

Extrapair paternity and the opportunity for sexual selection in long-distant migratory passerines

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Extrapair fertilizations (EPFs) are frequently documented in songbirds; however, the extent to which this reproductive tactic contributes to variance in male reproductive success and hence the strength of sexual selection on males remains little studied. Using 2 approaches, intraspecific and comparative, we test the hypothesis that the contribution of EPFs to variance in male fitness increases with migration distance in north temperate songbirds. Using data on the genetic mating system of the scarlet rosefinch *Carpodacus erythrinus*, a long-distance migrant, we show that the number of extrapair mates and within-pair paternity are the most important components of variance in male reproductive success. There was no evidence of a trade-off between extrapair and within-pair success of individual males as males successful in procuring EPFs were less likely to be cuckolded. Comparative data reveal that the opportunity for sexual selection due to EPFs is positively associated with both migration distance and breeding synchrony in north temperate passerines, and we discuss several mechanisms that could extend these relationships. In general, these data suggest that EPFs have a potential to play an important role in the evolution of sexually selected traits in long-distance migratory songbirds such as rosefinches. *Key words*: comparative analysis, mate choice, parentage assignment, promiscuity, scarlet rosefinch *Carpodacus erythrinus*, within-pair paternity. [*Behav Ecol* 18:477–486 (2007)]

The strength of sexual selection is proportional to variance in reproductive success, originally defined as the number of mates an individual is able to obtain (Crow 1958; Arnold and Wade 1984; Shuster and Wade 2003) and more widely quoted as the total number of offspring produced by an individual (Webster et al. 1995). Variation in the number and quality of social mates have traditionally been recognized as the 2 main sources of variance in reproductive output among males, leading to the evolution of male secondary ornaments and increased sexual dimorphism (Darwin 1871; Andersson 1994). However, it is now accepted that extrapair fertilizations (EPFs) are widespread in many bird species (Griffith et al. 2002; Westneat and Stewart 2003). Although rates of extrapair paternity appear to be positively correlated with the extent of plumage color dimorphism in birds (Owens and Hartley 1998; but see Dunn et al. 2001), it is not clear to what extent EPFs increase the opportunity for sexual selection (Freeman-Gallant et al. 2005). EPFs would have maximal impact on variance in male fitness if the males that excelled at within-pair paternity also achieve most EPFs at the expense of other males (Webster et al. 1995; Whittingham and Dunn 2005).

Assessing the relative contribution of EPFs to sexual selection requires an accurate assignment of dams and sires to all offspring within the study population. Despite recent advances in molecular tools (e.g., Webster et al. 2001), sufficient data are only available for a limited number of species and only 2 studies assigned paternity to all offspring (Hasselqvist et al. 1995; Whittingham and Lifjeld 1995). In most species

analyzed to date, extrapair matings increase variance in male reproductive success, but their relative contribution to variance in male fitness varies considerably across species for unknown reasons (but see Whittingham and Dunn 2005). However, failure to assign sires to offspring in some studies could have a big effect on reported estimates of opportunity for selection due to EPFs (Freeman-Gallant et al. 2005).

Rates of EPFs are higher among migrant species than residents (Spottiswoode and Møller 2004). Several mechanisms have been proposed to explain this relationship. First, migration could be associated with increased breeding synchrony due to strong selection on arrival time in most migratory species. Although a few studies have revealed a positive relationship between breeding synchrony and EPFs at the interspecific level (Stutchbury and Morton 1995; Stutchbury 1998b), there has been an ongoing debate as to the effect of breeding synchrony on extrapair mating strategies (see Møller and Ninni 1998; Stutchbury 1998a, 1998b; Weatherhead and Yezerinac 1998). However, when breeding is synchronized, many males are displaying simultaneously, and thus, females may have a better opportunity to compare their social mate with other males in the population (Stutchbury 1998a, 1998b). Similarly, if female migrants are obliged for ecological reasons to start breeding relatively quickly and synchronously after their arrival at the breeding grounds, choice of genetic mate could only occur after a choice of social mate, as reflected by high rates of EPFs (Westneat et al. 1990; Weatherhead and Yezerinac 1998; Spottiswoode and Møller 2004; but see Stutchbury 1998a). The short breeding season of some long-distance migrants might also prevent high-quality males from increasing the number of sired progeny in a season by mechanisms other than EPFs, such as by producing more than one brood per season with a social mate (e.g., Hill et al. 1994).

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In addition to the effects of the length of the breeding season and breeding synchrony on rates of EPFs, migration itself could increase rates of EPFs in bird populations by one of the evolutionary pathways hypothesized by Spottiswoode and Møller (2004). For example, it has been suggested that migration in birds generates additive genetic variation (Fitzpatrick 1994; Møller 1994, 1998; Spottiswoode and Møller 2004) and that this variation is positively associated with rates of EPFs in birds (Petrie et al. 1998). If genetic variation translates into either high variability in male attractiveness to females or high variance in male ability to obtain EPFs in competition with other males, simultaneous female choice of an extrapair mate and monopolization of EPFs by certain males might be commonplace in migrants. In that case, a significant contribution of EPFs to variance in male fitness should be expected. Surprisingly, however, no study thus far has attempted to evaluate the effects of migration on the opportunity for sexual selection via EPFs in birds.

Here we use 2 approaches, intraspecific and comparative, to examine the role of EPFs in enhancing variance in male reproductive success in songbirds breeding in the north temperate zone, with special emphasis on how long-distance migration affects the contribution of EPFs to male fitness. First, we use the scarlet rosefinch *Carpodacus erythrinus*, hereafter referred to as rosefinch, as a model species to evaluate the effects of EPFs on variance in male fitness in a typical long-distance migratory, single-brooded passerine. We specifically test the predictions that rosefinch males trade within pair for EPF success (e.g., Webster et al. 1995; Whittingham and Dunn 2005). In the absence of this trade-off, monopolization of EPFs by only a few males would strongly increase the contribution of EPFs to variance in male reproductive success. Breeding synchrony could affect the probability that a certain male would engage in EPFs (Webster et al. 2001). We evaluate how this parameter affects the occurrence of extrapair young (EPY) in nests of rosefinches. In a second approach, we perform a comparative analysis that includes rosefinch data from this study to test the prediction that the contribution of EPFs to male fitness is positively linked with migration in north temperate zone breeding passerines. Because breeding synchrony and length of the breeding season can covary with migration distance (Pitcher et al. 2005), these parameters are included in the analyses.

