

Proximate control and adaptive potential of protandrous migration in birds

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Synopsis Migration determines where, when, and in which order males and females converge for reproduction. Protandry, the earlier arrival of males relative to females at the site of reproduction, is a widespread phenomenon found in many migratory organisms. Detailed knowledge of the determinants of protandry is becoming increasingly important for predicting how migratory species and populations will respond to rapid phenological shifts caused by climatic change. Here, we review and discuss the potential mechanisms underlying protandrous migration in birds, focusing on evidence from passerine species. Latitudinal segregation during the non-breeding period and differences in the initiation of spring migration are probably the key determinants of protandrous arrival at the breeding sites, while sexual differences in speed of migration appear to play a minor role. Experimental evidence suggests that differences between the sexes in the onset of spring migratory activity are caused by differences in circannual rhythmicity or by photoperiodic responsiveness. Both of these mechanisms are hardwired and could prevent individuals from responding plastically to chronic changes in temperature at the breeding grounds. As a consequence, adaptive changes in both the timing of arrival in spring and of reproduction will require evolutionary (genetic) changes of the cue-response systems underlying the initiation and extent of migration in both males and females.

“In many cases special circumstances tend to make the struggle between the males particularly severe. Thus the males of our migratory birds generally arrive at their places of breeding before the females, so that many males are ready to contend for each female. I am informed by Mr. Jenner Weir, that the bird-catchers assert that this is invariably the case with the nightingale and blackcap, and with respect to the latter he can himself confirm the statement.”

Charles Darwin (1874)

“The young birds of the summer open the grand autumnal flight, unaccompanied by any old, the very finest old males at the close of the season bringing up the rear. In spring, however, quite the reverse invariably takes place, then the most perfect old males appear first, followed soon by old females, and later by younger birds of less perfect appearance.”

Heinrich Gätke (1879)

Introduction

Seasonal rhythms of animal hibernation, migration, emergence, and reproduction have evolved as a suite of co-adapted events in the life cycle that match the prevailing environmental conditions at a given latitude and elevation. Climatic change is affecting the seasonality and geography of suitable habitat conditions worldwide (Walther et al. 2002; Parmesan 2006). To be able to predict how species and populations of seasonally reproducing organisms will respond to these rapid changes, we urgently need a deeper understanding of the mechanisms that control and constrain the timing and duration of successive life-history stages (Coppack and Both 2002; Coppack and Pulido 2004; Pulido 2007; Bradshaw and Holzapfel 2008; Visser 2008; Wingfield 2008).

A consistent pattern found among seasonally migrating animals, including insects, salmonid fish, and the majority of birds, is the earlier arrival of males relative to conspecific females at the site of reproduction (Darwin 1871; Morbey and

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Ydenberg 2001). Protandrous migration is best explained by considering the fitness cost and benefits of early arrival of males relative to the emergence of females (Wiklund and Fagerström 1977; Morbey and Ydenberg 2001; Mills 2005; Kokko et al. 2006; Møller et al. 2009). However, there is no consensus about the relative importance of the components of selection involved (i.e., viability versus fecundity selection), nor is there a firm knowledge of the actual targets of selection, i.e., the behavioral and physiological mechanisms controlling the timing of arrival in the spring (Pulido 2007). In this article, we review the literature on the proximate control of avian protandry, focusing on evidence from passerine species. We discuss how behavioral and physiological mechanisms underlying protandry may potentially affect adaptive responses of migratory bird populations to ongoing climatic changes.

The first systematic account of sex-differentiated bird migration was published by Heinrich Gätke, who had spent more than 50 years on the North Sea island of Heligoland where bird migration is witnessed in its “full original purity” (Gätke 1879, 1895). Since this pioneering work, bird observatories worldwide have amassed extensive collections of phenological data, which confirm that protandrous migration and arrival in spring is the norm (Francis and Cooke 1986; Spina 1994; Stewart et al. 2002; Hüppop and Hüppop 2004; Mills 2005; Rainio et al. 2007; Cooper et al. 2009; for review, see Newton 2008; for a specific example, see Fig. 1). However, estimates of the degree of protandry derived from data on captures of birds at observatories must be interpreted with caution, because males and females caught during migration (and in different years) may not belong to the same breeding population. Recoveries of birds ringed during migration are rare and randomly scattered along the migratory routes. Hence, the origin of the majority of migrants is unknown. It is, therefore, uncertain whether the patterns of protandrous migration seen at bird observatories reflect the extent to which males appear before females at the site of reproduction. In addition to this problem, estimates of protandrous arrival at the breeding grounds may be biased due to different probabilities with which territorial (singing) males, non-territorial floaters, and females are detected.

Information on sexually asynchronous migration is naturally biased towards sexually dichromatic species that can be sexed in the field without difficulty. Consequently, the choice of species in comparative studies might be non-random with respect to the strength of sexual selection that influences protandry

