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EFFECTS OF SOCIAL AND EXTRA-PAIR MATING ON SEXUAL SELECTION IN BLUE TITS (*CYANISTES CAERULEUS*)

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ABSTRACT

The contribution of extra-pair paternity (EPP) to sexual selection has received considerable attention, particularly in socially monogamous species. However, the importance of EPP remains difficult to assess quantitatively, especially when many extra-pair young have unknown sires. Here we combine measurements of the opportunity for selection (I), the opportunity for sexual selection (I_s), and the strength of selection on mating success (Bateman gradient, β_{SS}) with a novel simulation of random mating tailored to the specific mating system of the blue tit (*Cyanistes caeruleus*). In a population where social polygyny and EPP are common, the opportunity for sexual selection was significantly stronger and Bateman gradients significantly steeper for resident males than for females. In general, success with the social mate(s) contributed most to variation in male reproductive success. Effects of EPP were small, but significantly higher than expected under random mating. We used sibship analysis to estimate the number of unknown sires in our population. Under the assumption that the unknown sires are non-breeding males, EPP reduced the variance in and the strength of selection on mating success, a possibility that hitherto has not been considered.

Key Words

Blue Tit (*Cyanistes caeruleus*), opportunity for selection, Bateman gradient, fitness components, sibship analysis, mating system

All data used in this manuscript are available as Supplementary Information.

In sexually reproducing organisms, fitness fundamentally depends on achieving matings. This generates selection on mating success and in turn selection on traits linked to mating success: sexual selection. Sexual selection is a major force in the evolution of phenotypic differences between the sexes, and of mating systems and sex roles (Andersson 1994).

Pair bonding with (social) monogamy is the apparent mating system in a wide range of animal taxa (Lack 1968; Caldwell 1997; Kvarnemo et al. 2000; Baeza 2008). Monogamy constrains the potential for sexual selection, because mating success can only vary from zero to one and – assuming an unbiased sex ratio – reproductive and mating success are equal for both sexes. However, the realized mating system is often genetic promiscuity with extra-pair paternity (EPP) (Griffith et al. 2002; Chapple 2003; Lodé and Lesbarrères 2004; Cohan and Allainé 2009), and extra-pair matings have the potential to dramatically alter the strength of sexual selection in one or both sexes.

The influence of EPP on the strength of sexual selection in males has been subject of extensive research effort (reviewed in Schlicht and Kempenaers 2010). Most studies are motivated by the idea that EPP increases the strength of sexual selection (e.g. Poesel et al. 2011), which is the case when EPP leads to a non-random reallocation of mating success from lower-ranked males to “top” males, resulting in highly skewed male mating success similar to that observed in lekking species (“hidden lek”, Wagner 1997). However, the strength of sexual selection could also remain unchanged by EPP, either if extra-pair mating is random, i.e. when all males have an equal probability to gain or lose paternity (Schlicht and Kempenaers 2010), or if paternity gain and loss cancel each other out, for instance as a consequence of a trade-off between protecting paternity with the social mate and pursuing extra-pair matings (Freeman-Gallant et al. 2005; Whittingham and Dunn 2005). Finally, EPP can even diminish the strength of sexual selection, if it reduces variation in mating success among males, for example if the extra-pair sires are males that failed to obtain a territory or a social mate (Lebigre et al. 2012). The aim of this study is to analyze the effect of EPP on the potential for sexual selection in a population of blue tits (*Cyanistes caeruleus*). Because blue tits are facultatively polygynous (Kempenaers 1994), we assess effects of variation in both social and extra-pair mating success on sexual selection.

It remains a matter of debate how to quantify mating systems and sexual selection independent from specific traits that may be sexually selected (e.g. Klug et al. 2010; Krakauer et al. 2011). One approach is to use a combination of three indices: the opportunity for selection I , the opportunity for sexual selection I_s , and the Bateman gradient β_{ss} (Arnold and Wade 1984; Wade and Arnold 1980). I and I_s estimate the variation available to

selection and are a measure of the upper limit of the response to selection (Crow 1958; O’Donald 1970). β_{ss} quantifies the link between mating success and fitness and is therefore a measure of the strength of selection on mating success. It is estimated as the slope of the (partial) least-squares regression of reproductive on mating success (Arnold and Duvall 1994). These three measurements have been proposed as adequate tools to quantify mating patterns and to characterize mating systems (Jones et al. 2004; Mills et al. 2007; Jones 2009; Croshaw 2010).

Here, we estimate I , I_s , and β_{ss} , combined with novel approaches that specifically address two issues that have been raised about these estimates. First, random mating can cause variation in mating success (and as a consequence variation in reproductive success) that is independent of male traits and that will thus not lead to sexual selection (Hubbell and Johnson 1987; Gowaty and Hubbell 2005; Klug et al. 2010; Jennions et al. 2012). To argue that selection and not drift is at work, it is therefore necessary to determine the level of variation expected by chance alone. Ideally, under randomness measurements of the opportunity for sexual selection should be similar for different study systems (Kokko et al. 1999). However, when describing random mating via a Poisson, binomial, or multinomial distribution, it can be shown that I and I_s increase with the number of individuals mating (randomly) and with the number of (randomly distributed) matings available, as determined for instance by clutch size (Downhower et al. 1987; Ruzzante et al. 1996; Fairbairn and Wilby 2001; Walsh and Lynch 2008). Hence, variance-based estimates reflect both trait-based and stochastic fitness variation. To solve this, various alternative indices have been derived that are standardized in relation to a given sampling distribution (e.g. Poisson, binomial), thus incorporating randomness (e.g. Morisita index I_{δ} , monopolization index Q , binomial skew index B ; Ruzzante et al. 1996, Kokko et al. 1999, Nonacs 2000, Fairbairn and Wilby 2001). With correct choice of a null model, the systematic effects are removed so that a comparison of selection opportunities becomes more meaningful (Jennions et al. 2012).

Similarly to the effect of clutch size, the rate of EPP may cause systematic effects on I and I_s , making it difficult to determine effects of EPP on sexual selection, unless a null model of random mating is included (Schlicht and Kempenaers 2010). However, the above mentioned null models based on simple sampling distributions probably do not correct for random mating in a way that is biologically relevant in a system with social polygyny and EPP, where mating takes place in two arenas: with social and with extra-pair mates. Here, we solve this problem by simulating random mating based on a model specifically derived for such a mating system.

The second issue is that sampling is often incomplete in studies on EPP, because (a) some young are sired by males that remain unsampled, leaving the paternity of these young unassigned, and (b) individuals included in the study may have sired offspring in unsampled broods. Comparisons based on opportunity measurements can be misleading due to such sampling limitations. A reduced number of assigned young increases estimates for the realized mating system (Møller and Ninni 1998; Freeman-Gallant et al. 2005) and the focal individuals may be a non-random sub-sample of the population (Webster et al. 1995; Jones et al. 2001). Our study provides no ultimate solution to this problem, but we (a) assess the number of unsampled sires via sibship analysis and (b) consider how sensitive estimates are to assumptions about the status of these unsampled individuals. We do this based on a scenario where unsampled individuals diverge strongly from the sampled population and effects are expected to be strong: we assume that unsampled individuals are unpaired males.

Neither opportunity estimates nor Bateman gradients are related to the strength of selection on an individual trait (e.g. Klug et al. 2010). However, here we seek to gain an understanding of the potential for sexual selection, without making prior assumptions about the traits under selection. I , I_s , and β_{ss} - when corrected for randomness - provide information relevant in this context (Krakauer et al. 2011). Values of I and I_s significantly above what is expected under random mating correspond to the inequality among individuals in their reproductive and mating success, unlikely to be generated by chance, but instead by the combination of all their traits. This allows a comprehensive quantification of sexual selection that can be compared among populations and is - assuming sufficient heritabilities - linked to overall phenotypic evolution.

Given a particular (sexual) selection potential among males, it is interesting to consider the sources of this reproductive skew. Variation between males may be mainly due to the contrast between those that successfully mate and reproduce and those that do not. Alternatively, most of the variation may lie within the class of successfully reproducing males. Further, variability in both extra- and within-pair reproductive success may arise through variation in mate number, in the number of offspring per mate, and in the proportion of these offspring sired (Webster et al. 1995). Calculating how much of the variation in male reproductive success can be assigned to each of these components then allows to assess the selection potential arising via extra- vs. within-pair reproduction. Such a calculation can be done analytically (Webster et al. 1995), but in addition, we here implement a statistical method to inspect fitness components. We also construct confidence intervals for these values, as well as for those obtained for I , I_s , and β_{ss} . This allows to assess the uncertainty around values that are customarily presented as point estimates.

METHODS

General Procedures

We studied a nest-box population of blue tits in a forest patch of high-quality habitat at Kolbeterberg, Vienna, Austria from 1998 to 2003. We captured mature individuals, banded them with a metal ring and a unique combination of three plastic color bands, and aged them as yearlings or older ("adults") following Svensson (1992). For birds with inconsistent aging between repeated captures (12 males and 20 females) age information was not used. Unless the hatch year is known from previous captures or breeding, the exact age of birds in adult plumage was unknown (43 males and 52 females). We visited nests regularly to monitor breeding activity. Identity of social pairs and socially polygynous males was determined via direct observation. Nestlings were banded with a metal ring 14-16 days after hatching. See the Supporting Information for a more detailed description of the study site and procedures.

From all adults and nestlings we collected a small (5-50 μ l) blood sample for molecular sexing and parentage analysis. We also collected unhatched eggs or dead nestlings for genotyping. We determined parentage of offspring using five to eight highly polymorphic autosomal microsatellite markers (combined probability of exclusion $P > 0.999$) following standard procedures detailed in Foerster et al. (2003) and Delhey et al. (2007) (probability of false inclusion $P \leq 4.77 \times 10^{-3}$ in all cases). For all young with unknown sires or unidentified social parents sibship analysis was performed using Colony 2.0 (Wang 2008), as described in the Supporting Information. Based on parentage and sibship analysis we constructed artificial IDs for unknown parents. No age variables were assigned to birds with artificial IDs.

Calculation of male and female reproductive success (RS) and mating success (MS) is based on a total of 4644 young (eggs, nestlings, or fledglings) from 473 breeding attempts, with a mean (\pm SD) brood size of 9.8 ± 2.8 . Of all breeding events, 262 (55%) contained extra-pair offspring. The mean number (proportion) of extra-pair young (EPY) in such clutches was 2.9 ± 2.2 (0.31 ± 0.24). We assigned paternity to 96% of the young ($N = 4476$). Of all offspring, 747 (16%) were extra-pair, and of these 22% (168) were sired by an unknown male. This could be (a) an *unrecognized breeder*, i.e. breeding in a natural cavity or in the low quality habitat surrounding the study site, (b) an *unsuccessful breeder*, i.e. with a breeding attempt that failed before parents were identified, or (c) a *non-breeder*, i.e. a male without a territory or mate.

Of 498 annual male breeders (376 individual males) we recorded, 187 (38%) sired extra-pair offspring (154 individual males, 41%). Of all resident males, 29 (8%) were socially polygynous, two of them in two years (31 annual breeders, 6%). Of all 449 annual female breeders (314

individual females), 202 (45%) had EPY (156 individual females, 47%).

