observed relationships between behavioral traits and siring routes do not automatically imply that the behavior causally affects overall siring success, and therefore that these relationships do not necessarily imply that the behavioral traits are under selection. In conclusion, acknowledging the notion that siring routes can vary and covary at multiple levels, and considering the particularities of the social environment as a source of phenotypic variation, can further our understanding of the evolution of the reproductive strategies of socially monogamous but genetically promiscuous species.

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Figure 1. Path diagram depicting the relative contributions of different routes to annual siring success. Pie charts represent the proportion of variation in each of the fertilization routes and annual siring success that is attributable to male and social female identity effects, spatiotemporal variation (plot-year effects) and unexplained environmental effects (residual variation). In brackets we present the path and model used to estimate the hypothesized relationship. Single-headed arrows represent causal effects of the fertilization routes in annual siring success (1-4) and the observed not-necessarily causal effects of behavior in the fertilization routes (9, 10, 13). Double-headed arrows represent hypothesized non-causal relationships between alternative fertilization routes that may affect annual siring success (5, 6).

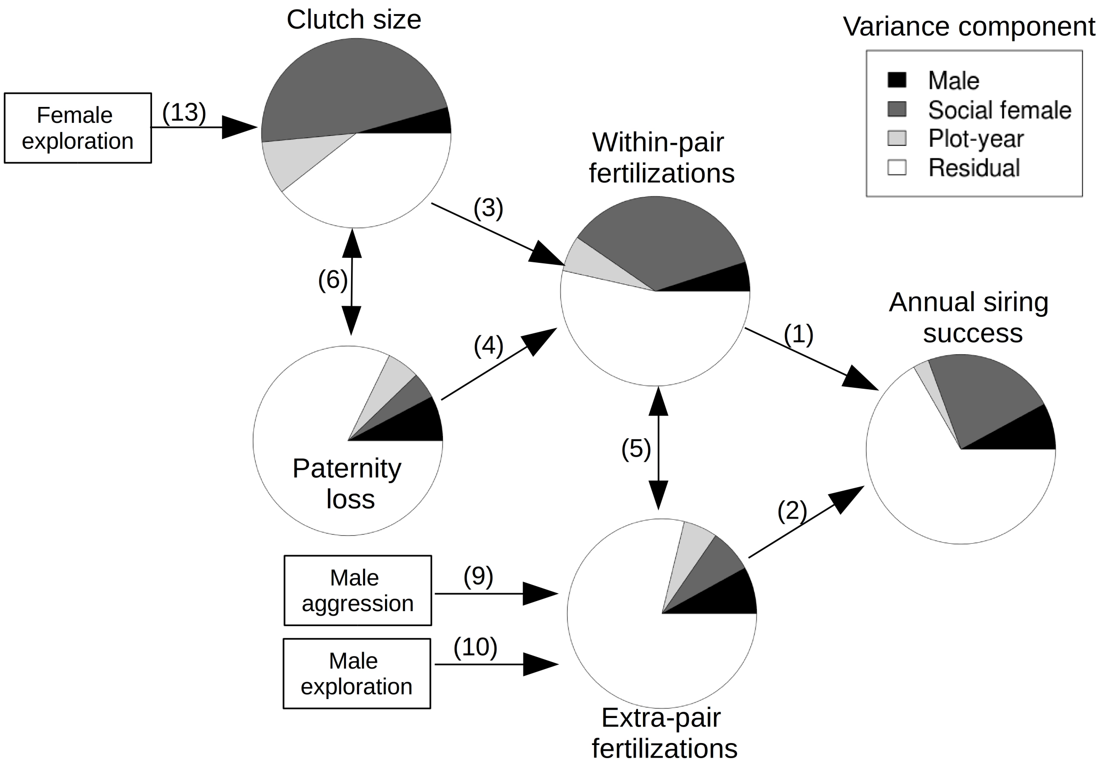

Table 1. Population mean and proportion of variance explained at the among-male, among-social-female, among-plot-year and residual level for annual siring success and its different components. Estimates presented are the mean of the posterior distribution and in parentheses the lower and upper credible interval limits (95% CI). Extra-pair fertilizations and paternity loss were modeled assuming a Poisson error distribution (see table S2 for results assuming other error distributions). Proportion of variance explained was calculated following Nakagawa and Schielzeth (2009).

