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Sex-specific timing of autumn migration in birds: the role of sexual size dimorphism, migration distance and differences in breeding investment

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Multiple studies have investigated differential migration of sexes during spring migration, while such differences during autumn migration are poorly studied. We tested several functional hypotheses explaining differences in autumn migration dates between sex and age classes and whether these patterns vary between short- and long-distance migrants (SDMs and LDMs, respectively). We used data of ringed birds from the Hanko and Lågskär Bird Observatory, Finland, North Europe. Altogether data for c. 200,000 ringed birds including 14 passerine species were used. Protogyny, with females migrating earlier than males, was common among young birds, and this difference was clearer in LDMs than in SDMs. However, in adults protogyny was not found, whereas protandy, males migrating earlier than females, was found in two species. Furthermore, species-specific sexual size dimorphism, SSD, was significantly connected with the time differences in migration between the sexes in SDMs, but not in LDMs. These results suggest that multiple factors are likely affecting differential timing of autumn migration in birds. It can be beneficial for males, especially young birds, to spend additional time at the breeding grounds to prospect for future nesting sites. The connection between SSD and autumn migration dates in SDM could be linked with the pattern where larger sized individuals can winter closer to the breeding grounds. In addition, later migration dates of adult females compared to adult males could suggest that larger reproductive investment by adult females on breeding may delay their autumn migration.

1. Introduction

Sex-specific differences in timing of the life cycle are common in nature. In protandry, timing of phenology in males is earlier than in females. For instance, the stamen of flowers develops earlier than pistils in the same plant individual likely to prevent self-pollination (Bertin and Newman 1993). In butterflies and spring migratory birds protandy has been suggested to provide a link with breeding strategies (Petersen 1892, Demoll 1908, Petersen 1947, Wiklund & Fagerström 1977, Morbey & Ydenberg 2001, Morbey *et al.* 2012).

In contrast to protandry, protogynous females

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have an earlier phenology than males. Protogyny is much rarer than protandry, but for instance in some migratory birds females migrate before males in spring in species where females are colourful and take care of establishing the breeding territory (Oring & Lank 1982, Reynolds *et al*. 1986). Furthermore, protogyny has been suggested to occur during autumn migration in birds, although evidence is equivocal (Ellegren 1991, Kjellén 1992, Mills 2005).

Many studies have addressed spring phenology, but little or no information is available on autumn phenology (recent review in Gallinat *et al.* 2015). In general sex-specific differences in timing of autumn migration have rarely been examined and even more seldom the potential causes have been addressed across multiple species. During autumn migration the situation differs from that in spring: there are two different age classes with potentially different migratory behaviour: adults and young birds, the latter being inexperienced since they have not yet migrated. The timing of migration of these two age groups often differs (Kjellén 1992, Newton 2008, Fox *et al.* 2016). For instance in species where adults moult at the breeding grounds young typically migrate earlier than adults.

The case is usually the opposite among species where adults do not moult at the breeding grounds (Kjellén 1992, Newton 2008). These different age classes also allows for investigation of the importance of different hypotheses explaining sex-specific differences in autumn migration. Furthermore, short- and long-distance migrants (hereafter SDMs and LDMs, respectively) have fundamental differences in migration strategy. Long-distance migrants need to leave much earlier to reach the tropical wintering areas whereas short-distance migrants can migrate much later to arrive in time at their wintering quarters in Europe and North Africa (Kjellén 1992, Newton 2008, Ozarowska & Zaniewicz 2015).

Several hypotheses may explain sex differences in autumn migration (e.g., Mills 2005). We briefly review these hypotheses and we introduce a new hypothesis that is linked to different investment of sexes during breeding (not mentioned by Mills 2005, but see Kjellén 1992). The hypotheses for differential timing of migration by the sexes during autumn migration are as follows:

i) Rank advantage hypothesis, which suggests that males should migrate later to protect their future breeding territory in both adult and young birds (Ketterson & Nolan 1976, Myers 1981a, Mills 2005). In the broad sense this could also mean time used for nest site prospecting at the breeding grounds for the future (Doligez *et al*. 2004).
ii) Mate opportunity hypothesis suggesting that males leave after females to maximize their mating probability (Wiklund & Fagerström 1977, Bulmer 1983, Mills 2005). This should however only apply to adult birds, because young are typically immature during the same breeding season as when they have hatched.
iii) Susceptibility hypothesis suggesting that the larger sex should be able to depart later because of lower susceptibility to deteriorating environmental conditions (Ketterson & Nolan 1976, 1983, Francis & Cooke 1986, Møller 2004, Mills 2005). According to this hypothesis the larger the size difference between the sexes in different species, the larger the difference in timing in both adult and young birds. This should apply both at the population and the individual level (Saino *et al.* 2010). As larger sized individuals are also often wintering closer to the breeding grounds (Ketterson & Nolan 1976, 1983), they do not necessarily need to depart as early as smaller sized individuals. This hypothesis could only concern SDMs, since LDMs spend their winter in areas where temperature is not restrictive (Newton 2008).
iv) Winter territory acquisition hypothesis suggests that in species, which have permanent winter territories at least some time during winter, subordinate individuals (young and females) should migrate earlier than dominant individuals (adult and males; Mills 2005). However, in species, which do not hold winter territories, such a connection should not exist.
v) Breeding investment hypothesis (our new hypothesis). Investment in breeding may have carry over effects and influence when either sex is able to start migration. For instance, in many wader species females depart soon after hatching of chicks, whereas males take care of brood rearing and can depart when chicks have grown older (Myers 1981b, Meissner & Ka-

mont 2005, Meissner & Krupa 2009). In birds of prey, females can start moult of the flight feathers already during brood rearing while males, which provide food for the young only start moult later (Schmutz & Schmutz 1975, Newton & Marquiss 1982, Arroyo & King 1996). This can cause delayed autumn migration of adult males compared to females (Kjellén 1992). In passerines, females typically invest more in breeding than males (Cramp *et al.* 1977–1994) and they often moult later than males (Jenni & Winkler 1994, Hemborg 1999). As species in this study are passerines, we could expect delayed departure dates of females compared to males. Furthermore, this should only occur in adult birds since young birds have not bred yet.

