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Degree of protandry reflects level of extrapair paternity in migratory songbirds

Abstract Males of most migratory organisms, including many birds, precede female conspecifics on their journey to the breeding areas. Several hypotheses have been proposed to explain the evolution of protandrous migration, yet they have rarely been tested at the interspecific level. Here, we provide correlational support for the "mate opportunity" hypothesis, which assumes that selection favours protandry in polygynous species where males gain significant fitness benefits from arriving earlier than females. Drawing on phenological data collected at two northern European stopover sites, we show that the time-lag in spring passage between males and females of five Palearctic migratory songbird species is positively associated with levels of extrapair paternity available from the literature. This suggests that males arrive relatively more in advance of females in species with high sperm competition where sexual selection through female choice is intense. Thus, protandry may arise from selection on the relative arrival timing of males and females rather than from selection within one of the sexes.

Keywords Extrapair paternity · Differential migration · Phenology · Sexual selection · Sperm competition

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Introduction

Protandrous migration, the earlier arrival of males at the breeding grounds relative to females, is widespread across animal taxa (Morbey and Ydenberg 2001). Long-term surveys have revealed that most migratory songbird species are protandrous during spring migration (e.g. Spina et al. 1994; Rubolini et al. 2004; Hüppop and Hüppop 2004), although the ultimate and proximate causes of intersexual differences in the timing and extent of bird migration remain hard to pin down (Ketterson and Nolan 1983; Berthold 1996).

At least seven (not mutually exclusive) hypotheses for the evolution of protandrous migration have been proposed (reviewed and classified by Morbey and Ydenberg 2001). Indirect selection hypotheses assume that selection acts in one of the sexes, whereas direct selection hypotheses for protandry consider evolutionary trade-offs between the timing of male and female arrival. Among the direct selection hypotheses, the "mate opportunity" hypothesis—originally conceived in insect studies (e.g. Wiklund and Fagerström 1977)—has received some attention in the ornithological literature (Morbey and Ydenberg 2001). Under this hypothesis, protandry is favoured in cases where males mate multiply and gain fitness benefits from early spring arrival because of reduced sperm competition and increased opportunities for extrapair copulations with receptive females (Morbey and Ydenberg 2001).

In birds, most support for the mate opportunity hypothesis comes from investigations on individual species or populations (e.g. Francis and Cooke 1986; Hasselquist 1998; Langefors et al. 1998). In comparison, evidence reflected at the interspecific level is scarce. Recently, Rubolini et al. (2004) analysed the association between protandrous spring migration and sexual plumage dichromatism in 21 trans-Saharan migratory bird species. Sexual dichromatism—a trait positively correlated with the level of extrapair paternity (EPP) across species (Møller and Birkhead 1994; Owens and

Hartley 1998)—was positively associated with the level of protandry, suggesting that protandrous migration may arise from sexual selection mediated by sperm competition and female choice. Consequently, protandrous timing of arrival should be more pronounced in species with high levels of EPP (cf. Rubolini et al. 2004).

Here, we test this prediction by relating the extent of protandrous migration derived from long-term surveys at two northern European stopover sites with species-specific differences in the level of EPP available from the literature.

Methods

Phenological data

Phenological data were obtained from long-term ringing schemes carried out on the islands of Heligoland, North Sea (54°12′N, 07°56′E), and Christiansø, Baltic Sea (55°19′N,15°11′E). Both sites are located several kilometres from the mainland and are characterised by a negligible proportion of terrestrial breeding birds. Thus, numbers of birds trapped over the years reflect species-specific phenological patterns of migration (for detailed descriptions of capture methods and protocols, see Hüppop and Hüppop 2004 and Tøttrup et al. 2006). For this analysis, we used pooled median trapping dates collected between 1960 and 2004 on Heligoland and between 1976 and 1997 on Christiansø. Median passage dates were available at both sites for five sexually dichromatic, migratory passerine species (Table 1). The intersexual time-lag in migration date for each species and site was defined as the difference between the median trapping date of females relative to that of males, with positive values signifying protandrous spring arrival (Table 1). Data on the Great Tit *Parus major* were excluded, as this species is not a regular migrant in most of its range and showed no signs of protandry at

Heligoland and a tendency towards protogyny at Christiansø.

