



Male mask size is correlated with mating success in the common yellowthroat

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Many socially monogamous species have sexually dimorphic traits. The evolution of these traits is puzzling as sexual selection is often thought to be relatively weak in monogamous species. However, sexual selection in monogamous species could be stronger than generally believed if the males possessing more dimorphic traits gain a reproductive advantage by increasing the probability of: (1) gaining a mate, (2) mating with a female of relatively higher quality (more fecund), or (3) gaining extrapair fertilizations. We used a combination of DNA fingerprinting and microsatellite markers to study male traits associated with social and extrapair mating success of males in the common yellowthroat, *Geothlypis trichas*. In this species the male has a black facial mask that is absent in females. The mask varies almost two times in size among males on our study area. We found that males with larger masks gained both a social and extrapair mating advantage. In terms of social mating success, males with larger masks were more likely to gain a mate. However, there was no clear evidence that these males also gained more fecund mates. In a populationwide analysis, males with larger masks were also more likely to gain extrapair fertilizations and they sired a larger number of extrapair young. Similarly, in a pairwise comparison, extrapair sires had larger masks than the males that they cuckolded. Over the season, males that obtained extrapair fertilizations sired more young (within-pair and extrapair) than males that failed to gain extrapair fertilizations. Most of this difference was due to extrapair rather than within-pair mating success. These results suggest that sexual selection has the potential to influence mask size as a consequence of variation in both the social and extrapair components of mating success.

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In general, the variance in male mating success is thought to be greater in polygynous than monogamous species and, thus, more likely to lead to the evolution of sexually dimorphic traits (Payne 1984; Andersson 1994). However, many monogamous species also have sexually dimorphic traits. Darwin (1871, Chapter 8) recognized that sexual selection might also be acting on traits in monogamous species and suggested an alternative mechanism of selection. He hypothesized that sexual selection could produce extravagant traits in monogamous species if males with the most developed traits are preferred by the most fecund females (see also Kirkpatrick et al. 1990). Thus more ornamented males receive a reproductive advantage in terms of mate quality, rather than number of mates. This female fecundity hypothesis has become known as the Darwin–Fisher hypothesis (Kirkpatrick et al. 1990). More recently, it has become evident that the mating success of monogamous males can also vary as a

consequence of matings outside the pair bond (extrapair fertilizations).

Genetic studies have shown that extrapair fertilizations are common in many species of socially monogamous birds (reviewed in Westneat & Webster 1994; Petrie & Kempenaers 1998). Extrapair fertilizations have the potential to increase the variance in male mating success and, thus, the opportunity for sexual selection on male traits (Webster et al. 1995). Furthermore, recent studies have found that extrapair mating success is correlated with male traits such as plumage (Sundberg & Dixon 1996; Yezerinac & Weatherhead 1997), tail length (Saino et al. 1997), timing of moult (Dunn & Cockburn 1999), body size (Kempenaers et al. 1992; Whittingham & Lifjeld 1995) and song (Hasselquist et al. 1996; Kempenaers et al. 1996). In these cases, extrapair paternity may play an important role in the evolution of sexual dimorphism. Nevertheless, many studies report no association between sexually dimorphic traits and the proportion of young sired in a male's own nest (i.e. paternity; Westneat 1990; Smith et al. 1991; Hill et al. 1994) or his extrapair mating success (Weatherhead & Boag 1995; Wetton et al. 1995).

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In these cases, other explanations such as the Darwin–Fisher hypothesis may be more applicable.

To date, few studies have examined variation in both social and extrapair mating success as mechanisms for the evolution of sexually dimorphic traits in birds (Hill et al. 1994; Sheldon & Ellegren 1999). We investigated these mechanisms as potential explanations for sexually dimorphic traits in the common yellowthroat, *Geothlypis trichas*, a socially monogamous warbler. One of the most conspicuous dimorphic traits in common yellowthroats is a black facial mask that is present only in males and varies about two times in size among males (Chen 1993; this study). A previous study (Chen 1993) found that males with a larger facial mask were more likely to attract a mate. Based on Chen's study, we predicted that males with larger masks would have greater social and extrapair mating success, in particular males with larger masks would: (1) be more likely to gain a mate, (2) mate earlier with more fecund females and (3) be more successful at extrapair matings. Although we were interested primarily in mask size, we also examined male body condition (Lens et al. 1997) and song rate (Hasselquist et al. 1996), which are correlated with mating success in other species.

METHODS

Study Area and Species

We studied common yellowthroats at the University of Wisconsin–Milwaukee Field Station in Saukville, Wisconsin (43°23'N, 88°01'W). A pilot study was conducted in 1997 during which all of the males on the study area were banded. In 1998 and 1999 there were 30 and 29 territories, respectively, on the study area. Territories were located in 5.4 ha of mostly contiguous swamp and open sedge marshes. Upland forest or fields isolated most of the study area from other occupied habitat.

Male common yellowthroats arrive on the breeding grounds 3–10 days before the arrival of females (Chen 1993; this study). Only males sing and their song repertoire consists of a single distinct perch song, a flight song and several calls (Ritchison 1995). Females build the nest on or within 0.5 m of the ground, predominantly in wet areas. Clutch size ranges from two to five eggs (Hofslund 1959; Guzy & Ritchison 1999). Only the female incubates the eggs, but both the male and female feed young at the nest and after fledging, which occurs at 8 days of age (Mousley 1933; Stewart 1953; Hofslund 1959).

