

## Module 8

### Phenological Responses To Climate Change III: Mating System Shifts

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#### Goals For Student Learning

This module was created to help students:

- Discuss the sensitivity of organisms' reproductive phenology to climate change
- Consider how a species' **mating system** might influence its response to climate change

#### Phenology and Reproduction

To date, there are few studies documenting reproductive changes in animals that have been caused by climate-mediated phenological shifts. This area of research has been the subject of increasing interest in recent years because the onset and duration of many species' breeding seasons is known to depend on local climatic conditions. Many of the studies designed to detect how phenological shifts may alter the process or outcome of **sexual selection** in organisms with different mating systems have focused on birds.

Birds exhibit a variety of mating behaviors, which are often coordinated with the timing of migration. In many migratory bird species, males and females segregate to different locations during the winter and/or use different cues to time their migration, subsequently arriving at breeding grounds at different times of the year. Researchers studying migratory birds have been concerned that phenological changes in **protandry** may cause certain individuals to have fewer mating opportunities or to experience increased competition for access to mates. Rainio et al. (2007) recently conducted a study in which they found that, despite strong phenological shifts in the timing of migration of four bird species, the degree of protandry has remained stable over a 33-year period.

#### Prior to the Seminar

Seminar participants should:

1. Read the following paper:  
Rainio, K., A. P. Tottrup, E. Lehikoinen, and T. Coppack. 2007. Effects of climate change on the degree of protandry in migratory songbirds. *Climate Research* 35:107-114.
2. Search for and select papers using *Web of Science* and/or *Google Scholar* on this topic. Students may choose to begin their searches with combinations of the following keywords: *mating system*, *protandry*, *climate change*, and *phenology*. They may also want to search for recent articles citing Rainio et al. (2007).
3. Prepare to provide brief verbal summaries of their selected articles in class.

### Suggested Discussion Questions

1. What is the NAO index? How does it provide an estimate of spring climate conditions? (Rainio et al. 2007)
2. What is the relationship between the NAO index and the migration times of the four focal bird species? (Rainio et al. 2007)
3. What phenological data did the researchers collect? Briefly describe the researchers' study design. (Rainio et al. 2007)
4. What did the study authors suggest might explain the parallel shifts in the timing of male and female migration? (Rainio et al. 2007)
5. What are some potential consequences of *increased* protandry in monogamous bird species? In polygamous species? (Rainio et al. 2007 **and student papers**)
6. What are some potential consequences of *decreased* protandry in monogamous bird species? In polygamous bird species? (Rainio et al. 2007 **and student papers**)
7. Did anyone find any studies that reported phenological reproductive shifts in other taxa (e.g., plants, fish, or mammals)?

### Glossary

- **Mating system:** the pattern of union of egg and sperm among individuals (in species with separate sexes) and/or within individuals (in species such as plants and some invertebrates that may include hermaphroditic individuals) in a population. For example, some birds are monogamous, whereas others are highly promiscuous. Other mating systems include sequential monogamy, polygamy, polyandry, and protandry.
- **Protandry:** In birds, this refers to the temporal difference between male and female arrival to a breeding grounds, where male arrival precedes female arrival.
- **Sexual selection:** a type of natural selection that acts on traits influencing an individual's ability to obtain or to choose a mate.



# Effects of climate change on the degree of protandry in migratory songbirds

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**ABSTRACT:** Current climate change is affecting the timing of life-history events of birds, such as the timing of spring arrival at the breeding grounds. Interspecific differences in the advancement of spring migration have hitherto been attributed to differences in exposure to climatic variables in winter or on migration, without a more detailed consideration of sex-specific differences in the timing and extent of migration. Since males and females migrate during different times of the season or may segregate into different wintering grounds, we expect climate change to differentially affect the arrival timing of males and females. Furthermore, sexual selection theory predicts that the degree of protandry (i.e. the time difference between male and female arrival) should increase when the forces of natural selection opposing early arrival relax and the earliest males benefit from improved mating opportunities. Here, we explore whether the degree of protandry has changed during a period of climatic warming using long-term phenological data collected at 5 North European bird observatories. We show for 4 sexually dichromatic songbird species that spring migration has generally advanced, but that the degree of protandry has not changed. Moreover, we provide evidence that variation in large-scale weather conditions, as reflected in the North Atlantic Oscillation (NAO) index, have not affected the degree of protandry. We hypothesize that a parallel shift in the timing of male and female migration may be due to similar phenotypic plastic responses of males and females to climatic changes or reflect a correlated selection response in males and females. In addition, we discuss the possibility that the observed variation in protandry could result from seasonal shifts in local environmental conditions under which birds of both sexes 'fall out' and are sampled.

