

# Extrapair Paternity Rates Vary with Latitude and Elevation in Emberizid Sparrows

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**ABSTRACT:** Mating systems can vary among species and populations and thus influence evolutionary trajectories, ecological traits, and population demography. The siring of offspring by an extrapair male, or extrapair paternity (EPP), is a widespread and varied phenomenon in all vertebrate classes. However, we do not understand all of the factors associated with variation in EPP rates. The breeding synchrony hypothesis suggests that EPP rates should increase with latitude and elevation, whereas the paternal care hypothesis predicts that EPP rates should decrease with elevation. To address these hypotheses, we investigated how population EPP rates vary over elevation and latitude in emberizid sparrows. In comparative analyses including the effects of phylogeny, the relationship between EPP rates and elevation depended on latitude. EPP rates were greater in higher-latitude populations. But within higher-latitude populations, EPP rates decreased with increasing elevation. These findings provide support for both the breeding synchrony and paternal care hypotheses, suggesting that in lower-latitude, higher-elevation populations, the need for male parental care does not outweigh the benefits of seeking extrapair fertilizations in populations with relatively synchronous breeding. In contrast, at higher-latitude, higher-elevation sites, the need for male parental care is greater and might drive lower rates of extrapair mating despite highly synchronous breeding.

**Keywords:** extrapair paternity, latitude, elevation, breeding synchrony hypothesis, paternal care hypothesis, Emberizidae.

## Introduction

Mating systems can influence a wide array of biological phenomena, including evolutionary trajectories and rates, ecological traits, and population demography. Although mating systems have received considerable research attention, we do not fully understand the causes or consequences of variation in mating systems either within or between species (Griffith et al. 2002; Macedo et al. 2008; Sardell et al. 2012).

The discovery that the occurrence of extrapair paternity (EPP) in socially monogamous birds is common was a major advance in the study of avian mating systems (Griffith et al. 2002). Males clearly benefit from engaging in extrapair fertilizations through gaining genetic paternity without incurring the concomitant costs of parental care. However, the reasons for females to engage in extrapair mating remain poorly understood. Extrapair mating might gain females genetic advantages for their offspring (Westneat et al. 1990; Gerlach et al. 2012; but see Sardell et al. 2012) and/or insure against the infertility of their social mate (Wetton and Parkin 1991).

Although EPP is a widespread phenomenon in birds, EPP rates can range widely, from rare occurrences to the most common form of paternity (Arnold and Owens 2002; Griffith et al. 2002). EPP rates vary among individuals, populations, and species, as well as geographically (Spottiswoode and Møller 2004), phylogenetically (Arnold and Owens 2002), and temporally (Westneat 1993). Extrapair offspring can increase among-individual variance in reproductive success, particularly among males, and thus have the potential to influence the intensity and outcome of sexual selection (Webster et al. 1995; Møller and Ninni 1998; Webster et al. 2007; Balenger et al. 2009). Indeed, indices of sexual selection, such as testis size, testosterone levels, and plumage dichromatism, are positively correlated with EPP rates in some avian species (Møller and Birkhead 1994; Møller and Briskie 1995; Garamszegi et al. 2005), and have been used as proxies of EPP in birds in some comparative analyses (Dunn et al. 2001).

Numerous hypotheses have been put forth to explain variation in extrapair paternity rates and are reviewed elsewhere (Griffith et al. 2002; Neudorf 2004; Macedo et al. 2008). Many of these hypotheses are not mutually exclusive, do not generate alternative predictions, and have not been tested with an experimental approach, and thus progress in identifying important causal mechanisms of variation in EPP rates has been slow. However, several broad

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patterns have been identified. For example, a phylogenetically controlled comparative study revealed that EPP rates in birds generally increase with latitude (Spottiswoode and Møller 2004). The mechanism underlying this pattern is unclear and possibly complex, with several factors that covary with latitude potentially influencing mating systems, such as population density (Westneat and Sherman 1997; Møller and Ninni 1998; Mayer and Pasinelli 2013), migratory distance (Spottiswoode and Møller 2004), and breeding synchrony (Stutchbury and Morton 1995; Stutchbury 1998). For example, high breeding synchrony at high latitudes might increase the likelihood of EPP because females can compare more easily between simultaneously displaying males, and males might have increased success in securing extrapair copulations (EPCs) because they are more likely to encounter fertile females (Stutchbury and Morton 1995; Stutchbury 1998). Additionally, the cost of seeking EPCs might be reduced in synchronously breeding populations, as males do not have to invest resources in maintaining an active reproductive system and engaging in mate-seeking and advertising behaviors across long time spans to capitalize on opportunities for EPP. The observation that in seasonally breeding birds, even those that breed relatively asynchronously, functional reproductive organs are maintained only during breeding life-history stages and regress during nonbreeding stages suggests that maintaining an active reproductive system is costly (Soma 2006). Elevated reproductive hormones can have negative effects on immune function and survival (Saino et al. 1995; Redpath et al. 2006; Soma 2006), and activities involved in mate attraction might also be associated with fitness costs (Hale 2004; Lima 2009). In an asynchronously breeding population, where extrapair mating opportunities are more broadly dispersed, both spatially and temporally, these costs could outweigh the fitness benefits that might be gained by maintaining reproductive competence and mate seeking behavior throughout the year in order to capitalize on these rare opportunities.