Size Measurements and Body Condition

We caught adults and fledglings in mist nets and marked them with a unique combination of three coloured leg bands and a United States Fish and Wildlife Service aluminium leg band. We measured wing chord and tail length (to the nearest 1.0 mm), tarsus length (to the nearest 0.1 mm) and body mass (to the nearest 0.1 g using an electronic balance). We estimated adult body condition by the residuals from the regression of residual body mass (adjusted for date) on tarsus length. We used

an 8-mm Sony video camera to record male mask size in front of a grid of 1-cm black and white squares. Two separate pictures of each side of the head were captured on a Macintosh G3 computer using a Computer Eyes[™] video capture card. All measurements of mask size were done by a single individual (K.T.) and were estimated by tracing the outline of the mask in an image analysis program (NIH *Image* version 1.44) after scaling the image with the 1-cm grid. An average area for each side of the mask was calculated and then summed together to estimate total mask size. Measurement error, calculated as within-individual percentage of total error was 6.8% (see Yezerinac & Weatherhead 1997) and, thus, mask size showed high repeatability ($r=0.93$; Lessells & Boag 1987).

Arrival Date, Breeding Stages and Experience

We determined arrival dates during daily surveys of the study area in early May. We estimated date of mating (pair bond formation) using the first date on which a male was seen following a female on his territory. Males also decreased their song rate once they gained a mate. Based on this change in behaviour and our daily surveys, we could estimate date of mating to within one day. We located nests by observing females building nests and by watching both parents feed nestlings. We used backdating from hatching to estimate laying date for nests that were found after laying was completed. For young located as fledglings ($N=27$ in 1998, $N=3$ in 1999), we estimated age by comparing their wing chord and tail length with those of known-age individuals. We captured all sampled fledglings prior to 21 days after fledging (mean capture age=13.7 days old) when they were weak flyers and relatively sedentary. A parallel study of brood division using fledglings colour-banded as nestlings never found any mixing of fledglings from different territories (Peterson et al. 2001), nor were any male traits (mask size, song rate or condition) related to the proportion of fledglings in the paternity sample (P values >0.69). Thus we assumed that fledglings were an unbiased sample with respect to the male traits of interest in this study. We defined stages of breeding for individual adults as: (1) 'pre mating', the period after the male arrived until he was mated; (2) 'pre laying', the period after the male was mated until the first egg was laid; (3) 'laying', the period from laying of the first egg to the penultimate egg; (4) 'incubation', the 12-day period after laying; (5) 'nestling', the 8-day period following hatching; and (6) 'fledgling', after young left the nest. We considered birds banded previously on the study area to be experienced breeders, whereas we considered unbanded males acquiring a territory on our study area to be inexperienced breeders. These experience categories should also be correlated with the yearling and older age classes because: (1) unbanded males were often (66%) 1-year-old birds based on the colour of the facial mask and eye ring (Pyle 1997), (2) few males were known to breed for more than two seasons (14%) and (3) site fidelity was high (92%; 24 of 26 returning males obtained the same territory or a territory adjacent to that held the previous year). Almost all males

were monogamous; there was one polygynous male each year.

Song Rate

We recorded song rates of males as the number of songs sung during 15-min observation periods between 0530 and 1100 hours. We chose a 15-min observation period as a representative sample of song rate after pilot data in 1997 indicated that cumulative estimates of mean song rate varied by less than 10% after 15 min of observation (30-min pilot observations). Our 15-min observation periods also produced similar estimates of pre-mating song rate (mean=117 songs/h) as a previous study that observed males 2–3 h per day (mean=125 songs/h; Ritchison 1995). We observed each male twice per week from his arrival on the breeding grounds until incubation began at the last nest in the population (late July). For mated males with an active nest, we examined pre-mating song rate as a potential cue for mate choice.

Parentage Analyses

We used a combination of multilocus DNA fingerprinting and microsatellite analyses to assign parentage to young and determine the reproductive success of males. We obtained paternity data from 46 broods: 32 were sampled during the nestling period and 14 were sampled as fledglings. We determined paternity for young in a total of 18 broods from 1998 and 28 broods from 1999. We collected blood samples (20–100 μ l) from the brachial vein of each adult and young and stored each sample in 1 ml of Queen's lysis buffer (Seutin et al. 1991). DNA was extracted from each blood sample by salt extraction (Miller et al. 1988).

DNA Fingerprinting

For all birds from 1998 ($N=94$) and a portion from 1999 ($N=33$), we used DNA fingerprinting to determine whether a bird was the result of an extrapair fertilization (details provided in Dunn et al. 1994). Briefly, we digested genomic DNA using the restriction enzyme *Hae* III. We separated digested DNA by electrophoresis in a 0.8% agarose gel (24 \times 20 cm) for approximately 40 h at 40 V. We transferred DNA fragments from the gel onto a nylon membrane (Hybond N+) by Southern blotting (Kirby 1990). We radioactively labelled the minisatellite probes, *per* (Shin et al. 1985) and 33.15 (Jeffreys et al. 1985) with [α - 32 P]-dCTP and hybridized them onto the membranes. We washed membranes and exposed them to autoradiograph film, and then developed the film for visualization after 1–10 days. To facilitate accurate scoring, we ran adults and putative young in adjacent lanes.

We excluded young as direct descendants of putative parents based on: (1) the presence of novel bands and (2) the proportion of bands shared between putative parents and young (Westneat 1990). We considered bands that were present in young and not found in either putative parent to be novel bands. Novel bands are expected to

arise from mutations at a rate of about five of every 1000 bands scored (Jeffreys et al. 1985; Burke & Bruford 1987) and occurred at a rate of one in 980 bands in this study. The probability of two novel fragments arising from mutation was less than 0.0001 (calculated from the Poisson distribution; see Burke & Bruford 1987). Thus, we considered a mutation to be the cause of a single novel band in any young and extrapair paternity to be the cause of two or more novel bands. The mean (\pm SD) number of bands scored for each individual was 16.0 (\pm 5.6). The mean (\pm SD) background band-sharing coefficient among unrelated adults (mated pairs, $N=26$) was 0.160 (\pm 0.13), whereas the band-sharing coefficient between mothers and their offspring was 0.496 (\pm 0.06, $N=78$). We excluded young with two or more novel bands as descendants of their putative parents if their band sharing fell below the one-tailed 99% confidence interval, which in this case was 0.436 (Peterson et al. 2001).