METHODS

Study area and study species

The study was conducted from the end of May to early July in the years 2000–2004 in the Vltava river valley, Šumava Mountains National Park, Czech Republic (48°49'N, 13°56'E). The study plot was an isolated patch of wet shrubby meadow (110 ha) surrounded by agricultural landscape mosaics (for a detailed description of the study site, see Albrecht 2004).

Scarlet rosefinches are small (ca., 20 g), semicolonial, sexually dimorphic cardueline finches with delayed plumage maturation in males (Stjernberg 1979). Second-year males resemble females in that they lack red feather ornament on the breast and rump. Most males do not breed until their third year, second-year males are only present infrequently on breeding grounds (Björklund 1989). Each year, but particularly in the 2001–2004 breeding seasons, we attempted to catch all birds in our study area when they first arrived on the breeding grounds using mist nets, although some birds were caught during the chick-provisioning stage. Each netted individual was banded with a National Museum of Prague aluminum ring and provided with a unique combination of 1 to 3 color rings for individual identification. This enabled us

to follow most individuals from their arrival upon the study area in May throughout the entire breeding season. Only resident birds, that is, those seen on the study plot repeatedly in the days following ringing, were considered in the analyses. Every 2 days, we determined the pairing status of resident males. Only a small proportion of resident males (and no resident female) appeared to be unpaired. Only males observed repeatedly feeding the female during the incubation, and feeding chicks, were considered the social fathers of young in a particular nest. Our estimates of realized reproductive success for males could be biased if males frequently sire young outside our study plot; however, this is unlikely because the nearest breeding colony of rosefinches is situated more than 3 km away from our study area. In a 5 year period before this study (1995–1999), a total of 51 male and 33 female rosefinches were color banded in both colonies. No birds banded in one of the colonies were ever recovered from the other, which suggests that rosefinches do not regularly move between the 2 colonies during the breeding season. However, for feeding, both sexes range over large distances and far from breeding areas (Stjernberg 1979); thus, we cannot exclude the possibility that birds from different breeding colonies encounter each other in a third area, where communal feeding takes place (also see Reyer et al. 1997; Westneat and Mays 2005).

Starting in late May, we systematically searched the study area for rosefinch nests. Each potential breeding site was visited at least 3 times per season except of the year 2000 when some places were visited less frequently. Hence, we are confident we were able to find most rosefinch nests on the study area in most years and to genotype the vast majority of young born on our study plot. All nests were found during the egg-laying or incubation stages. A geographic positioning system reading was taken at each nest, and these were used to calculate distances between nests. Rosefinches only rear a single brood per year, although one replacement clutch may be laid in response to the loss of the first (Stjernberg 1979). Relatively few nests were lost before fledging (predation rate 0–25%; Albrecht 2004), and our sample of nests includes predominantly first clutches, not replacements. Nests were checked every 1–4 days to determine the stage of breeding and nesting success. A blood sample (approximately 20 µl) was taken from 7-day-old nestlings and adult birds and stored in 96% ethanol.

Identification of parentage

Blood samples were dried, and DNA was extracted and purified using the DNeasy® Tissue Kit (Qiagen, Hilden, Germany). The parentage analysis was conducted using 3 microsatellite loci (*LOX2*, *LOX7*, and *LOX8*; Pierny et al. 1998) developed for the Scottish Crossbill *Loxia scotica*. Microsatellite loci were amplified individually using an MJ Research PTC-200 thermocycler. One primer of each primer pair was labeled with a different fluorochrome. The reaction conditions were slightly modified from Pierny et al. (1998). The reaction mixture contained the following: approximately 20 ng of genomic DNA, 0.5 units of *Taq* polymerase, 1× reaction buffer, 2 mM MgCl₂, 200 µM dNTPs, and 0.5 µM of each primer, in a final volume of 15 µl. The thermal profile consisted of 30 cycles of 92 °C for 30 s, followed by 54 °C for 30 s. No extension step was included in the cycles, except for a 5-min extension at 72 °C after the final cycle.

For each sample, polymerase chain reaction (PCR) products from each of the 3 loci were combined (0.7–1.5 µl of each reaction according to DNA concentration) and added to a denatured mixture of size standard (Genescan®, TAMRA 500, Applied Biosystems, Foster City, CA) and formamide. These mixes were denatured for 5 min at 95 °C, snap-cooled on ice, and loaded on an ABI Prism® 310 Genetic Analyzer (Applied

Biosystems) for separation and detection. DNA fragments were manually compared and analyzed using GeneScan® software (Applied Biosystems). Although the loci were described as tetranucleotide repeats in the Scottish Crossbill (Piertney et al. 1998), we frequently encountered differences smaller than one repeat unit size, which may suggest either indels in flanking regions or a more complex repeat structure (Primmer and Ellegren 1998). To avoid genotyping errors, we considered 2 fragments differing by less than one repeat unit to be different alleles only after very careful analysis. As a final check, we compared the fragment length of each locus for each individual in a family (i.e., the length of an allele did not usually vary within a family but differences were evident between families) and in doubtful cases, we repeated the fragment analysis or PCR.

The average probabilities of excluding a single randomly chosen unrelated individual from being a parent were calculated for each locus and for all 3 loci when the maternal genotype was known using the program Cervus 2.0 (Marshall et al. 1998). These analyses were based on all resident adult individuals genotyped in the course of the study (Table 1). The 3 microsatellite loci examined were extremely variable, had high heterozygosities, and each adult individual possessed a unique genotype. Thus, although we only used 3 loci, the total exclusionary power exceeded 99% for both the first and second parent (Table 1).