Elevation has also been proposed to influence sexual selection and EPP rates (Badyaev 1997a). However, few empirical studies have sought to describe variation in EPP rates over elevation. One previous within-species analysis failed to find differences in EPP rates across two populations breeding at different elevations (Balenger et al. 2009), but to our knowledge, no previous comparative studies across species have assessed relationships between elevation of breeding populations and EPP rates. Several avian species show similar patterns of variation in life-history traits across elevation, with high-elevation populations and species exhibiting a slower-paced lifestyle, with reduced annual fecundity, likely driven by increased survival of adults and possibly also of fledglings (Badyaev

1997b; Bears et al. 2009). In addition, challenges facing birds that breed at high elevations (e.g., cold temperatures) may require greater male parental care, thus altering the costs and benefits of extrapair mating strategies (Badyaev and Ghalambor 2001). Thus, EPP rates might also be expected to vary with elevation.

The two central hypotheses put forth to predict how EPP rates will vary over elevation generate opposing predictions. First, because high-elevation populations typically encounter shorter breeding seasons, and thus tend to breed more synchronously than lower-elevation populations, the breeding synchrony hypothesis predicts that the rate of EPP should increase with elevation (Stutchbury and Morton 1995; Stutchbury 1998). Supporting this hypothesis, we see coincident variation in a plausible mechanism controlling variation in EPP rates. Within species, testosterone can influence EPP rates (Raouf et al. 1998), and across species, testosterone concentrations increase with EPP rates, latitude, elevation, and breeding synchrony (Goymann et al. 2004; Garamszegi et al. 2005, 2008), although the relationship with elevation does not persist after control for phylogeny (Goymann et al. 2004). Alternatively, because the cost of raising offspring and thus the need for male parental care increases with elevation (Badyaev and Ghalambor 2001), the paternal care hypothesis predicts that EPP rates should decline with elevation (Birkhead and Møller 1996). As males invest more parental effort and resources into raising their offspring, they have a greater interest in paternity assurance and also less time available for seeking EPCs (Badyaev 1997a; Arnqvist and Kirkpatrick 2005). Indeed, male parental care declines with increasing EPP, both within and among species (Møller and Birkhead 1993; Dixon et al. 1994; Perlut et al. 2012; Matysioková and Remeš 2013). Further, in a comparative analysis that did not include population latitude or elevation, species with a greater fitness cost of the experimental removal of the male (an estimate of the importance of male parental care) had lower EPP rates (Møller 2000). To our knowledge, no one has directly investigated the predictions of these two hypotheses over elevation. However, a comparative analysis across 126 finch species (Carduelidae) revealed a reduction in plumage dimorphism with elevation, largely driven by increased brightness of male plumage at low elevations (Badyaev 1997a). This pattern is consistent with a reduction in the strength of sexual selection at high elevations, which might result from reduced EPP rates.

Although the breeding synchrony and paternal care hypotheses generate opposite predictions, they are not mutually exclusive, and they are not the only plausible hypotheses for how EPP rates might be shaped over elevation. Both breeding synchrony and the need for male parental care might contribute to the costs and benefits of seeking

EPCs, with the two factors pushing EPP rates in opposite directions. Additionally, EPP rates might also be influenced by population density, migratory distance, and other factors (Westneat and Sherman 1997; Møller and Ninni 1998; Spottiswoode and Møller 2004; Mayer and Pasinelli 2013). Importantly, none of these other factors are predicted to vary consistently across elevation, unlike the need for male parental care and breeding synchrony. Thus, by describing how EPP rates vary across latitude and elevation, we can better understand the outcome that these interacting forces have on shaping mating systems and provide valuable predictions for further experimental or comparative studies to assess the relative contributions of specific causal factors.

In this study, we employ a comparative approach to investigate how latitude and elevation of breeding are associated with EPP rates in the Emberizidae, a family of birds with a rich complement of studies on EPP variation. We compiled all available data for EPP rates in populations of socially monogamous emberizid species, and we conducted a phylogenetically controlled comparative analysis to determine whether a relationship exists between EPP rates and latitude and elevation of breeding. Whereas previous comparative analyses across species have combined available data to estimate a single, species-level mean EPP rate (and have assigned one species-level breeding latitude), we included all available data for populations of socially monogamous emberizids independently in our analyses, allowing a more refined analysis of the relationships between population-level variation in EPP and elevation and latitude of the breeding population.