Microsatellite Analyses

We used microsatellite primers developed for black-throated blue warblers, *Dendroica caerulescens* (Dca24 and Dca28; Webster et al., in press) and yellow warblers, *Dendroica petechia* (Dpu01 and Dpu16; Dawson et al. 1997) to determine parentage and assign extrapair sires. We analysed all birds in 1999 ($N=136$) at all four loci, and analysed all birds in 1998 ($N=94$) at one locus, or two to three loci in addition to DNA fingerprinting. We performed two polymerase chain reactions (PCR) to amplify each microsatellite. The initial 20 μ l reaction verified proper amplification sizes and the second 10 μ l reaction was used to radioactively label the amplified DNA. We used the following PCR conditions for Dpu01 (Dpu16, Dca24 and Dca28, respectively): 30–50 ng of genomic DNA, 0.5 (0.1, 0.5, 1.0) pmol of each primer, 50 mM KCl, 10 mM Tris-HCl (pH 8.3), 2.5 (3.75, 3.0, 2.75) mM MgCl₂, 0.2 (0.2, 0.15, 0.6) mM dNTPs and 0.5 U Taq polymerase. The thermal profile, began with an initial denaturing step at 94 °C for 3 min followed by 30 cycles at 94 °C for 30 (30, 60, 60) s, 52 °C (57, 44, 48) for 30 (30, 60, 60) s and 72 °C for 30 (30, 45, 45) s. The programme concluded with a final step of 72 °C for 5 min.

In the second step, we radioactively end-labelled the forward primer in a reaction containing 0.15 pmol forward primer, 40 mM Tris (pH 7.6), 10 mM MgCl₂, 5 mM DTT, 0.375 U T4 kinase and 0.375 μ Ci [γ - 32 P]-dATP at 37 °C for 30 min. Then we performed a radioactive PCR with 30–50 ng of the initial PCR product, 7.5 μ mol end-labelled forward primer, 3.0 μ mol reverse primer, 50 mM KCl, 10 mM Tris (pH 8.3), 1.5 mM MgCl₂, 2.4 mM dNTPs and 0.5 U Taq polymerase in a total volume of 10 μ l. The thermal profile was identical to the initial PCR, but we used only 10 cycles in the radioactive PCR. We ran labelled PCR products on a 6% polyacrylamide gel at approximately 1800 V for 2.5 h. We dried the gel for 2 h, exposed it to autoradiograph film for 1–5 days and then developed the film for visualization. At each of the four microsatellite loci, we determined allele sizes by reference to an M13 mp18 DNA sequence (Sequenase Version 2.0

DNA Sequence Kit; United States Biochemical US70770) run on each polyacrylamide gel.

The four microsatellite loci used in paternity analysis were highly polymorphic (Peterson et al. 2001). Briefly, we found that: (1) the number of alleles per locus ranged from 15 to 33, (2) the frequency of each allele ranged from 0.03 to 0.07, (3) the expected frequency of heterozygotes [$h_e = 1 - \sum(x_i)^2$] was similar to the observed frequency of heterozygotes (h_o ; range 0.85–0.95), (4) the average probability of paternal exclusion (Jamieson 1994) for each locus ranged from 0.712 to 0.901, and (5) the total probability of paternal exclusion at all four loci was 0.999. All young shared an allele with their putative mother at all loci. Young that possessed an allele that did not match the putative father at two or more loci were considered extrapair young. If a mismatch occurred at only one locus, we used multilocus DNA fingerprinting ($N=14$ young) to confirm paternity.

We used microsatellite analysis to assign paternity of excluded young to extrapair males by matching allele sizes of the paternally inherited alleles to those of other males in the population. For all excluded young we calculated the chance that any chosen male would share the same genotype as the extrapair young at all four loci as: $(2p_1 - p_1^2) * (2p_2 - p_2^2) * (2p_3 - p_3^2) * (2p_4 - p_4^2)$, where p_i is the frequency of the paternal allele at the i th locus (Jeffreys et al. 1992). The mean (\pm SD) of these probabilities was 0.00298 ± 0.00347 ($N=31$, range 2.0×10^{-4} –0.0117).

Within-pair paternity was the proportion of young sired by a male in his own nest. We analysed within-pair paternity using generalized linear models (GLM) with binomial errors and logit links (GLMStat, Beath 1997). For this analysis we used the number of within-pair young as the dependent (response) variable and the total number of young in the brood as the binomial denominator. We tested the significance of predictor variables by the change in deviance of the model with and without these predictors, using a chi-square approximation. We estimated extrapair mating success by: (1) the number of extrapair young sired (in nests of other females) and (2) whether a male sired any extrapair young (yes=1, no=0). We analysed these two variables using logistic regression models in JMP version 3.1 (SAS Institute 1995). We measured total reproductive success as the total number of offspring that survived to at least 5 days of age (when blood was sampled). Differences in sample sizes were due to incomplete data for some individuals. Means are presented \pm SE unless indicated otherwise.

RESULTS

Male Traits

Mask size

Mask size of males varied 1.9 times among individuals (range 195–376 mm²; Fig. 1). For all males, mask size averaged 292 ± 4.7 mm² and did not differ between years (independent sample t test: $t_{61}=0.95$, $P=0.35$). For males that were recaptured in multiple years, we examined the

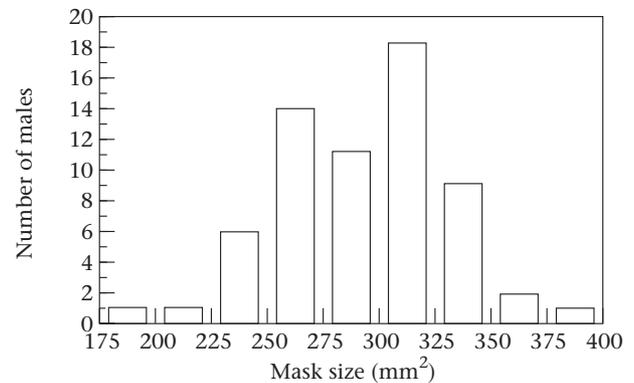


Figure 1. Distribution of mask size (mm²) in male common yellowthroats, Saukville, Wisconsin, 1998–1999 ($N=65$ males).