	Annual Siring success	Extra-pair fertilizations	Within-pair fertilizations	Clutch size	Paternity loss
Fixed effects	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)
Intercept	8.061 (7.875, 8.238)	0.180 (0.133, 0.227)	7.571 (7.377, 7.748)	8.288 (8.112, 8.482)	0.461 (0.375, 0.541)
Proportion of variance	R (95% CI)	R (95% CI)	R (95% CI)	R (95% CI)	R (95% CI)
$R_{\text{among-males}}$	0.079 (0.001, 0.183)	0.080 (0.004, 0.190)	0.050 (0.000, 0.143)	0.044 (0.000, 0.128)	0.068 (0.001, 0.174)
$R_{\text{among-females}}$	0.227 (0.123, 0.331)	0.074 (0.005, 0.194)	0.354 (0.263, 0.444)	0.471 (0.385, 0.549)	0.063 (0.000, 0.174)
$R_{\text{among-plot-years}}$	0.027 (0.001, 0.068)	0.058 (0.008, 0.122)	0.061 (0.026, 0.107)	0.091 (0.050, 0.144)	0.069 (0.012, 0.134)
R_{residual}	0.667 (0.546, 0.786)	0.788 (0.640, 0.911)	0.535 (0.431, 0.636)	0.394 (0.311, 0.485)	0.800 (0.656, 0.920)

Table 2. Multi-level pathways to annual siring success. Shown are total effects of the fertilization routes on annual siring success (β) and proportion of variance explained (R^2). Effect sizes and proportion of variance explained were also calculated at the among-male, among-female, among-plot-year and residual levels. Within-and extra-pair fertilizations directly affect annual siring success (paths and models 1 and 2), whereas paternity loss and clutch size can only affect annual siring success through their effects on within-pair fertilizations (paths and models 3 and 4). Effect sizes and proportion of variance explained were calculated from the multi-level covariance estimates extracted from bivariate-mixed effects models. The slopes (β) were calculated as the covariance between the variables divided by the variance of the focal route and the variance explained as the squared correlation (R^2). When the effect size (β) is not significant, the proportion of variance explained (R^2) is not interpretable and is printed in italics. We present the estimates of the models in the data scale for all variables so the effect sizes and variance explained can be interpreted in terms of number of fertilized eggs (see Table S3 for results assuming other error distributions). Estimates presented are the mean of the posterior distribution and in parentheses the lower and upper credible interval limits (95% CI).

Fertilization paths to annual siring success	Male	Female	Plot-year	Residual	Total
(1) Within-pair fertilizations⟶ annual siring success					
β	1.457	0.922	0.651	1.038	0.996
(95% CI)	(-0.872, 3.053)	(0.792, 1.048)	(0.308, 0.933)	(0.947, 1.113)	(0.956, 1.037)
R^2	*0.856*	0.986	0.905	0.627	0.720
(95% CI)	*(0.087, 0.997)*	(0.922, 1.048)	(0.566, 0.995)	(0.553, 0.693)	(0.687, 0.750)
(2) Extra-pair fertilizations⟶ annual siring success					
β	2.119	-4.745	-1.55	1.064	0.987
(95% CI)	(-1.54, 5.387)	(-15.25, 10.22)	(-4.655, 0.172)	(0.912, 1.21)	(0.875, 1.095)
R^2	*0.801*	*0.536*	*0.656*	0.427	0.273
(95% CI)	*(0.056, 0.994)*	*(0.002, 0.984)*	*(0.006, 0.980)*	(0.377, 0.502)	(0.220, 0.324)
(3) Clutch Size ⟶ within-pair fertilizations					
β	0.399	1.001	0.798	0.867	0.918
(95% CI)	(-2.586, 3.768)	(0.892, 1.106)	(0.540, 1.041	(0.749, 0.988)	(0.871, 0.962)
R^2	*0.577*	0.989	0.801	0.449	0.658
(95% CI)	*(0.004, 0.987)*	(0.941, 0.999)	(0.516, 0.988)	(0.360, 0.529)	(0.619, 0.695)
(4) Paternity loss ⟶ within-pair fertilizations					
β	-0.534	-0.196,	0.352	-0.861	-0.814
(95% CI)	(-3.398, 2.527)	(-19.38, 19.841)	(-1.11, 3.572)	(-0.989, -0.733)	(-0.921, -0.712)
R^2	*0.62*	*0.36*	*0.182*	0.422	0.231