We did not find any genetic mismatches between an offspring and its social mother. The offspring's paternal alleles were subsequently compared with the alleles of its putative father (the female's social partner). If alleles did not match at 2 or 3 loci, the putative father was excluded as a sire. One nestling did not match its putative father at just a single locus. We calculated the probability of resemblance for the 2 remaining loci using the method given in Ibaruchi et al. (2004, equations 1 and 3). Because the cumulative probability of resemblance (P_{RaCum} —the probability that the young and the sire match just by chance) is extremely low (1.51×10^{-5}) and the size difference between the offspring allele and that of the putative father was a single repeat unit, we assumed that a mutation is responsible for the difference and we did not exclude the father as the sire. The presence of null alleles (alleles that consistently fail to amplify to detected levels) can cause serious problems in paternity studies (Dakin and Avise 2004). As locus *LOX2* suggests that null alleles may be present at low frequency (Table 1), we paid particular attention to instance where the excluded putative father was homozygous at *LOX2*. In all such cases, the putative father was also excluded at the other 2 loci.

Sires of EPY were determined using the exclusion approach (Jones and Ardren 2003). We compared the paternal alleles of EPFs with the genotypes of all males in the population. The males that did not match the EPY at one or more loci were excluded as sires. If no male matched the particular EPY at all loci, the sire was categorized as “unknown.” For the remaining EPY, a single male was found to match at all 3 loci and was therefore assigned as the sire.

Variance in reproductive success of males, breeding synchrony

Apparent reproductive success was estimated by simply counting the number of the young in a male's nest, when the young were 7 days old. By contrast, realized reproductive success for each male was based on the total young sired by him, involving both losses of paternity in his own nest and extrapair offspring sired by him. Chick mortality before the age of 7 days was extremely low (only 4 young out of 270 died due to partial predation or starvation). As for eggs, about 5% remained unhatched in successful nests, but we were unable to extract DNA from any of them. Only the data from the years 2001–2004 were used to calculate the opportunity for sexual selection due to EPFs as we were not able to catch all males in 2000. We calculated standardized variances of realized and apparent success (I_s , I_{sapp} ; Arnold and Wade 1984) and used the ratio between I_s and I_{sapp} as an estimate of the relative contribution of EPFs to male fitness (Webster et al. 1995; Freeman-Gallant et al. 2005; Whittingham and Dunn 2005). The components of standardized variance in reproductive success among males were calculated following the method outlined in Webster et al. (1995). The total variance in male reproductive success (Tm) can be expressed as

$$\text{var}(Tm) = \text{var}(W) + \text{var}(E) + 2\text{cov}(W, E), \quad (1)$$

where W and E denote the variance in within-pair and extrapair success, respectively. Both W and E can be further partitioned into variance in number of mates (within [M_w] and extrapair [M_e]), proportion of young sired in a nest (P_w and P_e), and mate quality expressed as mate productivity (N_w and N_e ; Webster et al. 1995, equation 17), with the effects of extrapair terms being additive to those of within-pair terms. All means, variances, and covariances were calculated using only individuals with a defined value for the fitness component of interest (nonzero fitness in the previous episode of selection; see Webster et al. 1995). To avoid pseudoreplication, data were only used from the first breeding season of each male in the period 2001–2004

Table 1
Summary statistics of the microsatellite loci used to determine parentage in scarlet rosefinches

Locus	n^a	k^b	Allele size range	Het (exp) ^c	Het (obs) ^d	P (excl) 1 ^e	P (excl) 2 ^f	Estimated frequency of null alleles
LOX2	98	22	166–282	0.905	0.867	0.665	0.799	0.0204
LOX7	93	70	130–357	0.983	0.968	0.916	0.956	0.0055
LOX8	98	73	200–439	0.980	0.949	0.904	0.949	0.0134
Combined						0.997	>0.999	

^a Number of individuals tested.

^b Number of alleles.

^c Expected heterozygosity.

^d Observed heterozygosity.

^e Probability of maternal exclusion.

^f Probability of paternal exclusion.

(see also Whittingham and Dunn 2005). Three nests with known social parents were lost before we took blood samples from the young. Males from these nests as well as 3 EPY sired by one of them were excluded from calculations of variance in male reproductive success.

A breeding synchrony index (SI) for each breeding female in breeding population was calculated following Kempnaers (1993). We did not distinguish between “population level” and “local” breeding synchrony sensu Chuang et al. (1999) and treated the breeding colony as a unit where all birds are equally likely to encounter each other, as suggested by Martens and Kessler (2000). “Fertile period” was defined as the period starting 5 days before the first egg in a clutch was laid and ending with the penultimate egg in a clutch being laid (Stutchbury et al. 1997; Birkhead 1998), which reflects the potential for stored sperm to fertilize ovulated eggs later (Birkhead and Møller 1992). This fertile period in rosefinch females is also indicated by intensity of mate guarding because this appears to be high and stable over the whole period of 5 days before the first egg in a clutch appears (Albrecht T, unpublished data).

Statistical analysis

We performed multiple logistic regressions (general linear model procedures, S-Plus 6.0; Mathsoft 2001) with binary response variable to analyze how the timing of breeding (standardized around the median laying date) and breeding synchrony with other pairs in local population affects the likelihood of a male being cuckolded and losing paternity in his own nest. We repeated the analysis with the number of within-pair young as a dependent variable and the total number of young in the nest as the binomial denominator to account for the fact that different proportions of young in a nest were sired by social male parents. However, this second analysis led to the same conclusions and is not shown. All significance values of multiple tests are based on the Type III sum of squares (Crawley 2002). Numbers of EPY in nests were compared with the expected random values estimated from a prediction of multivariate hypergeometric distribution of EPY among nests (Neuhauser et al. 2001; Byers et al. 2004). Sufficient data were only available for broods of 5 young (the modal brood size). Differences in sample sizes between analyses were the result of incomplete data for some males or nests. Means are presented \pm standard error throughout.