Protandry estimates from the two sites were analysed both together and separately. A pooled analysis was performed to improve the accuracy of species-specific estimates. Pooled estimates were calculated for each species as the mean of the two protandry values for each site. Pooling data from the two sites is also biologically justifiable because ringing recoveries indicate that both migrant populations breed principally in Sweden and Finland, and those from Heligoland also farther west in Norway, implying that they form part of the same overall population (Rabøl and Rahbek 2002; Zink 1973–1985; Zink and Bairlein 1995). Nevertheless, we also checked whether results were broadly consistent for each site separately. Furthermore, we calculated protandry for each site and species on a yearly basis, to assess to what extent species-specific protandry estimates were repeatable among years and trapping localities. Repeatability estimates were derived from one-way ANOVA, following Lessels and Boag (1987).

Extrapair paternity (EPP)

Estimates of the degree of EPP—the average proportion of young sired by males other than the attending male—were drawn from a variety of published sources and one unpublished source, as compiled in Spottiswoode and Møller (2004). When EPP estimates were available from more than one study, we calculated a mean, weighted by the number of nestlings sampled in each study (Table 2).

Results

At both study sites and in all species, the numbers of trapped males peaked generally earlier during spring

Table 1 Median spring passage dates (given in Julian days: 1 = January 1) with 95% confidence intervals (CI; in parentheses) and sample sizes (*N*) of males and females of six migratory songbird species trapped between 1960 and 2004 on Heligoland, North Sea (54°12′N, 07°56′E), and between 1976 and 1997 on Christiansø, Baltic Sea (55°19′N, 15°11′E)

Location	Species	Males		Females		Protandry	*P*
		Median (95% CI)	*N*	Median (95% CI)	*N*		
Heligoland	*Emberiza schoeniclus*	102 (91–112)	102	129 (127–132)	198	27	< 0.001
	Ficedula hypoleuca	133 (132–134)	1,113	139 (138–139)	1,260	6	< 0.001
	Fringilla coelebs	87 (86–87)	4,166	99 (99–99)	5,708	12	< 0.001
	Lanius collurio	142 (141–144)	96	144 (142–47)	93	2	NS
	Turdus merula	79 (79–79)	22,593	88 (88–89)	30,459	9	< 0.001
Christiansø	*Emberiza schoeniclus*	99 (96–100)	222	106 (104–107)	338	7	< 0.05
	Ficedula hypoleuca	131 (130–131)	1,389	136 (136–137)	1,568	5	< 0.05
	Fringilla coelebs	95 (94–95)	715	105 (104–106)	969	10	< 0.001
	Lanius collurio	147 (142–148)	1,063	148 (146–149)	1,136	1	NS
	Turdus merula	87 (87–88)	732	94 (94–95)	1,194	7	< 0.001

The degree of protandry was defined as the difference between the median trapping date of females relative to that of males, with positive values signifying protandrous spring arrival. Level of significance of the median test

Table 2 Estimates of extrapair paternity (EPP)—defined as the percentage of young sired by males other than the male attending the nest—in five socially monogamous, migratory songbird species

Species	EPP (%)	N_{tot} for EPP estimate	References
Emberiza schoeniclus	43.20	842	Bouwman et al. (2005); Dixon et al. (1994); Kleven and Lifjeld (2005)
Ficedula hypoleuca	7.98	614	Brün et al. (1996); Ellegren et al. (1995); Gelter and Tegelström (1992); Lifjeld et al. (1991); Rätti et al. (1995)
Fringilla coelebs	17.00	47	Sheldon and Burke (1994)
Lanius collurio	5.26	19	Fornasari et al. (1994)
Turdus merula	17.77	467	Creighton (2000); A. Rasa (unpublished data, as cited in Spottiswoode and Møller 2004)

EPP values are averaged in cases for which information was available from more then one study site and are weighted by the number of sampled nestlings in each study

migration relative to females (Table 1). Intersexual differences in spring passage were significant for four of the species under study (Table 1). The repeatability (R) of protandry among years was statistically significant for each site (one-way ANOVA with species as factor; Heligoland, $F_{4, 196} = 4.03$, $P < 0.01$, $R = 0.07$; Christiansø, $F_{4, 105} = 7.46$, $P < 0.001$, $R = 0.23$), indicating that a small but significant amount of variation in protandry was due to differences among species. For protandry values averaged across all years, repeatability among sites was statistically nonsignificant (one-way ANOVA with species as factor; $F_{4, 5} = 1.69$, $P = 0.29$, $R = 0.25$).

