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Extrapair paternity and the evolution of bird song

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Bird song is usually considered to have evolved in the context of sexual selection. Because extrapair paternity is a major component of sexual selection, mating advantages at the social level for males that produce songs of high quality may be transformed into higher success in extrapair paternity. Therefore, males with longer and more complex songs should suffer less from extrapair paternity intraspecifically, whereas species with high rates of extrapair paternity, reflecting intense sperm competition, should produce more elaborate songs. Although some intraspecific studies demonstrated a negative link between features of songs and extrapair paternity in own nest, others failed to detect such a relationship. Contrary to expectation, a meta-analysis of all studies revealed no significant intraspecific evidence for songs being associated with extrapair paternity. In addition, in comparative analyses based on generalized least squares (GLS) models, we found that no measures of song complexity and temporal output were significantly related to extrapair paternity interspecifically, even when potentially confounding factors such as social mating system, life history, migration, habitat, or sexual dichromatism were held constant. Only plumage dichromatism was significantly related to extrapair paternity. The absence of both intra- and interspecific relationships between measures of song variability and extrapair paternity suggests that factors other than postmating sexual selection have been the important evolutionary forces shaping differences in song. *Key words:* bird song, evolution, extrapair paternity, generalized least squares, meta-analysis, repertoire size, sexual selection. *[Behav Ecol 15:508–519 (2004)]*

Sexual selection has been assumed to maintain extravagant song displays in birds, because bird song is used in both male-male competition and female choice (for reviews, see Catchpole and Slater, 1995; Searcy and Nowicki, 2000; Searcy and Yasukawa, 1986). A number of field and laboratory experiments demonstrated that males producing songs of high quality are more successful in deterring male competitors and attracting females. Comparative data also favor the hypothesis that songs are sexually selected. Interspecific variation in temporal organization and complexity of bird song has been associated with polygynous mating systems in which sexual selection is presumed to be more intense than that under social monogamy (Kroodsma, 1977; Payne, 1983; Read and Weary, 1992; but see also Catchpole, 1980, 1982; Catchpole and McGregor, 1985; Irwin, 1990; Shutler and Weatherhead, 1990). Migratory behavior is associated with measures of song complexity, which may be the result of intense competition for territories owing to time constraints in migratory species when arriving to the breeding grounds. Recent comparative studies of song repertoires revealed that an important function of song complexity is to signal male health, determining roles in sexual selection (Garamszegi et al., 2003; Møller et al., 2000).

Sexual selection occurs commonly at the level of sperm competition (Birkhead and Møller, 1998). Song has been hypothesized to be associated with avian sperm competition and thus to be a determinant of extrapair paternity (Møller, 1991). Attributes of song that reliably indicate the phenotypic quality of males, and thus their ability to defend their mates, may function as a paternity guard. Neighboring females are also hypothesized to respond to features of song displays, if they become reliable quality indicators. Therefore, males displaying elaborate songs in terms of complexity and temporal organization may be expected to enjoy advantages in sperm competition. This should result in negative intraspecific associations between the number of extrapaired offspring within the own nest and measures of song complexity, such as versatility, song, and syllable repertoire size, and measures of song output, such as song duration, song continuity, and song rate. These mechanisms acting within species could have evolutionary consequences that are reflected by patterns observed among species. Female choice requires a male phenotypic variance that allows discrimination among potential mates, and this usually leads to directional selection (Møller and Pomiankowski, 1993). Hence, interspecifically, song features should be positively related to the rate of extrapair paternity, because selection pressures arising from intense sperm competition may favor the evolution of sexually selected characters reflecting male quality.

Despite these obvious mechanisms, our view of the role of extrapair paternity in the evolution of avian vocal signals remains unclear owing to intraspecific studies that provide inconsistent results. Male great reed warblers, *Acrocephalus arundinaceus*, with a large song repertoire suffered less from extrapair paternity in their own broods and sired a larger number of extrapair offspring than did males with small repertoires (Hasselquist et al., 1996; Leisler et al., 2000). In contrast, there was no relationship between male repertoire size, song-flighting, and extrapair paternity in the closely related sedge warbler, *Acrocephalus schoenobaenus* (Buchanan and Catchpole, 2000). Female zebra finches, *Taenopygia guttata*, actively solicited and performed extrapair copulations with more attractive males having higher song rates (Houtman, 1992). In the serin, *Serinus serinus*, female, copulatory behavior was not significantly affected by song performance of the mate (Mota, 1999). Bluethroat, *Luscinia svecica*, males with extrapair offspring in their nest did not differ from those with full paternity with respect to song activity and song flight

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Table 1

Studies involved in the meta-analysis to investigate the intrasepcific relationship between extrapair paternity and song features in birds based on Cohen's d effect size (Cohen, 1988)

Species	Variable	*N*	*d*	Reference
Acrocephalus arundinaceus	repertoire size	20	1.174	Hasselquist et al., 1996
	repertoire size	4	0.656	Leisler et al., 2000
Acrocephalus schoenobaenus	repertoire size	19	0.758	Buchanan and Catchpole, 2000
	song flight	20	0.806	Buchanan and Catchpole, 2000
Ficedula albicollis	strophe length	16	−0.393	Garamszegi LZ, unpublished data
	song rate	16	−2.047	Garamszegi et al., 2003b
	repertoire size	16	−0.316	Garamszegi LZ, unpublished data
Hirundo rustica	song rate	26	1.397	Møller et al., 1998
	repertoire size	27	−0.308	Saino N, unpublished data
	song length	24	−0.039	Saino N, unpublished data
	no. of syllables	24	0.078	Saino N, unpublished data
	peak amplitude	24	−0.186	Saino N, unpublished data
	rattle impulse	24	−0.199	Saino N, unpublished data
Luscinia svecica	song rate	8	0.127	Krokene et al., 1996
	song flight	8	−0.396	Krokene et al., 1996
Melospiza melodia	repertoire size	28	0.246	Hill CE, unpublished data
	song sharing	28	−0.087	Hill CE, unpublished data
Parus caeruleus	intersong interval	25	0.063	Kempenaers et al., 1997
	strophe length	25	1.404	Kempenaers et al., 1997
Phylloscopus fuscatus	amplitude	7	3.208	Forstmeier et al., 2002
	repertoire size	7	−0.306	Forstmeier et al., 2002