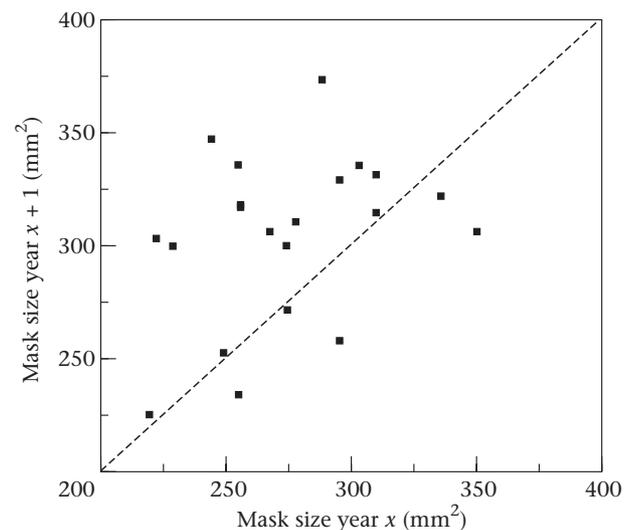


Figure 2. Change in individual male mask size (mm²) from one year to the next. Dashed line shows a one to one relationship indicating no change.

relationship between mask size and age. Mask size increased ($N=18$) more often than decreased ($N=4$) for an individual male between years (paired t test: $t_{21}=40.93$, $P=0.002$; Fig. 2). Four returning males were not included in this analysis because their mask size was not measured in one of the years. Mask size was related positively to breeding experience ($F_{1,56}=10.8$, $P=0.002$), which is a correlate of age, but it was not related to body mass (corrected for date of capture; $F_{1,56}=0.1$, $P=0.08$), wing ($F_{1,56}=1.3$, $P=0.3$) or tarsus length ($F_{1,56}=0.1$, $P=0.97$) in a multiple regression analysis ($R^2=0.17$, $F_{4,56}=2.8$, $P=0.036$).

Song rate

Song rate varied significantly with both calendar date (ANOVA: $F_{7,581}=11.59$, $P<0.001$) and breeding stage (ANOVA: $F_{5,372}=10.40$, $P<0.001$; Fig. 3). Song rate decreased after males gained a mate, but increased slightly during the incubation and fledgling periods. Song rate during the pre-mating period was not related to male mask size ($F_{1,32}<0.01$, $P=0.96$), body condition

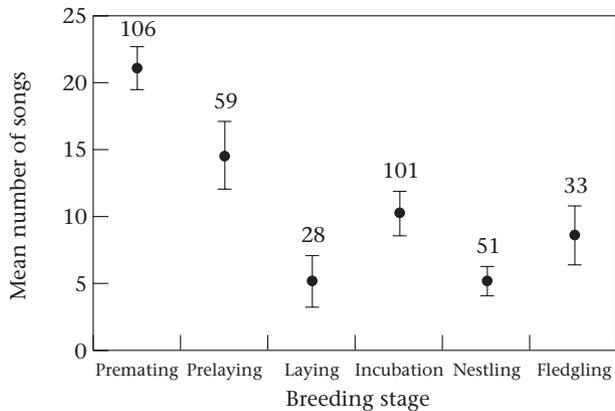


Figure 3. Variation in male song rate (songs/15 min) of all males in the population in relation to breeding stage. Numbers indicate observation sessions for each period.

Table 1. Pairing success (yes/no) of males in relation to male traits

Predictors	Estimate	χ^2	P
Mask size	0.04	5.1	0.02
Breeding experience	1.9	7.7	0.005
Body condition	1.2	2.0	0.15
Arrival date	0.2	16.8	<0.001
Year	3.2	7.8	0.005
Intercept	-17.9		

Likelihood chi-square values are from a logistic regression (SAS Institute 1995). Condition was estimated as the residual from the regression of body mass on tarsus length and date of measurement. Sample size was 61. For the whole model: $\chi^2_5=40.2$, $P<0.001$.

($F_{1,32}=0.7$, $P=0.39$), breeding experience ($F_{1,37}=1.0$, $P=0.31$) or year ($F_{1,37}=1.5$, $P=0.23$) in bivariate analyses.

Arrival Date, Male Traits and Mating Success

Males arrived 3.5 days prior to females in 1998 (males: 15.8 May \pm 1.1 days, $N=26$; females: 19.2 May \pm 1.4 days, $N=23$; independent sample t test: $t_{47}=1.88$, $P=0.07$), but male and female arrival dates were similar in 1999 (males: 16.7 May \pm 2.5 days, $N=42$; females: 15.8 May \pm 1.8 days, $N=26$; $t_{66}=0.46$, $P=0.64$). Of 69 males observed over the 2 years, 19 (28%) did not obtain a mate. In a multiple logistic regression that controlled for year effects, males were more likely to gain a mate when they arrived earlier ($P<0.001$), had a bigger mask ($P=0.02$) and had prior breeding experience on the study area ($P=0.005$; Table 1). Thus, arrival date, breeding experience and mask size all contributed independently to success at gaining a mate.