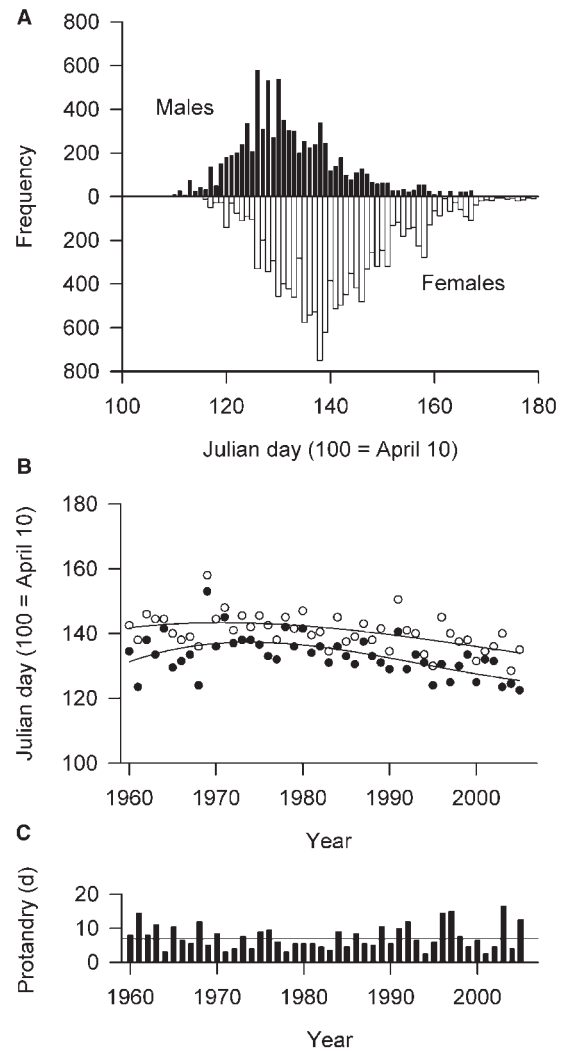


Fig. 1 Spring phenology of migrating male and female redstarts (*Phoenicurus phoenicurus*) caught between 1960 and 2005 at Heligoland Island, German North Sea (54°12'N, 07°56'E). (A) Cumulative frequency distributions of daily trapping totals. (B) Year-wise median passage dates of males (closed circle) and females (open circles). Lines are polynomial regression lines. (C) Yearly protandry values defined as the time lag between the median passage dates of males and females. The line indicates the average protandry value.

(cf. Coppack et al. 2006). So far, only a few studies have examined sex-differentiated migration patterns in sexually monomorphic species (Bédard and LaPointe 1984; Catry et al. 2004, 2005a; Bowlin 2007; Edwards and Forbes 2007).

There are at least seven, not mutually exclusive, hypotheses explaining the evolution of protandrous migration (classified and reviewed by Morbey and Ydenberg 2001; cf. Mills 2005). One hypothesis, applicable to birds, is the “mate-opportunity” hypothesis (Morbey and Ydenberg 2001; Kokko et al. 2006; Møller et al. 2009), which assumes

that polygynous males maximize their mating opportunities by arriving earlier. This hypothesis differs slightly from the traditional “rank advantage” hypothesis, which does not consider the consequences for fitness from changes in the timing of arrival of males relative to the timing of arrival of females (Morbey and Ydenberg 2001). Intraspecific studies on the conditional dependence of the early arrival of males and the consequences for fitness of early arrival (Møller 1994; Hasselquist 1998; Langefors et al. 1998; Ninni et al. 2004; Møller 2009; Reudink et al. 2009) provide empirical support for the “mate opportunity” hypothesis (but see Huyvaert et al. 2006). High-quality males tend to occupy prime breeding territories and reproduce earlier and more successfully than do late-arriving males of lower quality. The “mate-opportunity” hypothesis is further supported by the results of theoretical models (Kokko et al. 2006) and by interspecific comparisons showing that the degree of protandry is associated with indicators of the intensity of sexual selection through female choice. Among migratory songbirds, sexual dichromatism (Rubolini et al. 2004), sexual size dimorphism (Kissner et al. 2004; Förchler and Coppack 2008; but see Francis and Cooke 1986) and the rate of extra-pair paternity (Coppack et al. 2006) have been shown to be positively correlated with the lag in time between the spring migration of males and that of females.

The role of the mating system in the evolution of protandry is exemplified by the reverse phenomenon, i.e. protogyny, in which females precede males in migration (Morbey and Ydenberg 2001). This exception of Gätke’s rule, observed, for instance, in phalaropes (*Phalaropus* spp.) and a few other sequentially polyandrous shorebirds, is associated with reversed sexual dimorphism and with the reversal of sexual roles in competition for mates and in parental investment (Oring and Lank 1982; Reynolds et al. 1986; Eens and Pinxten 2000). Female phalaropes are larger and more brightly colored than are male conspecifics and they compete for males. Once female phalaropes have laid their eggs, they abandon the breeding site, leaving the males to incubate the eggs and care for the young. The rare cases of protogyny and reversal of sex-roles suggest that the physiological mechanisms underlying migration and mating behavior can evolve independently from the endocrine system controlling gametogenesis and ovulation. Furthermore, since neither sex of any phalarope species is territorial, sexually asynchronous migratory behavior need not be driven by territoriality (Reynolds et al. 1986).

The proximate control of protandrous migration in spring

While the ultimate (evolutionary) causes of protandrous spring migration have received much attention (Morbey and Ydenberg 2001), knowledge of the proximate (mechanistic) causes is still deficient (Berthold 2001; Coppack et al. 2006). In principle, sexual differences in time of arrival may be caused by three, not mutually exclusive, mechanisms: (1) Males may migrate faster than females by requiring less time for stopover. (2) Males may travel shorter distances by wintering closer to the breeding grounds. (3) Males may initiate migration in the spring earlier than do females (Fig. 2). We can