**KEY WORDS:** Differential migration · *Ficedula hypoleuca* · *Lanius collurio* · Migration timing · Phenology · *Phoenicurus phoenicurus* · Protandry · *Sylvia atricapilla*

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## 1. INTRODUCTION

Recent studies on avian phenology show trends towards earlier spring arrival and breeding, which are generally attributable to the environmental changes caused by global warming (Walther et al. 2002, Parmesan 2006). In Europe, first arrival dates of Eurasian bird species have generally advanced during the last 30 to 40 yr (Lehikoinen et al. 2004, Thorup et al. 2007, Rubolini et al. 2007, this issue). Similar results have been published from NE North America, where spring arrival of birds has advanced on average by 8 d during

the 20th century (Butler 2003, Marra et al. 2005). Short-distance migrants that overwinter in temperate and sub-tropical regions have generally advanced their arrival more than long-distance migrants (Lehikoinen et al. 2004), but several migrants returning from distant tropical winter quarters show equally strong responses (Stervander et al. 2005, Jonzén et al. 2006). It remains unclear to what degree these changes reflect immediate phenotypic responses or micro-evolutionary adaptations to changing environmental circumstances in breeding and non-breeding areas and while travelling between (Pulido & Berthold 2004, Both 2007, Jonzén

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et al. 2007). Numerous studies have linked long-term trends in the overall timing of spring migration and breeding to seasonal shifts in climatic conditions and resource availability (Coppack & Both 2002, Lehtikoinen et al. 2004, Visser et al. 2004). Yet, the within-season complexity of phenological patterns has, so far, received only limited attention (MacMynowski & Root 2007, Thorup et al. 2007).

Males of many migratory organisms, including the majority of songbirds, arrive on the breeding grounds before female conspecifics—a phenomenon termed protandry (Morbey & Ydenberg 2001). Avian protandry is usually explained by the ‘rank advantage’ hypothesis, which states that male–male competition over high-quality territories selects for the earliest arriving males (Morbey & Ydenberg 2001). However, selection could also act directly on the relative arrival of males and females in cases where males are polygynous and gain fitness benefits from earlier spring arrival with reduced sperm competition and increased opportunities for extra-pair copulations (‘mate opportunity’ hypothesis, see Morbey & Ydenberg 2001, Rubolini et al. 2004, Coppack et al. 2006, Kokko et al. 2006).

Intersexual time differences in migration potentially expose males and females of the same species to different patterns of climatic change, since both sexes pass through different latitudes and climatic conditions at different times of the year. Moreover, in cases where the sexes segregate into different wintering latitudes, with males typically wintering closer to the breeding grounds than females (Ketterson & Nolan 1976, Catry et al. 2005, Komar et al. 2005), males and females experience different climatic conditions throughout the entire non-breeding period. Any change in the relative arrival timing of males and females in immediate response to changing environmental conditions in winter or during migration (Ahola et al. 2004) will influence subsequent mating opportunities, with consequences for reproductive success, individual fitness and population viability.

Since the extent of protandrous migration can be viewed as a trait reflecting a balance between sexual and natural selection (Morbey & Ydenberg 2001, Coppack et al. 2006, Kokko et al. 2006, Møller 2007), we may expect the time lag between male and female arrival to increase when sexual selection outweighs the opposing forces of natural selection (Møller 2004, 2007). Recently, Møller (2004) showed that protandry had increased over the past 2 decades in a Danish barn swallow *Hirundo rustica* population, suggesting that the environmental constraints opposing earlier male arrival have relaxed and selection on male earliness has intensified. This assumption was supported by a parallel change of a sexually selected characteristic, i.e. tail length, which showed a trend towards larger

values (Møller 2004, Møller & Szép 2005). However, at the interspecific level, Spottiswoode et al. (2006) found that the relationship between the advancement of spring migration and the strength of sexual selection was stronger for changes in the median migration date of whole populations than for changes in the timing of first-arriving (male) individuals, suggesting that selection has not only acted on protandrous males.

In the present study, we explore whether the time lag between male and female migration of 4 sexually dichromatic songbird species has changed over a 20 yr period of climatic warming. Using phenological data collected at 5 northern European bird observatories, we analyse long-term trends in the degree of protandry and explore whether the relative arrival timing of males and females is related to large-scale fluctuations in climatic conditions.

## 2. MATERIALS AND METHODS

### 2.1. Phenological data

We used phenological data from constant-effort ringing stations on Helgoland, North Sea (54° 10' N, 7° 53' E; Germany) and Christiansø, southern Baltic Sea (55° 19' N, 15° 11' E; Denmark), as well as from 3 Finnish bird observatories in the northern Baltic Sea: Lågskär, (59° 50' N, 19° 56' E), Jurmo (59° 50' N, 21° 37' E) and Rönnskär (59° 56' N, 24° 24' E).

We selected 4 sexually dimorphic migratory species for which adequate phenological data were available: redstart *Phoenicurus phoenicurus*, red-backed shrike *Lanius collurio*, blackcap *Sylvia atricapilla* and pied flycatcher *Ficedula hypoleuca*. Our analysis was confined to these 4 migratory species, because they are the only ones that can be readily sexed in the field and occurred in sufficient numbers at all latitudes.