## Methods

### *Compilation of EPP Data for Emberizidae*

We compiled all the data that we could find on EPP rates and latitude and elevation of breeding for populations of socially monogamous Emberizidae—species where a paired male and female attend the offspring, and thus a social father can be identified, resulting in a sample of 24 populations of 12 species of emberizid sparrows, spanning 29° of latitude and more than 3,000 m elevation (table 1; Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3h771>; Bonnier et al. 2013). To determine which species belong to the family Emberizidae, we followed the classification as presented in the International Ornithologists' Union's World Bird List (ver. 2.10), which is based on continuous updates from newly published phylogenies (Gill and Donsker 2011). We extracted most data from the primary literature published until December 2012, with additional data from PhD dissertations and unpublished data kindly provided upon request by several researchers (table 1). For each

study, we defined EPP rate as the proportion of all broods sampled that contained at least one extrapair young (EPY). We also considered the proportion of nestlings sampled that were extrapair sired, a more commonly used metric of EPP, and conducted analyses and report results using both estimates. However, because the decision to mate with an extrapair male is, at least in part, made by the female, the proportion of broods containing EPY is a more appropriate EPP metric, as it does not treat offspring from the same brood (and same mother) as independent. When EPP estimates of the same population were reported in several studies, we included only the one we assessed to be more robust, favoring microsatellite analyses over minisatellites or allozymes, greater number of loci used, and larger sample size. When identical EPP estimates (same parentage analysis, population, and years) were reported in more than one publication, we only include data from one of these studies. We excluded a study on *Spizella pusilla* (Petter et al. 1990) from the data set because EPP estimates were based on only two loci, and might therefore have been inaccurate. We also only include EPP estimates from two equatorial populations of *Zonotrichia capensis* (Eikenaar et al. 2013) in supplementary analyses not presented here (app. A; apps. A–C available online) because they are latitudinal outliers (>6 SD from the mean latitude of the other emberizid populations). We defined latitude and elevation of breeding as the latitude and elevation of the study site at which the EPP data were collected. We obtained information on latitude and elevation of the study sites from the papers that we used to extract EPP data, either directly from the text or using a detailed geographic map (Google Earth: <http://www.google.com/earth/index.html>) and descriptions of study sites.

### *Statistical Analysis*

We conducted Bayesian mixed-effects meta-analyses (BMM) and Bayesian phylogenetic mixed-effects meta-analyses (BPMM) using the MCMCglmm package (Hadfield 2010) in R (ver. 2.14.0, [www.r-project.org](http://www.r-project.org)) to assess the relationship between EPP rates and latitude and elevation of breeding populations both without (BMM) and with (BPMM) consideration of phylogenetic effects. Following methods used in recent comparative studies (Cornwallis et al. 2010; Horvátová et al. 2012), we included species as a random factor in all models (app. A). To investigate the possible influence of phylogenetic nonindependence of our data, we constructed a phylogeny of all of the included emberizid populations and included it as a random factor in all BPMMs (see app. B for details).

We included latitude and elevation of the breeding population, along with an interaction term, as fixed effects. We standardized these two variables (setting the mean to

**Table 1:** Extrapair paternity (EPP) data used in the comparative analyses

Scientific name	Common name	Elevation (m)	Latitude (°N)	EPP rate (sample size) <sup>a</sup>	Source
<i>Ammodramus maritimus</i>	Seaside sparrow	0	32.77	.17 (18)	Hill and Post 2005
<i>Calamospiza melanocorys</i>	Lark bunting	1,500	40.81	.52 (153)	Chaine and Lyon 2008; A. Chaine, personal communication
<i>Emberiza citrinella</i>	Yellowhammer	22	59.90	.69 (32)	Sundberg and Dixon 1996
<i>Emberiza schoeniclus</i> (Switzerland)	Reed bunting	429	46.90	.64 (132)	Suter et al. 2009
<i>E. schoeniclus</i> (Norway)	Reed bunting	1,100	61.42	.54 (72)	Kleven and Lifjeld 2005
<i>E. schoeniclus</i> (Netherlands 1)	Reed bunting	0	51.75	.74 (121)	Bouwman et al. 2006
<i>E. schoeniclus</i> (Netherlands 2)	Reed bunting	0	53.35	.88 (17)	Bouwman 2005
<i>E. schoeniclus</i> (England)	Reed bunting	84	52.67	.86 (58)	Dixon et al. 1994
<i>E. schoeniclus</i> (Poland)	Reed bunting	107	51.52	.59 (70)	Buchanan 2001
<i>Junco hyemalis</i>	Dark-eyed junco	1,160	37.37	.39 (389)	Ketterson et al. 1997; McGlothlin et al. 2010; N. Gerlach, P. Parker, and E. Ketterson, personal communication
<i>Melospiza georgiana</i> (coastal)	Swamp sparrow	1	39.30	.39 (54)	Olsen et al. 2008
<i>M. georgiana</i> (inland)	Swamp sparrow	788	39.60	.44 (59)	Olsen et al. 2008
<i>Melospiza melodia</i> (Washington)	Song sparrow	100	47.66	.36 (72)	Hill et al. 2011
<i>M. melodia</i> (Nova Scotia)	Song sparrow	26	44.75	.30 (10)	Major and Barber 2004
<i>M. melodia</i> (British Columbia)	Song sparrow	1	48.63	.44 (811)	Sardell et al. 2010
<i>M. melodia</i> (Ontario)	Song sparrow	130	44.64	.24 (33)	E. MacDougall-Shackleton, personal communication
<i>Melozona (Pipilo) crissalis</i>	California towhee	710	36.21	.42 (31)	Benedict 2008
<i>Passerculus sandwichensis</i> (New Brunswick)	Savannah sparrow	10	44.58	.67 (159)	Freeman-Gallant et al. 2003, 2005
<i>P. sandwichensis</i> (Vermont)	Savannah sparrow	42	44.65	.71 (77)	Perlut et al. 2008
<i>Spizella pusilla</i>	Field sparrow	332	41.57	.12 (338)	Carey et al. 2008; M. Carey, personal communication
<i>Zonotrichia albicollis</i>	White-throated sparrow	460	44.19	.31 (32)	Tuttle 2003
<i>Zonotrichia leucophrys</i> (Washington)	White-crowned sparrow	20	47.61	.64 (28)	Bonier et al. 2007; F. Bonier, unpublished data
<i>Z. leucophrys</i> (California)	White-crowned sparrow	3,030	37.94	.56 (96)	MacDougall-Shackleton et al. 2002
<i>Z. leucophrys</i> (Oregon)	White-crowned sparrow	9	43.16	.32 (62)	Poesel et al. 2011