Comparative analysis

We first compared the contribution EPFs make with the variation in male reproductive success in species with similar breeding phenology as rosefinches (single brooded) and 2-brooded species. To do this, we used nonparametric Mann–Whitney statistics (see also Whittingham and Dunn 2005), with the I_s/I_{sapp} ratio as a dependent variable. Means were used when more than one I_s/I_{sapp} ratio was available for a single species. Single-brooded species were defined as those in which a second breeding attempt (not replacement clutch) in one season has never been recorded, or is rare. The data on the number of breeding attempts per season were obtained from Cramp et al. (1977–1994) and from The Birds of North America Online (Poole 2005). It has been argued that the data published on I_s/I_{sapp} ratios should be considered preliminary because studies where the paternity was assigned to only a low proportion of EPY tend to overestimate variance in realized male reproductive success (Freeman-Gallant et al. 2005). Therefore, we evaluated whether the groups of interest differed in this respect. When possible, we estimated the typical length of the main egg-laying period (an approxima-

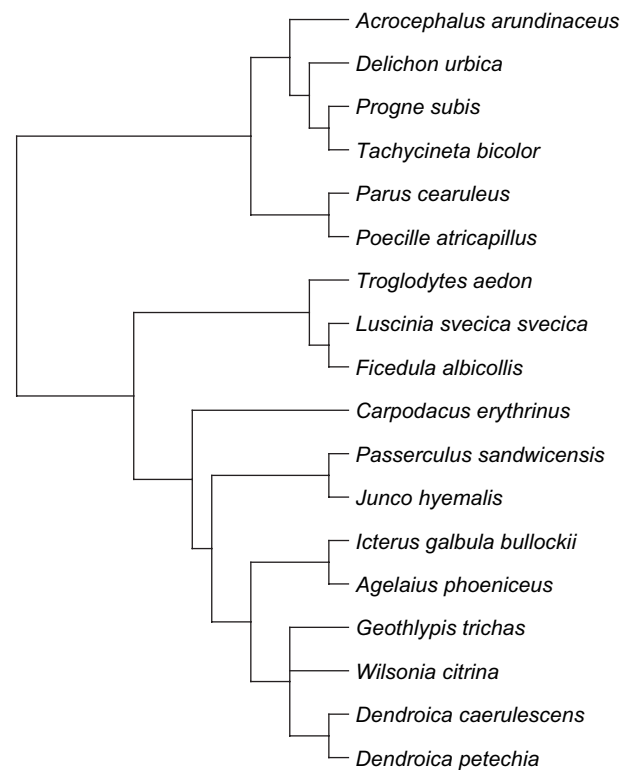


Figure 1

Phylogeny for passerine species used in the comparative analysis. Relationships among higher taxa were based on the phylogeny published in Barker et al. (2004). We used the phylogeny presented in Spottiswoode and Møller (2004) for Hirundinidae and Parulidae.

tion of the length of the breeding season) to the nearest week from the pie charts reported in Cramp et al. (1977–1994) and Poole (2005). We did not consider the tails signaling exceptionally early and exceptionally late breeding attempts. Data on mean migration distance (to the nearest 1000 km) and breeding synchrony were obtained from Spottiswoode and Møller (2004) and using the compendia cited above. We realize that our sample is restricted to northern temperate zone breeding passerines, in contrast to some previous comparative studies (e.g., Spottiswoode and Møller 2004; Pitcher et al. 2005). Hence, we did not include latitude as an explanatory variable; species vary relatively little for this parameter (range 38.96–52.07, sensu Spottiswoode and Møller 2004; ca., 1500 km along the meridian), and there is no relationship between mean latitude and the length of breeding season in our sample of species ($r_s = -0.25$, $P = 0.32$, $n = 18$).

We employed methods based on phylogenetically independent contrasts (Felsenstein 1985) to evaluate how the breeding season length, breeding synchrony (arcsin-root transformed), and migration distance affect the contribution of EPF to the opportunity for sexual selection across species. Relationships among higher taxa were based on molecular phylogeny presented in Barker et al. (2004), which is consistent with other phylogenies based on nucleotide sequence data (e.g., Ericson and Johansson 2003). For families Hirundinidae and Parulidae, detailed phylogenies presented in Spottiswoode and Møller (2004) were used (Figure 1). We assessed arbitrary branch lengths in our analysis assuming both a punctuated mode of evolution (equal branch length, hereafter PUNCT; Harvey and Pagel 1991) and a gradual mode of evolution (branch lengths proportional to the number of species in the clade, hereafter GRAD; Grafen 1989). Because the I_s/I_{sapp} ratio deviated from normality (Shapiro-Wilk’s test,

$P < 0.005$), we performed a Box-Cox transformation (Crawley 2002) in which the power transformation λ was set to -0.60 , that is, to the value equal to the minimum residual sum of squares. After this transformation, the I_s/I_{sapp} ratio was normally distributed (Shapiro-Wilk's test, $P = 0.55$). Phylogeny contrasts were calculated for the I_s/I_{sapp} ratio (transformed) as the dependent variable and the length of the breeding season, breeding synchrony, and migration distance as predictors, using COMPARE 4.6 (Martins 2004). In all regressions, results were statistically controlled for the variation among the proportion of EPY that had assigned sires (arcsin-root transformed). No correlation between the absolute values of independent contrasts and their standard deviation was detected for any variable under both modes of character evolution (PUNCT and GRAD); this indicates that the branch lengths successfully standardized the contrasts and, therefore, are reasonable for use in our analysis (Garland et al. 1992). Because the null expectation for a contrast at any given node is zero, all regressions in comparative analyses were forced through the origin (Harvey and Pagel 1991).

RESULTS

Rates of extrapair paternity

Over the 2000–2004 study period, 62 rosefinch nests were found to contain a total of 266 young of which 48 in 21 nests were EPY (mean: 2.29 ± 0.244 EPY per nest containing EPY). The proportion of nests containing EPY varied from 14% in 2000 ($n = 7$ nests) to 40% in 2004 ($n = 15$ nests). EPY were nonrandomly distributed in broods of 5 young, with zero and >3 EPY in a brood occurring more frequently than would be expected by chance ($\chi^2_5 = 33.59$, $P < 0.001$, $n = 23$ broods; Figure 2). Between 1 and 3, males sired EPY in broods with a mixed paternity (mean = 1.19 ± 0.136).