Calculation of Reproductive and Mating Success

Initially, we calculated both annual and lifetime (summed up across all years an individual was observed breeding on the study site) RS and MS , but we focus on annual estimates here. Both males and females gain additional matings and additional offspring with additional breeding seasons. This leads to an association between mating and reproductive success that is unrelated to sexual selection (see also Gerlach et al. 2012), but reflects the well-known differences between one- and multiple-year breeders (Dhondt 1989). Because covariance between EPP and survival was non-significant, EPP essentially operated within one year only. Our estimates of I and I_S for males reflect the inequality among males breeding in the same year, and we are interested in how this is affected by reallocation of paternity via EPP. In this sense, the length of one breeding season is the relevant timescale, given the question we study and the life-history of blue tits (Gerlach et al. 2012; Kokko et al. 2012). We do not present results for each year separately, because year-wise confidence intervals were large and showed great overlap, despite substantial differences in point estimates (Schlicht and Kempenaers 2010).

RS is defined as the number of young in the nest at day 14 to 16 post-hatch. We did not include information on unhatched eggs and dead nestlings, because sampling at this stage is often incomplete (e.g. due to predation). Breeding attempts that failed before the young were banded are thus included with RS set to zero. Based on the sibship analysis, we considered one scenario for the impact of unassigned EPY on the results; we assumed that all sires ($N = 64$, with artificial male IDs) were non-breeders, so that they only reproduced via EPP. Known males that sired EPY without breeding in one of the monitored nests (28 individuals, 29 annual breeders) were also included only here. We repeated all calculations using the number of fledged young instead of nestlings, a measurement that may reflect fitness more closely. Results remained qualitatively unchanged. Thus, we only report results based on nestlings.

MS is defined as the total number of mates with whom an individual has genetic offspring. We included information from unhatched eggs and dead nestlings here, because we seek a measure for the number of successful matings. Since we are lacking information on copulation behavior, we make use of all available information from the parentage analysis. All nesting males were assigned one apparent and within-pair mate (two for polygynous males), even when they did not sire a single offspring, because mating is considered successful on a behavioral basis. Following the scenario described above, the 92 males that are assumed to have only sired EPY are given zero apparent (within-pair) mates.

Estimates of Indices of Sexual Selection and Fitness Components

We calculated I , I_S , and β_{SS} following the standard definitions (e.g. Jones 2009):

$$I = \frac{\text{Var}(RS)}{[\text{mean}(RS)]^2}$$

$$I_S = \frac{\text{Var}(MS)}{[\text{mean}(MS)]^2}$$

$$\beta_{SS} = (\text{slope of the least-squares regression of } RS \text{ on } MS)$$

The slope was taken from a generalized linear mixed-effect model (Gaussian-GLMM) as described below (Statistical Analysis).

For the partitioning of variance in male RS , males were separated into two classes according to their actual RS (males without versus males with sired offspring), and according to their MS (genetically monogamous versus genetically promiscuous males).

We calculated the relative importance of variation within and between the two classes, using the fact that the variance of a variable X , split into a class a with frequency p_a and a class b with frequency p_b , can be written as

$$\text{Var}(X) = p_a \cdot \text{Var}_a(X) + p_b \cdot \text{Var}_b(X) + p_a \cdot p_b \cdot ((\bar{X})_a - (\bar{X})_b)^2,$$

where the first two variance terms reflect the within-class variances, and the last term reflects the between-class variance (modified from Wade and Shuster, 2004).

The contribution of different fitness components to male RS was inspected analytically and statistically. Total genetic reproductive success (G) can be partitioned as

$$G = W + E = M_W \cdot N_W \cdot P_W + M_E \cdot N_E \cdot P_E$$

with the parameters M , N , and P representing the total mate number, average brood size, and total percentage sired, respectively. The subscripts W and E denote within- or extra-pair parameters. Terms for the contribution of each of these six parameters and their covariances to the variance in male RS are derived analytically in Webster et al. (1995). The contributions of N_E and P_E are based only on individuals with non-zero M_E .

The statistical analysis of the contribution of the different fitness components to variance in male RS is based on R^2 -values from generalized linear mixed-effect models (GLMMs, see below). The R^2 -value of the full model, including all relevant fitness components as explanatory variables, was used as reference. The reduction in R^2 after removal of one of the variables is a measure of the variance explained by this variable (see Vedder et al. 2011 for a similar approach). Since maximum likelihood is the

Table 1. Effects of male age and social polygyny on paternity loss in blue tits. Binomial-GLMMs with (a) male perspective: paternity loss in at least one brood (yes/no, N = 305 males) and (b) brood perspective: brood containing EPY (yes/no, N = 333 broods) as dependent variables, and with year (1998-2003) and male identity as random factors. All estimates are back-transformed to the original scale (p-effect).

Explanatory variable	Effect (95% CI)	z	P
(a) Probability of paternity loss for a male			
Male mating status (social polygyny)	-0.04 (-0.34 to 0.29)	-0.25	0.80
Male age (yearling)	-0.03 (-0.18 to 0.13)	-0.40	0.69
Mating status \times age	0.44 (-0.07 to 0.50)	2.20	0.03
(b) Probability of containing EPY for a brood			
Male mating status (social polygyny)	-0.24 (-0.41 to 0.04)	-2.07	0.04
Male age (yearling)	-0.03 (-0.18 to 0.13)	-0.40	0.69
Mating status \times age	0.28 (-0.07 to 0.44)	1.98	0.05

criterion of fit in GLMMs, pseudo- R^2 -values are used following Nagelkerke (1991). For comparison, models were reduced to linear models and the procedure was repeated with adjusted R^2 -values. Results were almost identical and only the contributions based on pseudo- R^2 -values are reported here. To compare these results with those derived analytically, both were rescaled to sum up to 1 for all components included in the model.

Construction of Confidence Intervals

We estimated confidence intervals for opportunity estimates using the fact that the square root of opportunity estimates is the coefficient of variation (CV). We calculated confidence boundaries of the CV based on an approximation by Kelley (2007; R-package "MBESS": Kelley and Lai 2010) and squared them. For variance ratios, bootstrap confidence intervals were constructed using the R-package "boot", based on Davison and Hinkley (1997, chapter 5). Parameters were set to 10000 replicates, simulation-type "ordinary", "indices"-resampling, and interval-type "basic".

Construction of Reference Values for Estimates

To compare estimates of I , I_s and θ_{ss} to values expected under random mating, we simulated random within- and extra-pair mating, based on the original data. For random within-pair mating, the observed brood sizes and values of P_W were separated and randomly reallocated to each other. For random extra-pair mating, we used two approaches to assign EPY. In model A, each EPY was assigned a sire independently. Probabilities for siring young were initially equal for all potential sires, but decreased for a male with the number of young already sired by that male. In model B, the unit of assignment was not individual EPY, but instead the fraction of EPY in a brood sired by the same male. This takes into account that extra-pair fertilizations within the same brood may be non-independent (Brommer et al. 2007). Details of the simulation are given in the Supporting Information. Estimates of sexual selection were calculated for the

simulated populations in the same way as for the original population. The simulation was repeated 10000 times and the mean of the estimates from all simulations and their 95% confidence intervals (inner range of 95% of simulated values) are reported.

Statistical Analysis

All statistical analyses were performed with the software R 2.12.1 (R Development Core Team 2011). To account for annual differences and repeated measures from individuals breeding in several years we used generalized linear mixed-effect models (GLMMs, package "lme4": Bates et al. 2011) with year and ID as random factors. Depending on the distribution of the response variable, we used models with a Gaussian (identity-link function), Poisson (log-link function), or binomial (logit-link function) error structure. All estimates are presented on the original scale. Thus, estimates from a model with Poisson error structure (Poisson-GLMM) represent a multiplicative effect (referred to in the Results as m-effect), that is, a difference by a factor given by the back-transformed estimate (1 corresponds to no difference). Estimates from a model with binomial error structure (binomial-GLMM) represent a probability effect (p-effect), that is, a difference in probability as given by the back-transformed estimate (0 corresponds to no difference). For models with a Gaussian error structure, P -values and estimates were obtained by Markov-Chain Monte Carlo simulations (package "languageR": Baayen 2010, 100000 iterations). Credibility intervals are highest posterior density (HPD) intervals, from which the P -values are calculated. For models with a Poisson or binomial error structure, 95% confidence intervals (CI) were calculated by inference from the general linear hypothesis of the model (package "multcomp": Hothorn et al. 2008). 95%CI or HPD intervals are reported in parentheses behind effect sizes. We assessed effects of age (a) as a continuous variable, ranging from 1 to 6 years (mean for annual breeders: 1.5 ± 0.8 SD), (b) as the quadratic term of (a) to account for potential senescence in mating performance, and (c) as a

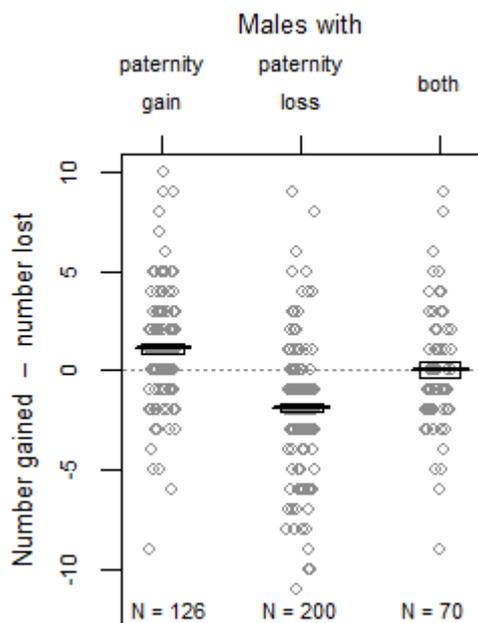


Figure 1. Net paternity gain or loss for subgroups of male blue tits. Boxes indicate mean and standard error. Values at the bottom indicate sample size.

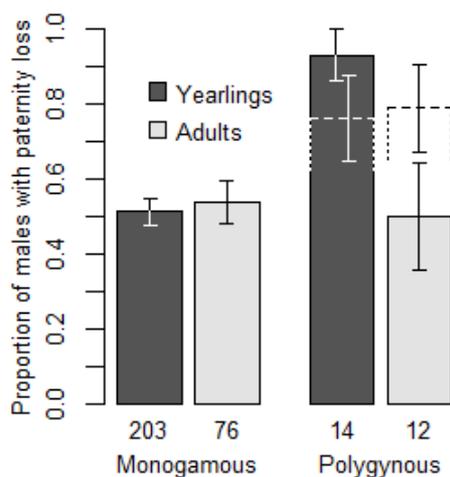


Figure 2. Relationship between paternity loss and social polygyny for yearling and older (adult) male blue tits (see **Table 1a** for statistical details). Values below bars are sample sizes (total $N = 305$) and error bars indicate the standard error. Dashed lines show f_p , the expected frequency of paternity loss for polygynous males, based on f_m , the observed frequency of paternity loss in monogamous males of the respective age class ($f_p = 2 f_m - f_m^2$).

categorical variable separating yearlings (477 annual breeders) from older birds (238 annual breeders). In all models, model fit was diminished when including (b) so that models were reduced to (a). Whenever age effects were solely due to differences between yearlings and older birds, we only report the effect of the categorical variable.

RESULTS

EPP Patterns

Of the 405 resident annual male breeders for which paternity loss could be determined, 70 both lost and gained paternity, while 56 gained paternity without loss and 130 lost paternity without gain. Reciprocal cuckoldry occurred rarely in three of the six study years (in total 9 out of 347 male-male pairs).

Considering all males, there was no association between measures of paternity gain and loss; for instance the probabilities to lose or gain paternity were unrelated (p -effect = 0.01 (-0.13 to 0.14), $N = 364$, $z = 0.09$, $P = 0.93$). However, considering only males that were involved in EPP, paternity gains and losses did not compensate each other (mean difference for males that gained paternity: 1.10 (0.49-1.69), $N = 126$, $P = 0.0004$; mean difference for males that lost paternity: -1.91 (-1.42 to -2.41), $P = 0.0002$; **Figure 1**).