(95% CI)	*(0.004, 0.989)*	*(0.001, 0.980)*	*(0.000, 0.931)*	(0.319, 0.514)	(0.179, 0.288)

Table 3. Correlations between the alternative fertilization routes to annual siring success. Estimates are extracted from bivariate mixed-effects models. Extra-pair fertilizations and paternity loss were modeled assuming a Poisson error distribution (see table S4 for results assuming other distributions). Estimates presented are the mean of the posterior distribution and in parentheses the lower and higher credible interval (95% CI).

Correlations between alternative fertilization paths	$r_{\textit{among-males}}$	$r_{\textit{among-females}}$	$r_{\textit{among-plot-years}}$	$r_{\textit{residual}}$	$r_{\textit{total}}$
(5) Extra-pair fertilizations ↔ within-pair fertilizations	0.179 (-0.755, 0.893)	-0.183 (-0.866, 0.693)	-0.410 (-0.887, 0.192)	0.084 (-0.117, 0.280)	0.006 (-0.104, 0.111)
(6) Paternity loss ↔ clutch size	0.038 (-0.820, 0.865)	0.034 (-0.758, 0.758)	0.339 (-0.155, 0.747)	0.295 (0.081, 0.508)	0.196 (0.073, 0.306)
(7) Extra-pair fertilizations ↔ clutch size	0.405 (-0.639, 0.993)	-0.334 (-0.896, 0.354)	0.420 (-0.118, 0.886)	0.093 (-0.146, 0.308)	0.046 (-0.058, 0.152)
(8) Extra pair fertilizations↔ paternity loss	0.303 (-0.750, 0.926)	-0.141 (-0.897, 0.901)	0.935 (0.795, 0.995)	-0.097 (-0.429, 0.250)	0.161 (-0.017, 0.340)

Table 4. Effects of male and female behavioral traits on the alternative fertilization routes: clutch size, paternity loss and extra-pair fertilizations. Effects were calculated at the among-male, among-female, among-plot-year and residual levels. The behavioral traits can only affect annual siring success through their effects on paternity loss, clutch size and extra-pair paternity gain. The pathways presented are hypothesized relations between behavior and the fertilization routes based on previous studies (see Introduction; paths and models 9-13). We present these relationships as slopes, which may represent causal effects depending on the specified level. Estimates presented are the mean of the posterior distribution and in parentheses the lower and upper credible interval limits (95% CI). Extra-pair fertilizations and paternity loss were modeled assuming a Poisson error distribution (see table S5 for results assuming other distributions)

Behavioral paths	Male	Female	Plot-year	Residual	Total
(9) Male aggression → extra-pair fertilizations					
β	-0.151	-0.089	0.458	0.247	0.204
(95% CI)	(-1.911, 1.508)	(-6.111, 5.778)	(-0.715. 1.843)	(-0.060, 0.551)	(0.026, 0.376)
(10) Male exploration → extra-pair fertilizations					
β	-0.899	0.251	-0.191	-0.069	-0.181
(95% CI)	(-0.998, -0.334)	(-0.975, 0.917)	(-0.964. 0.917)	(-0.286, 0.015)	(-0.290, -0.064)
(11) Male aggression → paternity loss					
β	0.783	-1.329	0.903	-0.118	0.044
(95% CI)	(-0.255, 2.241)	(-9.270, 7.909)	(-0.128. 2.201)	(-0.289, 0.088)	(-0.064, 0.161)
(12) Male exploration → paternity loss					
β	0.177	0.064	2.373	-0.104	0.030
(95% CI)	(-0.221, 0.563)	(-7.607, 7.703)	(-6.239. 8.278)	(-0.413, 0.176)	(-0.088, 0.154)
(13) Female exploration → paternity loss					
β	-1.384	0.488	1.373	-1.173	0.022
(95% CI)	(-8.850, 8.048)	(-0.062, 1.059)	(-4.361, 6.371)	(-0.414, 0.098)	(-0.098, 0.142)
(14) Female exploration → clutch size					
β	-0.897	0.457	-1.853	0.052	0.135
(95% CI)	(-8.002, 6.974)	(-0.046, 1.053)	(-8.943, 6.99)	(-0.134, 0.224)	(0.011, 0.262)

