

Sex-differentiated migration patterns, protandry and phenology in North European songbird populations

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Abstract This study aims to investigate causes and mechanisms controlling protandrous migration patterns (the earlier breeding area arrival of males relative to females) and inter-sexual differences in timing of migration in relation to the recent climate-driven changes in phenology. Using standardised ringing data from a single site for eight North European migratory passerines collected throughout 22 years, we analysed sex-differentiated migration patterns, protandry and phenology of the entire populations. Our results show protandrous patterns for the first as well as later arriving individuals for all studied species. Males show more synchronous migration patterns compared to females and, hence, first arriving females followed males more closely than later arriving individuals. However, we found no inter-sexual differences in arrival trends as both sexes advance spring arrival over time with the largest change for the first arriving individuals. These findings seem in support of the “mate opportunity” hypothesis, as the arrival of males and females is strongly coupled and both sexes seem to compete for early arrival. Changes in timing of arrival in males and females as a response to climatic changes may influence subsequent mating decisions, with subsequent feedbacks on population

dynamics such as reproductive success and individual fitness. However, during decades of consistent earlier spring arrival in all phases of migration we found no evidence of inter-sexual phenological differences.

Keywords Climate change · Northern Europe · Passerines · Phenology · Protandry

Introduction

Protandry, when males arrive earlier to the breeding grounds relative to females, is widespread across animal taxa. However, the adaptive significance is not fully understood (reviewed by Morbey and Ydenberg 2001). Protandry has been reported from, e.g., nematodes (Grewal et al. 1993), spiders (Gunnarsson and Johnsson 1990), grasshoppers (Wang et al. 1990), arthropods (Thornhill and Alcock 1983), ground squirrels (Michener 1983), and fish (Morbey 2000).

In birds, protandry has been widely reported (Ketterson and Nolan 1976; Myers 1981; Francis and Cooke 1986; Otahal 1995), and long-term surveys have revealed that most migratory bird species are protandrous during spring migration (e.g. Rubolini et al. 2004). Morbey and Ydenberg (2001) reviewed and classified seven not mutually exclusive hypotheses for the evolution of protandrous migration. Most former studies on birds have focused on: (1) the “rank advantage” hypothesis considering the advantages of early arrival in the territorial sex (e.g. Kokko 1999), and (2) the “mate opportunity” hypothesis considering costs and benefits of early male arrival relative to females (e.g. Hasselquist 1998).

Sex-differentiated migration strategies are known from several former studies on migratory songbirds: e.g. males migrate shorter distances compared to females in

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Chiffchaffs *Phylloscopus collobita* and *P. ibericus* (Catry et al. 2005) and in nine North American songbird species (Komar et al. 2005), while Catry et al. (2004) showed that male European Robins *Erithacus rubecula* depart earlier from wintering areas compared to females. However, basic knowledge on the proximate mechanisms which cause sex-differentiated migration strategies and the adaptive function behind the sex-biased timing is still lacking (Morbey and Ydenberg 2001).

Changes in migration phenology are likely to affect timing of breeding initiation. In species with sex-differentiated migration strategies, changes in timing of breeding area arrival may affect males and females differently. Thus, changes in relative arrival timing of males and females as a response to changing ecological conditions may influence subsequent mating decisions, with subsequent feedback on reproductive success, individual fitness and population viability (Morbey and Ydenberg 2001). Regardless, all recent phenological studies (Lehikoinen et al. 2004) showing changes in both spring arrival and autumn departure (e.g. Tøttrup et al. 2006a, b) with consistent patterns throughout Northern Europe (Jonzen et al. 2006; Thorup et al. 2007) have focused on inter-specific phenological changes with only a few studies considering the inter-sexual differences (Spottiswoode et al. 2006; Rainio et al. 2007).

We describe details of sex-specific migration patterns, to get a better understanding of the mechanisms controlling the migratory rhythms. This study analyses: (1) degree of protandry of three phases of migration; (2) inter-sexual synchronous migration patterns; and (3) the sex-differentiated phenological changes over time for the entire populations of migrants during spring migration.