We expected that the probability of paternity loss would be higher for socially polygynous than for socially monogamous males, because their risk is twice as high (two broods vs. one) and because males may not be able to guard two females simultaneously. However, this was only the case for yearling and not for older polygynous males (**Table 1a**, **Figure 2**). Similarly, the probability that a brood contained EPY was higher only when the owner was a yearling polygynous male (**Table 1b**). For polygynous males, paternity loss did not differ between primary and secondary broods (data not shown).

Effects of EPP on Selection Opportunities and Bateman Gradient

Taking EPP into account led to a significant increase in selection opportunities, (**Table 2**). For resident males, selection opportunities arising from the apparent mating system were systematically lower than the values obtained under the two simulations (**Table 2**). Regarding the realized mating system, the opportunity for selection I did not differ from the values obtained under the random mating simulations, but the opportunity for sexual selection I_s was significantly larger than expected under random mating (the 95% CIs do not overlap; **Table 2**). In contrast, the Bateman gradient was higher for the apparent mating system than expected from the random mating simulations, whereas the realized Bateman gradient was similar to that obtained from simulations (**Table 2**).

Assuming a non-breeder status for unknown males increased I , but not I_s , nor β_{ss} (**Table 2**). Among “non-breeding males” β_{ss} was slightly flatter than among resident males (**Table 2**, **Figure 3b**).

Table 2. Measurements of sexual selection based on reproductive (*RS*) and mating success (*MS*) for male and female blue tits. For males, different categories of birds are used. Resident males are those known to have bred in the study area. “Realized” and “apparent” refer to the genetic and social reproductive or mating success, respectively. “Extra-pair” and “within-pair” refer to selection arising from extra-pair and within-pair siring success, separately. “Unknown males” refers to unidentified sires under the assumption that they were unpaired. See text for details.

Category	<i>N</i>	Opportunity for selection (<i>RS</i>)				Opportunity for sexual selection (<i>MS</i>)				Bateman gradient (<i>MS~RS</i>)		
		<i>I</i>	95% CI	\bar{x}	σ^2	<i>I_s</i>	95% CI	\bar{x}	σ^2	β_{SS}	95% CI	<i>R</i> ²
Resident males realized	405	0.31 ^a	0.26 – 0.37	8.3	21.1	0.35	0.30 – 0.42	1.6	0.9	2.03	1.59 – 2.44	0.18 ^b
Resident males apparent	405	0.22	0.18 – 0.26	8.9	17.1	0.06	0.05 – 0.07	1.1	0.1	5.26	3.83 – 6.69	0.11 ^b
Resident males simulation A ^c	405	0.27	0.25 – 0.30	8.5	19.6	0.24	0.21 – 0.26	2.3	1.2	1.27	0.97 – 1.59	0.10 ^d
Resident males simulation B ^c	405	0.32	0.29 – 0.35	8.5	23.0	0.23	0.20 – 0.26	1.6	0.6	2.63	2.15 – 3.12	0.18 ^d
Resident males extra-pair	387	4.46	2.99 – 7.38	0.9	3.3	3.35	2.34 – 5.18	0.5	0.9	1.61	1.51 – 1.73	0.68 ^b
Resident males within-pair	364	0.17	0.14 – 0.20	8.3	11.5	0.063	0.05 – 0.07	1.1	0.1	3.76	2.53 – 4.99	0.09 ^b
Resident and unknown males realized	498	0.47	0.39 – 0.56	7.2	23.9	0.34	0.29 – 0.40	1.6	0.9	2.12	1.69 – 2.54	0.16 ^b
Resident and unknown males apparent	498	0.50	0.42 – 0.60	7.2	25.9	0.31	0.26 – 0.40	0.88	0.2	7.5	6.87 – 8.17	0.51 ^b
Unknown males only	93	1.13	0.72 – 2.08	2.2	5.3	0.26	0.19 – 0.39	1.5	0.6	1.48	0.87 – 2.02	0.22 ^b
Resident females	447	0.24 ^e	0.21 – 0.28	8.1	15.7	0.25	0.21 – 0.29	1.8	0.8	-0.01	-0.37 to 0.48	0.00 ^f

^aProbability for $I < 0.28$: $P = 0.16$, ^b $P < 0.0001$, ^cvalues are means across 10000 runs, ^dmean value, all $P < 0.01$, ^eProbability for $I > 0.26$: $P = 0.18$, ^f $P = 0.80$

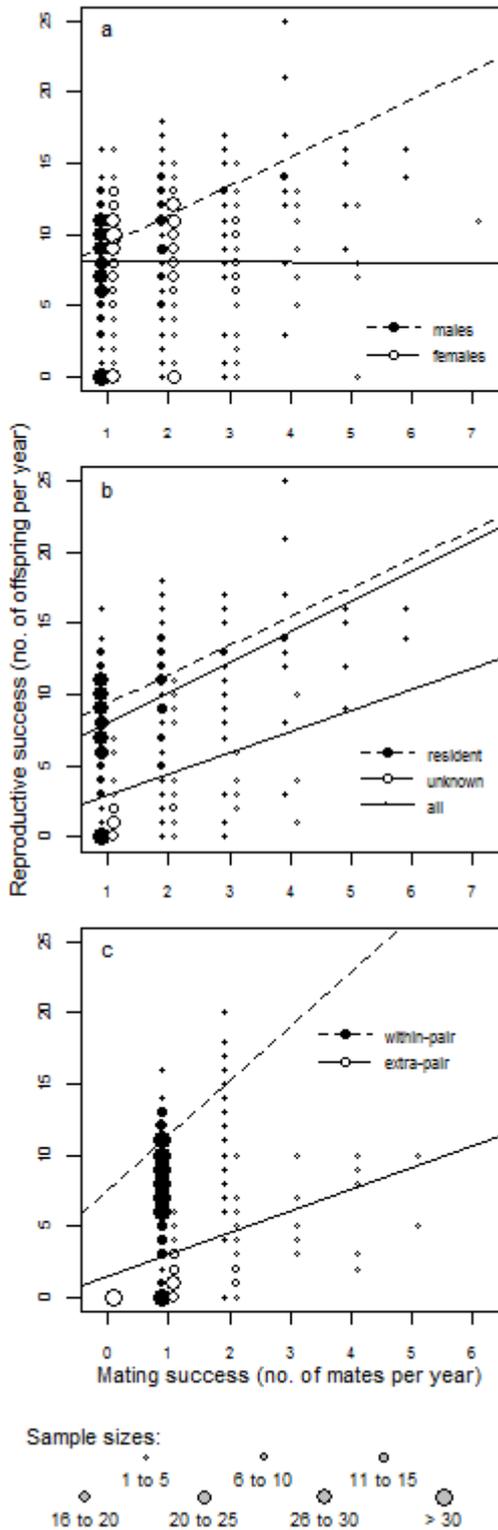


Figure 3. Relationship between reproductive and mating success (Bateman gradient) for (a) resident males versus females, (b) resident males versus unknown sires, assuming the latter were unpaired, as well as for both groups of males combined, and (c) separately for extra- and within-pair reproduction of resident males (see **Table 2** for details).

I , I_S , and θ_{SS} were higher for males than for females and confidence intervals showed only minimal overlap (**Table 2**, combined probability for $I_{males} < 0.28$ and $I_{females} > 0.26$: $P = 0.16 \cdot 0.18 = 0.03$). This was especially true for θ_{SS} , which is significantly positive for all categories of males, but essentially zero for females (**Table 2**, **Figure 3a**).

The frequency distributions of RS and MS showed similar levels of dispersion, asymmetry, and peakedness for males and females (**Figure 4a-d**), and they were well described by a two- (RS) or one-step (MS) Poisson distribution. The deviation from equality was also similar for both sexes (**Figure 4e, f**).

Variation within the group of successful ($RS > 0$) males produced more variance in RS than the variation between successful and unsuccessful ($RS = 0$) males: fraction within = 60% (70% with inclusion of unknown males as non-breeders). The opposite was the case for variance in male MS : variation between the groups of genetically monogamous versus promiscuous males contributed more than the variation within those groups (fraction between = 66%; 64% with inclusion of unknown males as non-breeders).

Among resident males, the selection opportunities arising from EPP were much higher than those from within-pair paternity (**Table 2**). However, θ_{SS} was much flatter for EPP than for within-pair paternity (**Table 2**, **Figure 3c**), indicating that an additional social mate (social polygyny) led to a larger increase in RS than an additional extra-pair mate.

Contribution of EPP to Fitness Components

Overall, the effect of within-pair success on variation in RS dominated that of extra-pair success both in the analytical and statistical analysis (**Table 3, 4**). Brood size of the social mate (N_W) was the most important component of variation in male RS , followed by success at protecting paternity in the own brood (P_W) and the number of social mates (M_W). Most influential for variation in extra-pair success was the number of extra-pair mates (M_E), whereas brood size of extra-pair mates (N_E) or the amount of paternity gained in the extra-pair broods (P_E) played a negligible role. Male extra-pair and within-pair success showed a small, but positive covariance. Results largely agreed between the analytical and statistical approach, although in the statistical approach the contribution of extra-pair success is more prominent (**Table 3, 4**).

The role of paternity gain for variance in male RS (as reflected in E) was enhanced for adult males compared to yearling males, whereas the contribution of paternity loss (measured by P_W) as well as the covariance between E and W was similar (**Table 3**). The covariance between within-pair paternity (proportion of the brood sired) and the number of social mates contributed little to the total

variance in male *RS*, but it was negative for yearlings (-6.6%) and positive for adults (3.8%).

Table 3. Partitioning of the total variance in *G* (annual male genetic reproductive success in a population of blue tits) into its within-pair (*W*) and extra-pair (*E*) components due to mate number (*M*), brood size (*N*), and siring success (proportion of the brood sired, *P*). Contributions are given as percent of total variance (95% CI), and represent the relative value (and its bootstrap confidence interval) of the corresponding variance term when total variance is partitioned analytically (see Methods for details).

Component of <i>RS</i>	All males ^a	Residents ^b	Resident yearlings ^c	Resident adults ^d
<i>G</i>	100.0 (<i>I</i> = 0.465)	100.0 (<i>I</i> = 0.305)	100.0 (<i>I</i> = 0.284)	100.0 (<i>I</i> = 0.253)
<i>W</i>	92.4 (85.7 to 98.6)	78.8 (72.9 to 84.5)	88.9 (83.1 to 95.0)	70.5 (60.2 to 79.0)
<i>M_W</i>	47.5 (38.2 to 55.9)	16.3 (10.3 to 21.4)	16.7 (7.9 to 23.9)	22.4 (10.1 to 31.6)
<i>N_W</i>	30.6 (24.6 to 35.9)	52.3 (43.6 to 60.0)	57.8 (47.3 to 67.5)	51.1 (35.2 to 63.9)
<i>P_W</i>	12.6 (9.0 to 15.8)	21.6 (15.8 to 26.8)	22.9 (15.0 to 29.9)	19.7 (10.0 to 27.8)
<i>E</i>	16.2 (11.8 to 20.1)	15.1 (10.2 to 19.4)	6.9 (2.9 to 10.1)	24.9 (13.8 to 33.0)
<i>M_E</i>	9.8 (6.6 to 12.4)	10.3 (5.8 to 13.7)	3.8 (0.6 to 6.0)	20.0 (8.6 to 27.8)
<i>N_E</i>	1.4 (0.9 to 1.8)	0.9 (0.5 to 1.3)	0.3 (0.0 to 0.4)	2.8 (0.7 to 4.1)
<i>P_E</i>	2.8 (1.5 to 3.8)	2.0 (0.7 to 2.9)	0.6 (0.1 to 1.0)	6.4 (0.4 to 10.3)
Covariance of <i>W</i> and <i>E</i>	-8.5 (-15.2 to -0.9)	6.1 (1.4 to 11.2)	4.2 (0.0 to 8.4)	4.6 (-4.9 to 17.1)

^aUnknown sires included under the assumption that they were unpaired (*N* = 498).