Table 5. Total effects (β) of clutch size, paternity loss and behavioral traits through either the within- or the extra-pair fertilization route. We also give the proportion of variance explained (R^2) by each of these traits on annual siring success. Total effects and variance explained were calculated by multiplying the effect sizes of the different steps in the path of each trait to annual siring success. When the effect size (β) is not significant, the proportion of variance explained (R^2) is not interpretable and is printed in italics. We present the estimates of the models in the data scale for all variables so the effect sizes and variance explained can be interpreted in terms of number of fertilized eggs. Estimates presented are the mean of the posterior distribution and in parentheses the lower and upper credible interval limits (95% CI).

Fertilization paths to annual siring success	Male	Female	Plot-year	Residual	Total
Clutch size → within-pair reproduction → annual siring success					
β	0.485	0.928	0.52	0.989	0.914
(95% CI)	(-4.185, 5.785)	(0.757, 1.107)	(0.200, 0.852)	(0.751, 1.057)	(0.852, 0.979)
R^2	*0.502*	0.975	0.727	0.279	0.473
(95% CI)	*(0.001, 0.962)*	(0.899, 0.998)	(0.375, 0.953)	(0.259, 0.298)	(0.438, 0.508)
Paternity loss → within-pair reproduction → annual siring success					
β	-1.33	-4.327	0.226	-1.896	-1.598
(95% CI)	(-6.313, 3.679)	(-17.418, 12.935)	(-1.07, 2.427)	(-2.314, -1.559)	(-1.950, -1.267)
R^2	*0.608*	*0.517*	*0.194*	0.617	0.398
(95% CI)	*(0.006, 0.976)*	*(0.003, 0.971)*	*(0.000, 0.893)*	(0.535, 0.681)	(0.309, 0.493)
Male aggression → extra-pair fertilizations → annual siring success					
β	-0.143	1.033	-0.688	0.25	0.197
(95% CI)	(-4.513, 3.99)	(-4. 96, 4.578)	(-4.277, 1,279)	(-0.061, 0.577)	(0.022, 0.347)
R^2	*0.482*	*0.273*	*0.320*	*0.012*	0.005
(95% CI)	*(0.002, 0.963)*	*(0.00, 0.789)*	*(0.000, 0.891)*	*(0.000, 0.041)*	(0.000, 0.016)
Male exploration → extra-pair fertilizations → annual siring success					
β	-0.578	-1.702	-0.576	-0.046	-0.109
(95% CI)	(-1.85, 0.229)	(-25.42, 21.98)	(-9.580, 6.963)	(-0.232, 0.116)	(-0.191, -0.032)
R^2	*0.558*	*0.287*	*0.256*	*0.002*	0.003
(95% CI)	*(0.009, 0.956)*	*(0.000, 0.812)*	*(0.000, 0.821)*	*(0.000, 0.010)*	(0.000, 0.008)
Female exploration → clutch size → within-pair reproduction → annual siring success					
β	-0.311	0.422	-0.946	0.047	0.123
(95% CI)	(-18.54, 20.15)	(-0.043, 1.003)	(-4.798, 3.501)	(-0.122, 0.215)	(0.010, 0.236)
R^2	*0.283*	*0.052*	*0.233*	*0.003*	0.004
(95% CI)	*(0.00, 0.848)*	*(0.000, 0.184)*	*(0.001, 0.755)*	*(0.003, 0.012)*	(0.000, 0.012)

Appendix S1. Model equations for the variance decomposition using univariate mixed effect models.