Methods

The dataset used in this study is derived from 22 years (1976–1997) of standardised mist-netting of night-migrating passerine species on the island of Christiansø (55°19'N, 15°11'E) in the Baltic Sea. Birds were trapped from 15 March to 15 June, covering the entire spring migration period of each species (for details see Rabøl and Rahbek 2002).

We only included data from years where no fewer than 10 individuals of each sex and species were trapped, and only species satisfying this criterion, for at least 20 years. Using these conditions, we included eight species all breeding in Scandinavia, Finland and the Baltic countries (Rabøl and Rahbek 2002); three short-distance migrants wintering in north-western Europe: Goldcrest *Regulus regulus*, Blackbird *Turdus merula* and Reed Bunting *Emberiza schoeniclus*; and five long-distance migrants wintering in sub-Saharan African: Pied Flycatcher *Ficedula hypoleuca*, Redstart *Phoenicurus phoenicurus*,

Whinchat *Saxicola rubetra*, Blackcap *Sylvia atricapilla* and Red-backed Shrike *Lanius collurio*.

Statistical analyses

We investigated three measures of population arrival for each spring season and species; the day of trapping (in Julian days: 1 = 1 January) when the first 5, 50 and 95% of the spring total were trapped, from here on referred to as migration phases (for details, see Tøttrup et al. 2006b). As a measure of migration synchronism between sexes, we used the duration of the migration period when 90% of the individuals of each sex and population (the time window between the 5% and 95% phases) have passed on migrating. Protandry was determined as the difference between the trapping dates of females relative to that of males, with positive values indicating protandrous spring arrival. We compared degree of protandry for the three phases of migration and tested differences between phases by use of a two-way ANOVA with degree of protandry as dependent variable. Species and phase were included as predictive variables, where species was regarded as a quantitative variable and phase as a qualitative variable. We tested for changes in degree of protandry over time for the three phases of migration, with time trend of protandry as dependant variable, and species and phase as predictive variables.

To describe changes in timing of migration, we applied a least square regression approach using the slope-value as a description of the phenological change over time for the three phases of migration. Besides estimating time trends for each species and sex, we tested differences between sexes by applying a general linear model approach using yearly arrival day of each sex as dependent variable testing for an overall inter-sexual difference in change of arrival timing. This model includes sex and year as predictive variables, where the interaction sex × year describes differences in slope-values between the sexes.

Results

Duration of the migration period

Our results show protandrous migration patterns for all species and all migration phases ($t = -9.17$, $P < 0.0001$, $n = 24$, pair-wise t -test; Fig. 1). Overall, males have a more synchronous migration period compared to females ($t = -2.54$, $P = 0.036$, pair-wise t -test; Table 1). The male population of Goldcrests passed through 5 days faster than females, whereas in Blackbird, Reed Bunting and Redstart, males migrated 3 days faster. We were not able to show significant differences between sexes on the species level.

Fig. 1 Sex-differentiated mean arrival days (in Julian days: 1 = 1 January) for the three migration phases: first 5% (black bar), first 50% (dark gray bar) and first 95% (light gray bar) of the total number of trapped birds each year (M males, F females)