In order to render data sets comparable, exactly the same span of years as available for Christiansø (1976 to 1997) was selected from all other sites that provide longer time series. To obtain continuous data sets for each spring, data from the Finnish observatories were pooled by calculating the daily mean number of birds trapped at all 3 sites. Phenological data from Christiansø and Helgoland (daily numbers of ringed individuals) were pooled by averaging median arrival dates, since these sites are situated at almost the same latitude. Pooling data from these 2 sites is also biologically justifiable, since ringing recoveries indicate that both migrant populations breed principally in Sweden and Finland (Zink 1973, Rabøl & Rahbek 2002, Bønløkke et al. 2006, the Finnish Museum of Natural History unpubl. data), and those from Helgoland also farther west in Norway (Zink 1973), implying that they belong to the same over-

all population (Spottiswoode et al. 2006). In the following, the Finnish data are referred to as 'north', and the combined data from Christiansø and Helgoland, as 'south'. Annual numbers of red-backed shrikes caught on Helgoland were considerably low, so that for this species, 'south' refers to data from Christiansø only.

## 2.2. Analyses of protandrous migration

We analysed sex-specific median migration dates, including geographical area, North Atlantic Oscillation (NAO) and year (and their interaction) as explanatory variables. Analyses were performed stepwise, whereby non-significant terms were dropped one-by-one, starting from the highest-level interaction until no term could be dropped.

The degree of protandry was calculated as the difference between median passage dates of females and males for each year between 1976 and 1997. We analysed changes in protandry by applying general linear models in which the degree of protandry was explained by year, winter NAO index (December to March, available from the website of the Climatic Research Unit at the University of East Anglia: [www.cru.uea.ac.uk/cru/data/nao.htm](http://www.cru.uea.ac.uk/cru/data/nao.htm)) and area (north and south) with all interactions. Analyses were weighted by the yearly totals of trapped birds. In Europe, the NAO affects winter weather most (Hurrell et al. 2003) and can be viewed as a proxy for spring conditions (Hüppop & Hüppop 2003, Stenseth et al. 2003). Using the NAO index closer to the actual migration period would appear more plausible, but shifting the NAO period closer to summer has little or no significant effect on the correlation coefficients between spring arrival of birds and the NAO (Rainio et al. 2006). The analyses were performed stepwise, similar to the sex-specific migration date analyses. We performed the analyses for each species separately.

## 3. RESULTS

Males of all 4 species arrived earlier than females, significantly in pied flycatcher *Ficedula hypoleuca* (north:  $t = 4.38$ ,  $p < 0.001$ ; south:  $t = 3.24$ ,  $p = 0.002$ ), redstart *Phoenicurus phoenicurus* (north:  $t = 5.78$ ,  $p < 0.001$ ; south:  $t = 5.16$ ,  $p < 0.001$ ) and blackcap *Sylvia atricapilla* in the south ( $t = 2.54$ ,  $p = 0.014$ ). The degree of protandry tended to be greater (statistically non-significant) in the south than in the north in all species except the pied flycatcher. The degree of protandry was greatest in the redstart (7.8 d in the north and 8.1 d in the south) and lowest in the red-backed shrike *Lanius collurio* (2.0 d north, 2.5 d south) (Table 1).

The sex-specific analyses are summarised in Table 2. All interactions were dropped in the stepwise regression. In the redstart and the pied flycatcher, both sexes correlated with NAO variability, arriving earlier after winters with high NAO indices. Of these 2 species, only female redstarts showed a statistically significant trend towards earlier arrival. In the blackcap, both sexes showed statistically significant trends towards earlier arrival dates, but the NAO had no significant effect. The arrival of red-backed shrikes was neither significantly affected by the NAO, nor was there a statistically significant trend towards earliness. The arrival times were later in the north for all species, except the red-backed shrike.

We found no trends in the degree of protandry in any of the species studied (Figs. 1 & 2, Table 3). Neither were there any statistically significant year-by-area interactions (Fig. 1, Table 3), indicating that the degree of protandry has remained unchanged in both areas. There were no significant NAO  $\times$  Area interactions or main effects of NAO on the degree of protandry in the redstart, blackcap, or pied flycatcher. In the red-backed shrike, the NAO  $\times$  Area interaction was statistically significant ( $F_{1,38} = 5.04$ ,  $SE \pm 0.47$ ,  $p = 0.031$ ), indicating different responses of protandry towards

Table 1. Mean of yearly protandry values with 95% CI, yearly range of observed individuals and mean passage dates of males and females in the 2 areas. The degree of protandry is measured as the difference in days between median passage dates of males and females