^bUnknown sires excluded (*N* = 405).

^cOnly resident males in their first breeding season included (*N* = 239).

^dOnly resident males after their first breeding season included (*N* = 153).

Including unknown males in the analysis, under the assumption that they were non-breeders, changes the conclusions. First, the overall contribution of extra-pair success to the total variance in annual male *RS* became smaller, and the covariance between extra-pair and within-pair *RS* turned negative. Second, the number of within-pair mates (*M_W*) became the most important contributor to variance in male *RS* (Table 3).

DISCUSSION

Influence of EPP on Proxies of Sexual Selection

The major aim of our study was to assess how EPP influences quantitative correlates of sexual selection on males. We found that the opportunity for sexual selection among resident male blue tits was higher than expected under random mating. Paternity gain and loss were overall uncorrelated, and the contribution of the covariation between extra-pair and within-pair success to total variation in *RS* was small (6.1%; Table 3). Nevertheless, males involved in EPP gained more offspring than they lost in their own brood and the confidence interval for the covariance was non-overlapping with zero (Table 3). The results therefore indicate that EPP enhances differences between resident males and elevates selection on mating success. However, the size of this effect is small. Reciprocal cuckoldry was rare but did occur and many males both lost and gained paternity. In both sexes reproductive skew (inequality) was low. The contribution of EPP to variation in male *RS* (15%) was small in comparison to the

contribution of within-pair success (79%). Thus, social success is the main arena for sexual selection among the resident males of this population.

Our results are similar to those reported in other studies that considered effects of EPP on estimates of sexual selection (Webster et al. 2001; Kraaijeveld et al. 2004; Freeman-Gallant et al. 2005; Whittingham and Dunn 2005; Westneat 2006). Often, the contribution of EPP to total variance in *RS* was low, or the covariance of extra-pair and within-pair success close to zero. In almost all studies to date, within-pair paternity remained the most influential component of male fitness (Schlicht and Kempenaers 2010; see also While et al. 2011; Lebigre et al. 2012). In our population, this results from two factors. First, clutches of blue tits are large and the proportion of a mixed paternity brood not sired by the social male was generally low (~30%). Second, social polygyny was important (measured by *M_W*). As a consequence, the Bateman gradients show that the effect of mating on reproduction was much stronger for within- than for extra-pair reproduction.

The importance of social polygyny is probably reduced when offspring quality is included in measurements of *RS*, because offspring of secondary females were in worse condition (see Supporting Information). Despite a strong link to fitness (*RS*), social polygyny may also come at a cost, particularly in the extra-pair arena. In a recent study on a Dutch blue tit population, yearling males were less successful at protecting paternity when mated polygynously, while this was not the case for older males,

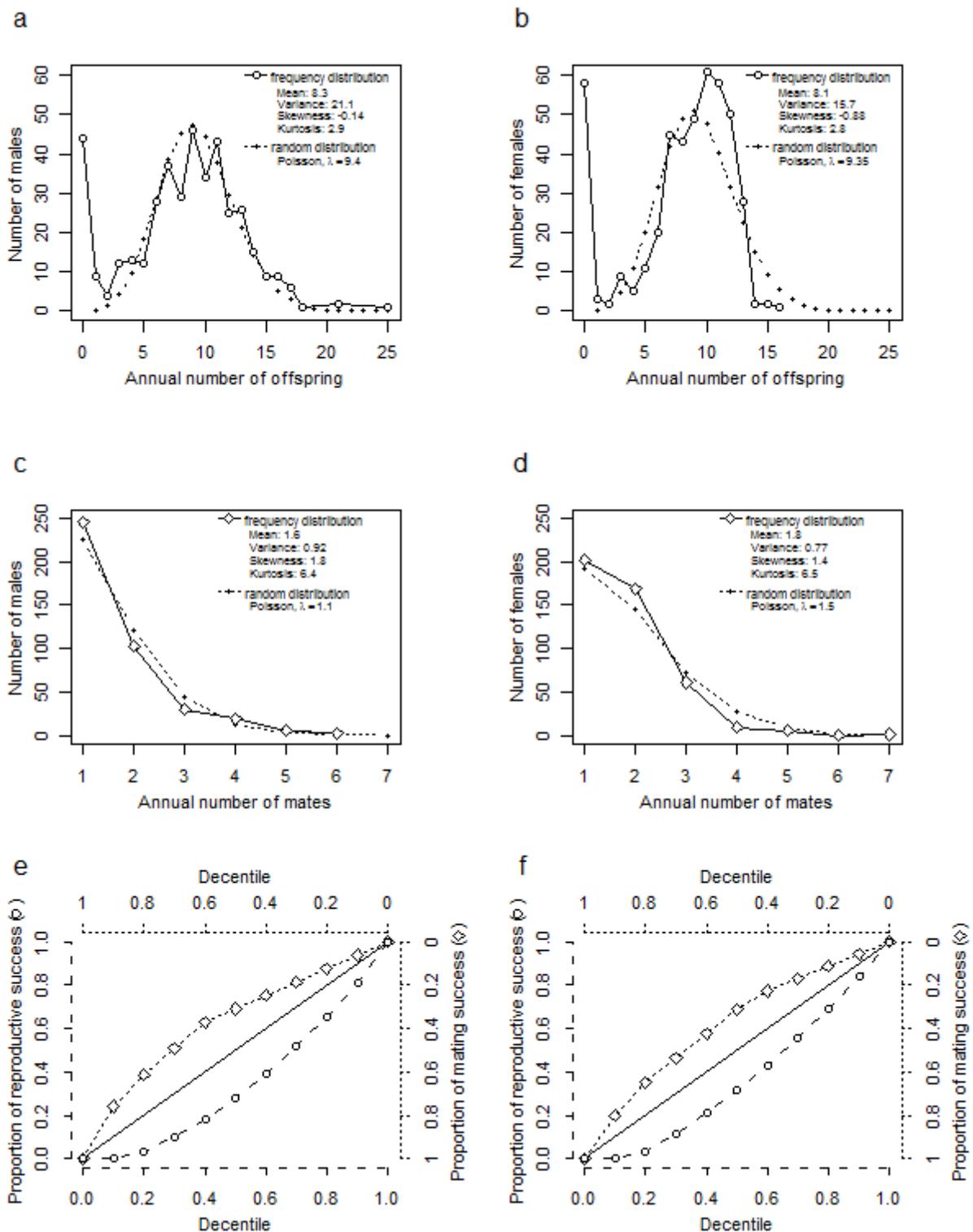


Figure 4. Distributions of reproductive and mating success for a population of blue tits. (a-d) Frequency distributions of reproductive success (a, b) and mating success (c, d) for males (a, c) and females (b, d). (e, f) Cumulative distributions for reproductive success (open circles, left and bottom axes) and mating success (open squares, right and top axes) for males (e) and females (f). Indication of inequality in a-d is given by dispersion (variance), symmetry (skewness), and peakedness (kurtosis) of distributions (calculations follow Zar 1984). Open circles refer to the actual data, filled circles show random distributions that were generated based on the observed frequencies by sampling from a Poisson distribution conditioned on an interval h of observed values >0 (a, b) or all observed values (c, d). The parameter λ was chosen such that the mean of this conditional distribution fitted the mean of the observed frequencies in h . Zero is excluded from h in a, b to account for zero-inflation in RS due to complete nest failures. In e and f, inequality is indicated by the deviation from the straight black line.

Table 4. Components of male total (G), within-pair (W) and extra-pair (E) genetic reproductive success in a population of blue tits, based on GLMMs with year (1998 -2003) and male identity as random factors. Relative contribution is the reduction in the pseudo- R^2 -value when the component is removed from the full model, rescaled to sum up to 1 for all components included in the model. Analytical results are based on Table 3 (residents), with values rescaled to sum up to 1 for all components included in the statistical model.

Dependent variable	Component	Statistical results			Analytical results
		Effect (95%-interval) ^c	χ^2 ^d	Relative contribution	Relative contribution (95% CI)
G (N = 364) ^a	W	0.94 (0.88 to 0.99)	507	0.74	0.84 (0.78 to 0.90)
	E	1.02 (0.93 to 1.11)	264	0.26	0.16 (0.11 to 0.21)
W (N = 364) ^a	M_w	5.78 (5.42 to 6.14)	487	0.23	0.18 (0.11 to 0.24)
	N_w	0.85 (0.81 to 0.88)	659	0.42	0.58 (0.48 to 0.67)
	P_w	8.05 (7.66 to 8.47)	603	0.35	0.24 (0.18 to 0.30)
E (N = 109) ^b	M_E	1.67 (1.49 to 1.87)	334	0.82	0.78 (0.44 to 1.00)
	N_E	1.17 (1.09 to 1.24)	158	0.12	0.07 (0.03 to 0.10)
	P_E	22.97 (10.85 to 48.61)	100	0.06	0.15 (0.05 to 0.22)

^aGaussian error structure

^bPoisson error structure, estimates back-transformed to original scale (m-effect).

^cHighest posterior density intervals (G , W) or confidence intervals (E).

^dAll df = 1, all $P < 0.0001$.

suggesting that the trade-off between increased social mating success and avoiding paternity loss is not straightforward (Vedder et al. 2011). Our results are similar: for yearlings, the fitness increase via acquisition of a secondary female is smaller than for adult males due to age-dependent paternity loss.

The Role of Unknown Sires

Most previous studies have only considered the resident male population (but see Sardell et al. 2010; Gerlach et al. 2012). However, often a substantial proportion of EPY cannot be assigned to any of these males (22% in this study). We specifically focused on unknown sires and by lower quality habitat without nest-boxes, so that the breeding density in the neighborhood is low. The occurrence of social polygyny also suggests that some males do not breed, unless the adult sex-ratio is female-biased (Kempnaers 1994; Vedder et al. 2011).

The presence of non-breeding males in a population can have substantial consequences (Penteriani et al. 2011; see also Courtiol et al. 2012). Amongst others, it may influence territorial strategies (Campioni et al. 2010), social organization (Smith 1987), movement-settlement patterns (Petit 1991; Delgado et al. 2009; Mannan 2010), or the timing of reproduction (Hogstad 1999). Non-breeding males may either fail to reproduce (Sergio et al. 2009) or sire offspring via second broods or EPP. The latter could be a conditional male strategy when initial mating has failed (Smith 1987; Marra and Holmes 1997), or even a way to obtain RS without having to care for an own brood (Kempnaers et al. 2001), comparable to alternative mating strategies in other species (e.g. Taborsky and Hudde 1987; Jukema and Piersma 2006).

determined their number via sibship analysis. Our results indicate that a surprisingly high number of individuals are missed when restricting evaluation to the resident male population (Gerlach et al. 2012). Unknown males could either be breeding in nests that were unsampled (natural cavities, nests outside the study area, nests failed early on), or they could be males that failed to obtain a territory or a mate (non-breeders). It seems unlikely that all unknown sires were unsampled breeders because (a) monitoring started before breeding behavior commenced and showed that early nest failures by unidentified individuals were rare, (b) intensive observations revealed only a low number of pairs breeding in natural cavities in the study site, and (c) the study area is surrounded

Non-breeding males were observed in several studies on EPP (Gibbs et al. 1990; Ketterson et al. 1997; Weatherhead and Boag 1997; Whittingham and Dunn 2005; Woolfenden et al. 2005; O'Connor et al. 2006; Albrecht et al. 2007; Balenger et al. 2009) and sometimes EPY could be assigned to these males (Freeland et al. 1995; Kempnaers et al. 2001; Kleven et al. 2006; Pearson et al. 2006; Cooper et al. 2009; Sardell et al. 2010; Lebigre et al. 2012). Non-breeding males could be present in many other populations where EPP is studied, but remain undetected.