<sup>a</sup> EPP rate is calculated as the proportion of broods containing at least one offspring sired by an extrapair male, and sample size is the number of broods sampled within the population.

0 and the standard deviation to 1) before analysis, to allow for direct comparison of effect sizes. This approach does not account for the differences in breadth of sampling between elevation and latitude. With a more than 3,000 m span of elevational sampling, a 1 SD change in this parameter represented a change of more than 700 m, whereas 1 SD deviation of latitude was only 7°. Arguably, these two changes might not be expected to be biologically comparable, and so we conducted analyses using unstandardized variables as well (app. A).

The response variable was a column-bind matrix (cbind in R) of the number of broods with at least one EPY and the number of broods without any EPY. This approach allows for consideration of the relative frequency of EPP as well as study sample size (the total number of broods

sampled), unlike approaches that use the proportion of extrapair broods or offspring as the response variable. We also conducted similar analyses with a matrix of the number of EPY and the number of within-pair young as the response variable. We ran three chains of each model to check for model convergence using the Gelman-Rubin diagnostic (Gelman and Rubin 1992), and report results of the first chain. We assessed relative likelihood of models through comparison of models with all possible combinations of fixed effects using comparison of the deviance information criterion (DIC) for each model (Spiegelhalter et al. 2002).

We also conducted supplemental analyses (app. C) investigating the possible contribution of population density and migratory distance to patterns of variation in EPP.

For these analyses, we compared model likelihood and estimates of fixed effects of several BPMMs that included estimates of density and migratory distance separately as well as in models along with latitude and elevation.

### Results

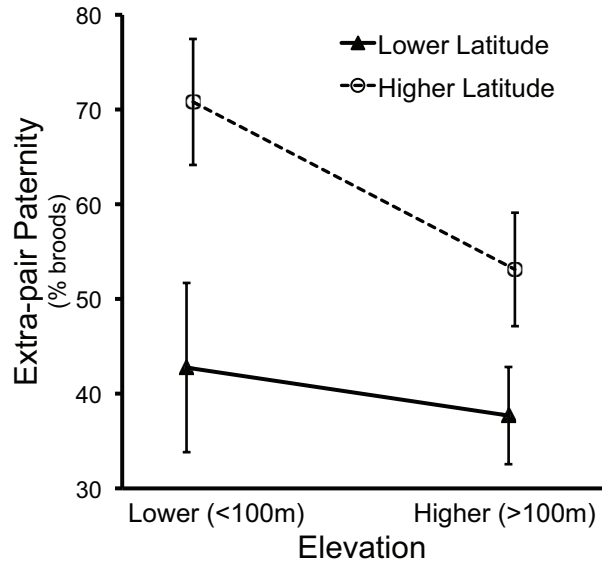
Across emberizid populations, EPP rates were greater at higher latitudes. Within higher-latitude populations, EPP rates decreased with increasing elevation (fig. 1). Results were similar when we ran analyses with the number of EPY and within-pair young as the response variable (fig. 2) and when we included the equatorial *Zonotrichia capensis* populations (app. A), except that the main effect of elevation was stronger (as indicated by narrower 95% confidence intervals that did not overlap zero) in models using EPY. Model simplification did not improve model fit; in all cases the saturated model was best fit (having the lowest DIC). Both phylogeny and species identity explained some of the variation in EPP rates (as indicated by 95% confidence intervals that did not overlap zero; fig. 2).

Supplemental analyses including estimates of population density and migratory distance did not improve model fit, and in all models with latitude and elevation, population density and migratory distance did not predict EPP rates (app. C). Elevation was uncorrelated with estimates of density and migratory distance ( $P > .21$ ). Latitude was positively correlated with estimated migratory distance ( $P < .001$ ) and uncorrelated with estimated density ( $P = .49$ ). Supplemental analyses using unstandardized latitude and elevation also reveal similar patterns (app. A), but with the sign of the main effect of elevation changing from slightly positive with unstandardized elevation to negative with standardized elevation and being stronger with unstandardized factors, as expected based on the broader sampling across elevation as compared to latitude.