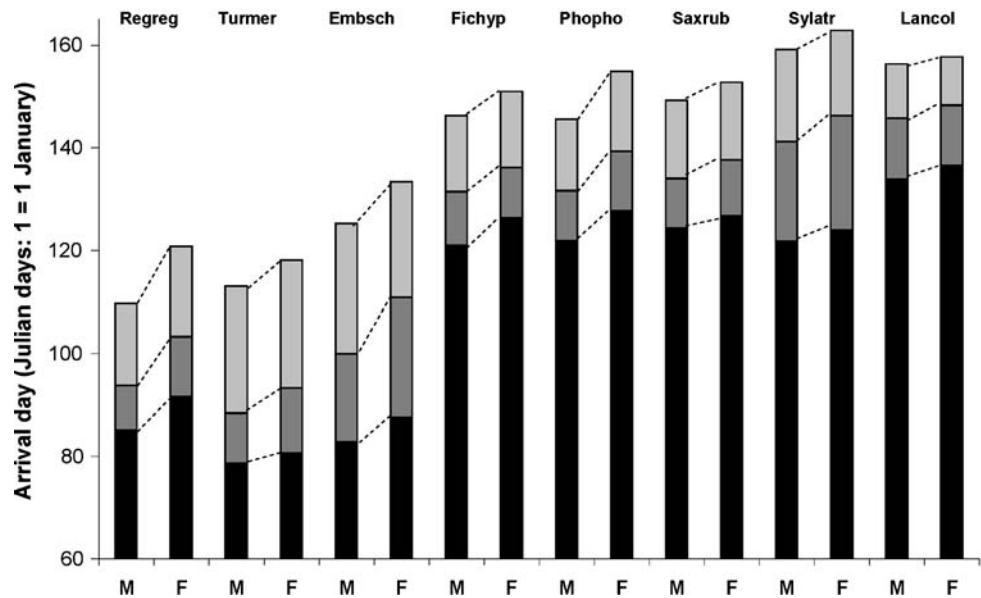


Table 1 The migration period for 90% of the populations (in number of days) for males and females, and the difference in duration of the migration period (Δ period; in number of days) between the sexes

Species	Males	Females	Δ period
Goldcrest <i>Regulus regulus</i>	25	29	5
Blackbird <i>Turdus merula</i>	34	38	3
Reed Bunting <i>Emberiza schoeniclus</i>	42	46	3
Pied Flycatcher <i>Ficedula hypoleuca</i>	25	25	-1
Redstart <i>Phoenicurus phoenicurus</i>	24	27	3
Whinchat <i>Saxicola rubetra</i>	25	26	1
Blackcap <i>Sylvia atricapilla</i>	37	39	2
Red-backed Shrike <i>Lanius collurio</i>	22	21	-1
Mean			1.9*

* $P < 0.05$, two-tailed

Although positive, we found no significant trend over time in the overall duration of migration period for males (0.25 days/year, $t = 2.28$, $P = 0.06$, $n = 8$), females (0.12 days/year, $t = 0.90$, $P = 0.38$, $n = 8$) or when pooling the two groups together (0.18 days/year, $t = 2.18$, $P = 0.06$, $n = 16$).

Degree of protandry

The inter-sexual difference in synchronous migration is causing degree of protandry to increase with degree of population arrival, i.e., protandry is smaller for the first compared to the later phases of migration ($F = 7.70$, $P = 0.014$). Table 2 presents degree of protandry for all migration phases with six of the eight species showing an increase in protandry with a significant mean slope of 0.02 days/degree of population arrival ($t = 2.61$, $P < 0.05$, $n = 8$). The largest increase in protandry was found for

Table 2 Degree of protandry (the number of days that males precede females) for eight migratory passerines and three phases of migration: the first 5%, first 50% and first 95% of the total number of individuals trapped

Species	5%	50%	95%	Slope
Goldcrest <i>Regulus regulus</i>	7	10	11	0.05
Blackbird <i>Turdus merula</i>	2	5	5	0.04
Reed Bunting <i>Emberiza schoeniclus</i>	9	15	14	0.06
Pied Flycatcher <i>Ficedula hypoleuca</i>	5	5	5	-0.01
Redstart <i>Phoenicurus phoenicurus</i>	6	8	9	0.04
Whinchat <i>Saxicola rubetra</i>	2	4	3	0.02
Blackcap <i>Sylvia atricapilla</i>	2	5	4	0.02
Red-backed Shrike <i>Lanius collurio</i>	3	2	1	-0.01
Mean change in protandry	4	7	7	0.02*

The slope values indicate change in degree of protandry comparing first 5%, 50% and 95%, (slope value is in days/degree of population arrival) (see also Fig. 2a–h)

* $P < 0.05$, two-tailed

Goldcrest and Blackbird with 0.05 and 0.06 days/degree of population arrival, respectively, whereas Pied Flycatcher and Red-backed Shrike showed a tendency of decreasing protandry with degree of population arrival (-0.01 days/degree of population arrival). We found no indication that degree of protandry is changing over time, for each population measure ($F = 0.46$, $P = 0.64$) and all species compared ($F = 0.72$, $P = 0.66$).