Taxon	Area	Mean protandry	Lower 95% CI	Upper 95% CI	N range		Passage date	
					♂♂	♀♀	♂♂	♀♀
Redstart	North	7.8	6.2	9.3	156–365	153–450	15 May	22 May
<i>Phoenicurus phoenicurus</i>	South	8.1	6.6	9.6	123–400	171–540	11 May	19 May
Blackcap	North	3.5	2.1	5.0	45–252	43–212	24 May	28 May
<i>Sylvia atricapilla</i>	South	4.6	2.7	6.5	85–425	87–462	14 May	19 May
Pied flycatcher	North	5.9	4.1	7.8	49–285	44–269	15 May	21 May
<i>Ficedula hypoleuca</i>	South	4.5	3.3	5.7	52–238	72–254	12 May	16 May
Red-backed shrike	North	2.0	1.1	2.8	18–226	10–243	25 May	27 May
<i>Lanius collurio</i>	South	2.5	1.3	3.8	12–112	14–136	26 May	28 May

Table 2. Sex- and species-specific effects of area, North Atlantic Oscillation (NAO) and year on the median spring arrival times. The analyses were performed stepwise so that non-significant terms were removed one-by-one, starting from the highest-level interaction. Only main effects are reported; all interactions were non-significant. For full taxonomic names, see Table 1

Species	Sex	Factor	Estimate	SE	df	F	p
Redstart	♂	Year	-0.11	0.10	1, 40	1.24	0.272
		NAO	-1.88	0.50	1, 41	14.08	<0.001
		Area	3.90	1.26	1, 41	9.56	0.004
	♀	Year	-0.24	0.10	1, 40	5.70	0.022
		NAO	-1.52	0.51	1, 40	8.80	0.005
		Area	3.58	1.24	1, 40	8.31	0.006
Blackcap	♂	Year	-0.37	0.13	1, 41	7.96	0.007
		NAO	-0.29	0.70	1, 40	0.18	0.676
		Area	9.64	1.67	1, 41	33.29	<0.001
	♀	Year	-0.44	0.12	1, 41	12.76	<0.001
		NAO	-0.86	0.64	1, 40	1.83	0.183
		Area	8.60	1.56	1, 41	30.47	<0.001
Pied flycatcher	♂	Year	-0.09	0.52	1, 40	0.73	0.399
		NAO	-2.05	0.50	1, 41	17.02	<0.001
		Area	2.85	1.25	1, 41	5.21	0.028
	♀	Year	-0.03	0.09	1, 40	0.12	0.730
		NAO	-1.51	0.45	1, 41	11.07	0.002
		Area	4.24	1.14	1, 41	13.88	0.001
Red-backed shrike	♂	Year	-0.13	0.13	1, 41	1.03	0.312
		NAO	0.81	0.68	1, 40	1.43	0.238
		Area	-0.92	1.67	1, 39	0.30	0.586
	♀	Year	-0.12	0.12	1, 41	0.92	0.343
		NAO	0.23	0.66	1, 39	0.13	0.725
		Area	-1.52	1.58	1, 40	0.93	0.341

NAO variability in the 2 areas. In the north, the NAO index was negatively correlated with protandry ( $b = -1.22$ ,  $SE \pm 0.25$ ,  $F_{1,20} = 23.72$ ,  $p < 0.001$ ); the degree of protandry was close to zero after high-NAO winters (Fig. 1), possibly because females tend to arrive earlier after such winters (Fig. 3). However, when sex-specific arrival times were analysed the NAO  $\times$  Sex interaction was not significant ( $F_{1,39} = 0.82$ ,  $p = 0.370$ ) (Fig. 3). In the south, the NAO had no significant effect on red-backed shrike protandry ( $b = 0.16$ ,  $SE \pm 0.59$ ,  $F_{1,19} = 0.15$ ,  $p = 0.702$ ) (Fig. 1).

#### 4. DISCUSSION

Males of all 4 species arrived earlier than females. The degree of protandry was greatest in the redstart *Phoenicurus phoenicurus*, 7.8 d in the north and 8.1 d in the south, and lowest in the red-backed shrike *Lanius collurio*, 2.0 and 2.5 d, respectively (Table 1). These protandry values are larger than those reported for the Mediterranean islands by Rubolini et al. (2004), where protandry averages around 5 d in the redstart, around 4 d in the pied flycatcher *Ficedula hypoleuca* (versus 5.9 d in the northern and 4.5 d in the southern