Here, we ask how assumptions about the status of unknown sires affect our estimates of the potential for sexual selection. We examined this by considering the most extreme case, namely that all unknown sires were non-breeders. Under this assumption there was a substantial change in the fitness components: even more of the variation in RS was due to variation in within-pair success. This implies that selection on "non-breeders" to

find a breeding opportunity is strong: the potential for sexual selection via this pathway was increased (compare M_w in **Table 3**). Importantly, variation in extra-pair and within-pair RS became negatively correlated. “Non-breeders” by definition had no social success while breeding males had a complete clutch: the apparent Bateman gradient is very steep (**Table 2**). This is partly compensated through EPP, leading to a negative covariance between within- and extra-pair success and a much lower realized β_{SS} . Thus, if non-breeding males father extra-pair offspring, EPP effectively lessens differences between males and leads to a reduction in the potential for sexual selection (Jones et al. 2001; Hauber and Lacey 2005; Singer et al. 2006; Webster et al. 2007; Lawler 2009; Collet et al. 2012; Lebigre et al. 2012).

Independent of the mechanisms of selection among unknown males, the estimates of the potential for sexual selection remained relatively stable, even under this anti-conservative assumption (**Figure 3 b**, **Table 2**). Perhaps a more realistic assumption is that some of the unknown sires are breeders elsewhere. One would then expect results from the sampled resident males to fit the total population more closely.

An alternative hypothesis is that there are many more males without a social mate than the ones that sire the unassigned EPY, namely males that do not reproduce at all. We assessed the sensitivity of the estimates to this possibility and found that variance both in reproductive and mating success can increase dramatically, depending on the size of the non-reproducing male population (see Supplementary Information; Figure S1). This highlights the importance in this type of study to collect and incorporate as much information about non-breeding individuals as possible.

The Potential for Sexual Selection in Blue Tits

We found that the opportunity for selection and for sexual selection observed for resident male and female blue tits fell within the lower range of estimates from other studies on vertebrates (Pröhl and Hödl 1999; Jones et al. 2002; Woolfenden et al. 2002; Mobley and Jones 2007; Schlicht and Kempenaers 2010; Bergeron et al. 2012; Courtiol et al. 2012). However, most previous studies did not consider the influence of random mating (but see Baena and Macías-Ordóñez 2012; Byers and Dunn 2012; Garg et al. 2012). Here, we show that empirical frequency distributions of reproductive and mating success were similar to those from related random frequency distributions and the level of inequality (“reproductive skew”) was low for both resident males and females. Thus, the variation on which sexual selection can act appears to be small in this population, and may be largely caused by stochastic processes, unlinked to traits that could be selected. Based on this, one would predict only a minor impact of sexual selection on the evolution of behavior and morphology in this population of blue tits, at least in the period under study.

This may explain the lack of a straightforward link between male mating success and presumably sexually selected traits, such as body size (Foerster et al. 2003), dawn song characteristics (Poesel et al. 2001), and crown coloration (Delhey et al. 2007) in this and other (Krokene et al. 1998; Charmantier et al. 2004) blue tit populations. Often, it is only the comparison between specific groups of males (e.g. extra-pair sires and the males they cuckold) that reveals effects of these traits (Kempenaers et al. 1992, 1997; Delhey et al. 2003; Foerster et al. 2003; Poesel et al. 2006), in line with the idea that sexual selection on these traits is not particularly strong.

Nevertheless, the Bateman gradient for resident male blue tits revealed that each additional mate leads to two additional offspring. Despite low variation in MS , there is strong positive selection on individuals to acquire additional mates through social polygyny or EPP, because this leads to significantly higher RS . Accordingly, the difference between genetically monogamous vs. promiscuous males generates most of the potential for sexual selection, while variance within the group of promiscuous males is less important. Our results therefore suggest that in this population sexual selection on males is mediated mainly via social polygyny. Future studies of sexual selection on particular traits could inspect this further by assessing correlations between the focal traits and the different components of fitness (e.g. Freeman-Gallant et al. 2009).

RS measured as the number of 14-day-old nestlings may not adequately reflect fitness variation when quality of young (e.g. condition) strongly influences their later survival and reproduction (e.g. López-Rull et al. 2011). We cannot exclude that the patterns we found become relatively unimportant when a better (more comprehensive) fitness estimate is used. At least, our results remained stable when fitness was measured as the number of fledged young (see also Dhondt 1989; Weatherhead and Dufour 2000). For several males, breeding attempts failed completely, leading to zero RS . Such failures may be largely stochastic, but may drive the relationship between RS and MS . However, the majority of the variance in RS among males was due to variance within the group of successful males.

Contrary to males, RS was uncorrelated to MS for resident females, as reflected by a Bateman gradient close to zero. Selection opportunities for females were also distinctly lower than those for males. In accordance with Bateman’s principles (Arnold 1994), variation in RS and MS , constituting selection potential, as well as their direct link, were reduced in females compared to males. This suggests that in this population sexual selection is likely to be more important in males than in females.

Our results further indicate that higher estimates for males emerged also when the additional matings (e.g., arising from EPP) are randomly allocated to males. This

means that the differences between males and females could at least partly be the result of a stochastic increase in mate number for some males, from which increased RS follows. On the other hand, there is no association between mate and offspring number for females, which would not occur if offspring from additional matings were randomly allocated to females (Gerlach et al. 2012). This implies that the sex differences in estimates arise not from enhancement in males, but from attenuation in females. Thus, it is the sex which shows *smaller* selection opportunities that shapes predictions about how sexual selection influences mating systems by non-random behavior (Jones et al. 2005; Shuster and Wade 2003; see also Krakauer et al. 2011).

Quantifying Sexual Selection

The aim of this study is to inspect the effect of EPP on the intensity of sexual selection. Yet we present estimates (I , I_s , and θ_{ss}) that do not directly measure the strength of sexual selection. These estimates capture both random and non-random variation and have no relation to any specified phenotypic trait (Jennions et al. 2012). Thus, in a hypothetical case where random processes have an important influence on mating allocation, inequality among individuals does not reflect the substrate for a selective response. Modeling random mating – in a biologically adequate way – should lead to similar inequality. If instead random processes play a minor role, the success of individuals should be predictable from a systematic factor that is a component of their identity, i.e. a trait or a combination of traits. In other words, under this scenario, phenotypic variation is linked to variation in mating or reproductive success, and the phenotypic traits are then under (sexual) selection. The estimates do not allow to detect which specific traits are under selection and the strength of selection on them. In fact, selection on a specific trait may be weak despite high selection opportunity. Still, the size of estimates quantifies selection acting on the complete phenotype, i.e. on all traits combined. In this interpretation, the presented estimates shed light on the strength of sexual selection, beyond the analysis of individual traits, e.g. via selection differentials.

To put this in practice, it is necessary to show that an estimate is significantly higher than expected under randomness. This is done by simulating random mating and assessing the uncertainty for realized as well as simulated estimates (Jennions et al. 2012, see Baena and Macías-Ordóñez 2012; Byers and Dunn 2012; Garg et al. 2012 for recent implementations). Simulation of random mating can also correct for the inherent bias in the correlation between mating and reproductive success (as established via θ_{ss}), that occurs because there is at least one offspring for every mate (Gerlach et al. 2012). This effect also applies to the estimate obtained in the simulation, which can therefore be used to take this issue into account.

It should be noted that the implemented estimates are corrected for random mating only in a statistical sense. There is always a chance that a particular pattern in a population is realized via purely random or purely directional processes. The simulation of random mating and the use of confidence intervals can only be used to assess the likelihood that the observed variation in mating and reproductive success as well as their association are due to random mating alone. This is different from the use of selection differentials, where any link between trait and fitness will – assuming sufficient heritability of the focal trait – lead to a selective response, even if the trait-fitness-correlation is a chance event.

Conclusions

Overall, the potential for sexual selection in our blue tit population showed no strong sensitivity to the incomplete sampling of sires. Estimates of sexual selection were higher for males than for females and mainly mediated by social success. In general, potential for sexual selection was low. However, the effect of EPP on sexual selection can either be positive or negative, depending on the presence of socially unsuccessful males in the population. In birds, these could commonly occur, either if populations contain (cryptic) non-breeding individuals, or if auxiliary males can offset low social success via EPP in cooperative breeders (Webster et al. 2007). In summary, our results suggest that knowledge about the socially non-reproducing part of a population may be essential to assess the role of EPP in the process of sexual selection.

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SUPPORTING INFORMATION

for

EFFECTS OF SOCIAL AND EXTRA-PAIR MATING ON SEXUAL SELECTION IN BLUE TITS (*CYANISTES CAERULEUS*)

Emmi Schlicht and Bart Kempenaers

METHODS

Study Species and Study Site

Blue tits are small, short-lived, cavity-nesting passerines resident in Europe. Many individuals reproduce only once in their life (Dhondt 1989). In the population under study, 83% of individuals were recorded breeding only once and the number of years breeding was the prior determinant of lifetime reproductive success, as is generally the case for this species (Dhondt 1989). Most individuals are socially monogamous, but facultative polygyny occurs at low frequency in most populations (Cramp et al. 1993). The proportion of broods with at least one extra-pair young (EPY) is commonly above 40%, resulting in 11-25% EPY, overall (e.g. Charmantier et al. 2004; Magrath et al. 2009).

The study area is located at Kolbeterberg, Vienna, Austria (48°13'17"N, 16° 14'12"E, altitude range 255-316 m, area approximately 50 ha). It comprises a patch of mixed deciduous forest primarily dominated by oak trees (*Quercus robur*), providing an optimal breeding habitat for blue tits (Cramp et al. 1993), and is surrounded by low quality habitat (houses, gardens/meadows, beech (*Fagus sylvatica*) forest). Nest-boxes excluding larger competitors (hole diameter 26 mm) were available at superabundance (uniform density of approximately 4 per ha). Nesting cavities are a limited resource in the natural habitat as shown by the fact that removal of nest-boxes led to an increase in intraspecific brood parasitism (Jacot et al. 2009; data not included in this study). Detailed observations during the first four years of the study revealed only five pairs breeding in natural cavities (Foerster et al. 2003).

General Procedures

We monitored breeding from nest-building (March-April) until fledging (May-June) by regular territory visits and nest-box checks. Mature individuals were captured in nest-boxes, either in winter while roosting or in late spring when feeding chicks, banded, and aged according to Svensson (1992) as yearlings or older ("adults"). Identity of social pairs was determined via observation of individuals at the nest, mostly during feeding. Males were identified as socially polygynous when present at two nests. There were no ambiguous cases, where no social father was observed, but (some of) the young could be assigned

in parentage analysis to a male breeding elsewhere. When performing parentage analysis, we had to exclude 177 young (from 60 broods) because of low quality DNA samples. For 20 breeding attempts no young (eggs, dead nestlings, banded nestlings) were sampled, because they failed early. Of these, the associated female is unknown for 9 breeding attempts and the associated male is unknown for 4 breeding attempts.