Effects of breeding synchrony and geography on extrapair paternity

Breeding synchrony as well as the geographical distribution of male–female interactions could affect the probability of cuckoldry. Over the 5 study years, the egg-laying period in rosefinches lasted 14 ± 2.4 days (range 10–22), and only few nests ($n = 11$) were established very late in the season (commencing ≥ 10 days after the first clutch of the season, hereafter described as late nests; also see Stjernberg 1979). Breeding synchrony (SI) averaged $57 \pm 2.8\%$ (range 2–96, $n = 62$). The probability a nest would contain at least one EPY was unrelated to standardized timing of breeding (partial effect: $\chi^2_1 = 0.01$, $P = 0.98$, $n = 62$) or breeding synchrony (SI) with other pairs on the study plot (partial effect: $\chi^2_1 = 0.082$, $P = 0.77$, $n = 62$). EPY occurred with equal probability in the nests of early and late breeders (15 of 51 vs. 6 of 11 nests, Fisher's exact test, $P = 0.17$). However, this result should be treated with caution because the power of the analysis is low (0.22).

The difference in the timing of breeding of males who sired EPY in nests and males they cuckolded was 6.6 ± 1.1 days (range = 1–14, $n = 12$), but there was no evidence that the cuckolders bred earlier or later than the males that lost paternity (Wilcoxon matched pairs test, $z = 1.02$, $P = 0.31$, $n = 12$). Similarly, there appeared to be no difference between cuckolded and extrapair sire in the value of SI (Wilcoxon matched pairs test, $z = 0.71$, $P = 0.48$, $n = 12$). In only one case was a male cuckolded by his closest neighbor. In all other cases, there was at least one other nest (median = 6, range 1–11) located closer to the nest of the cuckolded male than was the nest of the extrapair sire. In fact, nests of the extrapair sire and cuckolded male were sometimes situated at considerable

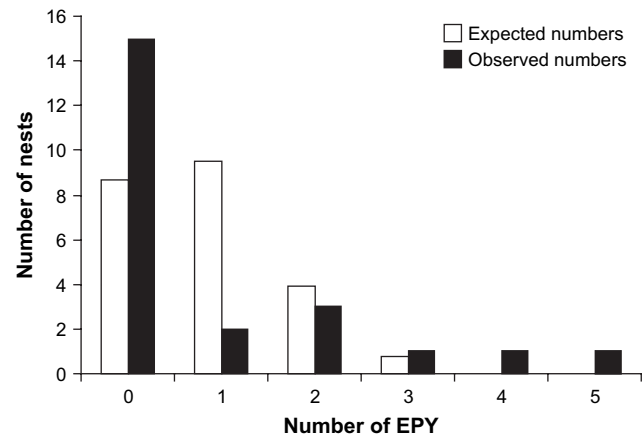


Figure 2

Expected and observed numbers of EPY in nests of scarlet rosefinches ($n = 23$) containing 5 young. Expected numbers of EPY were estimated from a prediction of multivariate hypergeometric distribution of EPY among nests (Neuhauser et al. 2001).

distances apart, in one case over the length of the study plot (mean 144 ± 28.3 m; range 25–920 m).

Variance in male reproductive success due to extrapair paternity

Over the restricted period 2001–2004, we examined the annual reproductive success of 46 male rosefinches, of which 2 were second-year males. Together, these males sired 24 of a total of 33 EPY uncovered in their nests. Each male sired 0–5 EPY (mean 0.54 ± 0.178 , $n = 46$), and males that sired EPY achieved this in either 1 or 2 nests. Variance in total reproductive success (T) was 7.02 greater for paired males than for paired females (variance ratio test: $F_{42,42} = 0.158$, $P < 0.001$; $I_{smales} = 0.344$, $I_{sfemales} = 0.049$). When we partitioned the variance in overall male reproductive success (T_m) into the variance due to the number of mates, the average number

Table 2

Standardized variance in male reproductive success in scarlet rosefinches attributable to within (W) and extrapair (E) success and a covariance between them

	total variance (%)
Variance in male reproductive success	
W	67.3
E	22.9
$2 \times \text{Cov}(W, E)$	9.8
Within-pair terms	
Due to variance in no. of mates (M_w)	17.4
Due to variance in no. of young/mate (N_w)	9.2
Due to variance in proportion of young sired (P_w)	28.7
Extrapair terms	
Due to variance in no. of mates (M_e)	18.9
Due to variance in no. of young/mate (N_e)	0.2
Due to variance in proportion of young sired (P_e)	1.3
Covariances + D	16.0

This variance is further partitioned into variance due to the number of mates (M), the average number of young produced per mate (N), and the proportion of young sired by male in mate's nest (P). The table shows also the proportion of variance in male fitness attributable to all covariance terms and D (remainder term that reflects multivariate skewness; Webster et al. 1995).

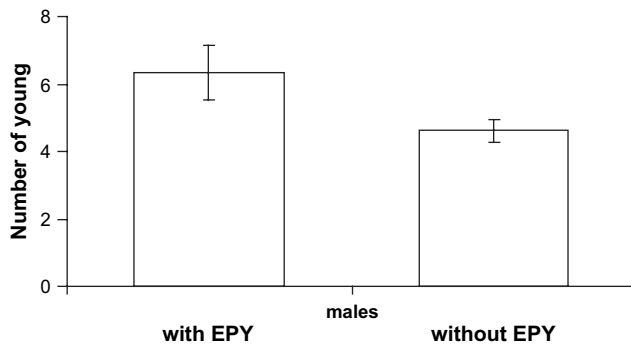


Figure 3

Mean annual reproductive success (number of young sired) of scarlet rosefinch males that were able to sire EPY (left column; $n = 9$ males) and those that avoided cuckoldry but did not sire any EPY (right column; $n = 22$). Only paired males are included. Vertical bars denote standard error.

of young per mate and the proportion of young sired through both within and extrapair mates. The major source of variance in male fitness was within-pair paternity (P_w) in combination with the number of extrapair mates (M_e) (Table 2), both positively correlated with Tm (only paired males; Spearman rank, $r_s = 0.74$, $P < 0.001$ and $r_s = 0.44$, $P < 0.001$, respectively, $n = 43$). The number of social mates (M_w) also contributed to variance in male fitness and was correlated with Tm

(all males: $r_s = 0.39$, $P < 0.01$, $n = 46$). Three bachelor males occurred on the study plot, one of which sired 3 young in 2 nests, and we recorded one case of simultaneous polygyny (1 male with 2 social mates).