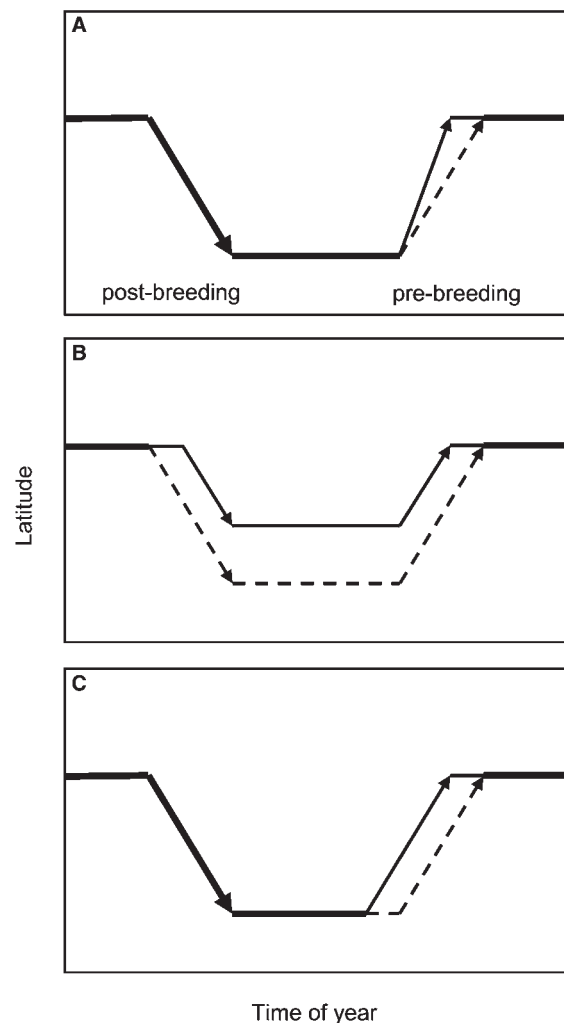


Fig. 2 Schematic representation of the three basic behavioral mechanisms controlling the timing of protandrous spring arrival: (A) Males (solid arrow) and females (dashed arrow) migrate from common wintering latitude but at different speeds. (B) Males and females segregate spatially during autumnal (postbreeding) migration, which leads to differential arrival in spring. (C) Males initiate spring (prebreeding) migration earlier than do females.

further distinguish between mechanisms that positively control the timing and progression of migration (circadian and circannual rhythms; Gwinner 1996; Berthold 2001; Coppack et al. 2008a, 2008b) and mechanisms that modify time of arrival through variation in environmental conditions experienced during migration (Tøttrup et al. 2008) or on the wintering grounds (Studds and Marra 2007; Reudink et al. 2009). The environmental conditions experienced in winter and spring are determined by the timing and extent of post-breeding migration (Nolan and Ketterson 1990), which, in turn, may be affected by responses to conditions experienced during the breeding period (carry-over effects; cf. Pulido 2007). This complex set of mechanistic explanations for protandrous migration is summarized in Table 1. We shall discuss some of these mechanisms below, drawing on evidence from the literature and from our own empirical investigations carried out at a migration hotspot in Central Europe, i.e., Heligoland Island.

Differential speed of migration

Overall, speed of migration is a function of flight speed and the frequency and duration of stopovers (Alerstam 2003; Hedenström 2008). Because the rate of energy expenditure steeply increases with higher flight speed, a higher speed of migration can only be achieved by increasing the rate at which energy is replenished during stopovers, which, in turn, is constrained by the physiological capacity to process ingested food (Hedenström 2008). Consequently, small birds with high mass-specific metabolic rates may spend up to seven times more time on refueling

than on actual flight (Hedenström and Alerstam 1997).

Trade-offs between the costs of energy-efficient long-distance flight and the costs of maneuverability after landfall could in theory give rise to sexual differences in wing morphology. Under this assumption, the faster migrating sex (in most species presumably the male) should have more pointed wings, since pointed wings are associated with energy efficient flight (Winkler and Leisler 1992; Mönkkönen 1995; Lockwood et al. 1998; Bowlin and Wikelski 2008) and lower wing load, which allows individuals to carry higher loads of fuel (Chandler and Mulvihill 1992). In willow warblers (*Phylloscopus trochilus*, Hedenström and Pettersson 1986), dark-eyed juncos (*Junco hyemalis*, Chandler and Mulvihill 1990a; Mulvihill and Chandler 1990) and Swainson's thrushes (*Catharus ustulatus*, Bowlin 2007), males do indeed have more pointed wings than do females, and in many species females have higher wing loading (Blem 1975; Chandler and Mulvihill 1992). The functional significance of these differences, however, remains ambiguous. It is unclear whether shape and loading of the wings relate to flight speed, migration distance or migration date (Bowlin 2007). Moreover, variation in wing morphology could also result from differences in habitat use and resource allocation strategies or could simply reflect correlated secondary sexual characteristics (sexual size dimorphism).

If protandrous migration was related to sexual differences in speed of migration or stopover strategy, males and females should differ in rates of fat deposition and in fuel loads at departure when measured at the same stopover site (Alerstam 2003; Hedenström 2008). In the Greenlandic/Icelandic subspecies of the Northern Wheatear (*Oenanthe oenanthe leucorhoa*), males showed a positive correlation between fuel load at departure and the deposition rate of fuel when supplemented with extra food in the field, whereas females departed with approximately constant fat stores independent of the deposition rate (Dierschke et al. 2005). However, this difference in stopover strategy between the sexes was not evident in the Scandinavian nominate form of the Northern Wheatear (*O. o. oenanthe*), which is protandrous during spring migration (Hantge 1958; Spina et al. 1994) and in arrival on the breeding grounds (Currie et al. 2000).