Males with larger masks also may have gained better-quality mates. Among those males that gained a mate, males with a larger mask arrived earlier ($R^2=0.39$, $F_{1,40}=5.0$, $P=0.032$) and mated earlier (multiple regression that included year: $R^2=0.23$, $F_{1,40}=5.5$, $P=0.02$; Fig. 4a, b). Males that arrived earlier mated earlier (multiple regression: $R^2=0.36$, $F_{1,44}=16.1$, $P<0.001$; Fig. 4c) and

had mates that laid their first clutch earlier ($R^2=0.16$, $F_{1,34}=6.8$, $P=0.01$; Fig. 4d). Females that arrived earlier also were in better body condition (bivariate regression: $r^2=0.18$, $N=29$, $P=0.02$). Thus, early-arriving males had a potential fecundity advantage because they gained a mate sooner who was in better body condition and whose first clutch was likely to be larger (clutch size of first nests was related negatively to laying date: bivariate regression: $r^2=0.16$, $N=30$, $P=0.03$). However, there were no direct correlations between potential indicators of male quality (mask size, premating song rate and male arrival date) and female fecundity (female condition or clutch size; P values >0.16). Male breeding experience, body condition and premating song rate did not contribute significantly to any of the above relationships in multiple regressions. Male body condition also was not related to success at gaining a mate (logistic regression: $\chi^2_1=2.87$, $P=0.09$) or to the date males gained a mate (bivariate regression: $r^2=0.03$, $N=41$, $P=0.32$).

Mated males had a lower mean song rate (12.8 ± 0.9 songs/15 min, $N=49$), averaged across the entire season, than unmated males (24.4 ± 5.4 , $N=8$; ANOVA: $F_{1,55}=14.2$, $P<0.001$). This difference occurred because unmated males sang throughout the entire breeding season, while mated males sang much less, or not at all, after they were mated (especially during the egg-laying period; Fig. 3). Premating song rate was not related to the date a male acquired a mate (bivariate regression: $r^2=0.01$, $N=39$, $P=0.62$).

Extrapair Paternity

In 1998, 7 of 57 (12.3%) young were the result of extrapair mating in 4 of 18 (22.2%) broods. In 1999, 24 of 96 (25.0%) young in 17 of 28 (60.7%) broods were the result of extrapair mating. Both the percentage of extrapair young per nest (Mann-Whitney U test: $Z=1.96$, $P=0.049$) and the percentage of broods containing extrapair young were greater in 1999 than in 1998 (chi-square test: $\chi^2_1=6.83$, $P=0.009$). Of the 24 extrapair young in 1999, four (17%) were mismatched with the social male at one locus, 15 (63%) at two loci, three (13%) at three loci and two (8%) at all four loci. For both years, the genotypes of all offspring matched those of the social mother, and therefore, we concluded that there was no intraspecific brood parasitism. All 27 extrapair young matched the assigned extrapair sire at all four loci. No other males matched at all four loci, however; there were two extrapair young in which another male matched at three loci, and, thus, the fourth locus determined the extrapair sire of these two young.

Correlates of Paternity

Within-pair paternity and male traits

Within-pair paternity, or the proportion of young sired within a male's own nests, averaged $80 \pm 4\%$ ($N=35$) for the entire season. Within-pair paternity was not correlated with mask size, premating song rate, male

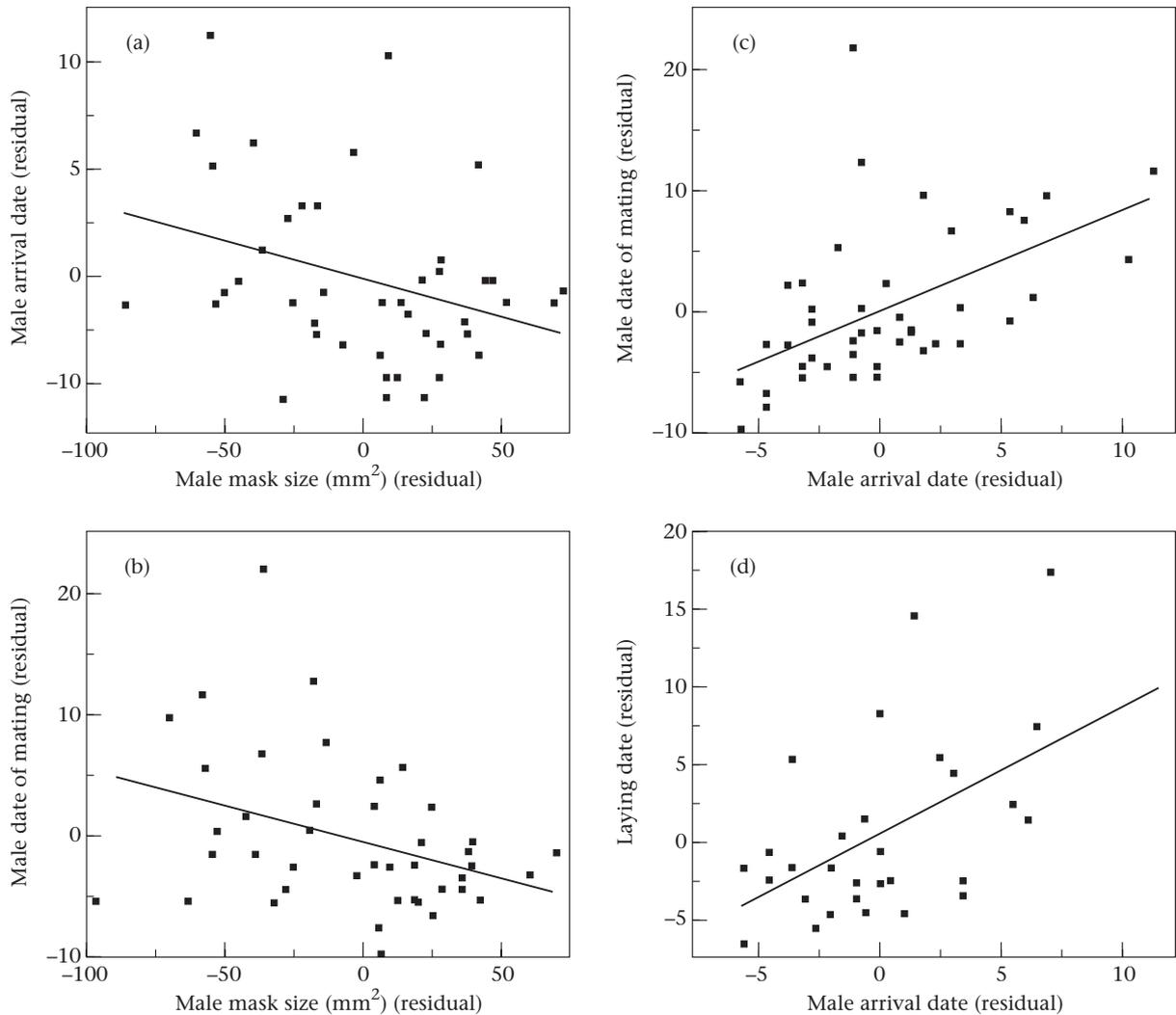


Figure 4. Relationships between (a) male arrival date and mask size, (b) male date of mating and male mask size, (c) male date of mating and male arrival date and (d) mate's laying date and male arrival date, using residuals corrected for year.

condition, or breeding experience in bivariate (Table 2) or multivariate analyses (Table 3).