### Discussion

Here, we describe for the first time a pattern of variation in EPP rates over breeding elevation among species and populations. Interestingly, EPP rates decreased with elevation at higher latitudes. EPP rates increased with latitude, most markedly at lower elevations (fig. 1).

The observed positive relationship between latitude and EPP rates, particularly at low elevations, follows the predictions of the breeding synchrony hypothesis. In birds, both latitude and elevation are important determinants of the length of the breeding season and hence breeding synchrony (Badyaev 1997b; Boehning-Gaese et al. 2000; Bears et al. 2009). The fact that EPP rates declined with elevation at higher latitudes, where breeding synchrony is expected

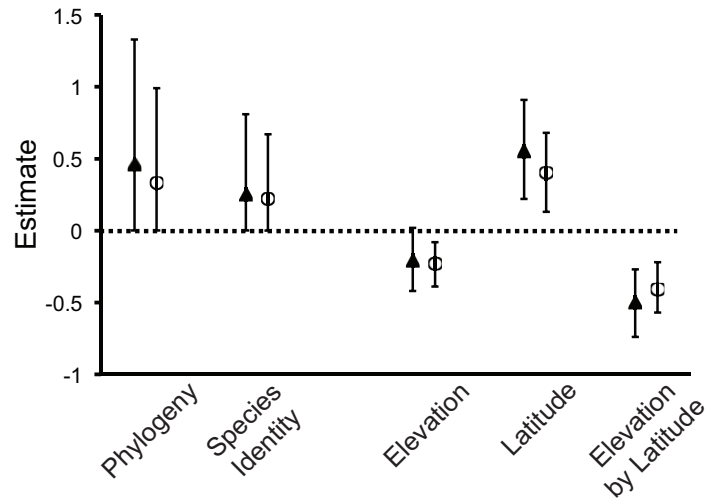


**Figure 1:** The relationship between elevation and extrapair paternity (EPP) rates in emberizid sparrows depends on population latitude. At lower latitudes (32.8°N–45°N), EPP rates are largely unchanged with increasing elevation. In contrast, at higher latitudes (45°N–61.4°N) EPP rates decline sharply with increasing elevation. Data shown are mean EPP rates ( $\pm$  SE) after dividing populations into groupings of lower and higher elevation and latitude to illustrate the interaction effect revealed in Bayesian mixed-effects models.

to be relatively high, suggests that factors other than synchrony are driving variation in EPP rates in these regions.

Our finding of decreased EPP rates with elevation at higher latitudes follows the predictions of the paternal care hypothesis, which suggests that EPP rates will decline with an increased need for paternal care. A suite of traits vary over elevation across avian taxa, such as plumage dimorphism, fecundity, survival, and male parental investment, which suggest reduced sexual selection and a slower-paced life history in high-elevation populations (Badyaev 1997a, 1997b; Bears et al. 2009), and that a greater need for paternal care at high elevations might lead to reduced EPP rates. Our results showing no apparent change in EPP rates over elevation at lower latitudes, however, suggest that the need for male parental care does not outweigh the benefits of extrapair fertilizations in these regions. Here, the need for male parental care might not increase as steeply with elevation as it does at higher latitudes, and thus other factors, such as increasing breeding synchrony, might more strongly influence variation in EPP rates in lower-latitude, high-elevation populations. Alternatively, high levels of male parental care might be compatible with high EPP rates (Sheldon 2002; Alonzo 2012).

All of the emberizid populations in our main analyses occur in the Northern Hemisphere at temperate latitudes.



**Figure 2:** Parameter estimates of relationships between phylogeny, species identity (random effects, *left*), and their interaction (fixed effects, *right*), with extrapair paternity (EPP) rates in populations of emberizid sparrows estimated using Bayesian phylogenetic mixed-effects meta-analyses. Results of analyses using two different estimates of EPP are shown (filled triangles = relative number of broods with at least one extrapair young; open circles = relative number of extrapair young), with 95% confidence intervals.

Thus, we must await better sampling of southern and tropical populations to determine whether the latitudinal and elevational patterns we report also hold in the tropics and in the southern temperate zone, where some avian life-history traits can more closely resemble those of tropical taxa (Martin 1996; Cardillo 2002). Results of analyses of relationships between latitude and elevation and EPP rates do not differ when we include two equatorial *Zonotrichia capensis* populations (app. A). However, these two tropical taxa had relative high EPP rates (with 64% and 60% of broods containing at least one EPY; Eikenaar et al. 2013), which does not follow expectations of a latitudinal increase in EPP.

Overall, we have found an interaction between elevation and latitude with EPP rates in emberizid sparrows, incorporating data from 24 populations and 12 species, spanning almost 30° latitude and more than 3,000 m elevation. Greater EPP rates in low-elevation, higher-latitude populations are consistent with variation in breeding synchrony contributing to the pattern, whereas lower EPP rates in high-elevation, higher-latitude populations suggest an influence of the need for paternal care in constraining EPP rates.