There is indirect evidence that males and females of migratory songbirds may employ different stopover strategies during spring migration. Females of some species are caught in higher numbers than are

Table 1 Mechanistic explanations of avian protandry and the potential factors that mediate the effect

Mechanism	Photoperiod	Other environmental variables	
		(e.g., food, temperature)	Social dominance
(A) Differential migration speed	+/-	+/-	+/-
(B) Latitudinal sexual segregation	+	+	+/-
(C) Differential onset of spring migration			
circannual rhythms	+	+/-	-
habitat segregation	-	+	+
carry-over effects across life-history stages	+/-	+/-	+/-

+: an effect; -: no effect; +/-: effect unknown.

males (Fig. 1A) and are more likely to be recaptured during stopover (Lavee et al. 1991; Morris et al. 1996). However, such differences could simply reflect sex-specific migration routes or seasonal variation in the environmental conditions that cause males and females to interrupt or resume migration (cf. Rainio et al. 2007).

Because asynchronously migrating males and females are exposed to different environmental conditions, it is impossible to separate intrinsic and environmental factors affecting their stopover and migratory behavior unless one can follow individuals over several days of their journey. One way of separating the intrinsic and environmental effects is to study birds in captivity, where the investigator can control environmental conditions (van Noordwijk

et al. 2006). In aviary-based investigations on male and female redstarts (*Phoenicurus phoenicurus*) caught on Heligoland Island and held under identical controlled conditions (Fig. 3), we found no significant sexual differences in search-settling time (i.e., the time elapsed from release into the aviary to settlement of the bird at the feeding dish), foraging activity, intake of food, and changes in body weight (one-way ANOVA with sex as a fixed factor, all P -values > 0.05 , cf. Coppack 2006). In an additional study on caged redstarts, we found no significant differences between the sexes in the circadian rhythm of nocturnal migratory activity (Coppack et al. 2008a). These indoor studies suggest that sexual differences in the speed of migration are not a determinant of protandrous spring migration

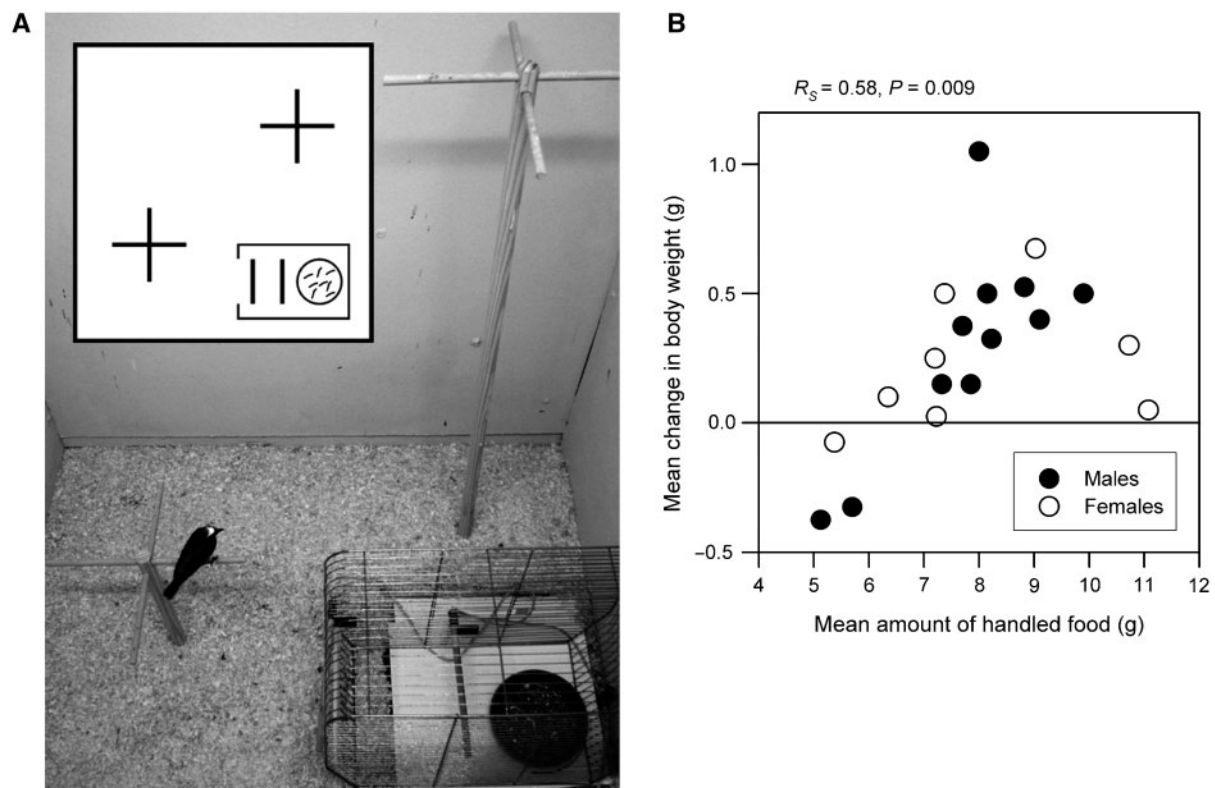


Fig. 3 Foraging and fuelling performance of migratory redstarts (*Phoenicurus phoenicurus*) at an artificial stopover site. Eleven male and nine female redstarts were randomly sampled between 27 April and 28 May 2005 on Heligoland Island (54°12'N, 07°56'E). Upon capture, birds were transferred individually to indoor aviaries (A) equipped with two perches and a feeding dish providing 30 g mealworms (*Tenebrio* sp.) in an enclosure (transformed bird cage fitted with two movable perches and connected to an event recorder). As soon as a bird entered the cage, the timing and duration of its visit was registered. Birds were kept at 19–22°C and under simulated local photoperiod (LD 16:8 h; 5:00–21:00 CEST) for 4 days and were released thereafter. Each evening, the redstarts were weighed (nearest 0.1 g). The amount of food that was left over was also weighed. Before the lights went off in the evening, birds were moved to separate aviaries. Food was refilled to exactly 30 g each morning. Shortly after the lights went on in the morning, birds were released into the arena through a flap door that could be opened remotely. (B) The mean amount of food that birds handled over the 4 days was significantly positively correlated with the mean gain in body weight over the 4 days (level of significance of Spearman's rank correlation). One-way ANOVA with sex as a fixed factor yielded no significant sexual differences in the intake of food and change in body weight ($P > 0.05$). Models including body size and fat load at capture as covariates yielded the same result (no significant sexual differences, all $P > 0.05$).