$siringsuccess_{ij} = mu + male_j + female_k + plot - year_l + e_{ij}$ Eq. 1

$with \in -pairfertilizations_{ij} = mu + male_j + female_k + plot - year_l + e_{ij}$ Eq. 2

$clutchij = mu + male_j + female_k + plot - year_l + e_{ij}$ Eq. 3

$log\left(with \in -pairpaternityloss_{ij}\right) = mu + male_j + female_k + plot - year_l + obs_{ij}$ Eq. 4

$log\left(extra - pairfertilizations_{ij}\right) = mu + male_j + female_k + plot - year_l + obs_{ij}$ Eq. 5

Here, the siring route or siring success of male j in the breeding attempt *i* is modeled as a function of the population mean siring success across years (*mu),* the male's (average) deviation from the population mean value ($male_j$), the effect of the female in her social mate siring route or success ($female_k$), spatio-temporal environmental effects associated to the plot and year where the breeding attempt took place ($plot - year_l$). Male ($male_j$), female ($female_k$) and plot-year ($plot - year_l$) deviations from the population-mean value (*mu)* are assumed to follow a normal distribution (N) with a mean of zero and variance ($V_{male}, V_{female}, V_{plot-year}$) to be estimated from the data. Siring success, within-pair fertilization success and clutch size were modeled in the data scale and the deviations from the predicted value (e_{ij}) are also assumed to be realizations of a Gaussian distribution with a mean of zero and an estimated residual variance (V_e). Within-pair paternity loss and extra-pair fertilization success were modeled with a poisson error distribution (log scale) and a observation level random effect was used to model over-dispersion (V_{obs}), which was also assumed to follow a normal distribution.

$\left[male_j\right] \sim N(0, \Omega_{male}) \quad : \Omega_{male} = [V_{male}]$ Eq. 6a

$[female_k] \sim N\left(0, \Omega_{female}\right) \quad : \Omega_{female} = \left[V_{female}\right]$ Eq. 6b

$[plot - year_l] \sim N\left(0, \Omega_{plot-year}\right) \; : \Omega_{plot-year} = \left[V_{plot-year}\right]$ Eq. 6c

$$[e_{ij}] \sim N(0, \Omega_e) \qquad :\Omega_e = [V_e] \qquad \text{Eq. 7a}$$

$$[ob_{ij}] \sim N(0, \Omega_{ob}) \qquad : \Omega_{ob} = [V_{ob}] \qquad \text{Eq. 7b}$$

Table S1. Bivariate models used to study the multi-level relations between annual siring routes, annual siring success and the behavioral traits. Bivariate models were an extension of the univariate models to calculate the covariances between variables at the different studied levels.

Bivariate model	y_1	y_1
1	Annual siring success	Within-pair fertilizations
2	Annual siring success	Extra-pair fertilizations
3	Within-pair fertilizations	Clutch size
4	Within-pair fertilizations	Within-pair paternity loss
5	Extra-pair fertilizations	Within-pair fertilizations
6	Within-pair paternity loss	Clutch size
7	Extra-pair fertilizations	Clutch size
8	Extra-pair fertilizations	Within-pair paternity loss
9	Extra-pair fertilizations	Male aggression
10	Extra-pair fertilizations	Male exploration
11	Within-pair paternity loss	Male aggression
12	Within-pair paternity loss	Male exploration
13	Within-pair paternity loss	Female exploration
14	Clutch size	Female exploration

Appendix S2. Additional models for the analysis of within-pair and extra-pair paternity

Table S2. Population mean and proportion of variance explained at the among-male, -female, -plot-year for paternity loss and extra-pair fertilization. Estimates presented are the mode of the posterior distribution and in parentheses the lower and upper credible interval limits (95%CI). Within-pair paternity loss and extra-pair paternity gain were considered as Gaussian and also binary variables, coded as zero (if there was no within-pair paternity loss or extra-pair fertilization success respectively) and 1 (if a male had "lost at least one within-pair chick or "gain" at least one extra-pair chick) .

