Protandry and sexual dimorphism in trans-Saharan migratory birds

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Earlier arrival to reproductive sites of males relative to females (protandry) is widespread among migratory organisms. Diverse mechanisms have been proposed that may select for protandry, including competition for limiting resources (e.g., territories) or mates. In species with large variation in male reproductive success, such as polygamous species and those with intense sperm competition, early arriving males may accrue a fitness advantage because they acquire more mates or have larger chances of paternity. Comparative studies of birds have shown that sexual size dimorphism (SSD) is positively associated with the level of polygyny, whereas intense sperm competition is associated with sexual dichromatism (SD). Positive correlations between protandry and SSD or SD can therefore be expected to exist across avian species. Because large males are predicted to be better able to cope with adverse ecological conditions early in the breeding season, selection for protandry, in turn, may have a correlated response on SSD among migratory species breeding in boreal latitudes. Although previous studies of birds have analyzed the association between SSD and protandry, none has analyzed SD in relation to protandry. Here we analyze the association between protandry during spring migration, SSD, and SD in 21 trans-Saharan monogamous migratory bird species. The difference in median migration dates between females and males, reflecting protandry, was positively associated with SD but not with SSD. Because dichromatism is positively related to sperm competition across species, present results are consistent with predictions derived from sexual selection hypotheses for the evolution of protandry mediated by sperm competition. *Key words:* arrival date, bird migration, comparative analysis, sexual dichromatism, sexual selection, sperm competition. *[Behav Ecol 15:592–601 (2004)]*

$\mathbf{E}$arlier migration or emergence of males relative to females, that is, protandry, is a common phenomenon across plants and animals (for review, see Morbey and Ydenberg, 2001). Several theoretical and empirical studies have tackled the issue of optimal timing of migration and arrival at breeding sites of either sex in individual species, taking the benefits and costs of early arrival into account (Brown and Brown, 2000; Kokko, 1999; McNamara et al., 1998; Møller, 1994a; Morbey and Ydenberg, 2001). A number of hypotheses have been proposed to explain the evolution of protandry, and these have been detailed in Morbey and Ydenberg (2001), the method of which we follow for terminology. In migratory birds, among which protandry is widespread, intrasexual competition for preferred territories is expected to select for early arrival at the breeding areas, because individuals that migrate and arrive early will acquire better territories compared with that of those that arrive late (Hasselquist, 1998; Ketterson and Nolan, 1976; Kokko, 1999; Lozano et al. 1996; Myers, 1981). This "rank advantage" hypothesis is supported by the observation that the territorial sex generally arrives earlier than does the other sex, and that often sexes tend to arrive together in nonterritorial species (Connors et al. 1979; Cooke et al. 1975; Myers, 1981; but see Reynolds et al., 1986). The "susceptibility" hypothesis proposes that protandry should evolve when early arriving individuals accrue a fitness advantage compared with those that arrive late and that environmental conditions at arrival on the breeding grounds differentially affect males and females, with male being better able to cope with conditions early in the

breeding season. For example, in boreal breeding bird species in which males are larger than females, males may afford arriving early because large individuals are likely to outcompete smaller ones for food, and a smaller area-to-volume ratio of large individuals should enhance metabolic efficiency and survival early in the breeding season, when ecological conditions can be harsh (see Kissner et al. 2003). The "mate opportunity" hypothesis predicts that individuals of the early arriving sex are more successful than are late arriving ones of the same sex in acquiring a mate. This has been demonstrated in some studies, in which mating success and level of polygamy have been shown to be larger among early compared with late arriving individuals (Hasselquist, 1998; Langefors et al. 1998; Lozano et al., 1996). Other hypotheses are less likely to apply to migratory bird species (see Morbey and Ydenberg, 2001), and thereafter, we limit our discussion to those presented above.

Independent of the mechanisms that lead to the evolution of protandry, selection for early male relative to female arrival is predicted to have consequences on body size of the two sexes in migratory bird species breeding at high latitudes. Weatherhead and Clark (1994) hypothesized that large size enhances the probability to survive harsh weather conditions at early arrival on the breeding grounds. This "energetic" hypothesis for the evolution of size differences between the sexes has been supported by comparative evidence in a study by Kissner et al. (2003) and is likely to apply widely to migratory birds breeding in the temperate region (but see Francis and Cooke, 1986). Thus, sexual size dimorphism (SSD) can represent a prerequisite condition for the evolution of protandry, as envisaged by the susceptibility hypothesis, but also a consequence of selection for early male relative to female arrival.