Extrapair success and male traits

Using microsatellites, we were able to assign 87% (27 of 31) of extrapair offspring in 15 separate broods to 15 different extrapair males. There were seven broods with two or more extrapair offspring and among these broods, five (71%) had two different extrapair sires. Over both years, 26.8% (15/56) of all males in the population were identified as extrapair sires. All of these were mated resident males. Sixteen extrapair young were sired by a neighbouring male on an adjacent territory, seven extrapair young were sired by males from two territories away, and four extrapair young were sired by males from three or more territories away.

In bivariate analyses, males with larger masks ($P=0.03$) and more breeding experience ($P=0.01$) sired a greater number of extrapair young (Table 2). There was no relationship with body condition or premating song rate (Table 2). In a multiple logistic regression that combined

mask size, breeding experience, male condition and premating song rate, only mask size was a significant predictor of the number of extrapair young sired ($N=22$, $P=0.036$; Model I, Table 4). Our sample size was reduced in this analysis ($N=22$) as data were not available for all traits of all males. To maintain a larger sample size, we reanalysed the data with a smaller set of variables, starting with mask size and breeding experience, which were significant in the bivariate analyses ($N=41$; Model II, Table 4). In a plot of the relationship between the number of extrapair young sired and male mask size, experienced males sired more young when they had a larger mask ($P=0.03$), but this was not true for inexperienced males ($P=0.54$; Fig. 5). This interaction was nearly significant ($P=0.051$) in a multiple logistic regression with mask size, breeding experience and their interaction (Model II, Table 4). Premating song rate ($P=0.99$) and body condition ($P=0.72$) were not significant when added to the model containing mask size and breeding experience (Models III and IV, Table 4). Arrival date and year had no significant influence when added to these models.

Table 2. Male mating success in relation to male traits

	Mask size			Breeding experience			Body condition			Premating song rate						
	χ^2 or <i>F</i>	<i>df</i>	<i>N</i>	<i>P</i>	χ^2 or <i>F</i>	<i>df</i>	<i>N</i>	<i>P</i>	χ^2 or <i>F</i>	<i>df</i>	<i>N</i>	<i>P</i>				
Male mating																
Within-pair*	0.23	1	35	0.63	0.42	1	35	0.52	0.28	1	32	0.59	0.32	1	26	0.57
Number of extrapair young sired*†	5.00	1	41	0.03	12.50	4	41	0.01	0.08	1	35	0.78	0.35	1	25	0.56
Success at siring at least one extrapair young*	3.86	1	41	0.049	3.98	1	41	0.046	0.38	1	35	0.54	0.21	1	25	0.65
Total number of young sired†‡	0.22	1,39	41	0.64	0.71	1,39	41	0.41	0.23	1,33	35	0.63	1.7	1,23	25	0.21

*Test statistics for the analysis of within-pair paternity, number of extrapair young sired and success at siring at least one extrapair young are likelihood chi-square values. A total of 35 males were available for the analysis of within-pair paternity as 10 of 45 males did not produce any young that survived to 5 days of age (when blood was sampled). Of the 35 males, 32 had data on body condition and 26 had data on song rate.

†A total of 41 males were examined for extrapair and total fertilization success; four additional males near the edge of the study area were excluded from analysis. Of the 41 males, 35 had data on body condition and 25 had data on song rate.

‡The total number of young sired was tested with *F* statistics. Total number of young sired only includes nestlings that survived to 5 days of age. Thus, the 10 males that did not produce any fledglings were assigned zero within-pair young sired.

Table 3. Within-pair paternity in relation to male traits

Predictors	Model I		Model II		Model III		Model IV	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Mask size	0.10	0.75	1.5	0.21	0.10	0.74	0.07	0.79
Premating song rate	0.76	0.38	0.82	0.37	0.47	0.50		
Body condition	<0.01	0.84	<0.01	0.92				
Breeding experience	<0.01	0.86	0.19	0.66			0.26	0.61
Arrival date	<0.01	0.91			1.7	0.20		
Year	<0.01	0.21			0.31	0.58		
Whole model								
χ^2	6.3		3.3		5.9		0.5	
<i>df</i>	6		4		4		2	
<i>P</i>	0.39		0.51		0.21		0.78	

Likelihood chi-square values are from generalized linear models with binomial errors and logit links (GLMStat, Beath 1997). In these analyses the number of within-pair young was the dependent (response) variable and the total number of young in the brood was the binomial denominator.

Table 4. Number of extrapair young sired in relation to male traits

Predictors	Model I		Model II		Model III		Model IV	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Mask size	4.4	0.03	0.30	0.58	5.9	0.01	4.5	0.04
Song rate	0.07	0.79					<0.01	0.84
Body condition	0.58	0.45			0.13	0.72		
Breeding experience	1.1	0.29	2.9	0.09	2.9	0.09	0.73	0.39
Mask*experience			3.8	0.051				
Whole model								
χ^2	8.3		12.5		13.6		7.2	
<i>df</i>	4		3		3		3	
<i>N</i>	22		41		35		25	
<i>P</i>	0.08		0.006		0.004		0.07	

Likelihood chi-square values are from ordinal logistic regressions (SAS Institute 1995).