Trends in timing of arrival

Table 3 presents arrival trends for each sex and the three phases of migration. We found significant overall earlier

Table 3 Changes in timing of spring migration for eight migratory species in a 22-year period (1976–1997) (see “Methods” for details)

Species	M	W	D	Sex	Years	<i>n</i>	5%	50%	95%
Goldcrest <i>Regulus regulus</i>	Short	E	1,500	M	22	4,680	−0.28	0.22	0.05
				F	22	6,326	0.01	−0.05	−0.26
Blackbird <i>Turdus merula</i>	Short	E	1,500	M	22	2,526	−0.64*	−0.72*	−0.32
				F	22	2,849	−0.75*	−0.43	0.11
Reed Bunting <i>Emberiza schoeniclus</i>	Short	E	2,000	M	21	357	−0.73*	−0.24	0.13
				F	22	556	−0.01	0.06	−0.28
Pied Flycatcher <i>Ficedula hypoleuca</i>	Long	WA	6,500	M	20	2,625	−0.20	−0.04	−0.02
				F	22	2,538	−0.29*	−0.03	0.00
Redstart <i>Phoenicurus phoenicurus</i>	Long	WA	6,000	M	22	3,859	−0.35*	−0.16	−0.59*
				F	22	4,095	−0.24	−0.37*	−0.37*
Whinchat <i>Saxicola rubetra</i>	Long	WA	6,000	M	21	526	−0.35*	−0.03	−0.15
				F	22	652	−0.14	−0.01	−0.13
Blackcap <i>Sylvia atricapilla</i>	Long	EA	5,500	M	22	2,719	−0.22	−0.25	−0.17
				F	22	2,560	−0.31	−0.33	−0.11
Red-backed Shrike <i>Lanius collurio</i>	Long	EA	9,000	M	21	1,066	−0.32	−0.14	−0.03
				F	21	1,142	−0.09	−0.14	0.17
Mean change of arrival				M		18,358	−0.39**	−0.17	−0.14
				F		20,718	−0.23*	−0.16*	−0.11

Three measures of population arrival (first 5%, 50% and 95% of the total number of individuals each year, and change in the migration period of 90% of the populations (95–5% population arrival))

M Migration strategy: short- and long-distance migrants; *W* wintering area: *E* Europe, *WA* West Africa, and *EA* East Africa; *D* migration distance in km; *Years* number of years included; *n* number of individuals included for each species and sex

* $P < 0.05$, ** $P < 0.01$, two-tailed

arrival over time for the first 5% of males (0.39 days/year, $t = -5.62$, $P < 0.01$), and the first 5% (0.23 days/year, $t = -2.66$, $P < 0.05$) and first 50% (0.16 days/year, $t = 2.47$, $P < 0.05$) of the females. In all species, males show earlier 5% arrivals, while in females, all species except Goldcrest advanced their migration. For 50% arrival, all species except Goldcrest (males) and Reed Bunting (females) showed advanced migration. The last migration phase showed advanced male migration in all species except Goldcrest and Reed Bunting, while in females, only Pied Flycatcher and Blackbird did not show advanced migration. Except for female Pied Flycatcher 95% arrival, all long-distance migrants showed earlier arrival in all phases of migration. In short-distance migrants, 10 out of 18 measures of phenology indicated advanced migration.

Sex-differentiated arrival trends of each migration phase and species are presented in Fig. 2. We found no differences in slopes and elevations between males and female arrival trends when testing the three migration phases of each species (24 models in total). Males showed a tendency of higher rate of change compared to females (Table 3). However, the lack of difference between the sexes (pairwise t -test for the entire group, $t = -1.25$, $P = 0.224$, $n = 24$) indicates that the different population parts change phenology at a similar rate in both males and females.

Discussion

Overall, males precede females in all three phases of migration, while in males, migration is more synchronous compared to females. As an effect of the latter, we found that degree of protandry is smaller for the first phases of migration compared to later phases. Further, both sexes are advancing spring arrival over time and therefore no intersexual differences in arrival trends were found, indicating that males and females are responding similarly to climate change. Hence, inter-sexual phenological differences do not seem to constitute a potential bias for the numerous studies on changes in timing of spring arrival related to climate change. This finding is also in support of Rainio et al. (2007) who found that degree of protandry was not affected by climate.