of the Redstart. This conclusion is further supported by the fact that protandrous migration in the Redstart and other Palearctic-African migrants is already apparent at lower latitudes, e.g. on the Tyrrhenian islands which provide one of the first available landfalls after crossing of the Saharan desert and the Mediterranean Sea (Spina et al. 1994; Rubolini et al. 2004). Thus, males and females may set off from tropical wintering grounds at different times of the year rather than migrate at different speeds.

Latitudinal sexual segregation

The sexes of many seasonally reproducing vertebrates are separated during the non-reproductive period. Spatial sexual segregation may arise due to differences in habitat preference, social affinity and energetic or nutritional requirements of males and females (Ruckstuhl 2007). Latitudinal sexual segregation, in which males tend to winter closer to the breeding grounds than do females, is known to occur in many temperate-zone bird species (Myers 1981; Nolan and Ketterson 1990; Catry et al. 2005b; Komar et al. 2005; for reviews see, Ketterson and Nolan 1983; Cristol et al. 1999; Newton 2008). Possibly the most prominent example among Palearctic passerines is the Chaffinch (*Fringilla coelebs*), which Carl von Linné named *coelebs*, meaning bachelor, with reference to the male's solitary social status during the non-breeding period (Newton 2008). In Palearctic-African migrants, however, there is currently no evidence from either ring recoveries (Berthold 2001; Newton 2008) or trace-element analyses of molted feathers (Szép et al. 2009) that males and females segregate into different wintering latitudes. Yet, ringing activity in Africa is very low and the number of species studied using stable-isotope analysis is too limited to draw general conclusions on differential migration of trans-Saharan migrants.

By wintering further north, male birds could expedite their return to the breeding grounds in two ways. First, the distance between non-breeding and breeding areas is shorter and traveling time is consequently reduced. Secondly, photoperiodic cues experienced by males wintering at higher latitudes could cause an earlier onset of vernal migration (Coppack and Pulido 2004; Coppack et al. 2008b). Hence, sexual segregation could account for differential arrival of males and females, without requiring specific adaptations in either the onset or the speed of migration.

Three hypotheses are recurrently mentioned in the ornithological literature to explain sex-specific differences in distance of migration (Myers 1981; Cristol et al. 1999; Holberton and Able 2000; Stouffer and Dwyer 2003; Catry et al. 2005b): The "body-size" or "cold-tolerance" hypothesis assumes that sexual segregation in winter is linked to differential susceptibility of males and females against cold weather, with larger-bodied males consequently wintering further north (Ketterson and Nolan 1976; 1979, Ketterson and King 1977; Stuebe and Ketterson 1982; Jenkins and Cristol 2002). The "social-dominance" hypothesis suggests that subordinate females are forced by dominant males to move to areas further away from the breeding territories (Terrill 1987; Choudhury and Black 1991). The "arrival-time" hypothesis considers differential advantages between males and females in the timing of arrival at the breeding grounds, with the territorial sex gaining benefits in fitness through wintering closer to the breeding grounds (Ketterson and Nolan 1976; Stouffer and Dwyer 2003).

This traditional set of hypotheses is confusing, because it does not distinguish clearly between the proximate and ultimate factors causing latitudinal segregation. Sexual differences in social dominance or in body size could drive latitudinal segregation either at a mechanistic level, evolutionary level, or both (Newton 2008). Using data on sex, age, date, and location from specimens collected south of the breeding range, Myers (1981) tested these three hypotheses for several species, including the protogynous Red Phalarope (*Phalaropus fulicarius*) and the Sanderling (*Calidris alba*). Neither red phalaropes nor adult sanderlings showed any sexual difference in wintering latitude. Combined with comparative data from other bird species, including songbirds, he concluded that patterns of latitudinal sexual segregation can only be explained by the "arrival time" hypothesis and not by intersexual differences in cold tolerance (body size) or social dominance.

Among North American songbird species, the Dark-eyed Junco represents the best studied differential migrant (Ketterson and Nolan 1983), for which the proximate basis of sexual segregation has been established in a laboratory investigation (Holberton 1993). When held under identical conditions, female juncos initiated autumnal migratory restlessness about 12 day earlier than did males, and continued to be active after males had stopped (Holberton 1993). This study suggests that the behavioral basis of latitudinal sexual segregation is developmentally fixed and controlled by endogenous circannual rhythms (Gwinner 1996; Berthold 2001).

Protogynous onset of post-breeding migration, which occurs in many songbird species (Gätke 1895; Newton 2008), can be viewed as an adaptation to the longer distances females need to cover during migration. Thus, the extent of autumnal protogyny may indirectly reflect the extent of latitudinal sexual segregation, which, in turn, may determine the extent of spring-time protandry. This assumption finds support in the fact that among Palearctic songbirds, species with high levels of autumnal protogyny exhibit the greatest extent of spring protandry (Fig. 4). Alternatively, autumnal protogyny may be explained by the extent to which males remain territorial after breeding (Wegglar 2000; Forstmeier 2002; for a review of hypotheses explaining autumnal protogyny, see Mills 2005).