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#### Literature Cited

- Alonzo, S. H. 2012. Sexual selection favours male parental care, when females can choose. *Proceedings of the Royal Society B: Biological Sciences* 279:1784–1790.
- Arnold, K. E., and I. P. F. Owens. 2002. Extra-pair paternity and egg dumping in birds: life history, parental care and the risk of retaliation. *Proceedings of the Royal Society B: Biological Sciences* 269: 1263–1269.
- Arnqvist, G., and M. Kirkpatrick. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. *American Naturalist* 165(suppl.):S26–S37.
- Badyaev, A. V. 1997a. Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. *Behavioral Ecology* 8:675–690.
- . 1997b. Avian life history variation along altitudinal gradients: an example with cardueline finches. *Oecologia (Berlin)* 111:365–374.
- Badyaev, A. V., and C. K. Ghalambor. 2001. Evolution of life histories along elevational gradients: trade-off between parental care and fecundity. *Ecology* 82:2948–2960.
- Balenger, S. L., L. Scott Johnson, H. L. Mays Jr., and B. S. Masters. 2009. Extra-pair paternity in the socially monogamous mountain bluebird *Sialia currucoides* and its effect on the potential for sexual selection. *Journal of Avian Biology* 40:173–180.

- Bears, H., K. Martin, and G. C. White. 2009. Breeding in high-elevation habitat results in shift to slower life-history strategy within a single species. *Journal of Animal Ecology* 78:365–375.
- Benedict, L. 2008. Unusually high levels of extrapair paternity in a duetting songbird with long-term pair bonds. *Behavioral Ecology and Sociobiology* 62:983–988.
- Birkhead, T. R., and A. P. Møller. 1996. Monogamy and sperm competition in birds. Pages 323–343 in J. M. Black, ed. *Partnerships in birds*. Oxford University Press, Oxford.
- Boehning-Gaese, K., B. Halbe, N. Lemoine, and R. Oberrath. 2000. Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. *Evolutionary Ecology Research* 2:823–839.
- Bonier, F., C. Eikenaar, P. R. Martin, and I. T. Moore. 2013. Data from: Extra-pair paternity rates vary with latitude and elevation in emberizid sparrows. *American Naturalist*, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.3h771>.
- Bonier, F., P. R. Martin, K. S. Sheldon, J. P. Jensen, S. L. Foltz, and J. C. Wingfield. 2007. Sex-specific consequences of life in the city. *Behavioral Ecology* 18:121–129.
- Bouwman, K. M. 2005. The illusion of monogamy. PhD thesis. University of Groningen.
- Bouwman, K. M., T. Burke, and J. Komdeur. 2006. How female reed buntings benefit from extra-pair mating behaviour: testing hypotheses through patterns of paternity in sequential broods. *Molecular Ecology* 15:2589–2600.
- Buchanan, G. 2001. Mate choice in reed buntings (*Emberiza schoeniclus*). PhD thesis. University of Sunderland.
- Cardillo, M. 2002. The life-history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator? *Journal of Animal Ecology* 71:79–87.
- Carey, M., D. E. Burhans, and D. A. Nelson. 2008. Field sparrow (*Spizella pusilla*). In A. Poole, ed. *The Birds of North America Online*. Cornell Lab of Ornithology, Ithaca, NY. [http://bna.birds.cornell.edu/bna/](http://bna.birds.cornell.edu.ezproxy.lib.vt.edu:8080/bna/species/103/articles/introduction%20for%20Virginia%20Tech%20Library%20users;public%20link:http://bna.birds.cornell.edu/bna/).
- Chaine, A. S., and B. E. Lyon. 2008. Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science* 319:459–462.
- Cornwallis, C. K., S. A. West, K. E. Davis, and A. S. Griffin. 2010. Promiscuity and the evolutionary transition to complex societies. *Nature* 466:969–972.
- Dixon, A., D. Ross, S. L. C. Omalley, and T. Burke. 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature* 371:698–700.
- Dunn, P. O., L. A. Whittingham, and T. E. Pitcher. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* 55:161–175.