Our aim was to test these hypotheses using migration data for 14 common bird species for which sexing is possible in both young and adult birds.

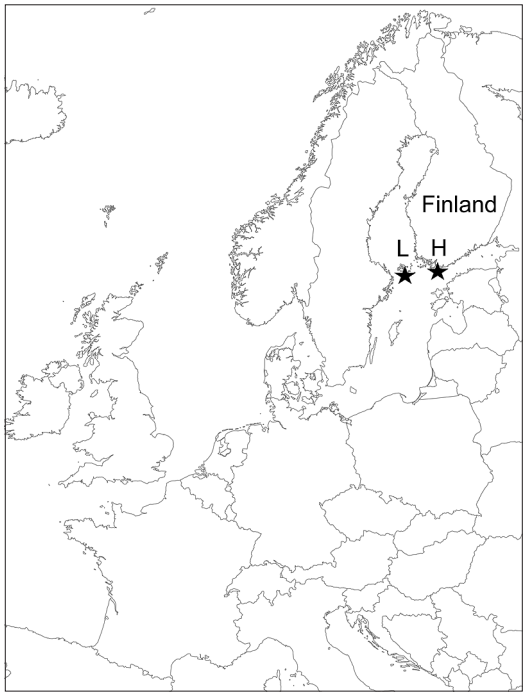

Fig. 1. A map showing the locations of the Hanko (H) and Lågskär (L) Bird Observatories.

2. Material and methods

2.1. Migration data

Migratory birds have been trapped with mist-nests at Hanko (59°49' N, 22°54' E) and Lågskär (59°50' N, 19°55' E) Bird Observatories in Southwest Finland during autumn migration in 1979–2014 and 1973–2012, respectively (Fig. 1). We used the study period 25 July till 15 November at both observatories. At Hanko trapping and observation effort has been relatively constant from 25 July till 5 November annually, and days without trapping are mainly caused by poor weather (rain or heavy wind) than actual observation gaps (e.g., Lehikoinen 2011). In recent years the season has continued until 15 November due to milder late autumns. This migration period does anyway cover the main migration period of all the study species (Lehikoinen & Vähätalo 2000). However, the Lågskär Bird Observatory has more trapping gaps especially in 1990s and 2000s, but we included the data, since another observatory can act as a replicate site because the same breeding population is migrating through the observatories, and the additional data can increase sample size for uncommon species. We do not believe that these observation gaps cause significant bias, since results with and without Lågskär data were almost identical (see Results and Table S1). In both observatories biometric measurements (such as maximum wing length and body weight; Svensson 1992) have been sporadically taken.

In the two observatories trapped birds have been ringed, aged and sexed according to the existing literature (Svensson 1975, 1984, 1992). In this study we used 14 bird species, which are sufficiently abundant to make appropriate analyses (at least 20 individuals or more of each of the sex and age categories in the combined data; *e.g.*, Vähätalo *et al.* 2004) in which individuals can be aged and sexed during autumn (Table 1). In Red-backed Shrike *Lanius collurio* young birds cannot be sexed based on plumage, but we included adult birds in the analyses. In the multi-species analyses all individuals were included even when sample sizes were smaller than 20 individuals per age/sex group. In addition, we did not include species with a main migration season that can continue during the winter outside the main trapping period (excluding e.g., Bohemian Waxwing *Bombycilla garrulus* and Fieldfare *Turdus pilaris*; Lehikoinen

Table 1. Sample sizes for different age and sex classes, migration period, sexual size dimorphism (SSD) and migration behaviour (Mig: short- and long-distance migrants, SDM and LDM, respectively) of 14 passerine species (1y = young, +1y = adult, M = male, F = female, fl = age unknown).