Estimates of protandry pooled across both sites were significantly positively correlated with the level of EPP ($r_S = 0.90$, $P < 0.05$; Fig. 1). Protandry was positively correlated with EPP for each site separately, yet

significantly only for Heligoland (Spearman's rank correlations; Heligoland, $r_S = 0.90$, $P < 0.05$; Christiansø, $r_S = 0.67$, $P = 0.22$).

Discussion

Spring arrival can be viewed as a trait that reflects a balance between sexual and natural selection (e.g. Møller 1994, 2004; Kokko 1999). When sexual selection outweighs the opposing forces of natural selection, we may expect protandry to increase (Møller 2004). Thus, in highly polygynous species, where sexual selection through sperm competition and female choice is intense, protandry should be more pronounced than in less polygynous species (Rubolini et al. 2004). The positive relationship between the degree of protandrous migration and the rate of EPP across passerine species, as found in our study, corroborates this general assumption that the strength of intersexual selection—which depends on a species' mating system—appears to be the main selective force shaping the degree of protandrous migration. Our interspecific comparative study provides suggestive support for the "mate-opportunity" hypothesis for protandry; that is, early-arriving polygynous males increase their mating opportunities by gaining priority access to the best territories and mates (cf. Morbey and Ydenberg 2001). This hypothesis differs from the indirect "rank advantage" hypothesis (Ketterson and Nolan 1976; Myers 1981; cf. Morbey and Ydenberg 2001) in that it considers the costs and benefits of arriving relative to females, i.e. the consequences of intersexual selection. However, territorial rank among males cannot be disregarded because it is relevant in female choice and male–male competition and could well be reflected in a species' mating system.

If males arrive before females, how can female choice affect male arrival date? This counterintuitive aspect of the role of sexual selection in shaping protandrous migration raises further questions about the ultimate benefits of early male arrival, about the mechanisms by which arrival advantages are upheld and signalled to females, and about the genetic consequences
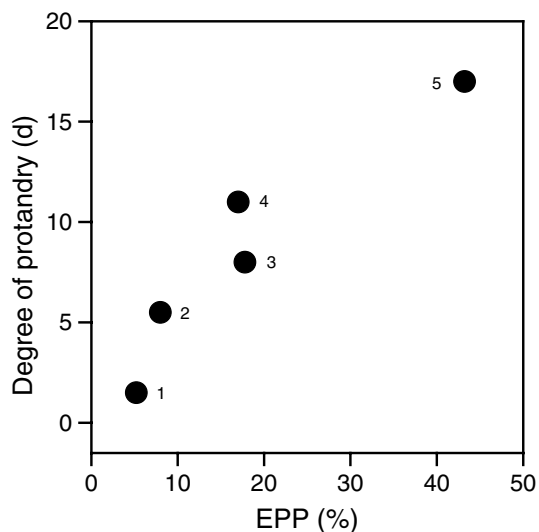
Fig. 1 Correlation between the intersexual time difference in spring migration (protandry) and the level of extrapair paternity (EPP) for five passerine migrants: **1** *Lanius collurio*, **2** *Ficedula hypoleuca*, **3** *Turdus merula*, **4** *Fringilla coelebs*, **5** *Emberiza schoeniclus*. Estimates of protandrous migration are the arithmetic means resulting from protandry values calculated at two northern European trapping sites (Heligoland, Germany, and Christiansø, Denmark;