In white-throated sparrows (*Zonotrichia albicollis*) breeding in Canada, differences in arrival between males and females (and among males) in the spring are associated with the latitude at which they winter (Mazerolle and Hobson 2007). Individuals arriving early wintered further north, as indicated by stable-isotope ratios in feathers that were molted on the wintering grounds. Differential migration with respect to distance may also correlate with wing shape. However, relationship between wing shape and the distance migrated have only rarely been considered. Mulvihill and Chandler (1990) found that male dark-eyed juncos had longer wings and larger proximal primary distances (corrected for body mass) than did females, which seems counterintuitive with regard to the shorter average distances migrating males need to cover, but is in accord with the hypothesis of higher migration speed of males compared to females (see above).

Differential onset of vernal migration

Apart from spending the non-breeding season closer to the breeding grounds, males may achieve an earlier arrival compared to females by initiating migration earlier. This could result either from differences between the sexes in the circannual program or differences in the response to environmental cues like photoperiod (Gwinner 1996; Berthold 2001; Coppack et al. 2008b), from habitat segregation on the wintering grounds (Marra and Holberton 1998; Marra et al. 1998), or from carry-over effects of conditions experienced during previous life-history stages (cf. Pulido 2007).

Evidence for earlier departure of males compared to females comes from studies that analyze seasonal changes in sex-ratios of birds sampled on, or near,

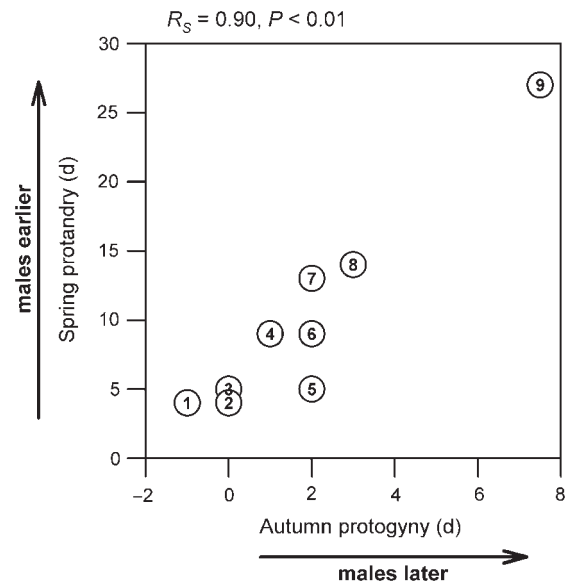


Fig. 4 Correlation between the extent of protandry during migration in the spring and the extent of protogyny in autumn among nine Palearctic passerine migrants trapped between 1960 and 2000 at Heligoland. Ringing recoveries indicate that migrants caught on Heligoland originate from Scandinavian breeding populations (Zink 1973–1985; Zink and Bairlein 1995). (1) Blackcap, *Sylvia atricapilla*; (2) Linnet, *Carduelis cannabina*; (3) Common Whitethroat, *Sylvia communis*; (4) Redstart, *Phoenicurus phoenicurus*; (5) Ring Ouzel, *Turdus torquatus*; (6) Blackbird, *Turdus merula*; (7) Goldcrest, *Regulus regulus*; (8) Chaffinch, *Fringilla coelebs*; and (9) Reed Bunting, *Emberiza schoeniclus*. Values derived from Hüppop and Hüppop (2004). Irruptive winter guests (Fieldfare, *Turdus pilaris*; Great Tit, *Parus major*; Brambling, *Fringilla montifringilla*; Greenfinch, *Carduelis chloris*) were omitted from the analysis. The degree of protandry is defined as the difference between the median trapping date of females relative to that of males, with positive values signifying earlier passage of males. The degree of protogyny in autumn is defined as the difference between the median trapping date of males relative to that of females, with positive values signifying earlier migration by females. Level of significance of Spearman's rank correlation. Autumnal protogyny remained significantly positively correlated with vernal protandry after correcting for phylogenetic nonindependence (Pearson product-moment correlation, $r = 0.95$, two-tailed $P < 0.0001$), applying the PDAP module (Midford et al. 2005) implemented in Mesquite (Maddison and Maddison 2009).

the wintering sites. Typically, the number of males decreases earlier in the course of spring. This has been demonstrated in a number of songbirds, for example in reed buntings (*Emberiza schoeniclus*) wintering in Spain (Villarán Adánez 1999) and northern Italy (Rubolini et al. 2000), in chiffchaffs (*Phylloscopus collybita*) wintering in Senegal (Catry et al. 2005), and in hermit thrushes (*Catharus guttatus*) wintering in the eastern United States and Mexico (Stouffer and Dwyner 2003). However, in

these observational studies, it is uncertain whether males and females belong to the same breeding populations.