Species	1y M	1y F	+1y M	+1y F	fl M	fl F	1y	+1y	Period	SSD (%)	Mig
Hanko Bird observatory											
Bluethroat (*Luscinia svecica*)	22	23	5	4	0	0	1	0	25.7.–15.11.	3.91	LDM
Common Redstart (*Phoenicurus phoenicurus*)	503	564	41	21	1	84	29	0	25.7.–15.11.	2.65	LDM
Eurasian Blackbird (*Turdus merula*)	228	264	39	31	0	3	13	1	20.9.–15.11.	3.32	SDM
Blackcap (*Sylvia atricapilla*)	804	858	10	16	5	40	75	0	1.8.–15.11.	0.13	LDM
Goldcrest (*Regulus regulus*)	15,746	11,716	260	252	311	211	396	6	15.8.–15.11.	4.15	SDM
Great Tit (*Parus major*)	11,465	25,593	1,926	2,708	71	71	949	38	1.9.–15.11.	4.12	SDM
Red-backed Shrike (*Lanius collurio*)	0	0	25	26	1	0	414	2	25.7.–15.11.	0.63	LDM
Chaffinch (*Fringilla coelebs*)	639	762	218	214	4	30	33	1	25.8.–15.11.	6.67	SDM
Brambling (*Fringilla montifringilla*)	249	251	36	19	2	0	15	0	25.7.–15.11.	5.81	SDM
Greenfinch (*Carduelis chloris*)	1,860	2,198	817	836	30	105	31	6	1.9.–15.11.	2.97	SDM
Eurasian Siskin (*Carduelis spinus*)	2,254	1,905	411	378	8	16	405	6	1.8–15.11.	2.66	SDM
Northern Bullfinch (*Pyrrhula pyrrhula*)	878	1423	190	155	13	4	13	2	20.9.–15.11.	2.26	SDM
Yellowhammer (*Emberiza citrinella*)	29	50	4	2	0	0	3	0	15.9.–15.11.	5.40	SDM
Reed Bunting (*Emberiza schoeniclus*)	127	196	3	4	2	0	14	0	1.9.–15.11.	6.93	SDM
Lågskär Bird Observatory											
Bluethroat (*Luscinia svecica*)	158	120	14	10	0	1	17	0	25.7.–15.11.	3.79	LDM
Common Redstart (*Phoenicurus phoenicurus*)	686	556	185	64	10	463	24	0	25.7.–15.11.	2.69	LDM
Eurasian Blackbird (*Turdus merula*)	623	634	206	214	3	10	36	3	20.9.–15.11.	4.45	SDM
Blackcap (*Sylvia atricapilla*)	958	795	33	40	13	115	87	1	1.8.–15.11.	0.40	LDM
Goldcrest (*Regulus regulus*)	35,870	28,157	1,302	1,198	1,386	1,192	409	9	15.8.–15.11.	3.97	SDM
Great Tit (*Parus major*)	4,939	11,883	503	752	78	81	123	2	1.9.–15.11.	4.11	SDM
Red-backed Shrike (*Lanius collurio*)	0	0	20	36	0	1	315	0	25.7.–15.11.	1.82	LDM
Chaffinch (*Fringilla coelebs*)	811	888	438	425	16	114	14	5	25.8.–15.11.	7.56	SDM
Brambling (*Fringilla montifringilla*)	323	339	195	112	5	22	8	1	25.7.–15.11.	6.76	SDM
Greenfinch (*Carduelis chloris*)	220	266	140	99	8	16	5	0	1.9.–15.11.	2.91	SDM
Eurasian Siskin (*Carduelis spinus*)	1,592	1,565	484	406	15	35	53	10	1.8.–15.11.	2.50	SDM
Northern Bullfinch (*Pyrrhula pyrrhula*)	2,166	3,523	460	537	29	35	38	4	20.9.–15.11.	2.18	SDM
Yellowhammer (*Emberiza citrinella*)	46	76	20	27	10	19	6	1	15.9.–15.11.	5.62	SDM
Reed Bunting (*Emberiza schoeniclus*)	244	310	36	42	14	14	20	2	1.9.–15.11.	7.96	SDM

& Vähätalo 2000). Last, we only included passerine species to minimize potential impacts of inclusion of orders with different migration and reproductive strategies. The study species were both long- and short-distance migrants including partial migratory species (Table 1).

The northern location of the two observatories guaranteed that the trapped birds originated from northern boreal and arctic breeding areas (Valkama *et al.* 2014), and thus birds from different populations within one species do not complicate the patterns. In addition, due to the northern location the trapping dates most likely reflect differences in departure dates (although it concerns passing through migration dates) as adults may migrate faster and catch up with slower young birds before they reach the wintering grounds (e.g., Hederström & Pettersson 1987, Moore *et al.* 2003).

We used data between 25 July and 15 November. However, in some species, which are often breeding near the observatories, we delayed the starting date based on the knowledge of the migration patterns so that breeding individuals would not affect the results (Lehikoinen & Vähätalo 2000). The species-specific sample sizes and migration seasons are shown in Table 1. After selection of species and migration season, the trapping numbers of the study species in both observatories were rather similar (Hanko total 92,723; on average 2,575/year, and Lågskär total 110,664; 2,766/year).

2.2. Statistical analyses

We conducted four different types of analyses. First we compared migration dates of sexes between different age classes for all species in the two observatories to get an overview of the frequency of protogyny and protandry among study species. In addition, these analyses would tell whether females and young birds migrate earlier than males and adults only in species which establish winter territories and e.g., do not winter in flocks (like finches and buntings; Cramp *et al.* 1977–1994). We estimated the rate of protogyny/protandry (Pro) using the method of Morbey (2000), see formula (1), where the difference is measured as the area (measure unit is days) between the cumulative percent distribution of male migration dates (M(t)) and female migration dates (F(t)):

$$\text{Pro} = \Sigma\,(\text{M}(t) - \text{F}(t))\,\text{d}t\,/\,100 \qquad (1)$$

where dt is = 1 day. Negative values mean protogyny and positive protandry. The statistical significance of the observed amount of protogyny or protandry was evaluated using randomization following the modified protocol of Morbey (2000). A null distribution of protandry was generated based on the empirical distribution of migration dates. For each species, age class and site we performed 10,000 iterations where the sex was randomized (but ensuring that the original sex ratio was maintained) and protogyny/protandry was calculated. Based on these two-tailed distributions we calculated the *P*-values for each group (number of simulated protogynies/protandries that are larger than the observed pattern multiplied by two because of the two-tailed distribution). Because of multiple testing (48 tests) we used sequential Bonferroni correction to adjust *P*-values for the significance level of 0.05 (Rice 1989). The analyses were conducted in Matlab version R2014b.