There was no evidence that males faced a trade-off between achieving EPFs and ensuring paternity within their own nests because the correlation between P_w and M_e was positive ($r_s = 0.31$, $P = 0.040$, $n = 43$), and, interestingly, no male that gained EPFs was cuckolded (comparison with other males, Fisher's exact test, $P = 0.044$, $n = 9$ and 34). As a result, males that were able to sire EPY achieved greater reproductive success than males that avoided cuckoldry but were not able to sire young outside their pair-bond (analysis of variance, $F_{1,29} = 6.13$, $P = 0.019$; Figure 3). The covariance term between within-pair and extrapair success of males was positive and amounted to 10% (Table 2). Standardized variance in realized reproductive success of males (I_s) was 3.31 times greater than variance in apparent reproductive success (0.402 vs. 0.122). Realized reproductive success of paired males (Tm) was unrelated to the timing of breeding ($r_s = -0.23$, $P = 0.13$, $n = 43$).

The opportunity for sexual selection due to extrapair paternity in north temperate zone passerines

In single-brooded species, such as rosefinches, EPFs tended to contribute relatively more to male fitness, defined as the I_s/I_{sapp} ratio, than in those with 2 breeding attempts per season ($n = 6$ and 12; Mann-Whitney U test, $Z = 2.43$, $P = 0.015$; Table 3). However, assignment success was higher in 2-brooded

Table 3

The contribution of EPFs to the opportunity for sexual selection expressed as the I_s/I_{sapp} ratio for temperate zone breeding songbirds

Species	I_{sapp}	I_s	I_s/I_{sapp}	%EPY	%EPY assigned	Mating system ^a	Breeding attempts/season	Migr ^b	SI ^c	Length ^d	Source ^e
<i>Acrocephalus arundinaceus</i>	1.00	1.02	1.0	3	100	Poly	2	8	30	8	1
<i>Agelaius phoeniceus</i> 1	0.25	0.39	1.1	26	78.5	Poly	2	5	36	11	2
<i>Agelaius phoeniceus</i> 2	0.34	0.49	1.4	25	60.0	Poly	2	5	36	11	3
<i>Agelaius phoeniceus</i> 3	0.25	0.39	1.6	28	93.0	Poly	2	5	36	11	4
<i>Carpodacus erythrinus</i>	0.12	0.40	3.3	18	73.0	Mono	1	6 ^c	57	4	5
<i>Delichon urbica</i>	0.06	0.31	5.2	19	100	Mono	2	8	60	10	6
<i>Dendroica caerulescens</i>	0.49	0.71	1.4	21	62.3	Mono	2	2	27	7	7
<i>Dendroica petechia</i>	0.04	0.53	13.3	37	35.4	Mono	1	6	47	3	8
<i>Ficedula albicollis</i>	0.03	0.14	4.7	16	53.8	Mono	1	7	—	5	9
<i>Geothlypis trichas</i>	0.28	0.48	1.7	26	83.0	Mono	2	5	25.5	5	10
<i>Icterus galbula bullockii</i>	0.07	0.17	2.4	32	44.6	Mono	1	3	—	8	11
<i>Junco hyemalis</i>	0.55	0.72	1.3	28	54.7	Mono	2	3	—	10	12
<i>Luscinia svecica svecica</i>	0.08	0.37	4.6	29	56	Mono	1	5	66	4	13
<i>Parus caeruleus</i>	0.16	0.27	1.7	11	72.3	Mono	2	0	57	12	14
<i>Passerculus sandwichensis</i>	0.27	0.48	1.8	47	92.3	Poly	2	4	34	8	15
<i>Poecile atricapillus</i>	0.04	0.10	2.5	9	46.9	Mono	2	0	53	6	16
<i>Progne subis</i>	0.05	0.33	6.6	19	53.8	Mono	2	7	28	6	17
<i>Tachycineta bicolor</i>	0.09	0.99	11.0	52	47.2	Mono	1	5	46	3	18
<i>Troglodytes aedon</i>	0.18	0.22	1.2	10	88.0	Poly	2	3	—	8	9
<i>Wilsonia citrina</i>	0.18	0.46	2.6	27	54.7	Mono	2	2	33	5	19

^a poly, socially polygynous, mono, socially monogamous.

^b Values for migration distance (migr; to the nearest thousand kilometer) and breeding SI obtained from Spottiswoode and Møller (2004) and from Cramp et al. (1977–1994).

^c Length in weeks of the main laying period from Cramp et al. (1977–1994) and Poole (2005); if possible, estimated to the nearest week from pie charts, without considering the tails signaling exceptionally early or exceptionally late breeding attempts.

^d Distance (to the nearest thousand kilometer) between breeding areas in Central Europe and wintering grounds in India (Cramp et al. 1977–1994).

^e Source for realized variance in male reproductive success (I_s , I_{sapp}), percentage of EPY in a population (%EPY) and %EPY for which extrapair sires were assigned (%EPY assigned): 1, Hasselqvist et al. (1995); 2, Weatherhead and Boag (1997); 3, Webster et al. (1995); 4, Gibbs et al. (1990); 5, this study; 6, Whittingham and Liffield (1995); 7, Webster et al. (2001); 8, Yezerinac et al. (1995); 9, Sheldon and Ellegren (1999); 10, Whittingham and Dunn (2005); 11, Richardson and Burke (2001); 12, Ketterson et al. (1997); Whittingham and Dunn (2005); 13, Johnsen et al. (2002); 14, Kempnaers et al. (1992); 15, Freeman-Gallant et al. (2005); 16, Otter et al. (1998); Whittingham and Dunn (2005); 17, Wagner et al. (1996); Møller (1998); 18, Kempnaers et al. (2001); 19, Stutchbury et al. (1997).