(Krokene et al., 1996). A comparison between extrapair and within-pair male blue tits, *Parus caeruleus*, showed that extrapair males, on average, sang longer strophes during the dawn chorus (Kempenaers et al., 1997). A study of barn swallows, *Hirundo rustica*, found that the proportion of extrapair offspring was negatively related to song rate independently of the effect of the size of a morphological secondary sexual character (Møller et al., 1998), but other song traits were not significantly related to paternity (Saino, Taramino, Galeotti, and Ferrario, unpublished data). An analysis of extrapair paternity in the dusky warbler, *Phylloscopus fuscatus*, revealed that females choose copulation partners on the basis of the quality but not of the quantity of song (Forstmeier et al., 2002). In the collared flycatcher, *Ficedula albicollis*, in which pathogen resistant males signaled health status with their song rate, resistant males tended to suffer from a higher rate of extrapair paternity in their own nests than did the average male (Garamszegi et al., 2004). In addition to this mixture of positive and negative evidence, the extent to which interspecific variation in extrapair paternity among birds is associated with features of bird song remains completely unknown. Given that polygyny explains very little of the interspecific variation in song features among birds (Read and Weary, 1992), it seems likely that unidentified general explanations have been overlooked.

The objective of the present study was to determine whether variation in extrapair paternity was associated with features of bird song both within and among species. First, we used a meta-analytic approach to assess intraspecifically the effect of songs on extrapair paternity in own nests. A recent meta-analysis showed that males with more extravagant secondary sexual characters had higher paternity in their own broods than did less adorned males (Møller and Ninni, 1998). Thus, we expected a similar relationship for different features of song subject to female preference. Second, in comparative analyses of passerines, we analyzed the interspecific relationship between extrapair paternity and song output, as well as song complexity after controlling for similarity owing to common descent and potentially confounding factors. We predicted that species with common extrapair paternity have more elaborate songs, as reflected by measures of song complexity and output. This prediction is based on the suggestion of studies on sexual dichromatism that indicated a role of sexual characters in sperm competition (Bennett and Owens, 2002; Møller and Birkhead, 1994). As a contrasts analysis, we also characterized the correlated evolution of extrapair paternity and sexual dichromatism.

METHODS

Meta-analysis

Meta-analytical techniques offer quantitative and objective methods to summarize a body of research by examining the magnitude and the generality of a predicted relationship, while taking sample size into account (Hedges and Olkin, 1985). The purpose of our meta-analysis was to obtain estimates of true effect sizes for the intraspecific relationship between extrapair paternity and song features in birds. We collected published and, in an effort to control for publication bias, unpublished results of studies investigating the association between songs and extrapair paternity within species. We included analyses from *t* tests (two-tailed), or other equivalent statistics testing the null hypothesis that males with more extravagant song display (measured as repertoire size, song rate, song length, and performance characteristics) have similar paternity in their own nests than do males with less extravagant song features. For these tests we calculated Cohen's *d* effect size (Cohen, 1988) and tested for the overall effect being significantly different from zero. We performed this analysis for the entire data and also for different subsets, testing for the effect of specific song features. We used random effects models. The list of studies used in the meta-analysis and the calculated effect sizes are given in Table 1.

Comparative analysis

The data set

The data set consisted of 65 bird species with quantitative information on extrapair paternity and song. We have used the relative frequency of extrapair offspring for a particular species as a measure of extrapair paternity, defined as the number of extrapair offspring divided by the total number of offspring. Extrapair paternity was determined by protein gel electrophoresis (only estimates corrected for probability of detection), DNA fingerprinting, and other DNA techniques. The present data set contains data until April 2002. For those species in which multiple estimates of extrapair paternity were available, analyses of repeatability showed consistently greater variance among than within species (Møller and Birkhead, 1994; Møller and Cuervo, 2000; Owens and Hartley, 1998; Petrie et al., 1998). We have redone the repeatability analysis for the currently available data, strengthening the previous findings ($F = 4.841$, df = 40,177, $p < .001$, $R = .583$). Therefore, we assumed that despite considerable intraspecific variation, the level of extrapair paternity can be considered a species-specific characteristic, which can be reliably estimated. Consequently, if more than one estimate was available for a species, we used the weighted-mean estimate in the analyses based on the particular sample sizes. Because island populations have a lower frequency of extrapair paternity than do mainland populations (Griffith 2000; Møller, 2001), perhaps owing to a reduced level of genetic variability (Frankham, 1997), we omitted data from islands, because information on song was generally absent from such populations. In experimental studies, only data for unmanipulated control treatments were considered. For cooperatively breeding birds, in which there is more than one social male, we classified an extrapair young as being the one that was fathered by a male outside the social group.

We used a number of variables to represent song output and song complexity following the definitions of Read and Weary (1992). First, song output was measured as (1) song duration (A, in seconds); (2) intersong interval (B, in seconds); (3) continuity ([A] / [A + B]); and (4) song rate (60 / [A + B]). Second, song complexity was measured as (1) song repertoire size (the mean number of different song types possessed by an individual, which represents a measure of between-song complexity), (2) syllable repertoire size (the mean number of different syllable types within a song, which represents a measure of within-song complexity), and (3) versatility scored as versatile (a score of two) if song types were rapidly switched, eventually versatile (a score of one) if song types were repeated several times before switching, or nonversatile (a score of zero) if a single song type was repeated continuously through a song bout. A song repertoire size scored as infinity by Read and Weary (1992) and MacDougall-Shackleton (1997) was assigned an arbitrary value of 1000. The results of the comparative analyses do not change if an infinite song repertoire size instead was set to 300 or 500 (see Appendix B). Versatility was treated as continuous, as done by Read and Weary (1992), because intermediate states are biologically meaningful. See Table 2 for sources of information on song variables. The proportion of extrapair paternity and song continuity were square-root arcsine-transformed, and song duration, intersong interval, song rate, song repertoire size, and syllable repertoire size were $\log_{10}$-transformed before analyses.