Second, we analysed whether there was a general pattern among species by combining the data of all the species of the two observatories. We conducted a linear mixed-effect model where ringing date of individuals was explained by fixed variables of sex, age, migration behaviour, the interaction between these three and year in factor format to account for differences between years. Random factors included sex and age and their interaction within species to account for species specific slopes for age and sex categories. The full model was thus

(1) Date ~ Sex*Age*Mig + Year + Site + (Sex*Age | Species),

where, Date is the timing of ringing, Sex and Age are sex and age of the bird, Mig is the migration strategy (SDM or LDM), Year is year (factor), Site is ringing location (Hanko or Lågskär) and Species is id of species. Based on this analysis we were able to investigate whether males or females migrate earlier in general and what is the role of age and migration distance in this pattern. According to the results of Mills (2005), we expected to find protogyny among migrants. If protogyny occurs in both age classes, it would support the rank advance hypothesis, but if protogyny is found only among adult birds, it would support the mate opportunity hypothesis, since only adults were capable of breeding during the same year when trapped. Furthermore, if protandry occurs among adult birds, it would suggest that larger investment of females in breeding would delay their breeding relative to breeding males, while such an effect should not occur among young birds. The analyses were conducted using function lmer and lmerTest in R version 3.3.1 (R Core Team 2016).

Third, we investigated whether species-specific sexual size dimorphism (size differences between males and females, SSD) explained the corresponding differences in the timing of migration. If species, which have larger differences in body mass between the sexes, also show increasing protogyny, it would support the susceptibility hypothesis – larger males are capable of staying longer near the breeding grounds than smaller females. We conducted a linear mixed effect model, where protogyny/protandry values calculated in the first analyses using the method of Morbey (2000) were explained by SSD, age, migration strategy and ringing location. Since closely related species may have similar responses due to common ancestry, we took the phylogeny of the species into account in the random structure of the model. We downloaded ten different combinations of phylogenies from *www.birdtree.org* (Jetz *et al.* 2012, Table S2). We start the analyses by test-

Table 2. Median trapping dates of different age and sex classes at Hanko and Lågskär Bird Observatories (1y = young, +1y = adult, M = male, F = female). If timing of sexes (Pro: positive values protandry, negative values protogyny) differed significantly based on randomizing tests (adjusted *P*-values; see methodology), the values are shown in bold. Negative values mean that females migrated earlier than males and vice versa.

Species	1y M	1y F	Pro	*P*	+1y M	+1y F	Pro	*P*
Hanko Bird Observatory								
Bluethroat (*Luscinia svecica*)	5 Sep	3 Sep	–4.48	0.043	–	–	–	–
Common Redstart (*Phoenicurus phoenicurus*)	**6 Sep**	**2 Sep**	**–4.37**	**<0.0001**	6 Sep	4 Sep	–1.73	0.256
Eurasian Blackbird (*Turdus merula*)	15 Oct	14 Oct	0.16	0.431	16 Oct	15 Oct	2.16	0.281
Blackcap (*Sylvia atricapilla*)	**10 Sep**	**9 Sep**	**–2.49**	**0.0012**	–	–	–	–
Goldcrest (*Regulus regulus*)	**4 Oct**	**2 Oct**	**–2.36**	**<0.0001**	8 Oct	11 Oct	1.57	0.086
Great Tit (*Parus major*)	**7 Oct**	**5 Oct**	**–1.32**	**<0.0001**	**12 Oct**	**13 Oct**	**0.97**	**0.0002**
Red–backed (Shrike *Lanius collurio*)	–	–	–	–	10 Aug	5 Aug	–4.85	0.031
Chaffinch (*Fringilla coelebs*)	**25 Sep**	**20 Sep**	**–3.67**	**0.0008**	12 Oct	8 Oct	–3.93	0.022
Brambling (*Fringilla montifringilla*)	17 Oct	11 Oct	–4.35	0.0031	–	–	–	–
Greenfinch (*Carduelis chloris*)	**26 Oct**	**24 Oct**	**–1.57**	**<0.0001**	26 Oct	27 Oct	1.05	0.0059
Eurasian Siskin (*Carduelis spinus*)	9 Oct	7 Oct	–0.89	0.03	6 Oct	9 Oct	0.057	0.482
Northern Bullfinch (*Pyrrhula pyrrhula*)	**22 Oct**	**21 Oct**	**–1.18**	**0.0016**	24 Oct	22 Oct	–0.16	0.429
Yellowhammer (*Emberiza citrinella*)	20 Oct	16 Oct	–7.08	0.004	–	–	–	–
Reed Bunting (*Emberiza schoeniclus*)	**30 Sep**	**23 Sep**	**–7.26**	**<0.0001**	–	–	–	–
Lågskär Bird Observatory								
Bluethroat (*Luscinia svecica*)	**4 Sep**	**29 Aug**	**–5.18**	**<0.0001**	–	–	–	–
Common Redstart (*Phoenicurus phoenicurus*)	**12 Sep**	**8 Sep**	**–4.01**	**<0.0001**	9 Sep	11 Sep	1.0769	0.267
Eurasian Blackbird (*Turdus merula*)	16 Oct	15 Oct	–0.51	0.191	16 Oct	17 Oct	0.3808	0.348
Blackcap (*Sylvia atricapilla*)	**24 Sep**	**23 Sep**	**–2.94**	**0.0001**	26 Sep	24 Sep	–2.7576	0.291
Goldcrest (*Regulus regulus*)	**2 Oct**	**2 Oct**	**–1.03**	**<0.0001**	**7 Oct**	**9 Oct**	**2.0035**	**<0.0001**
Great Tit (*Parus major*)	8 Oct	8 Oct	0.06	0.331	**10 Oct**	**12 Oct**	**2.2639**	**<0.0001**
Red-backed Shrike (*Lanius collurio*)	–	–	–	–	6 Aug	4 Aug	–0.4611	0.430
Chaffinch (*Fringilla coelebs*)	**4 Oct**	**30 Sep**	**–4.03**	**<0.0001**	4 Oct	2 Oct	–2.4153	0.0047
Brambling (*Fringilla montifringilla*)	12 Oct	10 Oct	–1.88	0.055	11 Oct	9 Oct	–0.5601	0.363
Greenfinch (*Carduelis chloris*)	20 Oct	19 Oct	–0.72	0.237	23 Oct	27 Oct	1.1756	0.198
Eurasian Siskin (*Carduelis spinus*)	**7 Oct**	**6 Oct**	**–1.46**	**0.0013**	4 Oct	7 Oct	1.6668	0.020
Northern Bullfinch (*Pyrrhula pyrrhula*)	**18 Oct**	**17 Oct**	**–0.85**	**0.0007**	19 Oct	19 Oct	0.8596	0.085
Yellowhammer (*Emberiza citrinella*)	21 Oct	24 Oct	3.00	0.0676	27 Oct	21 Oct	–0.937	0.437
Reed Bunting (*Emberiza schoeniclus*)	**6 Oct**	**30 Sep**	**–6.16**	**<0.0001**	6 Oct	1 Oct	–4.6865	0.012