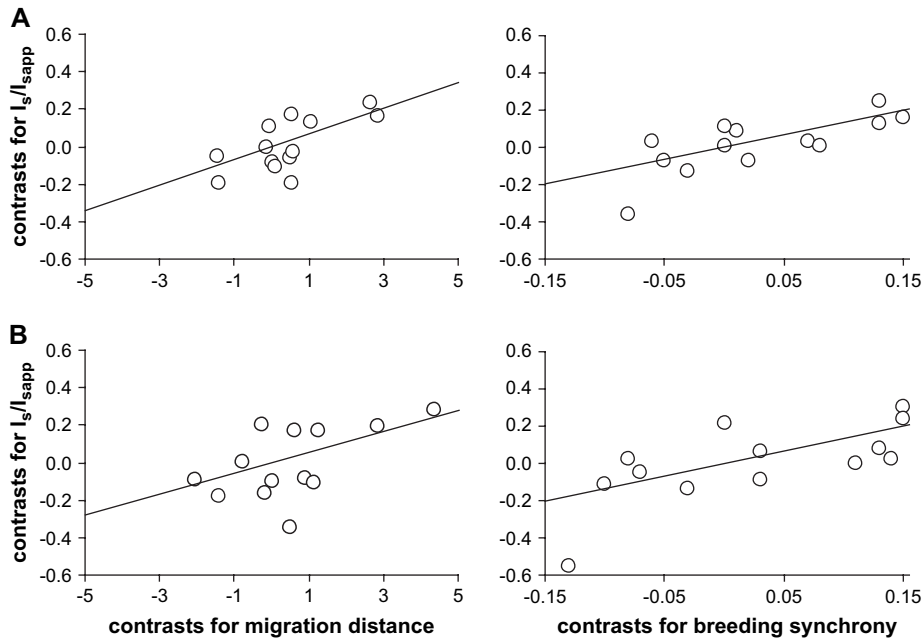


Figure 4 Migration distance (left column) and breeding synchrony (right column) as predictors of the opportunity for sexual selection due to EPFs (I_s/I_{sapp} ratio) in temperate zone breeding passerines. Effects controlled for percentage of young with assigned sire, the length breeding season, and migration distance or breeding synchrony, respectively. (A) Assuming gradual mode of evolution (Grafen 1989). (B) Assuming punctuated mode of evolution (Harvey and Pagel 1991). Regression lines are forced through the origin.

compared with single-brooded species (Mann–Whitney U test, $Z = 2.20$, $P = 0.023$) and for polygynous compared with socially monogamous species ($n = 4$ and 14 ; Mann–Whitney U test, $Z = 2.50$, $P = 0.012$). When the analysis was restricted to socially monogamous species, the difference in I_s/I_{sapp} ratio between single and 2-brooded species approached significance ($n = 6$ and 8 ; Mann–Whitney U test, $Z = 1.81$, $P = 0.07$) with no difference in assignment success between the groups (Mann–Whitney U test, $Z = 1.48$, $P = 0.13$).

The length of the breeding season tended to be inversely correlated with the opportunity for sexual selection to operate through extrapair paternity after being statistically controlled for percentage of EPY assigned (GRAD: $F = 6.20$, $P = 0.025$; PUNCT: $F = 4.16$, $P = 0.059$; $n = 18$). However, this effect was lost ($P = 0.057$ and 0.21 , respectively) when migration distance was added into the model. Migration distance tended to be a better predictor of I_s/I_{sapp} ratio than the length of the breeding season (partial effect of migration—GRAD: $F = 5.38$, $P = 0.036$; PUNCT: $F = 2.82$, $P = 0.11$). This pattern was even stronger when the analysis was restricted to socially monogamous species ($n = 14$; partial effect of migration—GRAD: $F = 13.59$, $P < 0.005$; PUNCT: $F = 8.14$, $P = 0.018$; partial effect of breeding season length—GRAD: $F = 3.46$, $P = 0.09$; PUNCT: $F = 2.53$, $P = 0.14$). In a more complex model, using a set of 14 species for which the effects of breeding season length, migration distance, and breeding synchrony could be simultaneously evaluated (Table 3), the length of breeding season again was no longer significant ($P > 0.40$ in both cases) and both migration distance (GRAD: $F = 8.36$, $P = 0.018$; PUNCT: $F = 2.32$, $P = 0.16$) and breeding synchrony (GRAD: $F = 15.13$, $P < 0.01$; PUNCT: $F = 10.03$, $P = 0.011$) tended to be positively correlated with the I_s/I_{sapp} ratio (Figure 4).

DISCUSSION

We show that EPFs considerably increase variance in reproductive success among rosefinch males despite only a moderate level of extrapair paternity (18% young in 30% nests were extrapair) in comparison with other passerines (reviewed in Griffith et al. 2002). Consistent with this result, EPYs were nonrandomly distributed across broods of 5 young. Because

we were able to identify genetic sires to a relatively large proportion of EPY in our study population over the period of 2001–2004, the relatively high value of the I_s/I_{sapp} ratio (a measure of the opportunity for sexual selection due to EPFs) is probably not due to bias resulting from an artificial overestimation of variance in realized reproductive success of males (e.g., Freeman-Gallant et al. 2005). Moreover, other lines of evidence highlight the contribution EPFs make in enhancing the reproductive success of certain males at the expense of others. There was a positive relationship between an individual male's success regarding within- and extrapair paternity, suggested also by a positive covariance term between these components of male fitness. Similarly, realized reproductive success was higher for males that achieved EPFs than in males that did not and was positively related to the number of extrapair mates.