Table 2

Results of GLS analyses of the relationship between song variables and extrapair paternity in birds

Extrapair paternity	κ	λ	Correlation	*p*	*N*
Song duration	0.267	0.678	−0.024	0.858	57
Intersong interval	0.000	0.000	0.101	0.533	38
Continuity	0.000	0.495	−0.014	0.929	38
Song rate	0.030	0.261	0.078	0.631	38
Song repertoire size	0.063	0.731	−0.067	0.611	58
Syllable repertoire size	0.108	0.000	−0.226	0.090	55
Versatility	0.092	0.553	−0.219	0.077	64

First, the contribution of scaling parameters was assessed by estimating the maximum-likelihood values of the branch length scaling parameters κ, and the phylogeny scaling factor λ. If a significant effect was found ($p < .05$, underlined), the estimated values were used in the final model, otherwise default (= 1) settings were used. Second, using the appropriate scaling parameters the partial correlation between pairs of traits (extrapair paternity and a song trait) was tested by log-likelihood ratio statistics comparing model H_0 that fits the data forcing the correlation to be zero with the alternative H_1 model, permitting correlated evolution of the two characters. The correlation estimated by H_1 is given. *p* values indicate the significance of the log-likelihood ratio test. Information on song variables originated from Cabe (1993), Catchpole (1980), Catchpole and Leisler (1989), Cramp (1985–1994), Cramp and Perrins (1993–1994), Eens et al. (1991), Eriksson (1991), Galeotti et al. (1997), Garamszegi et al. (2002), Gelter (1987), Glutz von Blotzheim (1985–1997), Langmore and Mulder (1992), Lowther and Cink (1992), MacDougall-Shackleton (1997), Møller et al. (2000), Poole and Gill (1992–1998), Read and Weary (1992), Robertson et al. (1992), Shutler and Weatherhead (1990), Smith (1993), Wiley and Wiley (1977), and R. Zann (unpublished data). Sources for extrapair paternity are given in Appendix A.

Before starting our analyses, we addressed the possibility of biases in the current data base. The comparability problem is a well-known difficulty met in studies of bird song that investigate interspecific patterns (Krebs and Kroodsma, 1980; MacDougall-Shackleton, 1997). This problem arises when measures of song variability in different species are not estimates of the same phenomenon. Investigators usually assume that repertoire size, as a measure of song complexity, in one species can be compared with repertoire size in another species (Gil and Gahr, 2002), although this is an untested assumption. We examined the correlation between different measures of song complexity, because we predicted positive relationships between variables that are designated to reflect song complexity if data are unbiased. By using data from Read and Weary (1992), we found significant associations among variables of song complexity (Pearson correlations: song repertoire size and syllable repertoire size $r = .494$; $N = 113$; $p < .001$; song repertoire size and song versatility $r = .608$; $N = 101$; $p < .001$; syllable repertoire size and song versatility $r = .288$; $N = 101$; $p = .004$, Table 3). An alternative measure for syllable repertoire size that is estimated by using sonagrams reported in handbooks (see details in Garamszegi et al., 2003) was also significantly related to that of Read and Weary's (1992) measure (Pearson correlation: $r = .438$; $N = 93$; $p < .001$). For a subset of birds for which multiple independent estimations for song repertoire size were available, we calculated repeatability that was very high ($F = 26.140$, df = 22,52, $p < .001$, $R = .917$). Based on this evidence, throughout the article we assume that song complexity variables can be reliably and repeatably estimated. Griffith et al. (2002) stressed that published extrapair paternity data are extremely heterogeneous in terms of sampling scheme, statistical methodology, and the type of population studied. The investigators suggested that comparative studies of extrapair paternity should make distinctions between different sorts of studies instead of lumping all available data irrespective of the source. Griffith et al. (2002) attempted to collate an unambiguous database of extrapair paternity estimates by following strict inclusion criteria. We found a very strong correlation between the estimates of extrapair paternity presented in Griffith et al. (2002) and in the present study (Pearson correlation: $r = .997$; $N = 49$; $p <$

Table 3

The relationship between extrapair paternity and sexual dichromatism in birds

Scaling parameters	κ = 0.097	λ = 0.542
Log-likelihood	model with zero covariance	−89.799
	model with nonzero covariance	−86.660
LR test	LR: 3.139, df = 1, $p = .012$	
Correlation	0.303	
Covariance	0.012	
Variance	extrapair paternity:	0.0073
	sexual dichromatism:	0.1975
Ancestral states (α)	extrapair paternity:	20.26%
	sexual dichromatism:	0.735

The results of an analysis by GLS models ($N = 65$ species). The maximum-likelihood values for κ and λ scaling parameters were estimated before testing assumptions.

.001). Furthermore, when we reinvestigated the relationships that are the focus of this study by using data from Griffith et al. (2002), our findings and conclusions remained the same (see Appendix B). Therefore, we present the results based on our estimates given in Appendix A.

A number of confounding factors may influence the evolution of bird song (Read and Weary, 1992). Males of polygynous species have been reported to have low song rates and large syllable repertoire sizes (Read and Weary, 1992). Species were classified as having either (1) no polygyny (a score of zero), (2) irregular polygyny (species with less than 5% of males attracting more than one female were given a score of one), or (3) regular polygyny (species with more than 5% of males attracting more than one female were given a score of two; mainly using Cramp, 1985–1994; Cramp and Perrins, 1993–1994; Møller, 1986; Poole and Gill, 1992–2001).

Species inhabiting open grassland habitats have been reported to have lower song rates and song versatility than do species of forested habitats (Read and Weary, 1992), because of different sound transmission properties in these two kinds of habitats (Ryan and Brenowitz, 1985; Wiley, 1991; Wiley and Richards, 1978). Species were classified as inhabiting open (score of zero) or forested habitats (score of one). Forested habitats were those with forest and woodland, or scrub, if habitat descriptions suggested that the preferred scrub was in forests or woodlands, with open habitats as the remainder. Species inhabiting both kinds of habitats were categorized as living in open habitats if they spend the majority of their time there. Information originates from Ehrlich et al. (1988), Harrison (1975, 1978), Heinzel et al. (1974) and National Geographic Society (1987).

Migratory species have been reported to have large song repertoires and large syllable repertoires (Read and Weary, 1992). Migratory behavior was scored on a three point scale as (1) resident (a score of zero), (2) partial migrant (species having resident and migratory populations; a score of one), or (3) migrant (a score of two). Information originates from Ehrlich et al. (1988), Harrison (1975, 1978), Heinzel et al. (1974) and National Geographic Society (1987). The polygyny, migration, and habitat variables were treated as continuous variables in the comparative analyses. This procedure also makes intuitive sense because intermediate states of these variables are biologically meaningful.