ing which phylogeny structure of the ten combinations fit best with the full model, which was:

(2) Pro ~ SSD*Age*Mig + Site + (1 | Species),

where Pro is protandry/protogyny of the species age group, SSD is sexual size dimorphism, Age is age class of species, Mig is migration strategy (SDM or LDM) and Site is ringing location. Species is a random factor with phylogenic tree. The model with the lowest Deviance Information Criterion (DIC, similar to AIC see Burnham & Anderson 2002) values (♂tree 7; Table S2) was used. Since wing length data from the observatories were insufficient for all species, we used published data of body size differences between the sexes from Finland (Piha & Lehikoinen 2016). The SSDs of species are given in Table 1. The modelling was conducted using function MCMCglmm in R version 3.2.2 (R Core Team 2016) using 505,000 iterations, where first 5,000 were used for "burning in" and thinning interval of 500. We used the following priors (R-structure: V=1, nu=0.00, G-structure: V=1, nu=0.02).

Last, we tested at the individual level whether larger individuals migrate later, which would support the susceptibility hypothesis. We used wing length as a proxy of body size as this typically correlate with other biometrical measurements of individuals (Ashton 2002). We used all individuals for which wing length had been measured and both age and sex had been identified. We used only

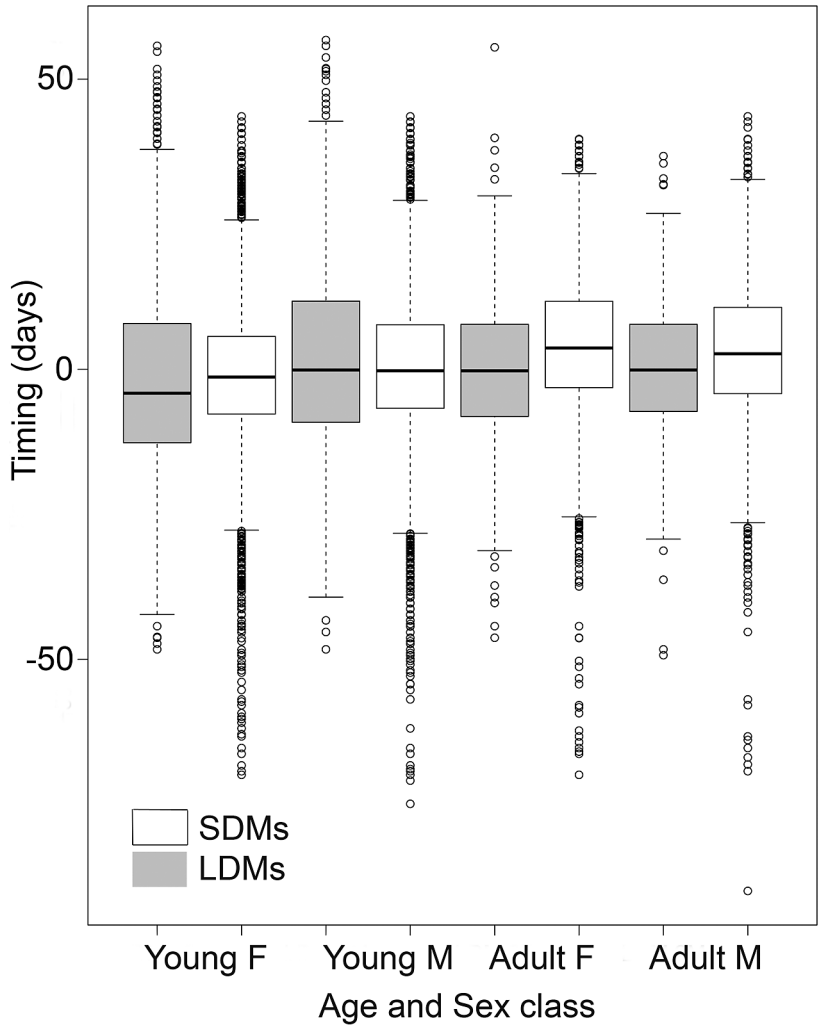

Fig. 2. Timing of migration in different age and sex groups (young and adults, females = F, and males = M) in short- (SDMs) and long-distance migrants (LDMs). The timing migration has been standardized (mean zero) species-specifically because of varying migration periods.

data from Hanko, where the data included altogether 865 individuals from all 14 species (mean *N* of individuals 61, min–max 8–151). Since in this data there was a trend that large sized species tend to migrate later than smaller sized species, especially in SDMs, and larger males migrate later than smaller females (especially in young birds; see results), we standardized (mean zero, standard deviation 1) the wing length of species age and sex group specifically before the analysis. We conducted a linear mixed-effect model, where the ringing date of the individual was explained by its standardized wing length and migration behaviour and their interaction. Random factors included were sex and age class (young male, young female, adult male, adult female) within species enabling species-specific slopes and year. The full model was

(3) Date ~ Wing*Mig + (1 | Species/SexAge) + (1 | Year),

where Date and Wing are ringing date and the standardized wing length of the individual, Mig is migration strategy (SDM or LDM), SexAge is sex and age class, Species is species id and Year is year. The analyses were conducted using function lmer and lmerTest in R version 3.3.1 (R Core Team 2016).