For broods where one (30 broods, 135 young) or both (5 broods, 41 young) of the social parents remained unidentified and parentage could not be assigned to any of the typed mature individuals, we checked whether allele count of the offspring conformed with a uniform paternal and maternal genotype. If this was the case, we assumed these parental genotypes. Otherwise, we excluded these broods from further analyses (27 young from 7 broods). This procedure will slightly bias our data towards broods with uniform paternity (proportion of mixed-paternity broods maximally 57% instead of the reported 55%), but it ensures that the number of broods excluded in this step is minimized.

Seven young from 6 broods resulted from intraspecific brood parasitism (Vedder et al. 2010) and were also excluded.

For our calculations, we included the replacement brood for individuals (25 males, 21 females) that started a new brood – with the same or a new mate – when their initial breeding attempt failed, because sampling was more complete for these broods than for the failed attempts. Results remained similar when using the failed broods instead. Breeders with brood(s) that could not be unequivocally classified as primary / secondary brood (of a socially polygynous male), replacement brood, or second brood (16 broods, 125 young) were excluded (8 males, 4 females). Nests that were subject to experiments (413 young from 50 broods; Foerster and Kempenaers 2004; Delhey et al. 2007) were included in the analysis (results remained qualitatively unchanged when these broods were removed).

Sibship Analysis

Sibship analysis was performed for all young with unknown parentage and unidentified social parents using Colony 2.0 (Wang 2008). No half-sibships among young with unidentified social parents, or between these and unassigned EPY, were recognized. Thus, young from different nests with unknown social fathers were not sired by the same male. Further, the unidentified social males were not among the unknown extra-pair sires.

Sibship analysis was then restricted to the 168 EPY with unassigned parentage. Here, shared sires were allowed within one year only, because (a) survival of blue tits between years is low (Dhondt 1989), and (b) it is unlikely that a male lived several years in the area, but was never caught, given that the study area is an insular patch of high-quality habitat with a superabundance of otherwise limited roosting and nesting sites. Parameters were set to full likelihood method with high precision and short run length. Analyses were repeated four times with different random number seeds as explained in the user guide of Colony. All four analyses resulted in a sire number of 64. The quality of the results derived via Colony was assessed as described in the next section.

Testing the results of the sibship analysis

To test the results of the sibship analysis of the 168 unassigned extra-pair young (EPY), we randomly sampled a group of 168 EPY from the population of assigned EPY, such that (a) for each brood in the original sample, a brood with at least as many assigned EPY was randomly selected and (b) from this brood the corresponding number of EPY were randomly selected. This ensured that the distribution of young among broods was exactly reproduced in each sample. This procedure was repeated 100 times.

The quality of the results derived via Colony was then assessed in three ways. First, we determined the true number of sires for each of the randomly selected samples. This number (mean \pm SD = 65.7 \pm 3.4) was very similar to the number of males assigned by Colony to the original sample (64 sires).

Second, for all 100 reproduced samples two sibship analyses were run in Colony, initially one with the same parameters as before (no shared sires across years) and then one allowing for shared sires across ± 1 year. Shared paternity across years, that is, a male producing offspring in several years, is more likely among assigned EPY (where the sires were breeding on the study site) than among unassigned EPY (sired by non-resident males). The latter parameter setting may thus be more appropriate when analyzing assigned EPY. Indeed, results of the initial analysis led to a slight overestimation of sire number (mean difference true – calculated sire number: -8.2 ± 4.4 SD) while the following analysis gave an underestimation of the same magnitude (mean difference true – calculated sire number: $+8.2\pm 3.2$ SD).

Third, the paternity assignment via Colony was compared to the true (known) paternity. For each of the 100 samples, the error rate was calculated by dividing the number of falsely assigned chicks by the total number of chicks. When a choice had to be made

which group of chicks was falsely vs. correctly assigned (e.g. when paternity was split up among too many sires) the smaller group was chosen as falsely assigned. The mean error rate under the original parameter settings (no shared paternity across years) was 0.04 ± 0.01 SD (range: 2-9%). Thus, the results generated via Colony give a reasonably good fit for this population and we used them as the best proxy for the reproductive success of unsampled males. For each paternal sibship derived via Colony, an artificial male ID was generated and the corresponding number of young and mates were assigned as measures of reproductive and mating success, respectively.

Simulation of random mating

Simulations assume a mating process similar to the model developed by Lee et al. (2008), where initially all males present in the population receive tokens in relation to their mating probability. Then, nesting males are chosen randomly without replacement from the collection of tokens (the urn). Selecting without replacement takes into account that in most natural populations, obtaining a mate reduces the probability of gaining another one. The simulation is performed separately for each breeding season and consists of two steps: random within-pair mating and random extra-pair mating.

For random within-pair mating, each male present in the population initially received the same number of tokens (one), representing equal success probabilities. The number of polygynous males N_{poly} from the original population is reproduced by choosing N_{poly} males randomly without replacement from the sample of males present in the original population. Thus, N_{poly} randomly chosen males have two tokens, whereas all other males have one. Next, the brood size of each nest is determined by selecting randomly without replacement from the brood sizes in the original data set. Finally, each nest is assigned a value between 0 and 1, representing the success of the attending male at securing paternity. This is again done by choosing randomly without replacement from the observed values of P_W in the original population. In this way, each male's within-pair success is determined.

Random extra-pair mating is modeled based on the frequency of EPP in the original population. We used two different approaches: in model A we assumed that extra-pair fertilizations occurred independently of each other and separately assigned each EPY a sire; in model B we took into account that extra-pair fertilizations within the same brood often are non-independent (Haydock and Koenig 2003; Brommer et al. 2007). In the original population each nest contained young sired by N_{sire} males, so there are N_{sire} proportions (P_W being one of them), each representing

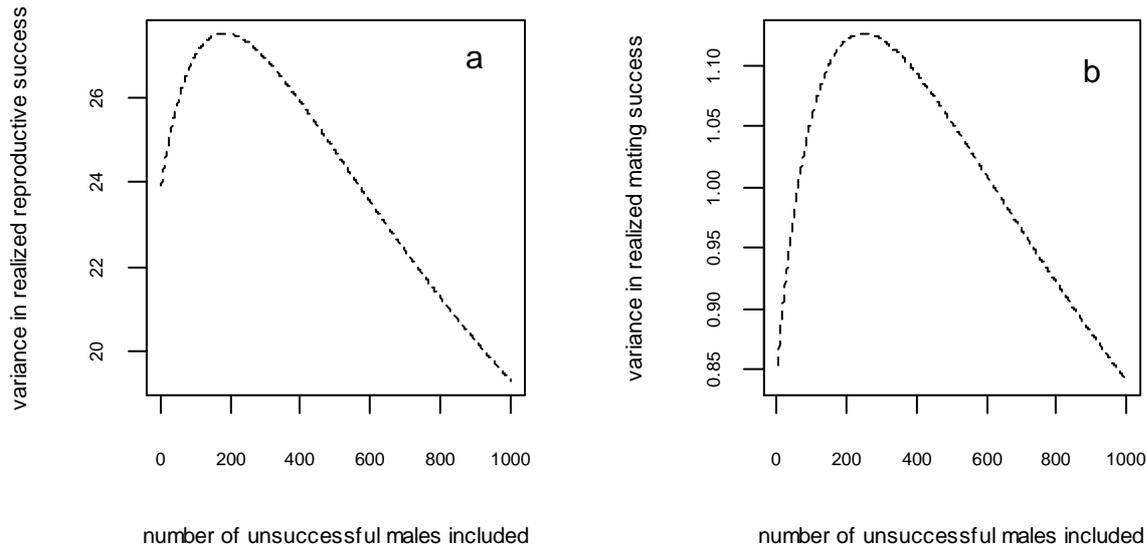


Figure S1 Change of variance in realized reproductive (a) and mating success (b) with an increasing number of non-reproducing males added to the population. Variance in reproductive success (mean \pm SE: 24.6 \pm 1.1; range: 19.3 to 27.5) reached its maximum for an added 172 non-reproducing males, variance in mating success (mean \pm SE: 1.0 \pm 0.03; range: 0.8 to 1.1) for 236 additional males.

the fraction of young sired by one male. For model B, we assigned together with P_W all corresponding N_{sire} proportions in the last step of simulating within-pair success. In this way, we reproduced the clustering of paternity found in the original population. Each “cluster” is then separately assigned a sire. Thus, the unit of assignment is individual EPY in model A and clusters of EPY in model B. The steps of the simulation procedure for model A and B are further identical. The sire of each EPY (model A) or cluster of EPY (model B) is chosen randomly without replacement from an urn containing tokens for each potential sire. The number of tokens for each male in the population is identical (random mating) and equals the number of EPY (or clusters). Tokens of the social father are excluded from the urn when choosing a sire. EPY (or clusters) were assigned paternity in randomized order. This completes the simulation of random within- and extra-pair mating.

Assessing the Influence of Non-Reproducing Males

We inspected how the presence of males that did not sire extra- or within-pair young, i.e. males that did not reproduce at all, would influence our estimates. We did this by adding males without mating or reproductive success to our real data set. We successively increased the number of these males up to 1000 and inspected the results for the population-wide proxies of sexual selection. It should be noted that the regression coefficient of reproductive on mating success (β_{ss}) will not change when adding points at the origin. Further, I and I_s will increase

linearly with the number of additional non-reproducing males. Consider adding x non-reproducing males to a population of n males with the success of the i -th male denoted as s_i , which is zero for the last x males. The mean success and the variance in success prior to adding males are

$$1/n \sum s_i = m/n$$

and

$$1/n \sum s_i^2 - m^2/n^2 = v/n - m^2/n^2,$$

respectively, giving a selection opportunity of $(v/n - m^2/n^2)/(m/n)^2 = (vn/m^2) - 1$.

Adding x non-reproducing males leaves v and m unaffected, resulting in mean

$$m/(n+x),$$

variance

$$v/(n+x) - m^2/(n+x)^2,$$

and selection opportunity

$$(v(n+x)/m^2) - 1 = (v/m^2)x + (vn/m^2) - 1,$$

the latter of which is a linear increasing function of x . In contrast, the variance term shows no simple relationship with x . The informative comparison is therefore the inspection of the variances in reproductive and mating success.

RESULTS

Descriptive Patterns of Reproductive and Mating Success

Of all 4644 young, 1021 (22%) were unhatched eggs or nestlings that died before banding. Fledging success of banded nestlings was 95%. Brood sizes of secondary, but not primary, females of socially polygynous males were smaller than those of females mated to socially monogamous males (primary broods: mean difference 0.0, m-effect = 1.01 (0.85-1.21), $N = 405$, $z = 0.13$, $P =$

0.90; secondary broods: mean difference 3.2, m-effect = 0.62 (0.50-0.76), $N = 405$, $z = -5.10$, $P < 0.0001$). Secondary females of polygynous males had an increased probability of nest failure compared to all other females (p-effect = 0.40 (0.11 -0.48), $N = 314$, $z = 2.79$, $P = 0.005$) and young from secondary broods were lighter and in worse condition (weight/tarsus) than other young (linear mixed effects models with year and IDs of mother, social father, and genetic father as random factors and extra-pair status (yes/no), measuring day (14-16 posthatch), first egg date, and brood status (secondary yes/no) as fixed effects; weight [g]: -0.42 (-0.67 to -0.17), $N = 3140$, $P = 0.001$; condition [g/mm]: -0.02 (-0.03 to -0.01), $N = 3088$, $P = 0.004$). Socially polygynous males did not differ in age from monogamous males (m-effect = 1.11 (0.77-1.60), $N = 355$, $P = 0.52$), but yearling females had a higher

probability than older females to be secondary female to a polygynous male (p-effect = 0.47 (0.34-0.50), $N = 362$, $z = 4.06$, $P < 0.0001$).