Response variable	Extra-pair fert. (Gaussian)	Extra-pair fert. (binomial)	Paternity loss (Gaussian)	Paternity loss (binomial)
Fixed effects	β (95% CI)	β (95% CI)	β (95% CI)	β (95% CI)
Intercept	0.46 (0.376, 0.544)	0.361* (0.305, 0.420)	0.715 (0.609, 0.815)	0.173* (0.125, 0.221)
Proportion of variance	R (95% CI)	R (95% CI)	R (95% CI)	R (95% CI)
R_{males}	0.025 (0.001, 0.310)	0.122 (0.001, 0.310)	0.077 (0.008, 0.165)	0.060 (0.000, 0.132)
$R_{females}$	0.021 (0.000, 0.161)	0.056 (0.000, 0.161)	0.045 (0.002, 0.119)	0.162 (0.008, 0.329)
$R_{plot\text{-}year}$	0.12 (0.537, 0.931)	0.748 (0.537, 0.931)	0.056 (0.017, 0.103)	0.036 (0.000, 0.095)
$R_{residual}$	0.942 (0.899, 0.78)	1	0.822 (0.712, 0.971)	1

*Back transformed estimates from a generalized mixed effect models with binomial error distribution, should be interpreted as a probability.

Table S3. Multi-level pathways to annual siring success. Shown are total effects of the fertilization routes on annual siring success (β) and proportion of variance explained (R^2). Effect sizes and proportion of variance explained were calculated at the among-male, among-female, among-plot-year and residual levels. Within-and extra-pair fertilizations directly affect annual siring success (paths and models 1 and 2), whereas paternity loss and clutch size can only affect annual siring success through their effects on within-pair fertilizations (paths and models 3 and 4). Effect sizes and proportion of variance explained were calculated from the multi-level covariance estimates extracted from bivariate-mixed effects models. The slopes (β) were calculated as the covariance between the variables divided by the variance of the focal route and the variance explained as the squared correlation (R^2). When the effect size (β) is not significant, the proportion of variance explained (R^2) is not interpretable and is printed in italics. We present the estimates of the models for extra-pair fertilizations and paternity loss in the log scale as they were estimated using a Poisson error distribution. Estimates presented are the mean of the posterior distribution and in parentheses the lower and upper credible interval limits (95% CI).

Fertilization paths to annual siring success	Male	Female	Plot-year	Within-male-cross-year	Total
(1) Within-pair fertilizations⟶ annual siring success					
β	1.457	0.922	0.651	1.038	0.996
(95% CI)	(-0.872, 3.053)	(0.792, 1.048)	(0.308, 0.933)	(0.947, 1.113)	(0.956, 1.037)
R^2	*0.856*	0.986	0.905	0.627	0.720
(95% CI)	*(0.087, 0.997)*	(0.922, 1.048)	(0.566, 0.995)	(0.553, 0.693)	(0.687, 0.750)
(2) Extra-pair fertilizations⟶ annual siring success					
β	1.165	-1.551	-0.931	1.545	1.381
(95% CI)	(-5.764, 7.326)	(-16.32, 15.123)	(-4.175, 2.131)	(1.341, 1.809)	(1.313, 1.648)
R^2	*0.66*	*0.549*	*0.579*	0.988	0.603
(95% CI)	*(0.004, 0.993)*	*(0.002, 0.984)*	*(0.003, 0.983)*	(0.9341, 1.00)	(0.490, 0.718)
(3) Clutch Size ⟶ within-pair fertilizations					
β	0.399	1.001	0.798	0.867	0.918
(95% CI)	(-2.586, 3.768)	(0.892, 1.106)	(0.540, 1.041	(0.749, 0.988)	(0.871, 0.962)
R^2	*0.577*	0.989	0.801	0.449	0.658
(95% CI)	*(0.004, 0.987)*	(0.941, 0.999)	(0.516, 0.988)	(0.360, 0.529)	(0.619, 0.695)
(4) Paternity loss ⟶ within-pair fertilizations					
β	-0.948	-4.854,	0.345	-1.891	-1.605
(95% CI)	(-4.107, 2.266)	(-18.902, 13.189)	(-1.150, 3.675)	(-2.159, -1.522)	(-1.945, -1.311)
R^2	*0.78*	*0.510*	*0.226*	0.987	0.556
(95% CI)	*(0.009, 0.992)*	*(0.002, 0.975)*	*(0.000, 0.956)*	(0.921, 0.999)	(0.424, 0.691)