In each model, we first fitted the full model and tested the significance of the three-way interaction term (models 1 & 2) or two-way interaction terms

Table 3. Parameter estimates and test values of mixed-effect models where autumn migration dates are explained by the fixed factors of age, sex and migration strategy (Mig: SDM and LDM, short- and long-distance migrants, respectively) their interaction and site. The test-values of the years (1974–2014) are not shown, but all years except 1990 differed significantly from the starting year 1973 (all P < 0.001).

Parameter	β ± *SE*	*df*	*t*	*P*
Intercept	237.4 ± 6.4	18	36.73	< 0.001
Sex (males compared to females)	5.26 ± 1.01	12	5.12	< 0.001
Age (adults compared to young)	3.05 ± 1.70	20	1.78	0.088
Mig (SDMs compared to LDMs)	41.06 ± 7.63	17	5.38	< 0.001
Sex × Age (adult males compared to others)	–4.97 ± 1.12	222	–4.42	< 0.001
Sex × Mig (male SDMs compared to others)	–3.23 ± 1.17	11	–2.76	0.018
Age × Mig (adult SDM compared to others)	0.48 ± 1.89	17	0.26	0.801
Sex × Age × Mig (adult male SDMs compared to others)	3.10 ± 1.16	123	2.67	0.009
Site (Lågskär compared to Hanko)	1.86 ± 0.06	194943	31.26	< 0.001

(model 3). If this was significant, we considered that to be the best model (Zuur *et al.* 2009). If the highest level interaction was not significant, we removed this interaction and investigated the simplified model.

3. Results

At the Hanko Bird Observatory eight out of 13 species showed significant protogyny after Bonferroni correction and no protandry was observed among young birds. Among adults one out of 9 species (Great Tit *Parus major*) showed significant protandy at Hanko after Bonferroni correction, and no significant protogyny was observed (Table 2, Fig. 2). At the Lågskär Bird Observatory eight out of 13 species showed significant protogyny among young after Bonferroni correction, and no protandry was observed. Among adults two species (Goldcrest *Regulus regulus* and Great Tit) showed significant protandry at Lågskär after Bonferroni correction, and no significant protogyny was observed (Table 2, Fig. 2).

The mixed effect model revealed that there was significant three-way interaction between sex, age and migration behaviour connected with the migration date of species in the combined data of the observatories. Based on the coefficients of the models, this interaction means that young females migrated earlier than young males, but this difference was larger in LDMs compared to SDMs. Among adults there was no such difference and

Table 4. Parameter estimates, effective sample sizes and *P*-values of MCMC mixed-effect models where species-specific timing differences of sex were explained by sexual size dimorphism (SSD), migration strategy (Mig: SDM and LDM, short- and long-distance migrants, respectively), age (adult or young) and ringing location.

Parameter	β (min, max 95% c.i.)	Effective sample	*P*
Intercept	–4.04 (–6.56, –1.28)	1,000	0.008
SSD	1.18 (–0.21, 2.72)	1,000	0.130
Mig (SDMs compared to LDMs)	8.34 (4.49, 12.33)	1,000	< 0.001
Age (young compared to adults)	0.86 (–2.32, 4.32)	1,000	0.594
Location (Lågskär compared to Hanko)	1.16 (0.25, 2.07)	1,000	0.020
SSD × Age (young compared to adults)	–1.77 (–3.27, –0.05)	1,000	0.038
SSD × Mig (SDMs compared to LDMs)	–2.30 (–3.74, –0.54)	1,000	0.008
Age × Mig (young SDMs compared to others)	–3.19 (–7.44, 1.17)	1,000	0.168
SSD × Age × Mig (young SDMs compared to others)	1.89 (0.10, 3.63)	1,000	0.044