of assortative mating in relation to migration timing (e.g. Bearhop et al. 2005). Studies on single species and populations have shown that male arrival date is positively associated with mating success and male quality (based mostly on plumage characteristics or body condition): High-quality males tend to occupy prime territories first and mate earlier and more successfully than late-arriving individuals of less perfect appearance (e.g. Møller 1994, 2004; Lozano et al. 1996; Møller et al. 2003; Smith and Moore 2005). However, the detailed mechanism by which the extent of protandrous migration is shaped by selection remains unresolved because the physiological link between migration-related traits that cause protandrous migration and the characteristics that are directly subject to sexual selection through female choice (e.g. plumage characteristics or body size) is unknown. In addition, basic knowledge of the proximate mechanisms that cause males to migrate earlier than females is still lacking (especially in Palearctic-African migrants), since it remains to be determined from either ringing recoveries or observations to what extent males and females of the same population segregate into different wintering areas (e.g. Catry et al. 2005; Komar et al. 2005), migrate at different speeds, or initiate migration at different dates (e.g. Terrill and Berthold 1990). Future studies could incorporate physiological correlates that are associated with male earliness and the development of sexually selected characters (e.g. antioxidants, Ninni et al. 2004). However, despite these intrinsic factors, female choice could also depend on cues such as territory or nest-site quality (see, for example, Alatalo et al. 1986).

The significance of our result is clearly limited by the small number of species for which estimates of EPP and protandry values were available—the latter restricted to sexually dichromatic species. Moreover, since dichromatism and EPP are positively related (Møller and Birkhead 1994; Owens and Hartley 1998), information may generally be biased towards species with higher levels of EPP and missing at the other end of the scale. The small number of species does not allow controlling for covariates such as migration date, migration distance, geographic origin, or phylogenetic dependence. If one of these factors covaries with protandry in the same way as EPP, the association between protandrous migration and EPP need not be a cause–effect relationship. Moreover, many factors may affect among-species variation in EPP (Griffith et al. 2002; Neudorf 2004). In an interspecific comparative study, Spottiswoode and Møller (2004) showed that migration distance is positively related to the level of EPP and that migration can statistically explain a latitudinal trend in EPP. Likewise, the degree of protandry could vary, depending on a species' or population's geographic origin. Hence, alternative explanations for the relationship between protandry and EPP may be feasible, and further studies are needed to validate our interpretation of among-species variation in protandry. In principle, molecular sexing of individuals trapped at bird observatories would enable estimation of the degree of protandrous migration in sexually monochromatic species with well-studied mating systems, such as acrocephaline warblers (Leisler and Wink 2000; Leisler et al. 2002), thus increasing the number of species with known levels of protandry and EPP.

One advantage of our approach is that the protandry values we use are based on trapping totals from long-term, constant-effort surveys and are not derived from observational first-arrival dates, which are likely to be biased. We believe that our pooled protandry estimates are a good proxy for species-specific arrival patterns in northern Europe. On the other hand, some EPP estimates used in this analysis do not stem from northern European populations or are based on studies with low sample sizes (*Lanius collurio*, Fornasari et al. 1994; *Turdus merula*, Creighton 2000) and must be handled with caution. Furthermore, estimates of EPP from different populations may vary considerably between sites and among years (i.e. Pied Flycatcher *Ficedula hypoleuca*, summarised in Lubjuhn et al. 2000), questioning the biological significance of our averaged EPP estimates.

Many aspects of animal behaviour, including mating decisions, are relevant to the conservation of species (Quader 2005). An in-depth understanding of the causes and consequences of protandrous spring arrival is important in our attempt to predict whether populations of migratory birds will be able to adapt to human-related environmental changes (Møller et al. 2004). Any change in relative arrival timing of males and females in response to changing ecological conditions in winter (e.g. Saino et al. 2004) or during migration (e.g. Ahola et al. 2004) will influence subsequent mating decisions, with consequent feedback on reproductive success, individual fitness, and population viability. Recently, Møller (2004) showed that protandry had increased over the past two decades in a Danish barn swallow *Hirundo rustica* population, which indicated that natural selection apposing early male arrival had relaxed, leading to increased sexual selection for early arrival. This assumption was supported by a parallel change of a sexually selected characteristic, tail length, which showed a trend towards larger values (Møller 2004; Møller and Szép 2005). This highlights the potential role of sexual selection in shaping the degree of protandrous spring migration.

Zusammenfassung

Geschlechtsspezifische Unterschiede in den Heimzugterminen von Singvögeln spiegeln Unterschiede im Paarungssystem wider

Bei den meisten wandernden Tierarten, darunter viele Vögel, sind es die Männchen, die den Weibchen auf ihrem Zug zu den Brutplätzen voraneilen. Zum differenzierten Heimzug der Geschlechter (Protandrie) liegen

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