Extrapair paternity has been reported to be strongly positively associated with sexual dichromatism (Bennett and Owens, 2002; Møller and Birkhead, 1994). Two observers, unaware of the hypotheses under test, independently scored differences in plumage coloration between males and females on a scale ranging from zero to five (zero for monochromatic species, five for species with very dull females and very striking males). Sexual dichromatism was scored simply with respect to all forms of coloration. See Møller and Birkhead (1994) and Bennett and Owens (2002) for further details.

Arnold and Owens (2002) have shown that a large amount of the interspecific variation in extrapair paternity is owing to ancient divergence in life history. From their study we extracted data for adult mortality, annual fecundity, clutch size, and male contribution to parental care to control for these life-history traits in our analysis. However, data for adult mortality were limited, restricting the power of multivariate tests. In our data set on song and extrapair paternity, we found information on mortality for 19 species. Because, in our sample there was no significant correlation between adult mortality and extrapair paternity (Pearson correlation: $r = -.086$; $N = 32$; $p = .641$), to achieve larger sample size in the multivariate tests we excluded this variable from our analysis. Following the scoring criteria used by Arnold and Owens (2002), we collected additional information on annual fecundity, clutch size, and male contribution to parental care from Cramp and Perrins (1993–1994) and Poole and Gill (1992–2001). The entire data set is given in Appendix A.

Phylogenetic information

The phylogenetic information for the comparative analyses originated from a number of sources that estimated phylogenetic relationships by using molecular techniques. We used Sibley and Ahlquist (1990) as a basic source of information. For several taxa we obtained additional data: Hirundinidae (Winkler and Sheldon, 1993), Sylvidae (Leisler et al., 1997), Paridae (Sheldon et al., 1992), Emberizidae (Grapputo et al., 2001), and references from Møller and Cuervo (2000). We resolved the phylogeny with complete bifurcation, and excluded species with information on song and extrapair paternity with uncertain phylogenetic positions (mainly Parulidae), instead of using several alternative phylogenies. We applied branch lengths from the tapestry tree of Sibley and Ahlquist (1990) for higher taxonomic levels. Within families, the distance between different genera was set to 3.4 $\mathrm{D}T_{50}H$ units, and we used 1.1 $\mathrm{D}T_{50}H$ units between species within genera (see also Bennett and Owens, 2002; and Sibley and Ahlquist, 1990). The entire phylogeny is given in Figure 1.

The comparative method

We applied the general method of comparative analysis for continuous variables based on generalized least squares (GLS) models by using the statistical software Continuous (Pagel, 1997, 1999). This model offers hypothesis testing unavailable in earlier phylogenetic approaches, and simultaneously avoids difficulties of those methods. The GLS approach controls for similarity owing to common descent and allows investigation of correlated evolution between pairs of characters, estimates ancestral states, examines random-walk versus directional change models, assesses the tempo and mode of trait evolution, and also estimates the importance of phylogenetic corrections. In addition, it is possible to obtain information about the temporal order of changes. Hence, this approach may be ideal to investigate the potential relationship between extrapair paternity and song features while obtaining information on the mode of trait evolution. The GLS model characterizes evolutionary changes along each branch of a phylogenetic tree through the variance components of traits (Martins and Hansen, 1997; Pagel, 1997). Hypotheses are tested with likelihood ratio statistics. This compares the log-likelihood of the model corresponding to a null hypothesis

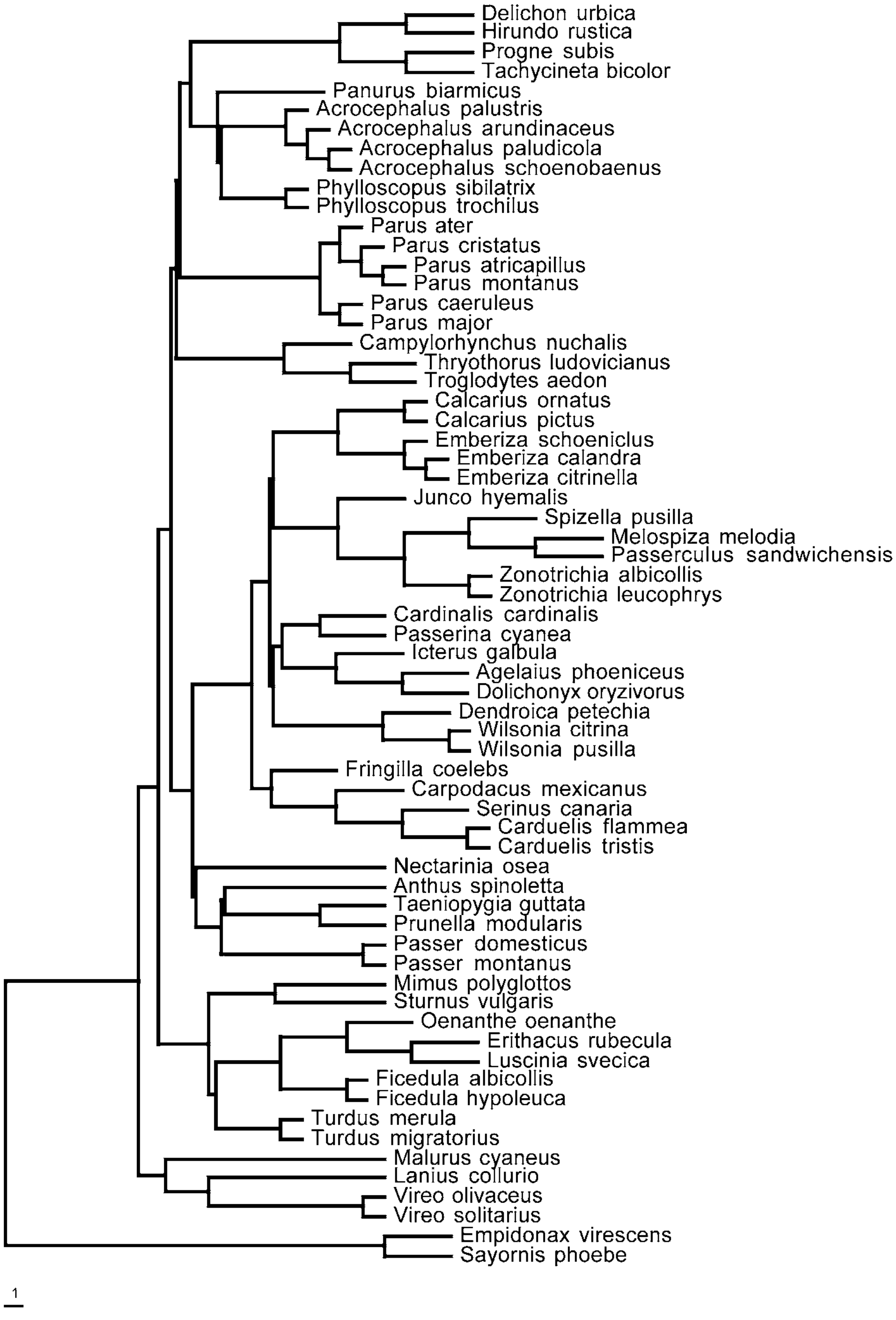

Figure 1
Phylogeny of passerine birds used for the comparative analyses of song variables. The scale for branch lengths is given in the bottom left corner. For sources, see Methods.