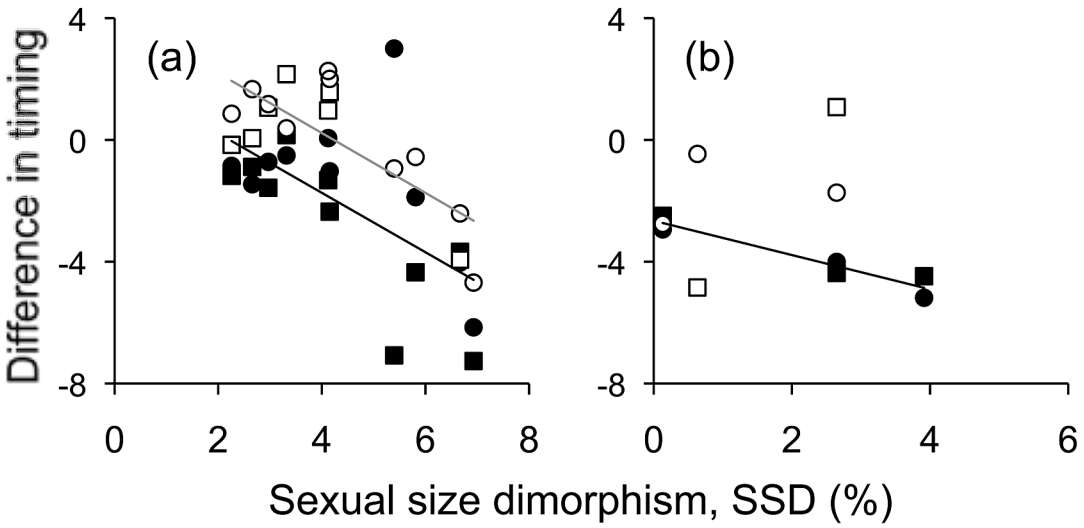

Fig. 3. Migration time difference between the sexes in relation to sexual size dimorphism (SSD) in (a) short- and (b) long-distance migrants in young (black symbols) and adult birds (white symbols) using combined data of Hanko (squares) and Lågskär (dots) Bird Observatories. Solid lines represent least squares lines between the significantly correlating variables.

sexes migrated on average at the same time in both migratory groups (Fig. 2, Table 3). Species-specific timing of different age and sex groups are shown in Supplementary Figs 1 & 2.

There was a significant interaction between SSD, age and migration strategy in the model explaining species-specific protandry/protogyny. This interaction suggests that protogyny was significantly stronger in young compared to adults, and the slope between timing difference of sexes and SSD was more negative in SDM and young LDMs than in adult LDMs (Table 4, Fig. 3a–b). In addition, at Lågskär time difference between females and males was shorter than at Hanko (Table 4, Fig. 3a–b).

Last, the interaction between wing length and migration strategy was significant and this suggested that the connection between migration date and wing length was dependent on migration strategy. Based on the coefficients, SDMs show more positive connection between migration date and wing-length than LDMs. In LDMs long-winged birds tend to migrate earlier than short-winged birds, but in SDMs the pattern was opposite. However, in neither of the cases the coefficients were different from zero (Table 5).

4. Discussion

Our first analyses showed that protogyny is common among young birds during autumn migration,

Table 5. Parameter estimates and test values of mixed-effect models where autumn migration dates are explained by the fixed factors of wing length and migration strategy (Mig: SDM and LDM, short- and long-distance migrants, respectively) their interaction. The test-values of the years (1974–2014) are not shown, but all years except 1990 differed significantly from the starting year 1973 (all $P < 0.001$).

Parameter	β ± *SE*	*df*	*t*	*P*
Intercept	296.7 ± 31.7	111	9.34	< 0.001
Wing	–0.63 ± 0.38	136	–1.67	0.10
Mig (SDMs compared to LDMs)	–61.36 ± 34.13	81	–1.80	0.076
Wing × Mig (SDMs compared to LDMs)	1.15 ± 0.40	101	2.86	0.005

whereas among adults two SDM species showed significant protandry and no significant protogyny was found. This does not support the mate opportunity hypothesis (ii). Furthermore, since protogyny is also observed among species that winter in flocks and do not establish territories (finches and buntings; Cramp *et al.* 1977–1994), we rejected the winter territory acquisition hypothesis (iv). However, the rest of the hypotheses were at least partly supported.

The connection between SSD and migration dates of the two sexes especially in SDMs supports the susceptibility hypothesis (iii). However, since protogyny was not observed in adults and at least in two species adult females migrated later than adult males, finding could also support the breeding investment hypothesis (v). Since adult females likely invest more on breeding compared to adult males this can lead into a delayed post-breeding moult and autumn migration of females (Cramp *et al.* 1977–1994, Jenni & Winkler 1994, Hemborg 1999). In contrast, among young protogyny was common as one would expect based on the rank advanced hypothesis (ii). We cannot fully separate these three hypotheses and they are not mutually exclusive.

The reason why protogyny is common among young birds could be that inexperienced young males use the additional days before autumn migration to prospect for suitable future nesting territories (rank advantage hypothesis). Nest site prospecting is common among birds even before sexual maturity (Boulinier & Danchin 1997, Doligez *et al.* 2004). Since males have higher natal philopatry than females among birds (Greenwood 1980, Pakanen *et al*. 2015), nest site prospecting can be important for young males that need to find the first suitable nesting site next spring. Adult males can start nest site prospecting already during the breeding season. In collared flycatchers *Ficedula albicollis* adult males visit nests of other pairs during the breeding season and acquire cues of territory quality for the future (Doligez *et al.* 2004), but in pied flycatchers both males and females prospect equally during the breeding season (Thomson *et al.* 2013). In addition, adult males know the surroundings of their breeding territory already during the first breeding season, and they do not need to spend as much time during post-breeding period as young males on prospecting. The reason why protogyny of young birds was larger in LDMs compared to SDMs could be that SDMs migrate in general later compared to LDMs. Because of this SDMs have in general more time for nest site prospecting and there is no need to allocate as much time as in young male LDMs. An alternative hypothesis could be that SDM females are more philopatric than LDM females and as a consequence SDM females spend more time inspecting their natal territories than LDM females.

The significant connection between migration timing difference of sexes and SSD at the population level in SDMs supports the susceptibility hypothesis in this migratory group: larger males can tolerate cold environmental conditions better than females. This was observed only in SDMs, which is logical since larger males can winter closer to the breeding grounds (King *et al.* 1965, Ketterson & Nolan 1976, 1983, Prescott & Middleton 1990). All LDMs migrate to tropical areas where coldness is unlikely the limiting factor and birds typically migrate before coldness starts to limit their food availability. In SDMs this could be also linked to the rank advantage hypothesis, according to which SSD determines how much more time young males can use for prospecting compared to young females. In addition, nest site prospecting after the breeding season could be the reason why departure dates of passerines have hardly changed in recent years despite arrival and breeding dates having advanced due to climate change (Dunn & Winkler 2010, Lehikoinen & Sparks 2010, Lehikoinen 2011). Additional time after breeding could be used for prospecting for future nesting sites, but only if this provides fitness benefits and/or there is no selective pressure for early arrival at the wintering grounds. One such benefit of early arrival at the winter quarters could be better timing of moult relative to timing of food availability.