- Eikenaar, C., F. Bonier, P. R. Martin, and I. T. Moore. 2013. High rates of extra-pair paternity in two equatorial populations of rufous-collared sparrow, *Zonotrichia capensis*. *Journal of Avian Biology*. doi:10.1111/j.1600-048X.2013.00212.x.
- Freeman-Gallant, C. R., M. Meguerdichian, N. T. Wheelwright, and S. V. Sollecito. 2003. Social pairing and female mating fidelity predicted by restriction fragment length polymorphism similarity at the major histocompatibility complex in a songbird. *Molecular Ecology* 12:3077–3083.
- Freeman-Gallant, C. R., N. T. Wheelwright, K. E. Meiklejohn, S. L. States, and S. V. Sollecito. 2005. Little effect of extrapair paternity on the opportunity for sexual selection in savannah sparrows (*Passerulus sandwichensis*). *Evolution* 59:422–430.
- Garamszegi, L. Z., M. Eens, S. Hurtrez-Boussès, and A. P. Møller. 2005. Testosterone, testes size, and mating success in birds: a comparative study. *Hormones and Behavior* 47:389–409.
- Garamszegi, L. Z., K. Hirschenhauser, V. Bókony, M. Eens, S. Hurtrez-Boussès, A. P. Møller, R. F. Oliveira, et al. 2008. Latitudinal distribution, migration, and testosterone levels in birds. *American Naturalist* 172:533–546.
- Gelman, A., and D. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–472.
- Gerlach, N. M., J. W. McGlothlin, P. G. Parker, and E. D. Ketterson. 2012. Promiscuous mating produces offspring with higher lifetime fitness. *Proceedings of the Royal Society B: Biological Sciences* 279: 860–866.
- Gill, F., and D. Donsker. 2011. IOC World Bird List (version 2.10). Accessed November 25, 2011. <http://www.worldbirdnames.org>.
- Goymann, W., I. T. Moore, A. Scheuerlein, K. Hirschenhauser, A. Grafen, and J. C. Wingfield. 2004. Testosterone in tropical birds: effects of environmental and social factors. *American Naturalist* 164:327–334.
- Griffith, S. C., I. P. F. Owens, and K. A. Thuman. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* 11:2195–2212.
- Hadfield, J. D. 2010. MCMC methods for multi-response generalised linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* 33:1–22.
- Hale, A. M. 2004. Predation risk associated with group singing in a Neotropical wood-quail. *Wilson Bulletin* 116:167–171.
- Hill, C. E., C. Akçay, S. E. Campbell, and M. D. Beecher. 2011. Extrapair paternity, song, and genetic quality in song sparrows. *Behavioral Ecology* 22:73–81.
- Hill, C. E., and W. Post. 2005. Extra-pair paternity in seaside sparrows. *Journal of Field Ornithology* 76:119–126.
- Horvátová, T., S. Nakagawa, and T. Uller. 2012. Strategic female reproductive investment in response to male attractiveness in birds. *Proceedings of the Royal Society B: Biological Sciences* 279:163–170.
- Ketterson, E. D., P. G. Parker, S. A. Raouf, V. Nolan, C. Ziegenfuss, and C. R. Chandler. 1997. The relative impact of extra-pair fertilizations on variation in male and female reproductive success in dark-eyed juncos (*Junco hyemalis*). Pages 81–101 in *Avian reproductive tactics: female and male perspectives*. Ornithological Monographs. University of California Press, Berkeley.
- Kleven, O., and J. T. Lifjeld. 2005. No evidence for increased offspring heterozygosity from extrapair mating in the reed bunting (*Emberiza schoeniclus*). *Behavioral Ecology* 16:561–565.
- Lima, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews* 84:485–513.
- MacDougall-Shackleton, E. A., E. P. Derryberry, and T. P. Hahn. 2002. Nonlocal male mountain white-crowned sparrows have lower paternity and higher parasite loads than males singing local dialect. *Behavioral Ecology* 13:682–689.
- Macedo, R. H., J. Karubian, and M. S. Webster. 2008. Extrapair paternity and sexual selection in socially monogamous birds: are tropical birds different? *Auk* 125:769–777.
- Major, D. L., and C. A. Barber. 2004. Extra-pair paternity in first and second broods of eastern song sparrows. *Journal of Field Ornithology* 75:152–156.
- Martin, T. E. 1996. Life history evolution in tropical and south tem-