Table S4. Correlations between the different fertilization routes. Estimates are extracted from bivariate mixed-effects models. Estimates presented are the mean of the posterior distribution and in parentheses the lower and higher credible interval (95% CI). Within-pair paternity loss and extra-pair paternity gain are model with binomial error distributions in A and assuming a Gaussian error distribution in B.

A)

Correlations between alternative fertilization paths	$r_{among\text{-}males}$	$r_{among\text{-}females}$	$r_{among\text{-}plot\text{-}years}$
(5) Extra-pair fertilizations ↔ within-pair fertilizations	0.202 (-0.473, 0.709)	-0.148 (-0.617, 0.362)	-0.206 (-0.639, 0.291)
6) Paternity loss ↔ clutch size	0.377 (-0.315, 0.824)	0.186 (-0.116, 0.459)	0.351 (-0.168, 0.731)
(7) Extra-pair fertilizations ↔ clutch size	0.380 (-0.295, 0.790)	-0.297 (-0.691, 0.185)	0.330 (-0.120, 0.713)
8) Extra pair fertilizations↔ *paternity loss*	0.144 (-0.515, 0.719)	-0.141 (-0.710, 0.492)	0.781 (0.544, 0.917)

B)

Correlations between alternative fertilization paths	$r_{among\text{-}males}$	$r_{among\text{-}females}$	$r_{among\text{-}plot\text{-}years}$	$r_{within\text{-}male\text{-}cross\text{-}year}$	r_{total}
(5) Extra-pair fertilizations ↔ within-pair fertilizations	0.733 (-0.910, 0.996)	-0.592 (-0.989, 0.623)	-0.844 (-0.993, -0.323)	0.041 (-0.073, 0.155)	-0.007 (-0.077, 0.059)
(6) Paternity loss ↔ clutch size	0.090 (-0.984, 0.991)	-0.005 (-0.966, 0.951)	0.466 (-0.093, 0.961)	0.148 (0.031, 0.262)	0.122 (0.053, 0.123)
(7) Extra-pair fertilizations ↔ clutch size	0.833 (0.017, 0.997)	-0.787 (-0.992, -0.041)	0.053 (-0.158, 01986)	0.053 (-0.068, 0.175)	0.034 (-0.058, 0.152)
(8) Extra pair fertilizations↔ paternity loss	0.642 (-0.842, 0.993)	-0.322 (-0.987, 0.951)	-0.976 (-0.905, 0.997)	-0.022 (-0.121, 0.073)	0.065 (-0.006, 0.141)

Table S5. Effects of male and female behavioral traits on the alternative fertilization routes: clutch size, paternity loss and extra-pair fertilizations. Effects were calculated at the among-male, among-female, among-plot-year and residual levels. The behavioral traits can only affect annual siring success through their effects on paternity loss, clutch size and extra-pair paternity gain. The pathways presented are hypothesized relations between behavior and the fertilization routes based on previous studies (see Introduction; paths and models 9-13). We present these relationships as slopes, which may represent causal effects depending on the specified level. Estimates presented are the mean of the posterior distribution and in parentheses the lower and upper credible interval limits (95% CI). Extra-pair fertilizations and paternity loss were modeled assuming a Gaussian error distribution.