We also examined male traits in relation to whether or not a male sired any extrapair young, which may be less influenced by incomplete sampling of male reproductive success near the edges of a study area. These results were similar to the analyses of the number of extrapair young sired (e.g. Table 2).

Paired comparison of extrapair and social mates

In the above analyses, we included all males in the population. Because it is likely that females are not able to assess all males in the population, a more realistic and powerful comparison may be of the extrapair sire and the male he cuckolded. In a paired comparison, males that sired extrapair young had higher within-pair paternity ($84.2 \pm 4\%$) than the males that they cuckolded ($54.8 \pm 5\%$; paired *t* test: $t_{15}=0.29$, $P<0.001$). The black facial mask of extrapair males was larger than the mask of the males that they cuckolded (25 mm² larger or 9% of mean mask size; paired *t* test: $t=24.7$, $P=0.035$). Extrapair males were also more experienced than the males they cuckolded. In nine broods the extrapair male was more experienced than the cuckolded male, in 13 broods they did not differ in experience and in two broods the

extrapair male was less experienced than the social mate (chi-square test: $\chi^2_1=7.8$, $N=24$ broods, $P=0.006$). Results were similar when we analysed each nestling as an independent observation ($N=27$). Extrapair sires and the males they cuckolded did not differ in body condition (paired *t* test: $t_{15}=0.82$, $P=0.43$) or premating song rate ($t_{12}=1.77$, $P=0.10$).

Total reproductive success

Males that sired extrapair young had significantly greater total reproductive success (4.9 ± 0.70 young) than males that did not gain extrapair fertilizations (2.5 ± 0.42 young; Table 5). This relationship was influenced more by extrapair rather than within-pair reproductive success (Table 5). Total reproductive success averaged 3.43 ± 0.41 offspring over the entire season (range 0–11, $N=41$ males) and was not related to mask size ($r^2_{1,39}=0.01$, $P=0.64$), male condition ($r^2_{1,33}<0.01$, $P=0.63$), breeding experience ($P=0.41$) or premating song rate ($r^2_{1,23}=0.07$, $P=0.21$) in bivariate analyses (Table 2). In a multivariate analysis, there was also no relationship between any of these variables and total reproductive success (all NS).

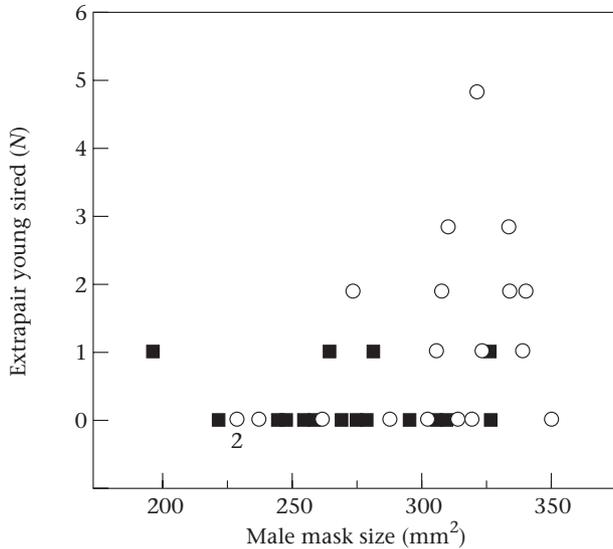


Figure 5. Relationship between the number of extrapair young sired (in nests of other females) and the size of the male’s facial mask for males with prior breeding experience on the study area (○) and males without prior experience (■). The relationship was significant for experienced males (ordinal logistic regression: $\chi^2_1=4.7$, $N=19$, $P=0.03$), but not for inexperienced males ($\chi^2_1=0.4$, $N=22$, $P=0.54$).

DISCUSSION

We investigated both social and extrapair mating success of male common yellowthroats in relation to mask size, body condition and premating song rate of males. Males with larger masks were more likely to get a social mate, and they mated earlier in the season with females that laid clutches earlier and were in better body condition. These males were also more likely to sire extrapair offspring. Thus, both social and extrapair mating success have the potential to influence sexual selection on mask size in common yellowthroats. Males that had prior breeding experience on our study area were also more likely to get a social mate and extrapair fertilizations, but the latter result was influenced by mask size as older and, thus, more experienced males also had larger masks (Fig. 2). Song rate and body condition of males were not

related to any measure of mating success we studied and, thus, may be influenced by other types of selection.

In common yellowthroats, males with larger masks had two potential advantages in terms of social mating success. First, males with larger masks were more likely to obtain a mate. As 87% of our extrapair young were sired by mated resident males and none were sired by unmated residents, it seems unlikely that males without a mate (unmated residents or floater males) have much opportunity to compensate for their lack of a mate by gaining extrapair fertilizations. Note that the effect of mask size was in addition to the effects of arrival date and breeding experience, which also had significant effects on mating success. Second, the Darwin–Fisher hypothesis suggests that earlier-arriving females are in better condition and prefer to mate with the most ornamented males (Kirkpatrick et al. 1990). Female common yellowthroats that arrived earlier were in better condition and started laying earlier. As in many other birds, first clutches in common yellowthroats were larger when they were laid earlier in the season. However, we found no direct correlation between male mask size and female condition or clutch size. Nevertheless, males with larger masks could gain a fecundity advantage if: (1) their mates nested earlier and this allowed males to produce more broods in a season or (2) young produced from earlier nests have a greater probability of survival as a consequence of a longer period for development or better environmental conditions earlier in the season (e.g. Verhulst et al. 1995).