(H_0) over the model for an alternative hypothesis (H_1), where the likelihood ratio $= -2\ \log_e[H_0\ /\ H_1]$. The likelihood ratio statistic is asymptotically distributed as a chi-square variate with degrees of freedom equal to the difference in the number of parameters between the two models. Models contain three scaling parameters that can be used to scale branch lengths in the tree (κ), scale total (root to tip) path in the tree (δ), and assess the contribution of phylogeny (λ). The κ parameter by differentially stretching long and short branches would yield a punctuational mode of trait evolution as $\kappa = 0$, whereas $\kappa \geq 1$ indicates the importance of long branches in trait evolution (gradualism). By scaling the overall path lengths in the phylogeny, parameter δ would detect early and rapid evolution as $\delta < 1$, whereas $\delta > 1$ would be the signature of accelerating evolution (contribution of longer paths). Recent simulations showed that the estimation of δ is biased (Freckleton et al., 2002), thus we avoided estimating this parameter. Values of $\lambda < 1$ would correspond to traits being less similar amongst species than expected from their phylogenetic relationship, whereas $\lambda = 1$ suggests the reverse. Any of these potential effects present in the data can be detected by comparing the log-likelihood of a H_0 model containing default ($= 1$) values for the scaling parameters with the log-likelihood of an alternative H_1 model in which one parameter is permitted to take its maximum-likelihood value. Once an appropriate model with adjusted scaling parameters has been selected, it can be used to study correlated evolution by comparing the goodness of fit of model H_0 fitting to the data by allowing only independent evolution with that alternative H_1 model that permits correlated evolution of the two characters. The best model can be used to estimate ancestral states, variance parameters

Table 4

Pairwise correlations among song traits by GLS models

	κ	λ	Correlation	p	N
Song duration					
Intersong interval	0.309	0.817	−0.019	0.909	38
Song repertoire size	0.738	0.935	0.195	0.151	53
Syllable repertoire size	0.230	0.679	0.289	0.039	49
Versatility	0.741	0.922	0.015	0.912	57
Intersong interval					
Song repertoire size	0.122	0.676	−0.489	0.001	38
Syllable repertoire size	0.065	0.000	−0.337	0.035	37
Versatility	0.078	0.374	−0.243	0.128	38
Song repertoire size					
Syllable repertoire size	0.495	0.764	0.468	<0.001	50
Versatility	0.402	0.846	0.380	0.003	57
Syllable repertoire size					
Versatility	0.397	0.574	0.144	0.282	55

Scaling parameters (κ and l) and phylogenetic correlations were derived as in Table 1. A model including all song variables also revealed significant evidence for correlated trait evolution ($\kappa = 0.132$, $\lambda = 0.515$; log-likelihood ratio statistics: model with zero covariance versus model with nonzero covariance, LR = 18.082, df = 10, $p < .001$).

for each trait, and also the correlation and covariance between traits.

RESULTS

Meta-analysis

There was no significant intraspecific evidence for within own brood extrapair paternity being related to song. When we included all studies, the mean effect size was 0.245 (SE = 0.195; $t = 1.258$, $p = .209$ $N = 396$). Similarly, no significant effect was found when we investigated the effects of specific song traits, such as song complexity (repertoire size: mean effect = 0.277 [SE = 0.239]; $t = 1.163$, $p = .247$, $N = 121$), temporal organization (song length, intersong interval: mean effect = 0.288 [SE = 0.400]; $t = 0.719$, $p = .474$, $N = 90$), and song performance (song rate, song flight, amplitude, rattle impulse: mean effect = 0.303 [SE = 0.476]; $t = 0.637$, $p = .525$, $N = 133$).

Comparative analysis

Song, extrapair paternity, and sexual dichromatism

Applying the GLS approach, all song variables were unrelated to extrapair paternity across species (Table 2). The scaling parameters in the models showed that traits follow punctuational evolution ($\kappa < 0.267$ in Table 2, LR test of $\kappa = 0$ to $\kappa = 0.267 : 0.699$, df = 1, $p = .237$), and that phylogenetic history has minimal effects ($\lambda < 1$ in all cases) (Table 2).

Because sexual dichromatism has previously been reported to be associated with extrapair paternity, we characterized the correlated evolution of these traits by GLS approach as a contrast for the song analysis above (Table 3). In this analysis we found that contrary to song features, sexual dichromatism was significantly and positively related to extrapair paternity. There was no significant interspecific relationship between song characteristics and sexual dichromatism (phylogenetic correlations: $-.138 < r < .093$, all $p > .264$).

Potentially confounding factors

We investigated the correlated evolution of independent song traits (thus excluding derived variables such as continuity and song rate). After identifying the suitable scaling parameters, we found significant evidence for correlated evolution of song features (Table 4). Because song variables were interrelated (see also Methods) and, in addition, sexual dichromatism, life history, migration, habitat type and polygyny may have confounding effects, we intended to test our hypotheses by a multiple regression approach to control for these potential biases. Previously, we detected that phylogeny explained minimal covariance among species on traits considered ($\lambda < 1$). Hence, we performed a stepwise multiple regression analysis by using the raw species data with extrapair paternity as the dependent variable, and song traits and potentially confounding variables as independent variables. In the best model, only sexual dichromatism was significantly associated to extrapair paternity ($F = 2.769$, df = 5, 51, $r^2 = .214$, $p = .027$; sexual dichromatism, slope: 0.046 [SE = 0.023], $p = .049$; fecundity, slope: −0.016 [SE = 0.008], $p = .060$; clutch size, slope: −0.018 [SE = 0.018], $p = .313$; song duration, slope: −0.042 [SE = 0.048], $p = .382$; habitat, slope: −0.014 [SE = 0.049], $p = .781$). When we repeated this analysis with phylogenetically independent contrasts (thus assuming $\lambda = 1$) calculated by CAIC (Purvis and Rambaut, 1995), the results remained unchanged (see Appendix B).