The seven hypotheses on the adaptive significance of protandrous arrival (or appearance) to breeding areas reviewed by Morbey and Ydenberg (2001) are divided into two main groups: (1) indirect selection hypotheses, with selection acting within sexes but not between sexes, and (2) direct selection hypotheses based on the relative arrival timing of males and females having fitness consequences for both sexes. Most studies on birds have found support for the “rank advantage” hypothesis (indirect selection)

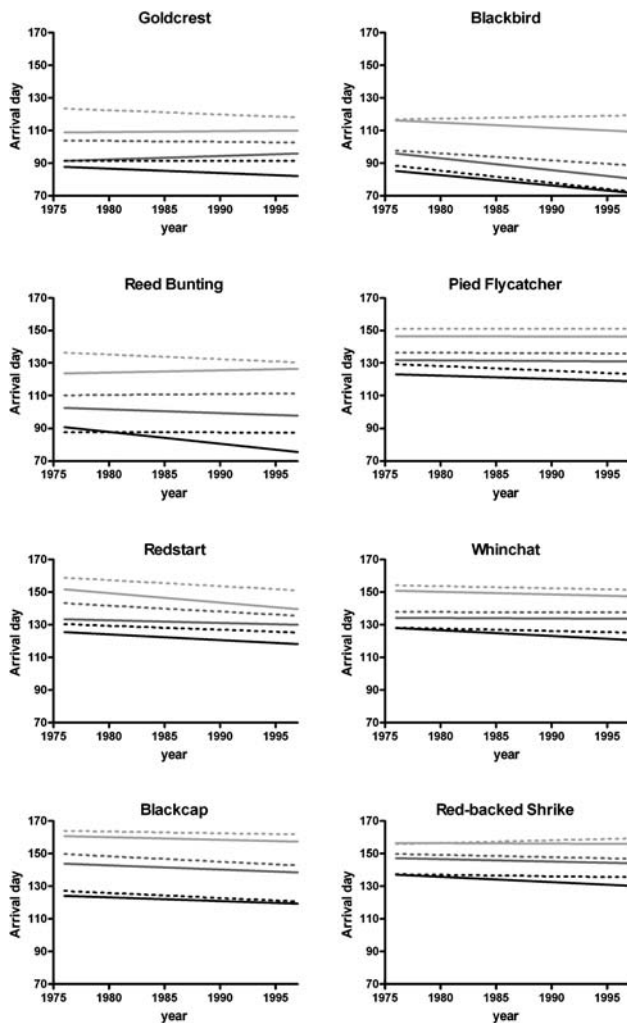


Fig. 2 Trends in the sex-differentiated population arrival for three phases of migration. *Solid lines* are males; *dotted lines* are females. The two *lower lines* in each figure are the 5% phase (*black*), the next two *lines* are the 50% phase (*dark gray*), and the two *upper lines* are the 95% phase (*light grey*)

(e.g. Kokko 1999) and the “mate opportunity” hypothesis (direct selection) (e.g. Rubolini et al. 2004).

In support of the “mate opportunity” hypothesis, Rubolini et al. (2004) found that sexual selection is driving the protandrous migration patterns in sub-Saharan migrants. Hence, competition for mates, rather than male–male competition for territories, is determining degree of protandry. Coppack et al. (2006) showed that degree of protandry reflects level of sexual selection in migratory songbirds, also suggesting that protandrous migration may arise from sexual selection. Further, Spottiswoode et al. (2006) showed that species with a stronger index of sexual selection have advanced their date of spring passage the most, indicating that spring arrival is controlled by female choice. Finally, Kokko et al. (2006) showed, by modelling the evolution of protandrous patterns, that the “rank advantage” hypothesis

alone could not explain protandry and that the implications of the “mate opportunity” hypothesis explains why protandry is the common pattern found in migratory birds.

We found that males and females show similar degrees of change in migration phenology in all phases of migration. Hence, the close coupling between the sexes in phenological changes indicates that selection for early arrival is operating in both sexes (direct selection).