Assessing the Influence of Non-Reproducing Males

Both variance in reproductive and mating success increased initially when non-reproducing males were added to the population, reached a maximum at approximately 200 additional males, and then declined again with addition of further males (Figure S1).

Males with

paternity

paternity

both

gain

loss

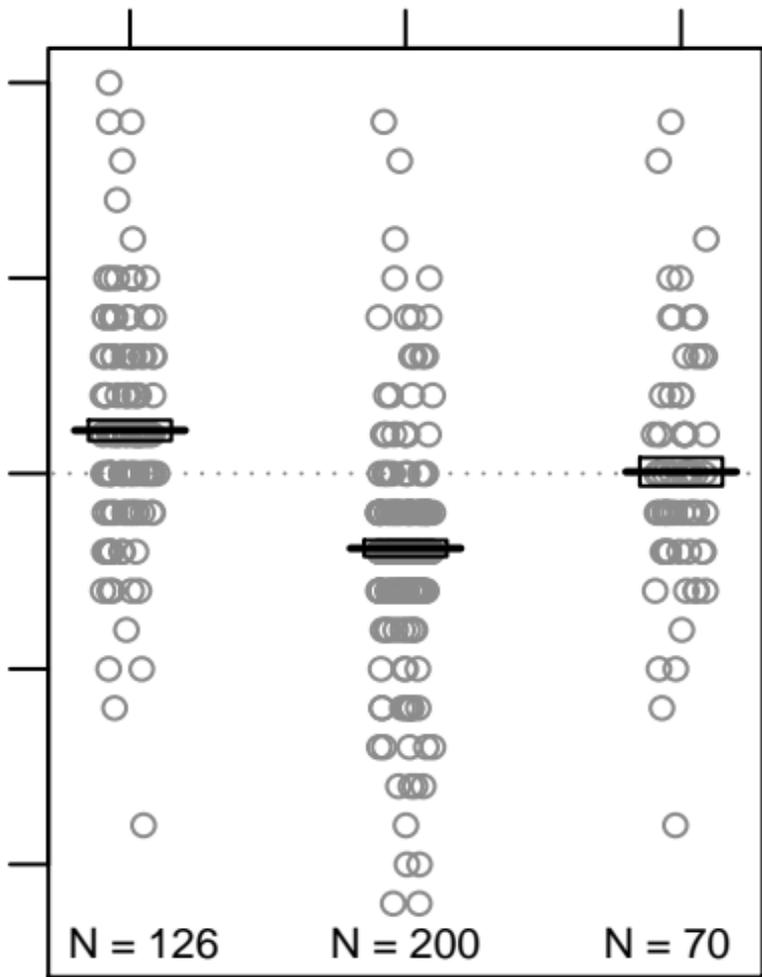
Number gained - number lost

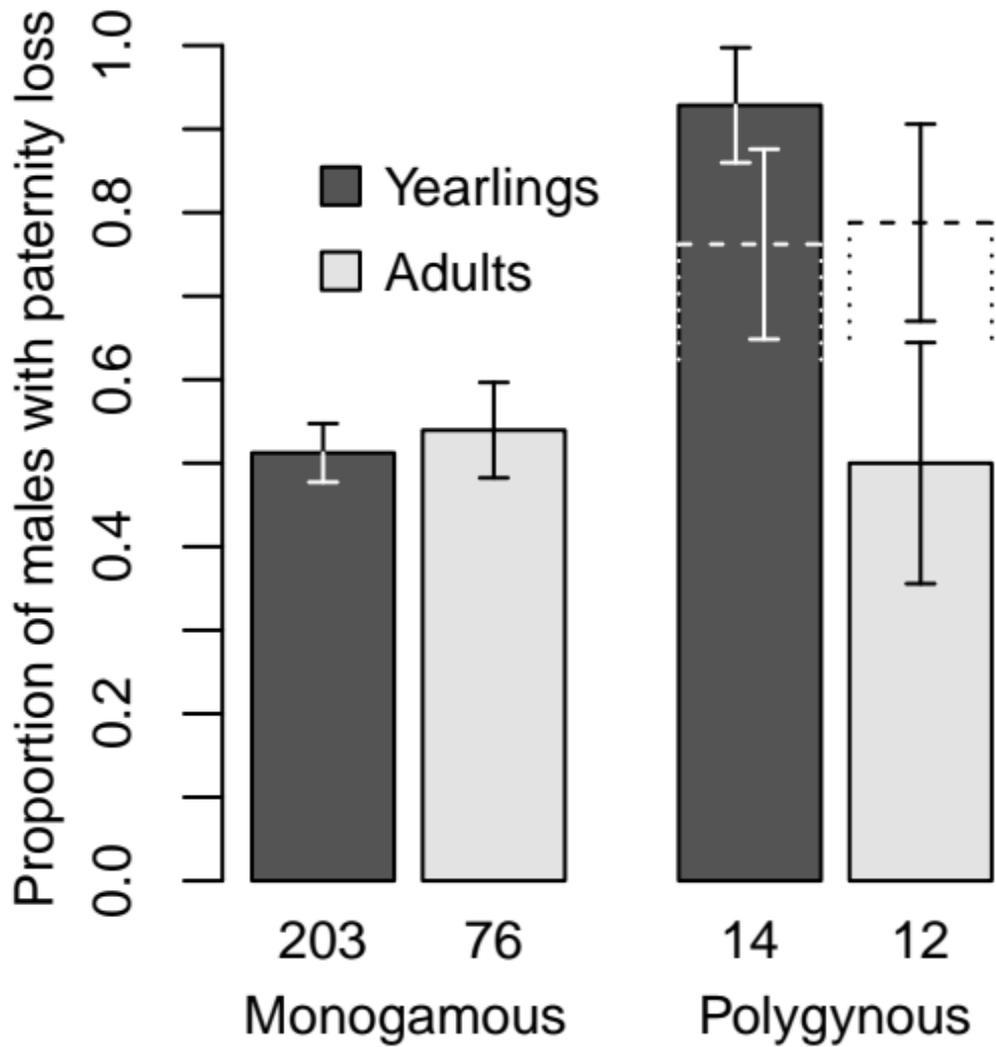
10
5
0
-5
-10

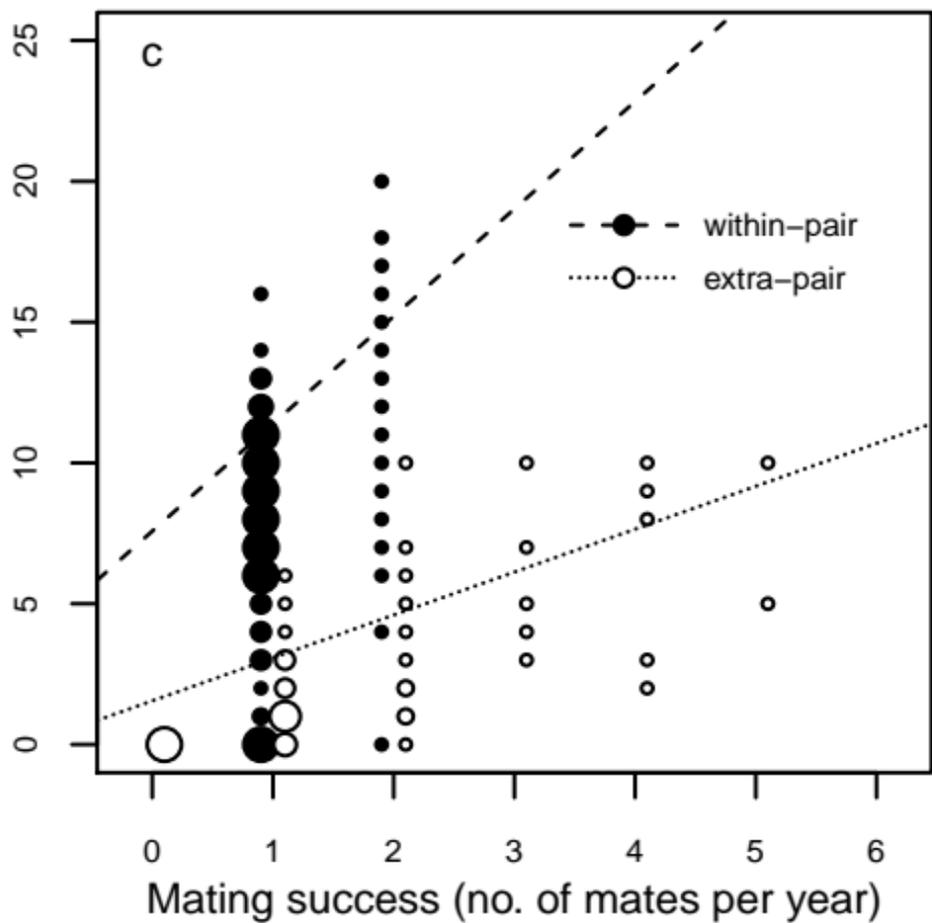
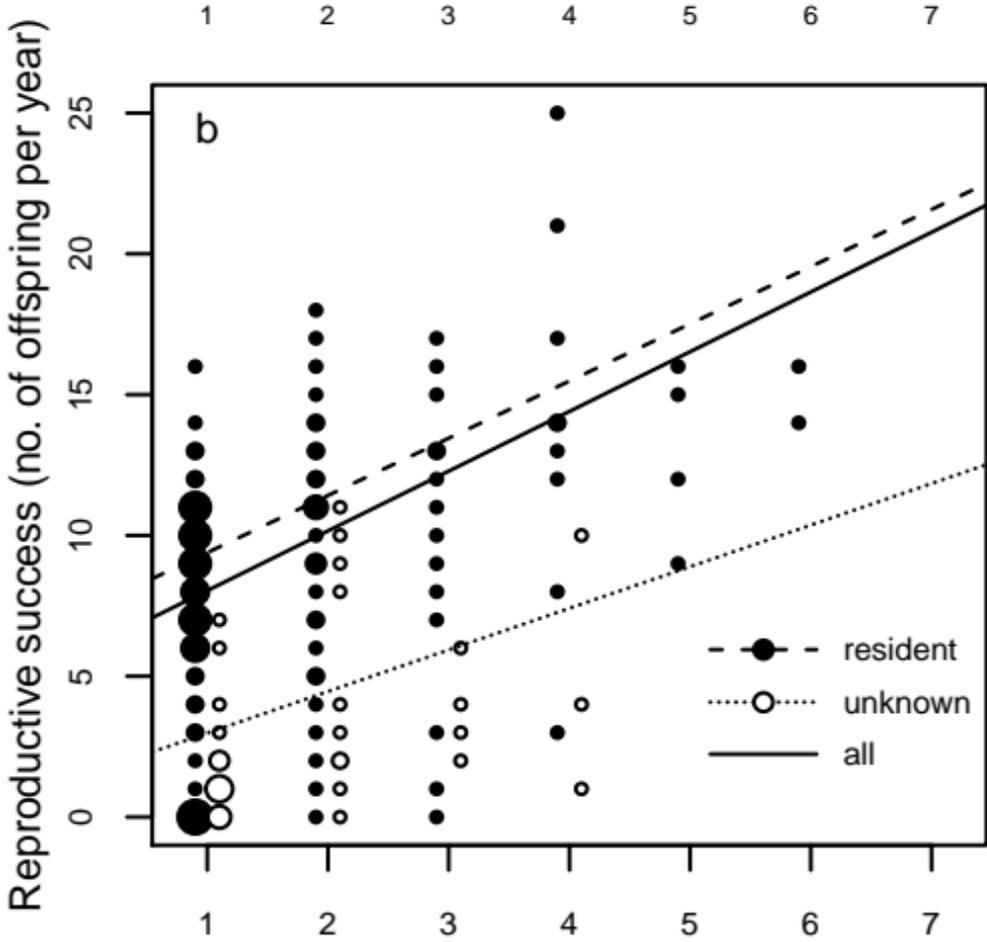
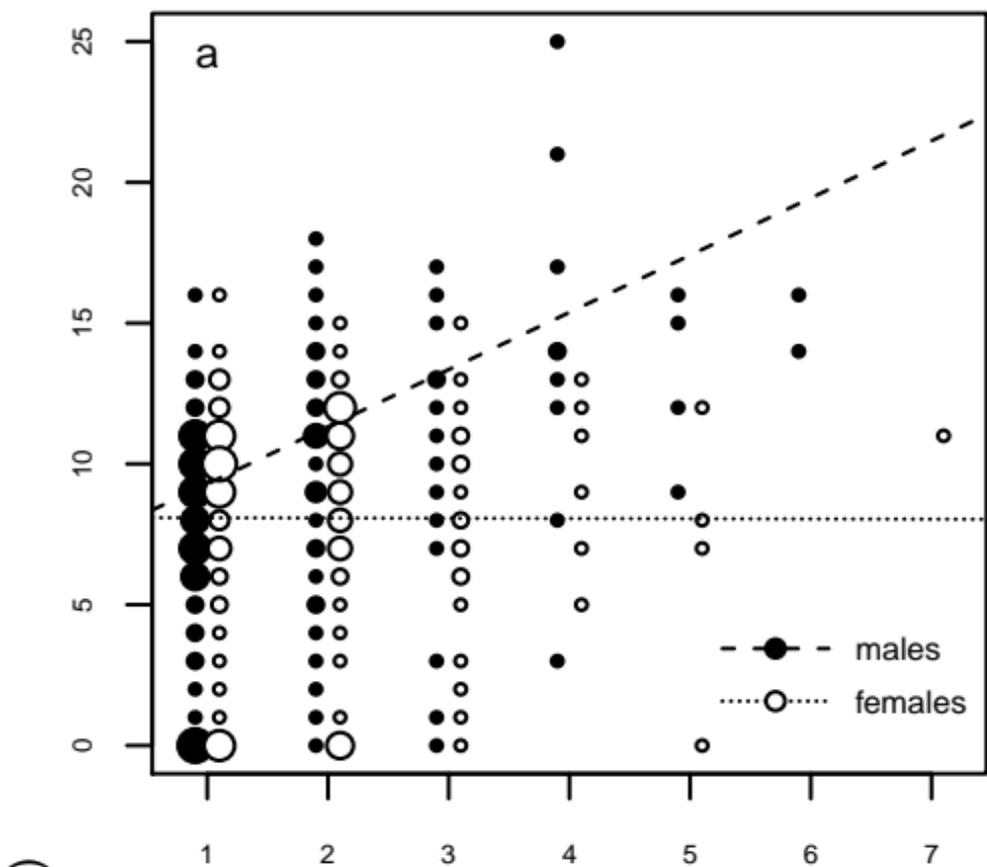
N = 126