DISCUSSION

Variation in song output and complexity was hypothesized to be related to extrapair paternity both within and among birds. Interestingly, meta-analytic and comparative tests of this hypothesis revealed that no feature of song was significantly related to extrapair paternity. Although some studies demonstrated that males with elaborate songs may experience an advantage in extrapair paternity (see Introduction), our findings at the intraspecific level show that this cannot be a general phenomenon. Our interspecific results are inconsistent with a previous comparative study of bird song, which suggested that greater song complexity was associated with sexual selection (Read and Weary, 1992).

Studies providing evidence of a correlation between extrapair paternity and male coloration among and within species suggested that extrapair paternity is associated with the expression of sexually selected characters (see Bennett and Owens, 2002; Johnsen et al., 1998; Møller, 1997; Møller and Birkhead, 1994; Møller and Ninni, 1998; Owens and Hartley, 1998; Yezerinac and Weatherhead, 1997; but see also Hill et al., 1994; Rätti et al., 1995). An evolutionary relationship between sexual signals and extrapair paternity could be interpreted in two different ways: (1) extrapair paternity may have given rise to evolutionary modifications of male traits, or (2) female choice based on male displays may have resulted in a change in the rate of extrapair paternity (Møller, 1997). Although it is difficult to disentangle the causal links based on correlative evidences, these mechanisms link sperm competition directly to sexual selection. In accordance with sexual selection theory, we found that sexual dichromatism was significantly and positively related to extrapair paternity among species but, obviously, based on our negative results, this relationship does not hold for songs.

Bird song has been repeatedly shown to be associated with sexual selection in intra- and interspecific studies of birds (see Introduction). Mating advantages for males that produce songs of superior quality indicate that song features, which give rise to differences in mating success, may be transformed into differences in mating success as reflected by extrapair paternity. This suggests that there should be a relationship between song traits and extrapair paternity, a pattern that we failed to detect.

We assume that our results are of biological relevance, and the lack of correlation is not owing to methodological problems. Our repeatability and reliability analyses of song variables and extrapair paternity (Table 4, Methods) showed that the investigated traits are comparable among species. In addition, when we controlled statistically for several potentially confounding factors, the results remained unchanged. It might be possible that the relevant song variable that is under direct selection was not measured. For example, Forstmeier et al. (2002) suggested that sound amplitude reflecting individual physiological limitations can be a determinant of extrapair paternity decisions. However, if similarly constrained song traits are interrelated (Methods), we predict that selection arising from extrapair paternity will similarly affect them. Hence, song performance traits such as song rate or sound amplitude may be expected to relate to extrapair paternity among species with comparable exponents. Moreover, a list of intra- and interspecific evidence indicates that the measured song traits are sexually selected.

Why should extrapair paternity not be associated with interspecific variation in bird song—a trait that is extremely variable—when such a relationship occurs for visual signals? There are at least five reasons for no consistent association between song features and extrapair paternity. First, intense directional sexual selection on song features may have resulted in exaggeration of bird song, but simultaneously depleted genetic variance in male viability or attractiveness. Female choice of extrapair males for genetic reasons may thus be unimportant. This explanation seems unlikely because the same song features are important in precopulation sexual selection in several species (see Introduction). Second, several direct and indirect benefits may accrue to females from their choice of multiple copulation partners without requiring preferences for traits indicating the quality of males (e.g., higher probability of fertilization; for review, see Birkhead and Møller, 1998). This view can be rejected because evidence shows associations between extrapair paternity and plumage coloration, indicating the importance of signaling mechanisms in sperm competition. Third, females may adopt threshold criteria for their choice of mates, and all males with the most elaborate songs may exceed this minimum threshold. Females may not choose males with superior sexual displays but rather avoid males with inferior displays, such as males with deleterious mutations. Again, this explanation seems unlikely, because song features are important for precopulation sexual selection. Fourth, males of species with intense competition may apply alternative strategies (such as frequent copulation or mate guarding) to increase their paternity instead of singing. In these cases, females no longer select songs. Nevertheless, it has been suggested that female choice rather than male-male competition plays a major role in determining extrapair paternity in birds (for review, see Møller and Birkhead, 1994). Fifth, different sampling strategies of females in precopulatory and copulatory sexual selection may result in females not using song cues in their choice of extrapair copulation partners. Differences between the interests of females in social and extrapair mate choice imply that different rules may be used when choosing breeding and copulatory partners. In addition, different circumstances (e.g., time constraints on mate sampling) may also determine that different signals used in different contexts. If extrapair copulatory decisions are made quickly, it may be difficult to assess male quality by complex songs in species with intensive sexual selection for song complexity. In some species, the time of singing does not match the fertile period of females when copulations occur (for review, see Gil et al., 1999). Hence, in these cases the choice of extrapair mate should be based on other male traits. However, this cannot be of general importance, as most species do sing, often at high rates, during the fertile period (Møller, 1991).

In conclusion, we found that none of the measures of song complexity and temporal organization of song was significantly associated with extrapair paternity in birds both intra- and interspecifically, although sexual selection arising from extrapair paternity is likely to be closely related to sexual dichromatism. Clearly, the difference that we have observed between song and sexual dichromatism suggests these two forms of sexual character are the results of different selective pressures. The lack of general intraspecific evidence for songs being related to extrapair paternity may indicate that females do not use song cues in their copulatory decisions in the majority of species. However, we need further empirical information on female sampling behavior during extrapair copulations. If the choice of extrapair mates is based upon other male traits, selection arising from extrapair paternity may not favor song traits evolutionary, and this would lead to the absence of interspecific associations.