Behavioral paths	Male	Female	Plot-year	Within-male-cross-year	Total
(9) Male aggression → extra-pair fertilizations					
β	-0.015	-0.099	0.395	0.089	0.094
(95% CI)	(-0.887, 0.691)	(-2.821, 3.224)	(-0.099. 1.043)	(-0.041, 0.213)	(0.014, 0.173)
(10) Male exploration → extra-pair fertilizations					
β	-0.267	0.494	-0.195	-0.042	-0.112
(95% CI)	(-0.528, -0.038)	(-3.198, 3.772)	(-3.22. 3.681)	(-0.221, 0.119)	(-0.190, -0.035)
(11) Male aggression → paternity loss					
β	0.586	-0.415	0.579	-0.073	0.043
(95% CI)	(-0.094, 1.563)	(-3.764, 3.318)	(-0.067. 1.390)	(-0.200, 0.068)	(-0.032, 0.130)
(12) Male exploration → paternity loss					
β	0.099	-0.161	1.760	-0.057	0.018
(95% CI)	(-0.309, 0.958)	(-3.266, 3.487)	(-3.873. 6.053)	(-0.220, 0.120)	(-0.067, 0.100)
(13) Female exploration → paternity loss					
β	1.071	-0.184	0.229	-0.025	0.017
(95% CI)	(-5.860, 8.003)	(-1.779, 1.388)	(-0.227, 0.689)	(-0.122, 0.074)	(-0.054, 0.084)
(13) Female exploration → clutch size					
β	-0.897	0.457	-1.853	0.052	0.135
(95% CI)	(-8.002, 6.974)	(-0.046, 1.053)	(-8.943, 6.99)	(-0.134, 0.224)	(0.011, 0.262)

Table S6. Proportion of variance explained in annual siring success by each fertilization route and their correlation based on the point estimates of the bivariate models' results.

Fertilization paths to annual siring success	*Male*	*Female*	*Plot-year*	*Within-male -cross-year*	*Total*
Variance in Annual siring success (ANS)	0.396	1.136	0.138	3.330	4.999
Proportion of variance in ANS associated with within-pair fertilizations p(V)	0.464	1.13	1.61	0.582	0.726
Proportion of variance in ANS associated with Extra-pair fertilizations p(V)	0.211	0.063	0.31	0.363	0.282
Proportion of variance in ANS associated to covariation between extra- and within fertilizations p(V)	0.403	-0.171	-0.954	0.039	-0.07
Sum of the estimated proportions p(V)	1.079	1.025	0.968	0.984	1.001
Variance in within-pair fertilizations (WPF)	0.184	1.286	0.222	1.937	3.629
Proportion of variance in WPF associated with clutch size p(V)	0.689	1.047	1.176	0.580	0.788
Proportion of variance in WPR associated with within-pair paternity loss p(V)	0.537	0.045	0.321	0.541	0.352
Proportion of variance in WPR associated to covariation between clutch size and within pair loss p(V)	-0.074	-0.002	-0.456	-0.178	-0.128
Sum of the estimated proportions p(V)	1.152	1.09	1.041	0.943	1.012

Table S7. Age effects on within-pair paternity loss and extra-pair paternity gain derived from mixed-effect models. Parental age is based on birth year for locally born birds or plumage characteristics at first catching for immigrants (Svensson 1992). Immigrants first caught with adult plumage are assigned a minimal age of 2 years (following Bouwhuis et al. 2009). Estimates presented are the mode of the posterior distribution and in parentheses the credible interval (95%CI). Paternity loss and extra-pair paternity gain are modeled assuming over-dispersed Poisson error distributions.

Response variable	Within-pair paternity loss	Extra-pair paternity gain
Fixed effects	β (95% CI)	β (95% CI)
Intercept	-0.83 (-1.01, -0.61)	-2.12 (-2.46, -1.79)
Age	0.07 (-0.02, 0.18)	0.37 (0.23, 0.52)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
$V_{\text{among-males}}$	0.150 (0.001, 0.398)	0.321 (0.002, 0.926)
$V_{\text{among-females}}$	0.129 (0.001, 0.398)	0.280 (0.001, 0.914)
$V_{\text{among-plot-years}}$	0.133 (0.035, 0.275)	0.143 (0.001, 0.422)
$V_{\text{within-male-cross-year}}$	1.714 (1.372, 2.110)	3.847 (3.010, 4.903)

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