Day length (photoperiod) is the most important environmental cue controlling the onset of migration in songbirds (Gwinner 1996; Berthold 2001; Coppack and Pulido 2004; Coppack et al. 2008b). Therefore, differences between the sexes in the timing of departure from the wintering grounds are likely to be caused by sexual differences in photosensitivity. Circumstantial evidence for this proposition comes from observations of individual consistency in departure from the wintering grounds in spring (Kok et al. 1991; Battley 2006) and consistency of protandry among years (Fig. 1; Rainio et al. 2007). Clearer evidence for sexual differences in circannual rhythmicity and photoperiodicity as a cause of protandrous migration in spring is provided by laboratory studies. When individuals of species that show protandrous arrival are kept under controlled laboratory conditions (i.e., ad libitum food, constant temperature and humidity, simulated photoperiodic conditions), males initiate spring migratory activity before females. This has been shown, so far, in dark-eyed juncos (Ketterson and Nolan 1985), Palearctic *Sylvia* warblers (*Sylvia atricapilla*, Terrill and Berthold 1990; *Sylvia borin*, Widmer 1999), the Pied Flycatcher (*Ficedula hypoleuca*, unpubl. data) and the Redstart (Fig. 5). In all these studies, sexual differences in the onset of migratory activity were as large as, or even larger than, the sexual difference in arrival observed in the populations from which birds were sampled. This suggests that in these species, sex-specific differences in the onset of migration are primarily caused by different endogenous cycles or photoperiodic sensitivities. Common-garden experiments simulating different photoperiodic regimes (Terrill and Berthold 1990; Widmer 1999) indicate that males and females may have different norms of reaction to photoperiod.

Besides these hardwired endogenous and photoperiodic control mechanisms, the timing of migration in spring may be modified by physical condition or by physiological state (Gordo 2007; Pulido 2007). Several studies provide evidence for an influence of habitat quality and physical condition on the timing of migration (Marra and Holmes 2001; Bearhop et al. 2004; Norris et al. 2004; Saino et al. 2004a, 2004b; Norris 2005; Studds and Marra 2005). Individuals that spend the non-breeding season in high-quality habitats are in better condition and are able to accumulate the fat deposits necessary for migrating faster. Consequently, birds wintering under optimal conditions may be able to

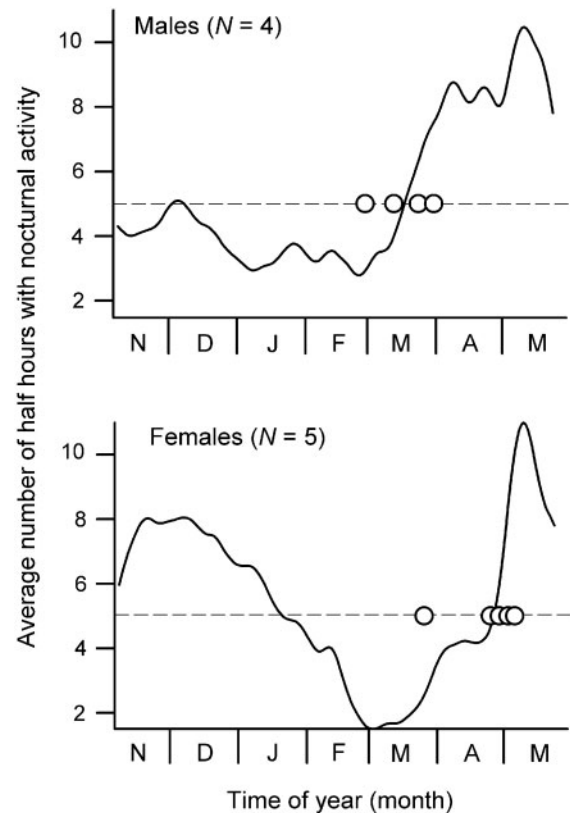


Fig. 5 Experimental evidence for a sex-specific difference in the onset of vernal migration in the Redstart (*Phoenicurus phoenicurus*). During the migratory period, night-migrating songbirds develop nocturnal locomotory activity (German: *Zugunruhe*), which reflects the timing and extent of migratory behavior found in the wild (Gwinner 1996; Berthold 2001). Yearling redstarts were caught during autumnal migration on Heligoland Island and were kept for 8 months in individual registration cages under constant laboratory conditions (LD 12:12, ad libitum food and water, room temperature). The number of movements per unit of time was measured using event recorders connected to vibration detectors. Spline curves are locally weighted within optimal bandwidths and represent the average nocturnal activity in each sex over 7 months. Circles mark the individual onset dates of vernal migration, defined as the dates on which activity reached 5 half hour units on average. Male redstarts showed a significantly earlier onset of nocturnal activity (males, 16 March \pm 14 days; females, 23 April \pm 16 days; mean \pm SD; Wilcoxon two-sample test, $S = 11$, $Z = -2.08$, $P < 0.05$), suggesting that they would have left the wintering site several days before females would have gone.

leave the wintering sites earlier than can birds wintering under sub-optimal conditions. The distribution of individuals among habitats differing in quality could result from differences in social dominance, with males generally being dominant over females (Marra 2001). In American redstarts (*Setophaga ruticilla*), sexual differences in date of departure from wintering sites in Jamaica are

primarily due to sexual segregation while in the winter habitat. The settlement of males and females in different habitats is apparently caused by dominance. Males winter predominantly in mangrove forest, females in second-growth scrub. The difference in availability and quality of food among these habitats results in clear sexual differences in survival, weight-gain, and condition, and, finally, date of departure (Marra et al. 1998; Marra and Holmes 2001). Note, however, that in some years, sexual differences in departure dates were found to be independent of the quality of the habitat (Marra et al. 1998), indicating that other timing cues had been used.

Apart from habitat conditions experienced during the non-breeding period, conditions during the previous breeding season may influence the timing of return to the breeding areas. For example, hatching date, rearing conditions and parental investment may potentially determine how individuals perform during their first migratory cycle (Sternberg and Grinkov 2006). In many species, males and females differ in their parental investment and may therefore differ in physical condition after reproduction. Carry-over effects of previous breeding conditions on the timing and extent of migration could potentially shape the degree of protandry. If this were the case, protandry should be most pronounced in species in which female reproductive investment is much higher than in males. We should also find correlations between yearly protandry values and environmental conditions of the preceding breeding seasons. If settlement in a high-quality wintering territory depends on arrival date and physical condition, birds that leave the breeding areas late would tend to settle in habitats of lower quality, and would consequently return to the breeding areas later. Likewise, birds breeding early and in high-quality territories should be able to occupy the best territories in winter and to return earlier to the breeding grounds the following season (Gunnarsson et al. 2005). Other carry-over effects could result from migrating at different times of the season, and therefore, being exposed to different climatic conditions en route (Both and te Marvelde 2007) and to different photoperiods either on the wintering site (see above) or en route (Helm and Gwinner 2005).