Saino *et al.* (2010) have previously found a connection between SSD and differences in timing of migration between the sexes among spring migratory LDM species in a Mediterranean stop-over site, but found only weak support at the individual level. Our study found that the individual level connection can be linked with migration strategy and SDMs can show more positive connection between migration dates and wing length than LDMs. However, we could not show that the coef-

ficients of the SDMs would have differed from zero. In our case, the wing length analyses had relatively small sample sizes, and we suggest this topic to be investigated with larger datasets. Optimally, this pattern should be studied in high latitude study sites, where mixture of multiple populations with potentially partly different migration dates cannot complicate detection of any of the patterns compared to southern latitudes.

The reason why we did not observe significant associations between sex difference in timing of migration as often in adults as in young birds could partly be due to sample sizes for young birds being much larger than for adults. We must also emphasize that our data on LDMs is limited to four species and our results thus mainly concern SDMs. Furthermore, we have only included phylogeny in the SSD analyses and in rest of the models species are considered to be independent. We do not believe that this is major weakness, since all species are passerines and e.g., the same families of our study species include also SDMs and LDMs (e.g., thrushes or warblers; Cramp *et al.* 1977–1994).

In conclusion, multiple factors may cause differential timing of autumn migration among males and females in birds. SSD can influence the timing of autumn migration in SDMs. Later migration of larger males could be caused by higher cold-tolerance, which enables wintering closer to the breeding grounds compared to smaller females. It may also be beneficial for males, especially young males, to spend additional time at the breeding grounds to prospect for future nesting sites. In addition, larger reproductive investment by adult females may cause at least in some species delaying their autumn migration compared to adult males. We strongly encourage both empirical and theoretical investigation of differential migration between the sexes during autumn migration in other model systems.

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Sukupuolten väliset ajoituserot syysmuuttavilla varpuslinnuilla

Sukupuolten eriaikaista kevätmuuton ajoitusta on tutkittu lukuisissa tutkimuksissa, kun taas mahdolliset ajoituserot sukupuolten välillä syysmuutolla tunnetaan puutteellisesti. Tarkastelimme useita hypoteesejä, jotka voivat selittää eri sukupuoli- ja ikäluokkien syysmuutonaikaisia ajoituseroja. Selvitimme, voivatko nämä mahdolliset erot poiketa Euroopassa talvehtivien lähimuuttajien ja tropiikissa talvehtivien kaukomuuttajien välillä. Käytimme aineistona Lounais-Suomessa sijaitsevien Hangon ja Lågskärin lintuasemien rengastustietoja. Aineisto käsitti yhteensä noin 200,000 rengastettua lintua sisältäen 14 varpuslintulajia, joiden sukupuoli ja ikä ovat määritettävissä luotettavasti syksyisin.

Nuorilla linnuilla naaraat muuttivat merkitsevästi ennen koiraita, ja tämä sukupuolien välinen aikaero oli suurempi kaukomuuttajille verrattuna lähimuuttajiin. Vanhoilla linnuilla sukupuolten välinen ajoitusero oli vähäisempää, ja vain kahdella lajilla koiraat muuttivat merkitsevästi aikaisemmin kuin naaraat. Koiraiden ja naaraiden välinen ajoitusero oli yhteydessä lajin sukupuolidimorfiaan lähimuuttajilla. Mitä isompi koiras oli suhteessa naaraaseen, sitä myöhemmin koiraat muuttivat suhteessa naaraisiin. Tulokset viittaavat siihen, että useat tekijät vaikuttanevat syksyiseen sukupuolten väliseen muutonajoittumiseen. Koska koiraat ovat paikkauskollisempia kuin naaraat, etenkin nuorten koiraiden kannattaa viivästyttää syysmuuttoa ja käyttää ylimääräistä aikaa tulevan pesimäpaikan etsintään. Vanhat koiraat tuntevat jo pesimäalueen edellisen pesimäkauden ansiosta, jonka takia niiden ei tarvitse erityisesti viivyttää syysmuuttoa. Sen sijaan joillakin lajeilla vanhojen naaraiden muuttaminen vanhojen koiraiden jälkeen voi johtua siitä, että naaraat panostavat pesintään koiraita enemmän, mikä viivästyttää niiden valmistumista syysmuuttoon.

Sukupuolidimorfian ja muuttoajoituseron välinen yhteys viittaa siihen, että suurikokoisemmat koiraat pärjäävät kylmemmässä ilmastossa kuin pienikokoiset naaraat ja voivat siksi muuttaa naaraita myöhemmin ja talvehtia pohjoisempana kuin naaraat. Tämä yhteys havaittiin kuitenkin vain lähimuuttajilla, koska tropiikissa talvehtivilla kaukomuuttajilla molemmat sukupuolet muuttavat

keskimäärin niin aikaisin, että kylmät säät eivät ehdi rajoittaa niiden hengissäsäilymistä.

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Online supplementary material

Figure S1. Species-specific migration dates for different sex and age classes at the Hanko Bird Observatory.

Figure S2. Species-specific migration dates for different sex and age classes at the Lågskär Bird Observatory.

Table S1. Test results of mixed-effect models explaining autumn migration dates at Hanko Bird Observatory.

Table S2. Comparison of the models with different phylogenic structures explaining protandry/protogyny in species.