APPENDIX A

Data on frequency of extrapair paternity (EPP, %), song duration (DUR, s), intersong interval (INT, s), song repertoire size (REP), syllable repertoire size (SYL), versatility (VER), and potentially confounding variables, such as polygyny (PG), habitat (HAB), migration (MIG), sexual dichromatism (DICR), annual fecundity (FEC), clutch size (CLS), and male parental care (MPC) in birds

Species	EPP	DUR	INT	REP	SYL	VER	PG	HAB	MIG	DICR	FEC	CLS	MPC	REF
Acrocephalus arundinaceus	4.02	3.2	2	>100	5	2	2	0	2	0	5	5	2	1, 2
Acrocephalus paludicola	39.10	2.18	—	>100	20	1	2	0	2	0	10	5	0	3, 4
Acrocephalus palustris	3.05	5	0.01	>100	90	1	0	0	2	0	4	4	4	4
Acrocephalus schoenobaenus	7.85	19.5	1.31	>100	7.7	2	1	0	2	0	5	5	2	5, 6
Agelaius phoeniceus	28.27	1.25	14	4	3	1	2	0	1	2	8	4	2	7–9
Anthus spinoletta	5.23	10.64	—	1	—	0	0	0	1	0	12	6	2	10
Calcarius ornatus	17.64	2.25	—	—	7.5	1	0	0	2	2	4	4	2	11
Calcarius pictus	0.90	1.63	—	1	—	1	1	0	2	2	4	4	1	12
Campylorhynchus nuchalis	1.40		—	5	—	1	0	1	0	0	6	3	2	13
Cardinalis cardinalis	13.51	1.8	6.9	9	1	0	0	1	0	2	6	3	2	14
Carduelis flammea	4.55	100	—	16	—	1	0	1	1	1	9	4.5	2	15
Carduelis tristis	14.29	100	—	>100	—	1	0	1	1	2	10	5	4	16
Carpodacus mexicanus	8.40	1.9	4.9	4	1.3	2	0	0	1	2	8	4	2	17
Delichon urbica	17.04	—	—	—	4	0	0	0	2	0	8	4	6	18, 19
Dendroica petechia	31.14	1.3	7.1	12	3.7	2	1	0	2	1	4.5	4.5	2	20, 21
Dolichonyx oryzivorus	14.60	3.5	—	10	—	0	2	0	2	2	5.5	5.5	2	22
Emberiza calandra	4.50	1.6	10.89	2	20	1	2	0	0	0	5	5	2	23
Emberiza citrinella	37.40	2.1	7.01	2.1	3	1	1	0	0	2	8	4	2	24
Emberiza schoeniclus	54.63	1.98	4.02	20	3	1	1	0	1	1	5	5	4	25
Empidonax virescens	30.00	—	—	3	—	—	—	1	2	0	6	3	2	26
Erithacus rubecula	4.00	2.18	3.27	>100	4	2	0	1	1	0	10	5	2	27
Ficedula albicollis	17.44	2.95	18.88	>100	8.4	2	2	1	2	1	6	6	2	28
Ficedula hypoleuca	7.98	2	6.11	>100	9	2	2	1	2	2	6	6	2	29–33
Fringilla coelebs	17.00	2.1	8.09	3	5	1	0	1	1	2	4	4	2	34
Hirundo rustica	28.78	4.01	0.05	>100	19.8	2	1	0	2	1	10	5	4	35–37
Icterus galbula	32.18	1.4	10.59	6.5	10.7	2	2	1	2	3	8	4	4	38
Junco hyemalis	28.34	1.4	4.5	5	1	1	1	1	1	0	6	4	2	39
Lanius collurio	5.26	—	—	—	12	2	0	0	2	1	5	5	2	40
Luscinia svecica	31.37	5	—	—	5	2	1	0	2	2	6	6	2	41, 42
Malurus cyaneus	66.99	2.9	—	1	3	0	0	1	0	4	6	3	2	43
Melospiza melodia	8.80	2.62	6.07	9	5	1	1	0	1	0	12	4	2	44
Mimus polyglottos	8.00	3.06	1.1	190	20	2	1	1	1	0	9	4.5	4	45
Nectarinia osea	26.00	1.6	—	—	—	0	1	1	0	4	5	3	2	46
Oenanthe oenanthe	10.96	—	—	—	18	2	1	0	1	2	12	6	2	47
Panurus biarmicus	14.40	2	—	—	—	0	0	1	1	1	12	6	6	48
Parus ater	25.32	2.1	—	14	2	1	0	1	0	0	9	9	4	49
Parus atricapillus	8.91	—	—	1	2.5	0	0	1	0	0	7	7	4	50
Parus caeruleus	12.03	2.4	4.6	5	2	1	1	1	0	0	0.5	9	4	51–53
Parus cristatus	12.40	3.2	7.1	1	2	0	0	1	0	0	6	6	4	54
Parus major	9.63	3	—	3	2	1	1	1	0	1	11	11	2	52, 55–58
Parus montanus	0.96	1	—	1	1	0	0	1	0	0	8	8	4	59
Passer domesticus	11.74	0.17	—	1	1	0	2	0	0	2	10	5	6	60–65
Passer montanus	9.06	0.11	7.1	1	6	0	0	0	0	0	15	5	6	66
Passerculus sandwichensis	23.10	2.25	6.3	1	5	0	1	0	2	0	5	5	2	67
Passerina cyanea	36.37	2.2	8.59	1	9	0	1	0	2	2	6	3	0	68, 69
Phylloscopus sibilatrix	0.00	3.4	4.6	2	1.5	2	2	1	2	0	6	6	2	70
Phylloscopus trochilus	18.52	3.31	7.28	31	9	2	1	1	2	0	6	6	2	70–72
Progne subis	23.90	3	17	1	10	0	0	0	2	0	4	4	4	73–75
Prunella modularis	0.80	3	—	4	12	1	2	1	0	0	10	5	2	76
Sayornis phoebe	11.84	0.4	1.7	2	2	2	0	1	2	0	10	5	4	77
Serinus canaria	0.00	—	—	>100	400	2	0	1	0	2	10.5	3.5	2	78
Spizella pusilla	15.10	3	—	1	2	0	0	0	1	0	8	4	2	79
Sturnus vulgaris	9.09	24.77	5	49	15	1	1	0	1	0	10	5	5	80, 81
Tachycineta bicolor	54.06	—	—	2.6	2.5	0	1	0	2	0	5	5	2	82–85
Taeniopygia guttata	2.40	0.9	—	1	6.8	0	0	0	0	2	15	5	6	86
Thryothorus ludovicianus	0.00	1.6	3.6	36	2.5	1	0	1	0	0	10	5	2	87
Troglodytes aedon	8.35	1.7	—	>100	6	1	2	1	2	0	12	6	2	88
Turdus merula	17.77	2.4	1.6	34	6	2	0	1	0	2	10.5	3.5	2	89, 90
Turdus migratorius	53.00	1.93	2.28	13	—	2	0	1	1	0	7	3.5	2	91
Vireo olivaceus	57.89	0.35	1.42	43	2	2	0	1	0	0	4	4	2	92
Vireo solitarius	2.70	0.34	2.3	15	2	2	0	1	0	0	8	4	6	92