N = 200

N = 70

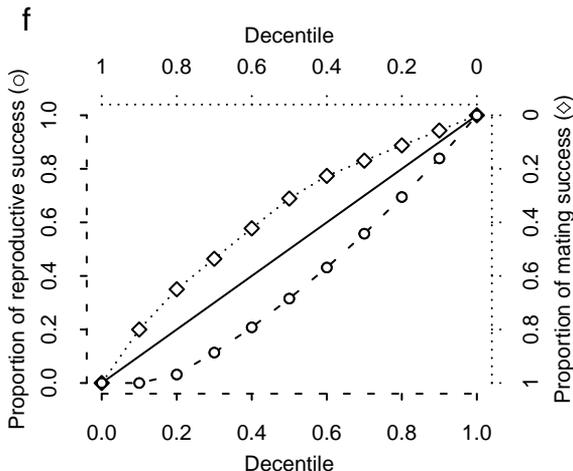
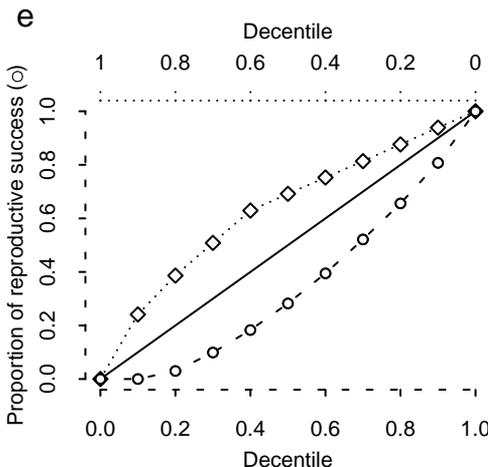
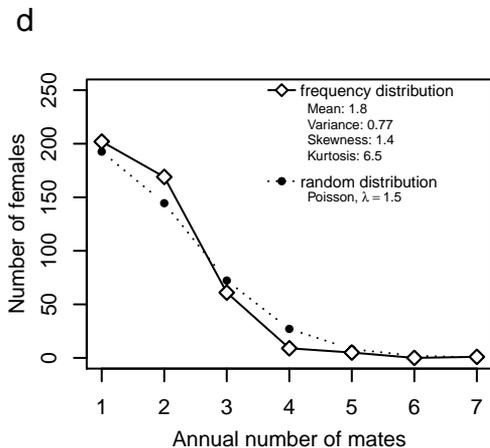
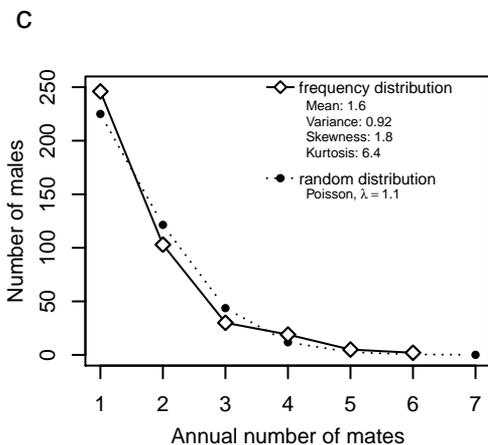
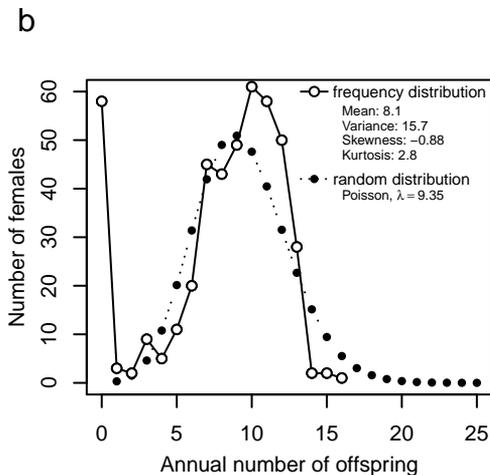
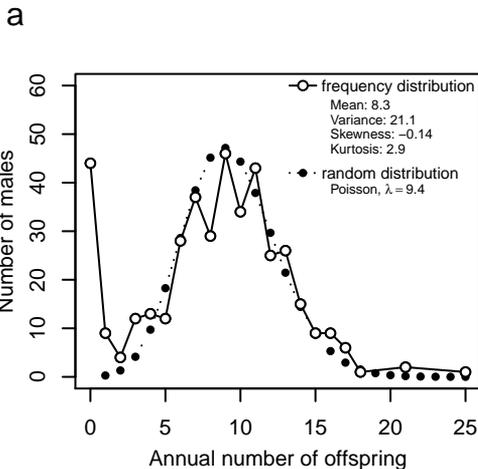




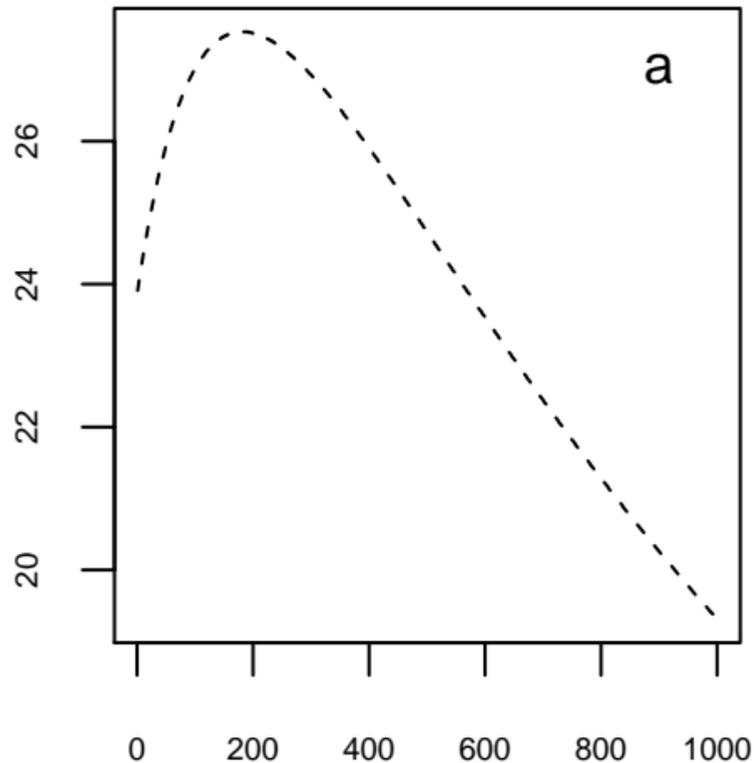


Sample sizes:



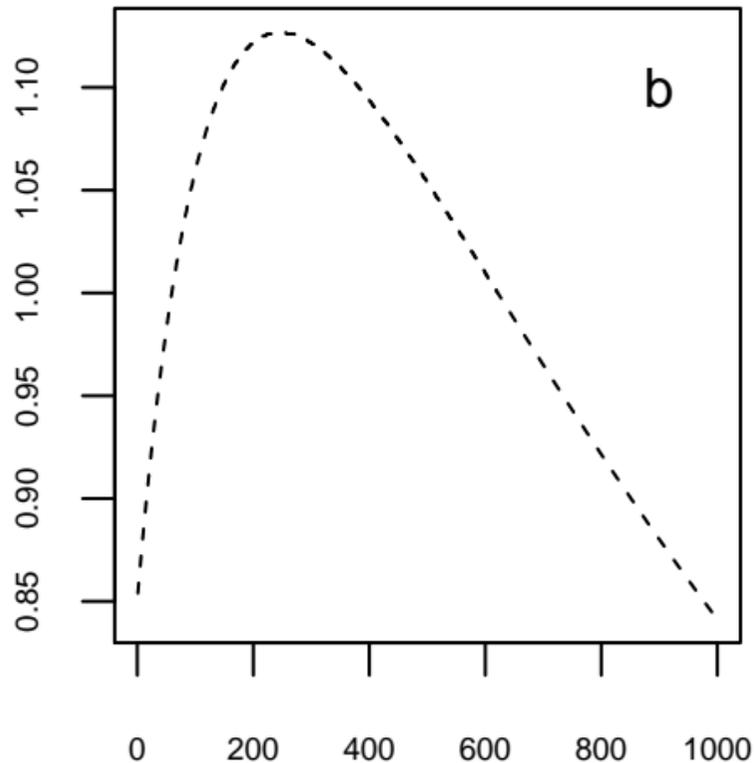


variance in realized reproductive success



number of unsuccessful males included

variance in realized mating success



number of unsuccessful males included