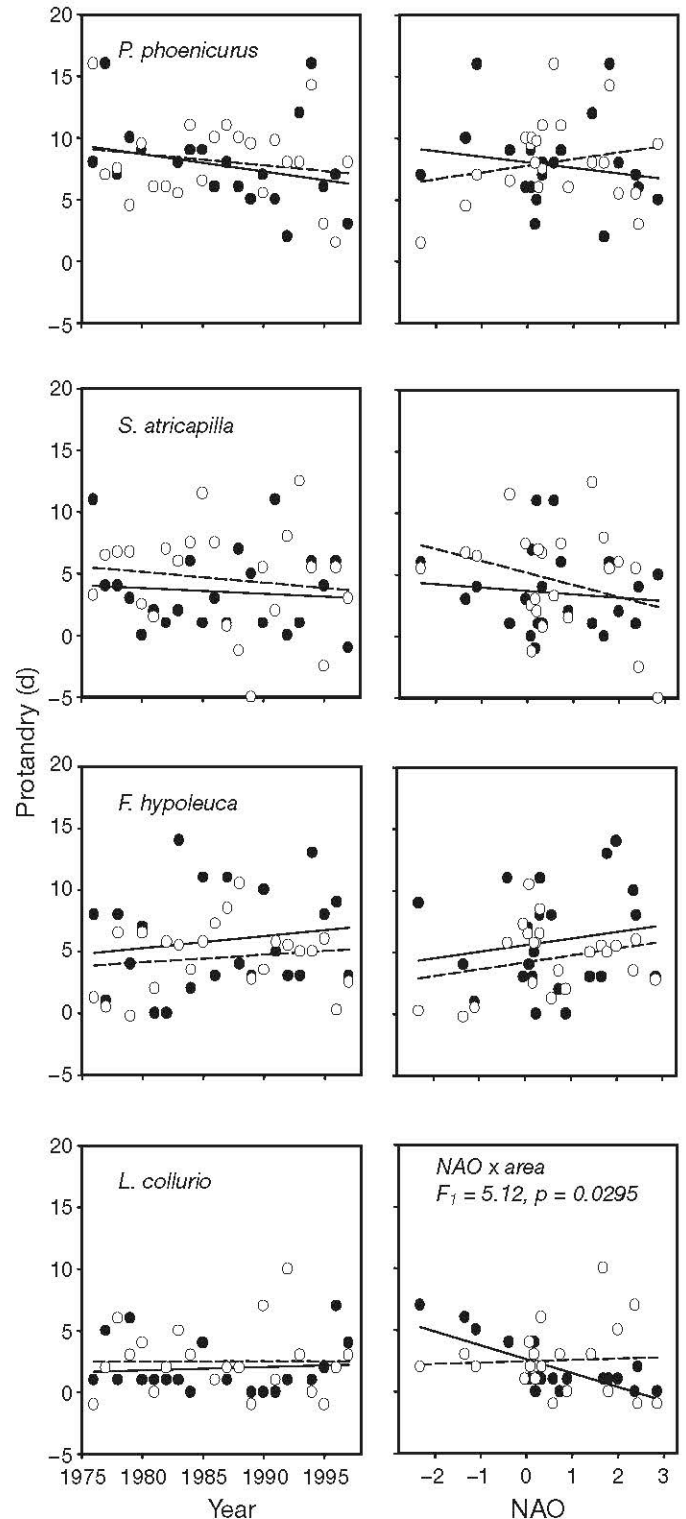


Fig. 1. Species-specific trends in protandry (the difference in days between median passage dates of males and females) from 1976 to 1997 and the effects of winter NAO (North Atlantic Oscillation) in the south (Christiansø, Denmark; and Helgoland, Germany: filled circles, solid line) and the north (Lågsjär, Jurmo and Rönnskär, Finland: open circles, dashed line). For full taxonomic names, see Table 1