APPENDIX A, continued

Species	EPP	DUR	INT	REP	SYL	VER	PG	HAB	MIG	DICR	FEC	CLS	MPC	REF
Wilsonia citrina	26.69	1.1	6.7	7	4	0	0	1	2	2	6	3	2	93
Wilsonia pusilla	32.00	1.2	4	3	2	2	0	1	2	2	4.5	4.5	2	94
Zonotrichia albicollis	12.80	2.87	5.83	1	4	0	0	0	1	0	4.5	4.5	2	95
Zonotrichia leucophrys	36.00	1.9	11	1	4	0	0	0	1	0	4	4	2	96

See Methods for definitions and sources of information. References for extrapair paternity is given here.

1 indicates Hasselquist et al. (1996); 2, Leisler et al. (2000); 3, Schulze-Hagen et al. (1993); 4, Leisler and Wink (2000); 5, Langefors et al. (1998); 6, Buchanan and Catchpole (2000); 7, Gray (1996); 8, Weatherhead and Boag (1995); 9, Westneat (1993); 10, Reyer et al. (1997); 11, Hill and Gould (1997); 12, Briskie et al. (1998); 13, Rabenold et al. (1990); 14, Ritchison et al. (1994); 15, Angst (1998); 16, Gissing et al. (1998); 17, Hill et al. (1994); 18, Riley et al. (1995); 19, Whittingham and Lifjeld (1995); 20, Yezerinac et al. (1999); 21, Yezerinac et al. (1996); 22, Bollinger and Gavin (1991); 23, Hartley et al. (1993); 24, Sundberg and Dixon (1996); 25. Dixon et al. (1994); 26, Woolfenden L, unpublished data; 27, Tobias (1996); 28, Garamszegi et al. (2004); 29, Gelter and Tegelström (1992); 30, Brün et al. (1996); 31, Rätti et al. (1995); 32, Lifjeld et al. (1991); 33, Ellegren et al. (1995); 34, Sheldon and Burke (1994); 35, Saino et al. (1997); 36, Wellbourn M, personal communication; 37, Møller and Tegelström (1997); 38, Richardson and Burke (1999); 39, Raouf et al. (1997); 40, Fornasari et al. (1994); 41, Krokene et al. (1996); 42, Questiau et al. (1999); 43, Dunn and Cockburn (1999); 44, Smith (1991); 45, Derrickson and Breitwisch (1992); 46, Zilberman et al. (1999); 47, Currie et al. (1998); 48, Hoi and Hoi-Leitner (1997); 49, Lubjuhn et al. (1999a); 50, Otter et al. (1998); 51, Kempenaers et al. (1997); 52, Gullberg et al. (1992); 53, Leech et al. (2001); 54, Lens et al. (1997); 55, Strohbach et al. (1998); 56, Lubjuhn et al. (1999b); 57, Blakey (1994); 58, Otter et al. (2001); 59, Orell et al. (1997); 60, Wetton and Parkin (1991); 61, Cordero et al. (1999); 62, Whitekiller et al. (2000); 63, Veiga and Boto (2000); 64, Griffith et al. (1999); 65, Kimball R, unpublished data; 66, Cordero et al. (2002); 67, Freeman-Gallant (1997); 68, Westneat (1990); 68, Westneat (1987); 70, Gyllensten et al. (1990); 71, Fridolfsson et al. (1997); 72, Bjørnstad and Lifjeld (1997); 73, Morton et al. (1990); 74, Wagner et al. (1996a); 75, Wagner et al. (1996b); 76, Burke et al. (1989); 77, Conrad et al. (1998); 78, Voight et al. (1997); 79, Carey et al. (1994); 80, Smith and von Schantz (1993); 81, Pinxten et al. (1993); 82, Dunn et al. (1994a); 83, Kempenaers et al. (1999); 84, Dunn et al. (1994b); 85, Barber et al. (1996), ; 86, Birkhead et al. (1990); 87, Haggerty et al. (2001); 88, Soukup and Thompson (1997); 89, Creighton (2000); 90, Rasa A, personal communication; 91, Montgomerie in Briskie et al. (1997); 92, Morton et al. (1998); 93, Stutchbury et al. (1997); 94, Bereson R, unpublished data; 95, Tuttle (1993); and 96, Sherman and Morton (1988).

APPENDIX B

Additional analyses that were performed to confirm the use of different data and different phylogenetic approaches (See Methods and Results).

Phylogenetic relationship between extrapair paternity and song type repertoire size when infinite song type repertoire size was set to 300 or 500: using 300, $\kappa = 0.065$, $\lambda = 0.720$, phylogenetic correlation $= -0.065$, $p = .618$; using 500, $\kappa = 0.065$, $\lambda = 0.726$, phylogenetic correlation $= -0.066$, $p = .616$.

Phylogenetic relationships between extrapair paternity and song variables when using data from Griffith et al. (2002) for extrapair paternity

Extrapair paternity	κ	λ	Correlation	p
Song duration	0.208	0.000	−0.047	0.761
Intersong interval	0.000	0.000	0.098	0.611
Continuity	0.000	0.482	−0.038	0.844
Song rate	0.000	0.447	0.075	0.695
Song repertoire size	0.303	0.743	0.091	0.555
Syllable repertoire size	0.236	0.353	−0.041	0.792
Versatility	0.276	0.486	−0.229	0.107

Stepwise multiple regression analysis forced to the origin when using statistically independent contrast generated by CAIC (Purvis and Rambaut, 1995) with extrapair paternity as the dependent variable, and song traits and potentially confounding variables as independent variables: $F = 2.911$, df = 4, 36, $r^2 = .220$, $p = .037$; variables in the model: sexual dichromatism, slope: 0.063 [SE = 0.056], $p = .181$; polygyny, slope: −0.076 [SE = 0.048], $p = .119$; migration, slope: 0.106 [SE = 0.052], $p = .048$); male parental care, slope: −0.046 [SE = 0.025], $p = .071$).

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