In both sexes, degree of change is largest for the first phases of migration, indicating that competition for early arrival is acting within both males and females. Arguably, female migrants compete for an equally scarce resource (territories occupied by males) compared to males (competing for vacant territories). Hence, our findings seem to support that competition within the territorial sex (“rank advantage” hypothesis) cannot alone explain the patterns (see Kokko et al. 2006). Therefore, our results seem mostly in support of the “mate opportunity” hypothesis, as competition for mates are acting in both males and females.

Irrespective of trends, females show a less synchronous migration period (i.e. longer period) compared to males. This indicates less selection pressure within females compared to males (at least for later migration phases). It can be argued that females compete for a resource that is initially scarce (occupied territories) becoming more common over time. In contrast, males compete for vacant territories becoming scarce over time. Hence, our results may indicate that female competition for occupied territories is relaxed compared to males during the migration period.

Patterns of overall advanced female phenology, but consistently later arrival compared to males, could be caused by: (1) both sexes being selected to arrive early because of competition for mates, whereas females benefit by waiting until males have established territories (Francis and Cooke 1990; see also “waiting costs” hypothesis, cf. Morbey and Ydenberg 2001), or (2) female arrival is controlled by the actual breeding conditions. The latter implies that female phenology is a direct result of changes in the timing of food resource availability in the breeding areas and that males adjust arrival according to actual female arrival, thereby ensuring a territory and mating opportunities. However, there is a tendency (not significant) of males advancing spring arrival at a greater rate compared to females. If future studies corroborate this pattern, it would indicate indirect selection for earlier breeding area arrival.

Sex-differentiated changes in timing of arrival to breeding areas as a response to ecological changes in winter areas (Rubolini et al. 2004; Rainio et al. 2006) or during migration (Ahola et al. 2004) may influence subsequent mating decisions, with subsequent feedback on population dynamics such as reproductive success and individual fitness (Quader 2005). However, during decades of consistent earlier arrival of northern hemisphere

migratory birds (Bairlein and Winkel 2001; Lehikoinen et al. 2004; Thorup et al. 2007) we have found no evidence of sex-specific phenological changes.

Zusammenfassung

Geschlechtsverschiedene Zugmuster, Protandrie und Phänologie in nordeuropäischen Singvogelpopulationen

Diese Studie hat zum Ziel, Ursachen und Mechanismen zu untersuchen, die protandrische Zugmuster (die im Vergleich zu den Weibchen frühere Ankunft der Männchen im Brutgebiet) und intersexuelle Unterschiede im zeitlichen Zugverhalten angesichts der aktuellen phänologischen Änderungen durch den Klimawandel kontrollieren. Unter Verwendung von standardisierten Beringungsdaten von einem einzelnen Ort, von acht nordeuropäischen Singvogelarten über 22 Jahre gesammelt, untersuchten wir geschlechtsunterschiedliche Zugmuster, Protandrie und Phänologie der gesamten Population. Unsere Ergebnisse zeigen protandrische Muster für sowohl die ersten als auch die später ankommenden Individuen bei allen untersuchten Arten. Die Ankunftsdaten der einzelnen Männchen liegen dichter beieinander als die der Weibchen, so dass die ersten ankommenden Weibchen den Männchen zeitlich dichter folgen als die später ankommenden. Allerdings fanden wir keine geschlechtsspezifischen Unterschiede in der Verschiebung der Ankunftsdaten, da beide Geschlechter ihre Frühjahrsankunft mit der Zeit vorverlegen, wobei die größten Änderungen bei den am frühesten eintreffenden Individuen stattfinden. Diese Ergebnisse scheinen die „mate opportunity“-Hypothese zu unterstützen, da die Ankunftszeit von Männchen und Weibchen stark gekoppelt ist und beide Geschlechter um eine frühe Ankunft wetteifern. Änderungen in den Ankunftszeiten bei Männchen und Weibchen als Antwort auf klimatische Änderungen könnten die folgende Partnerwahl beeinflussen, was wiederum zu einer Rückkopplung auf die Populationsdynamik, z.B. durch Reproduktionserfolg und individuelle Fitness, führen könnte. Allerdings fanden wir während Jahrzehnten immer früherer Frühjahrsankünfte in allen Phasen des Zugs keinen Hinweis auf phänologische Unterschiede zwischen den Geschlechtern.

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