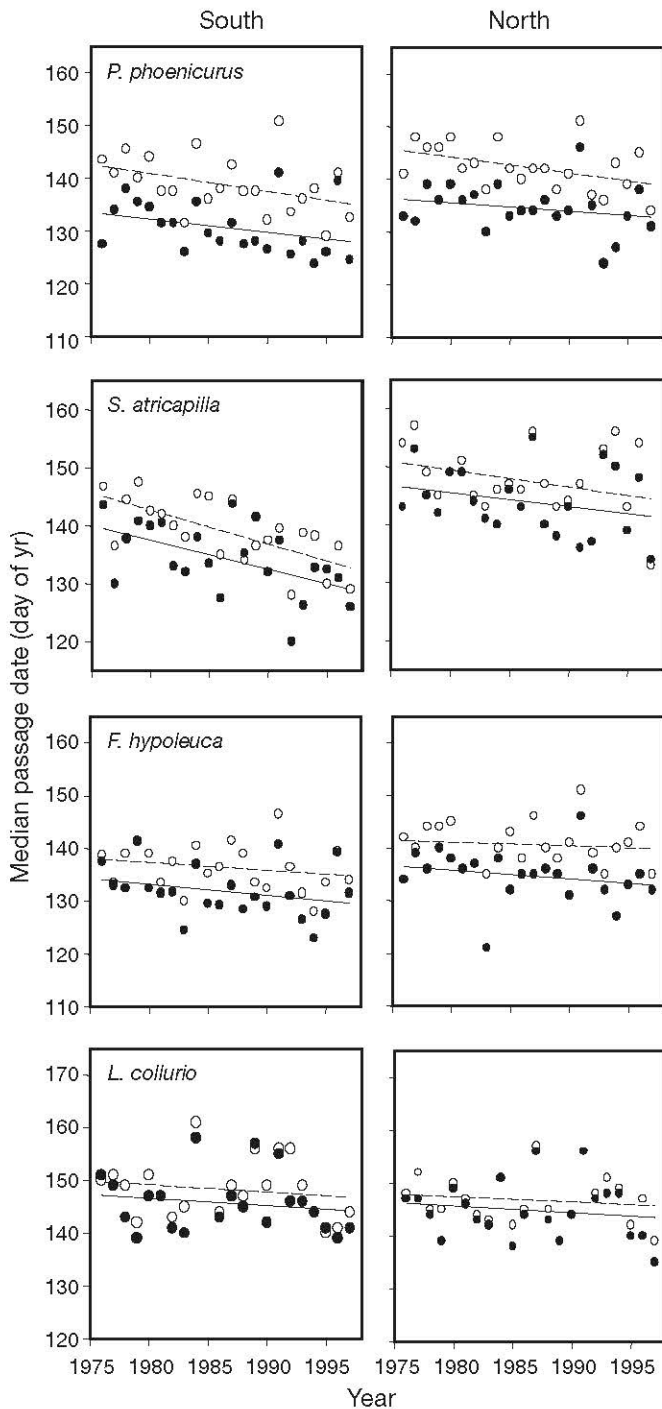


Fig. 2. Trends in sex-specific, median passage dates of 4 song-bird species in the south (Christiansø, Helgoland) and the north (Lågskär, Jurmo, Rönnskär) from 1976 to 1997. Filled circles, solid line: males; open circles, dashed line: females

group of our study), and around 1 d in the blackcap *Sylvia atricapilla* (versus 3.5 d in the northern and 4.6 d in the southern group of our study). This general trend towards higher protandry values in northern Europe as compared to southern Europe may indicate that males

Table 3. Results of general linear modelling in which the degree of protandry was explained by year, winter NAO index and area. The analyses were performed stepwise, whereby non-significant terms were dropped one-by-one, starting from the highest-level interaction, and were weighted by yearly sample size

Factor	df	F	p
<b>Redstart <i>Phoenicurus phoenicurus</i></b>			
<i>Removed fixed effects</i>			
Year × NAO × Area	1, 36	2.09	0.157
Year × Area	1, 37	0.00	0.993
Year × NAO	1, 38	1.75	0.194
NAO × Area	1, 39	2.09	0.156
Area	1, 40	0.25	0.619
NAO	1, 41	0.30	0.584
Year	1, 42	2.48	0.123
<b>Blackcap <i>Sylvia atricapilla</i></b>			
<i>Removed fixed effects</i>			
Year × NAO × Area	1, 36	0.17	0.681
Year × NAO	1, 37	0.00	0.958
NAO × Area	1, 38	0.13	0.725
Year × Area	1, 39	0.24	0.628
Year	1, 40	0.02	0.886
Area	1, 41	0.49	0.487
NAO	1, 42	1.06	0.309
<b>Pied flycatcher <i>Ficedula hypoleuca</i></b>			
<i>Removed fixed effects</i>			
Year × NAO × Area	1, 36	0.33	0.570
NAO × Area	1, 37	0.05	0.818
Year × Area	1, 38	0.34	0.566
Year × NAO	1, 39	0.66	0.423
NAO	1, 40	0.62	0.436
Area	1, 41	0.98	0.328
Year	1, 42	1.39	0.246
<b>Red-backed shrike <i>Lanius collurio</i></b>			
<i>Fixed effects-final model</i>			
Year	1, 38	0.50	0.485
NAO	1, 38	9.00	0.005
Area	1, 38	0.30	0.586
NAO × Area	1	5.04	0.031
<i>Removed fixed effects</i>			
Year × NAO × Area	1, 35	0.83	0.369
Year × Area	1, 36	0.19	0.667
Year × NAO	1, 37	1.32	0.259

and females migrate at different speeds, in which case males would stopover less frequently and for shorter periods than females. However, comparisons between phenological estimates at different localities and time periods must be handled with caution, since birds passing different observatories at different times of the year may not belong to the same overall breeding populations and may be subject to different ecological conditions and selection regimes. Furthermore, our study only considers sexually dichromatic species, which can be readily sexed in the field. Rubolini et al. (2004) have shown that more dichromatic species tend to be more protandrous. Thus, our sample of species might be non-random with respect to the strength of sexual selection that influences protandry (cf. Coppack et al. 2006).