Protandry and the response of migratory birds to climatic change

Global climatic change is expected, and has been shown, to profoundly affect the timing and extent

of avian migration (Berthold 1991; Coppack and Both 2002; Lehikoinen et al. 2004; Jonzén et al. 2006; Rubolini et al. 2007; Møller et al. 2008). Several studies have linked long-term trends in the overall timing of migration and breeding in spring to seasonal shifts in climatic conditions or resource availability (Coppack and Both 2002; Lehikoinen et al. 2004; Visser et al. 2004; Gordo 2007). Yet, the within-season complexity of phenological patterns has, so far, received only limited attention (MacMynowski and Root 2007; Rainio et al. 2007; Møller 2008).

Intersexual differences in the timing and extent of migration may expose males and females of the same species to different patterns of seasonal environmental change, since both sexes pass through different latitudes and climatic conditions at different times of the year and may also use different habitats during winter (cf. Both and te Marvelde 2007; Studds and Marra 2007). Furthermore, selection on the time of arrival differs between males and females (Morbey and Yedenberg 2001; Kokko et al. 2006; Møller 2007). Any change in the relative timing of arrival of males and females in immediate response to changing environmental conditions in winter or during migration could influence subsequent mating opportunities, with consequences for reproductive success, individual fitness, and population viability.

Elevated spring temperatures could increase pre-breeding survival rates, thereby making it possible for early-arriving males competing for territories to arrive even earlier (Møller 2004, 2007; Spottiswoode et al. 2006). Therefore, climatic change may lead to an increased time lag between the arrival of males and females. This was found in a population of Danish barn swallows, *Hirundo rustica* (Møller 2004). The role of sexual selection in driving the increase in protandry in this population was supported by a parallel change of a sexually selected trait, i.e. tail length, which showed a trend towards larger values in early-arriving males (Møller 2004; Møller and Szép 2005). In contrast, Rainio et al. (2007) found that the degree of protandry had not changed consistently in four sexually dichromatic songbird species in which migration dates in spring had advanced. Variation in large-scale weather conditions, as reflected in the North Atlantic Oscillation (NAO) index, did not explain among-year variation in protandry. Moreover, Spottiswoode et al. (2006) found that the positive relationship between the advancement of vernal migration and indices of sexual selection was stronger for changes in the median date of migration of whole populations than for changes in the timing

of first-arriving (male) individuals, suggesting that changes in selection have not only affected protandrous males. However, unlike in Møller's study (Møller 2004), phenological analyses based on passage dates of migrants do not include information on how individual males and females from defined populations behave in different years or on how progeny of known origin deviates from its mid-parental value. Thus, results from these studies need to be interpreted with caution.

The adaptability of migratory behavior to environmental change could be constrained by positive intersexual genetic correlations, if optimal dates of migration differ between males and females, as suggested by empirical studies (Møller 2004, 2007, 2009) and theoretical models (Kokko et al. 2006), or if changes in selection on the dates of arrival of males and females are in different directions, for which there is also some evidence (Møller 2004, 2007). Moreover, if arrival in spring is primarily determined by environmental conditions on the wintering sites or en route, and there is temporal or spatial segregation among males and females during the non-breeding season or during migration, then the relationship between the dates of arrival of males and females will change, although not necessarily adaptively (since shifts in environmental conditions are not correlated with the "needs" of an individual). If the degree of protandry is an adaptive trait, as shown in the Barn Swallow (Møller et al. 2009), the responsiveness of females or males to environmental cues experienced en route or on the non-breeding grounds would need to evolve. Again, genetic correlation could prevent adaptation to an optimum. Hence, it seems that the key for predicting future changes in the timing of migration will be to determine the genetic co-variation between the arrival dates of males and females and the traits determining the timing of arrival.

Conclusion

Protandrous arrival at the site of reproduction is common among birds and other migratory organisms. In most cases, however, it is uncertain how sexual differences in the timing of arrival are controlled. Empirical studies on a few model songbird species suggest that two mechanisms (which are not mutually exclusive) most likely control avian protandry: spatial sexual segregation over latitude and differential onset of migration in the spring as a consequence of sexual differences in responsiveness to photoperiodic cues. However, we do not know

how genetic and environmental influences contribute to these different mechanisms, nor do we know what consequences they may have for the adaptability of migratory routines to global environmental change.

Our current knowledge on the patterns and processes of animal migration are based mostly on correlative field observations at the level of the species or population or is derived from behavioral and/or physiological correlates measured in captive specimens under controlled conditions. In contrast to most morphological, physiological or behavioral attributes that can be directly measured, migration is a phenomenon that is notoriously difficult to study in either the field or laboratory. Currently, we simply do not know whether results from laboratory experiments give us realistic insight into the mechanisms controlling actual migration. A major breakthrough in the study of animal migration is expected from recent advances in telemetric methods but judged by the quantity of small-animal species for which an appropriate tracking system is still unavailable (Wikelski et al. 2007), it seems we are only just beginning to understand the migratory process as such and the genetic and physiological links between migration and other life-history stages.

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