- perate birds: what do we really know? *Journal of Avian Biology* 27:263–272.
- Matysioková, B., and V. Remeš. 2013. Faithful females receive more help: the extent of male parental care during incubation in relation to extra-pair paternity in songbirds. *Journal of Evolutionary Biology* 26:155–162.
- Mayer, C., and G. Pasinelli. 2013. New support for an old hypothesis: density affects extra-pair paternity. *Ecology and Evolution* 3:694–705.
- McGlothlin, J. W., D. J. Whittaker, S. E. Schrock, N. M. Gerlach, J. M. Jawor, E. A. Snajdr, and E. D. Ketterson. 2010. Natural selection on testosterone production in a wild songbird population. *American Naturalist* 175:687–701.
- Møller, A. P. 2000. Male parental care, female reproductive success, and extrapair paternity. *Behavioral Ecology* 11:161–168.
- Møller, A. P., and T. R. Birkhead. 1993. Certainty of paternity covaries with paternal care in birds. *Behavioral Ecology and Sociobiology* 33:261–268.
- . 1994. The evolution of plumage brightness in birds is related to extrapair paternity. *Evolution* 48:1089–1100.
- Møller, A. P., and J. V. Briskie. 1995. Extra-pair paternity, sperm competition and the evolution of testis size in birds. *Behavioral Ecology and Sociobiology* 36:357–365.
- Møller, A. P., and P. Ninni. 1998. Sperm competition and sexual selection: a meta-analysis of paternity studies of birds. *Behavioral Ecology and Sociobiology* 43:345–358.
- Neudorf, D. L. H. 2004. Extrapair paternity in birds: understanding variation among species. *Auk* 121:302–307.
- Olsen, B. J., R. Greenberg, R. C. Fleischer, and J. R. Walters. 2008. Extrapair paternity in the swamp sparrow, *Melospiza georgiana*: male access or female preference? *Behavioral Ecology and Sociobiology* 63:285–294.
- Perlut, N. G., C. R. Freeman-Gallant, A. M. Strong, T. M. Donovan, C. W. Kilpatrick, and N. J. Zalik. 2008. Agricultural management affects evolutionary processes in a migratory songbird. *Molecular Ecology* 17:1248–1255.
- Perlut, N. G., L. M. Kelly, N. J. Zalik, and A. M. Strong. 2012. Male savannah sparrows provide less parental care with increasing paternity loss. *Northeastern Naturalist* 19:335–344.
- Petter, S. C., D. B. Miles, and M. M. White. 1990. Genetic evidence of mixed reproductive strategy in a monogamous bird. *Condor* 92:702–708.
- Poesel, A., H. L. Gibbs, and D. A. Nelson. 2011. Extrapair fertilizations and the potential for sexual selection in a socially monogamous songbird. *Auk* 128:770–776.
- Raouf, S. A., P. G. Parker, E. D. Ketterson, V. Nolan, and C. Ziegenfus. 1998. Testosterone affects reproductive success by influencing extra-pair fertilizations in male dark-eyed juncos (*Aves: Junco hyemalis*). *Proceedings of the Royal Society B: Biological Sciences* 265:2453–2453.
- Redpath, S. M., F. Mougeot, F. M. Leckie, and S. A. Evans. 2006. The effects of autumn testosterone on survival and productivity in red grouse, *Lagopus lagopus scoticus*. *Animal Behaviour* 71:1297–1305.
- Saino, N., A. P. Møller, and A. M. Bolzerna. 1995. Testosterone effects on the immune system and parasite infestations in the barn swallow (*Hirundo rustica*): an experimental test of the immunocompetence hypothesis. *Behavioral Ecology* 6:397–404.
- Sardell, R. J., P. Arcese, L. F. Keller, and J. M. Reid. 2012. Are there indirect fitness benefits of female extra-pair reproduction? lifetime reproductive success of within-pair and extra-pair offspring. *American Naturalist* 179:779–793.
- Sardell, R. J., L. F. Keller, P. Arcese, T. Bucher, and J. M. Reid. 2010. Comprehensive paternity assignment: genotype, spatial location and social status in song sparrows, *Melospiza melodia*. *Molecular Ecology* 19:4352–4364.
- Sheldon, B. C. 2002. Relating paternity to paternal care. *Philosophical Transactions of the Royal Society B: Biological Sciences* 357:341–350.
- Soma, K. K. 2006. Testosterone and aggression: Berthold, birds and beyond. *Journal of Neuroendocrinology* 18:543–551.
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. Van Der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society: B: Statistical Methodology* 64:583–639.
- Spottiswoode, C., and A. P. Møller. 2004. Extrapair paternity, migration, and breeding synchrony in birds. *Behavioral Ecology* 15:41–57.
- Stutchbury, B. J., and E. S. Morton. 1995. The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour* 132:675–690.
- Stutchbury, B. J. M. 1998. Breeding synchrony best explains variation in extra-pair mating system among avian species. *Behavioral Ecology and Sociobiology* 43:221–222.
- Sundberg, J., and A. Dixon. 1996. Old, colourful male yellowhammers, *Emberiza citrinella*, benefit from extra-pair copulations. *Animal Behaviour* 52:113–122.
- Suter, S. M., D. Ermacora, N. Rieille, and D. R. Meyer. 2009. A distinct reed bunting dawn song and its relation to extrapair paternity. *Animal Behaviour* 77:473–480.
- Tuttle, E. M. 2003. Alternative reproductive strategies in the white-throated sparrow: behavioral and genetic evidence. *Behavioral Ecology* 14:425–432.
- Webster, M. S., S. Pruett-Jones, D. F. Westneat, and S. J. Arnold. 1995. Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. *Evolution* 49:1147–1157.
- Webster, M. S., K. A. Tarvin, E. M. Tuttle, and S. Pruett-Jones. 2007. Promiscuity drives sexual selection in a socially monogamous bird. *Evolution* 61:2205–2211.
- Westneat, D. F. 1993. Temporal patterns of within-pair copulations, male mate-guarding, and extra-pair events in eastern red-winged blackbirds (*Agelaius phoeniceus*). *Behaviour* 124:267–290.
- Westneat, D. F., and P. W. Sherman. 1997. Density and extra-pair fertilizations in birds: a comparative analysis. *Behavioral Ecology and Sociobiology* 41:205–215.
- Westneat, D. F., P. W. Sherman, and M. L. Morton. 1990. The ecology and evolution of extra-pair copulation in birds. Pages 331–369 in D. M. Power, ed. *Current ornithology*. Plenum, New York.
- Wetton, J. H., and D. T. Parkin. 1991. An association between fertility and cuckoldry in the house sparrow, *Passer domesticus*. *Proceedings of the Royal Society B: Biological Sciences* 245:227–233.