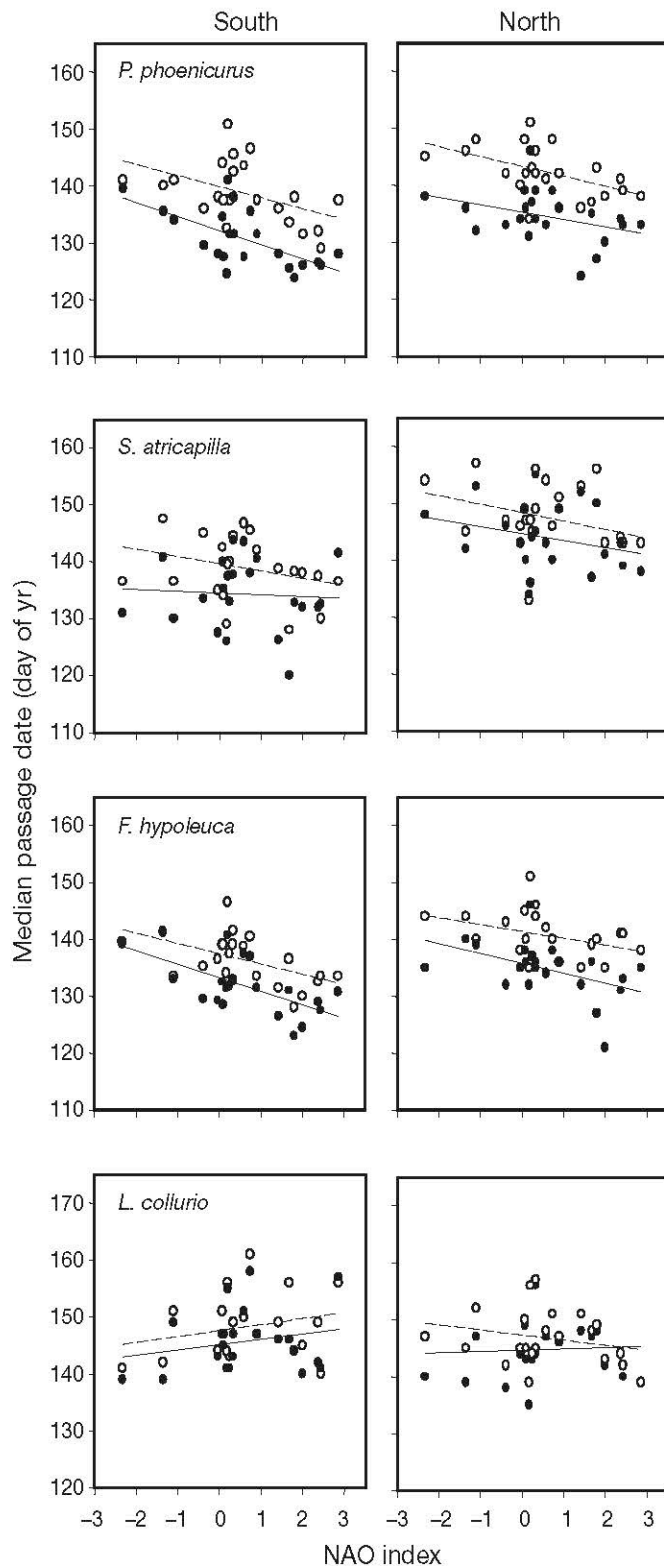


Fig. 3. Sex-specific, median passage dates of 4 songbird species in the south (Christiansø, Helgoland) and the north (Lågskär, Jurmo, Rönnskär) in relation to the winter NAO index (1976 to 1997). Filled circles, solid line: males; open circles, dashed line: females

#### 4.1. Long-term trends in protandry

We found no effect of year on the degree of protandry in any of the 4 long-distance migrant songbird species under study, meaning that during the last decades there has not been any consistent change in the arrival time difference between males and females. Thus, recent changes in environmental conditions appear to have affected both sexes in a similar way. This general pattern differs from the results of Møller (2004), who found that the degree of protandry in a Danish barn swallow population had increased during the last decades of climate warming.

There are 3 hypothetical, not mutually exclusive, explanations why we did not detect any consistent changes in protandry despite the overall trend towards earlier migration. (1) Both sexes show similar phenotypic plastic responses to environmental changes at the wintering grounds and/or en route. (2) Selection has acted on both sexes to the same degree. (3) Local conditions under which birds of both sexes 'fall out' have advanced, leading to parallel a shift in sampling frequency.

Hypotheses 1 and 2 assume that migratory birds are actually shifting the mean timing of their migration (see Fig. 4a) and that males and females of the same species are responding to phenological changes in their environment in the same way. Changes in migratory behaviour could be taking place at a phenotypically plastic level (Hypothesis 1), for instance, through an increase in migration speed due to milder conditions en route (see Ahola et al. 2004, Marra et al. 2005, Hüppop & Winkel 2006) and/or through selection on the timing mechanism of spring migration (Hypothesis 2), which would involve genetic changes in circannual rhythms and cue response thresholds (van Noordwijk 2003, Pulido 2007a). These 2 alternatives cannot be distinguished by analysing trapping numbers that do not include repeated measurements of individuals (see Pulido 2007b, this issue).