Other studies of monogamous birds have found male traits related to social mating success, in terms of simply gaining a mate (e.g. Price 1984) or gaining a mate with greater fecundity, as suggested by the Darwin–Fisher mechanism (e.g. O’Donald 1980; Price 1984; Møller 1990, 1991; Norris 1990). For example, Norris (1990) found that male great tits, *Parus major*, with larger breast stripes mate with females that lay their clutches early. Hill et al. (1994) also tested the hypothesis that extrapair fertilizations contribute to sexual selection on plumage colour in male house finches, *Carpodacus mexicanus*. They did not find a relationship between plumage colour and extrapair mating success; however, males with brighter plumage obtain

Table 5. Reproductive success of males (mean±SE) that did and did not gain extrapair fertilizations

	Number of broods	Number of within-pair young	Number of extrapair young	Total reproductive success
Gained extrapair fertilizations (N)	1.2±0.14 (10)	3.1±0.64 (15)	1.8±0.30 (15)	4.9±0.70 (15)
Did not gain extrapair fertilization (N)	1.3±0.11 (17)	2.5±0.42 (26)	0.0±0.00 (26)	2.5±0.42 (26)
<i>t*</i>	0.52	0.92	8.08	3.2
<i>df</i>	25	39	39	39
<i>P</i>	0.61	0.36	<0.001	0.002

N=number of males sampled. Number of broods was the number of nesting attempts per season for each male. The 10 males that did not produce any young that survived to blood sampling were assigned zero within-pair young in this analysis. When these males were excluded the number of within-pair young sired did not differ between males that gained (*N*=11) or failed to gain (*N*=20) extrapair fertilization (independent sample *t* test: $t_{29}=1.6$, $P=0.13$).

*Independent sample *t* test.

a mate and begin nesting earlier than duller males, as predicted by the Darwin–Fisher hypothesis. In summary, male yellowthroats with larger masks were more likely to gain a mate, which provides a strong advantage in social mating success. Whether males with larger masks also gain a fecundity advantage is unclear and requires further study.

Sexual selection also has the potential to act on mask size through extrapair mating success, as extrapair sires had larger masks than the female's social mate, and males with larger masks were more likely to sire extrapair young. Over the entire season, males that gained extrapair young also sired a greater number of offspring; this was a consequence of siring extrapair young rather than maintaining greater within-pair paternity, (Table 5). As found in several other studies (Ketterson et al. 1998; Dunn & Cockburn 1999), males that gain extrapair matings also lose some within-pair paternity, but overall these males are more successful. We found no relationship between mask size and total reproductive success, but this relationship may have been obscured by random factors that influence nest success, such as predation (41% of nests were depredated). Similar results have been reported in yellow warblers in which males with more plumage streaking are more likely to be extrapair sires and, as a group, have higher annual mating success (Yezerinac & Weatherhead 1997). To date, evidence of sexual selection on males as a consequence of both variation in social and extrapair mating success has only been reported in barn swallows, *Hirundo rustica*. Male swallows with longer tails gain a reproductive advantage by mating with earlier-arriving females that lay larger clutches (Møller 1991) and by gaining more extrapair fertilizations (Saino et al. 1997). Male common yellowthroats with larger masks also gained a reproductive advantage through both social and extrapair components of mating success.

Other studies have reported similar relationships between specific male traits and extrapair mating success, but in many cases it is unknown or unclear whether females are choosing the trait or simply older or more experienced males (reviewed by Dunn & Cockburn 1999; Richardson & Burke 1999). Male traits are often strongly correlated with age, making it difficult to disentangle the variables. For example, in our analysis of the number of extrapair young sired, there was a significant interaction between mask size and breeding experience, and closer inspection of the data revealed that mask size influences mating success of experienced males, but not of inexperienced males (Fig. 5). Thus, experience appears to influence mating success, but mask size increases with age, so the experience effect may simply be a consequence of an age-related change in mask size. Although age and breeding experience are correlated, they may not always be equivalent in terms of mating success. In American redstarts, *Setophaga ruticilla*, Perreault et al. (1997) found that among adult males, new residents were more likely to have extrapair young in their nest than males with prior residency. Thus, prior breeding experience on the study area was associated with greater paternity in a male's own nest, even after controlling for age.

Our study also suggests that breeding experience was important to mating success, but we cannot separate the effects of age from experience in our study, as older males were also more experienced, by definition. In the future, data from known-aged birds (using banding returns) will allow us to tease apart the effect of experience from age, as done by Perrault et al. (1997).

Mask size of common yellowthroats may be important in male–male competition (intrasexual selection) as well as female choice (intersexual selection). For instance, males with larger masks may have the ability to defend territories more efficiently. In one of the first field experiments on sexual selection in birds, Lewis (1972) found evidence that mask size in common yellowthroats plays a role in male–male competition. Lewis painted the black facial mask of the males to look like females. Experimentally manipulated males without a mask had more aggressive male–male encounters than unmanipulated males, suggesting that masks may play a role in territory defence. Similarly, increased territorial aggression and loss of territories occurred in red-winged blackbirds, *Agelaius phoeniceus*, when the size of the male's red epaulet was reduced or eliminated (Smith 1972; Hansen & Rohwer 1986). Thus, it is possible that a number of selective forces influence mask size in common yellowthroats, including male–male competition and female choice through both within-pair and extrapair mate choice. Natural selection may also play a role if larger black masks are more costly to produce or maintain (see Rohwer 1982; Viega & Puerta 1996).

In this study, we have shown that variation in both social and extrapair mating success was related to the size of the black facial mask in common yellowthroats. Males with a larger mask arrived earlier and were more likely to gain a social mate. There was no clear evidence that these males also gained a fecundity advantage, as predicted by the Darwin–Fisher hypothesis. Also, extrapair sires had larger masks than the males they cuckolded. These results suggest that larger mask size in common yellowthroats may be favoured by sexual selection through variation in both social and extrapair mating success. The relative importance of these two components, as well as the roles of female choice and male–male competition remain to be determined. Recently, there has been much interest in extrapair fertilizations as a potentially large source of variation in male reproductive success and, consequently, an important selective factor in the evolution of male ornamental traits (Møller & Birkhead 1994). However, more traditional explanations for the evolution of these traits that are based on social mating success have not been examined thoroughly and should also be considered in future studies (see also Hill et al. 1994; Dunn et al. 2001).

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