There are several explanations that may account for high variance in male fertilization success in rosefinches. If, for example, high-quality males successful in EPFs were those that started to breed earlier than the rest of males, those males may not have to trade-off pursuing extrapair copulations against investments to protect within-pair paternity (Birkhead and Møller 1992). However, in this study, no systematic difference in the timing of breeding or breeding synchrony was found between males that lost paternity and those that sired EPY in their nests. Moreover, neither breeding synchrony nor timing of breeding influenced occurrence of EPY in rosefinch nests. It is possible that too few nests in our sample were asynchronous for any intraspecific effects of breeding synchrony to be detectable. Whether breeding synchrony affects extrapair paternity remains an area of debate (Westneat and Stewart 2003). Consistent with other within-species studies, we failed to detect any significant effects, either positive or negative, of breeding synchrony on extrapair paternity (reviewed in Griffith et al. 2002; see also Møller and Ninni 1998). Territoriality is another factor that may limit access of high-quality males to extrapair females, as well as sampling among an adequate number of males by females (Webster et al. 2001). However, indeed, we found that even males up to 920 m away could sire EPY. This indicates that choice of extrapair mates may not be restricted to a local spatial scale (closest

neighbors) in rosefinches, a finding reported in other songbirds (e.g., Reyer et al. 1997; Westneat and Mays 2005; Woolfenden et al. 2005; Kleven et al. 2006).

The fact that males that achieve EPFs were not cuckolded themselves could be a result of congruent female preference for a particular male phenotype combined with the willingness of females paired with low-quality males to accept extrapair mates of higher quality. It has been argued that high rates of extrapair paternity in long-distance migrants, such as rosefinches, indicate that females in these species accept an extrapair male to offset their hasty or inappropriate choice of social mates (e.g., Weatherhead and Yezerinac 1998; Spottiswoode and Møller 2004). Females may be less “choosy” during social pairing if any delay in breeding incurs fitness costs to them (Westneat et al. 1990), and these costs of delay can be expected high in long-distance migratory species. Whether this explanation applies to rosefinches remains unclear. However, in line with this “compensatory” hypothesis, social pairing in rosefinches seems to be random with respect to morphological and plumage characters of males, possibly as a result of time constraints that appear to limit female choice (Björklund 1990). To date, however, no data are available on extrapair mating preferences. Monopolization of EPFs by certain males could also be a result of male–male competition and male pursuit tactics (Westneat and Stewart 2003).

Using comparative methods, we tested the prediction that patterns of contribution of EPFs to the opportunity for sexual selection in rosefinches can be explained by explicit hypotheses related to migration. Although effects of migration on rates of EPFs and/or the level of sperm competition in birds have been already evaluated (e.g., Spottiswoode and Møller 2004; Pitcher et al. 2005), our analysis extends previous studies by focusing on variance in fertilization success among males due to EPFs. We found that the potential role of EPFs in sexual selection is higher in species with short breeding seasons than in species with a prolonged breeding season where high-quality males could increase their number of annual progeny by multiple breeding with high-quality females (e.g., Hill 1994). However, a more detailed analysis reveals that migration may be a confounding factor in this relationship. In fact, breeding season length lost its effect when migration was added to the model. This suggests, all else being equal, that EPFs contribute more to variance in male reproductive success and thus result in a greater opportunity for selection in migratory species compared with sedentary species. This result is consistent with the finding that migratory species tend to exhibit more sexual dichromatism (Fitzpatrick 1994, 1998).

Migration can covary with breeding synchrony (e.g., Spottiswoode and Møller 2004; Pitcher et al. 2005). Although breeding synchrony seemed to have no effect on the fertilization success of rosefinch males, it was an important predictor of variance in male success due to EPFs in the interspecific comparison. Such a discrepancy between the results of intra- and interspecific analyses seems to be relatively common in evolutionary ecology (e.g., Martin et al. 2001) and was also reported for the effect of breeding synchrony on rates of EPFs in socially monogamous passerines (slight negative intraspecific effect, Møller and Ninni 1998 vs. positive interspecific trend, Stutchbury 1998b). Here we demonstrate a positive interspecific effect, independent of migration, of breeding synchrony on variance in fertilization success among males. These results are in line with the prediction that synchrony allows females to compare potential extrapair males that are competing and displaying for EPFs at the same time (Stutchbury and Morton 1995) and simultaneously provides high-quality males more EPF opportunities. However, data seem to support the idea that the effect of migration is direct and independent of breeding synchrony, as breeding syn-

chrony did not significantly changed a positive relationship between migration and I_s/I_{sapp} ratio at least under one (gradual) mode of evolution.

A set of non-mutually exclusive hypotheses has already been invoked to explain the direct effects of migration on rates of EPFs in birds (Spottiswoode and Møller 2004), all of them also applicable to the relationship between opportunity for sexual selection due to EPFs and migration demonstrated in our study. Unfortunately, most are difficult to distinguish using comparative methods. For example, the above-mentioned “compensatory” hypothesis as well as “higher variance in male quality in migrants” hypothesis (Fitzpatrick 1994) would lead to the same relationship between I_s/I_{sapp} ratio and migration, despite evolutionary mechanisms being different. The latter would attribute either higher fertilization success of certain males to their superior genetic and phenotypic qualities (that could involve, e.g., quality of ejaculate and the ability to gain EPFs in competition with other males) or higher attractiveness of certain males to all females in a population and greater benefits from EPFs to females. It specifically demands that migration generates additive variation in genetic quality among individuals, a prediction that has biological relevance (Fitzpatrick 1994, 1998). However, whether long-distance migration in birds is associated with higher genetic variability deserves further investigation.

Using a large set of species from several geographic regions, Pitcher et al. (2005) found that strength of sperm competition, as measured by relative testes size, is related to social mating system and breeding density rather than to migration in birds. However, these authors treated migration as a 2-level categorical variable used also as an index of breeding synchrony. We demonstrate that EPFs have the potential to increase the opportunity for sexual selection particularly in long-distance migratory songbirds such as rosefinches, and analyses should distinguish between sedentary species, short-distance, and long-distance migrants. Moreover, our data indicate that migration and breeding synchrony could promote sexual selection via EPFs through independent pathways, at least in passerine species from the north temperate zone. Our findings agree with the prediction that at a given latitude and implicit level of seasonality, long-distance migration and high breeding synchrony could be associated with increased strength of sexual selection through extrapair paternity.

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