In the third case (Hypothesis 3), we assume that the climatic conditions under which birds of both sexes 'fall out' and stopover have shifted, with the consequence that both males and females are sampled earlier in the season (see Fig. 4b). Under this assumption, phenological changes in spring passage would not involve populational changes in behaviour or physiology, but would simply reflect changes in local sampling conditions, resulting in different observation frequencies at different times of the year. If, however, males migrate earlier than females, proportionally more males should be trapped earlier in the season, potentially leading to an inflation of protandry. This prediction could be tested by analysing trends in sex ratios relative to the degree of protandry.



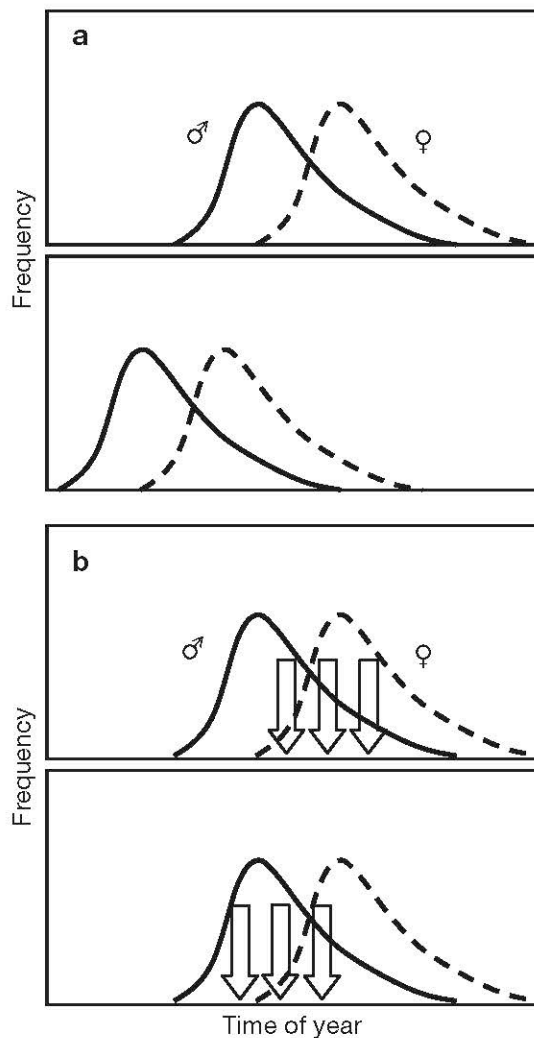


Fig. 4. Hypothetical frequency distributions of male and female migrants, showing at which levels overall phenology and the degree of protandry may change: (a) the timing of migration of the entire population shifts; (b) no changes in ‘true’ migration, but a change in local sampling conditions occurs, causing males and females to ‘fall out’ earlier (arrows)

Generally, the question of whether migrants have changed their behaviour or whether climate change has simply altered the conditions under which certain fractions of migratory populations are observed needs further attention (see Knudsen et al. 2007, this issue).

#### 4.2. The effect of NAO on protandry

The effect of the NAO on the degree of protandry was not significant in most cases. The sex-specific response slopes are parallel, which indicates a similar response of both sexes to fluctuation of the NAO. How-

ever, in the red-backed shrike, the NAO  $\times$  Area interaction remained significant in the model, indicating that change in protandry in relation to the NAO was different between northern and southern trapping sites. At northern sites, the degree of protandry seems to be smaller after high-NAO winters; females are advancing, while males are not, and so the females are catching up to the males and arriving at breeding areas at approximately the same time as males (Fig. 3). This could lead to situations where males have less time to find and defend high-quality territories before potential mates arrive.

The responses in arrival time to the NAO fade with the progression of the migration season, i.e. early fractions of migratory populations are more sensitive to fluctuations in the NAO (Vähätalo et al. 2004, Rainio et al. 2006, Tøttrup et al. 2006). This fading of response could result from increased protandry (Rainio et al. 2006)—males would be more sensitive to the overall advancement in phenology, which they experience along their migration route after high-NAO winters, thus shifting the early part of migratory populations towards earlier arrival. Since we did not detect significant changes in the degree of protandry, its role may not be an important factor creating different phase responses. However, Rubolini et al. (2007) showed that the arrival time responses of birds to climate change are species specific: when the effects of phylogeny were analysed, the most important taxonomic level was species. Thus, the results of our study may not apply to other species.

In conclusion, our results suggest that protandry has not changed in populations of migrating songbirds. However, phenological data collected at bird observatories do not include information on how individual males and females behave in different years and on how progeny of known origin deviates from its mid-parent value. This information is needed to be able to distinguish between phenotypic plastic responses and genetic (evolutionary) processes that underlie recent phenological changes in response to global environmental change (Pulido 2007b). Thus, we need to continue established—and initiate new—long-term studies that follow-up life-history and behavioural traits in individually marked or tracked bird populations.

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