Sexual selection arises from differences in reproductive success among individuals (Andersson, 1994; Darwin, 1871; Møller, 1994b) and is believed to lead to the evolution of male

Table 1

Predictions of possible associations between protandry during spring migration and sexual size dimorphism (SSD) or sexual dichromatism (SD) in monogamous migratory birds, based on different hypotheses for the evolution of protandry (defined after Morbey and Ydenberg, 2001) and different natural and sexual selection mechanisms

Hypotheses for the evolution of protandry	Selection mechanism	Predictions
Rank advantage	Male-male competition for territories	Protandry positively related to SSD, no relation with SD
Susceptibility	Differential susceptibility to environmental condition in relation to sex	Protandry positively related to SSD, no relation with SD
Mate opportunity	Male-male competition for females Female choice	Protandry positively related to SD and SSD Protandry positively related to SSD, no relation with SD

For further details, see Introduction.

secondary sexual traits, such as large size and ornamental characters, relevant to male intrasexual competition over territories and mates, as well as female mate choice. Comparative studies of birds have identified a positive association between the intensity of different mechanisms of sexual selection (e.g., variation in number of mates or extrapair offspring) and different forms of sexual dimorphism (Dunn et al., 2001; Møller and Birkhead, 1994; Owens and Hartley, 1998). Sexual dichromatism (SD) is mainly associated with sperm competition mediated by cryptic female preference for brightly colored males as extrapair partners, as positive associations have repeatedly been found between dichromatism and frequency of extrapair paternity across species (Møller and Birkhead, 1994; Owens and Hartley, 1998; but see Dunn et al., 2001), whereas size dimorphism is mainly associated with variation in social mating system, with polygamous species showing relatively large differences between the sexes (Dunn et al., 2001; Owens and Hartley, 1998).

When opportunities for sexual selection are large, such as in monogamous species with high frequency of extrapair paternity, selection for early male arrival at the breeding areas is likely to be more intense than is selection in species with small variation in male reproductive success. For example, early arriving (and therefore breeding) males may have greater chances of paternity of the offspring generated by their social mate because of low levels of sperm competition by the few males already present (Birkhead and Møller, 1992, 1998). In addition, mates of early arriving males will have already completed their first clutch when many females in the population are still receptive. Early arriving males will thus have more chances of fertilizing extrapair females because they will not have to guard for paternity when other females are fertile (Birkhead and Møller, 1992, 1998). High levels of sperm competition in socially monogamous species may thus select for early male arrival and a high degree of SD (albeit through separate selection mechanisms, i.e., intrasexual competition for mates and cryptic female choice, respectively), resulting in a positive correlation between protandry and dichromatism across species.

Under monogamy, sexual selection mediated by female mate choice may also select for early male arrival, if extensive

overlap in migration spread and arrival dates exists between males and females, as is the case in most passerine and near-passerine avian species (see Francis and Cooke, 1986; Spina et al., 1994; current study). Females can take several days before choosing a mate (see Møller, 1994b) and can thus discriminate between males according to arrival date. If male arrival is condition-dependent and only males of high phenotypic/genetic quality can afford arriving early (Andersson and Gustafsson, 1995; Arvidsson and Neergaard, 1991; Lozano, 1994; Marra et al., 1998; Stolt and Fransson, 1995), females may acquire direct or indirect benefits by choosing early arriving males. Thus, female choice may select for early male arrival because early arrival functions as a reliable signal of mate quality. If early arriving females are more fecund, as originally proposed by Darwin (1871) and Fisher (1930; see also Kirkpatrick et al., 1990), early arriving males would achieve greater reproductive success compared with the success of late arriving ones. In addition, in multibrooded species, variance in male breeding success is influenced by the number of clutches achieved during the breeding season, and early arriving males should have relatively more chances of multiple breeding attempts (see Møller, 1992, 1994b). Therefore, in species in which variance in male quality, and thus condition-dependent arrival date, is relatively large, greater protandry is expected. However, in these species, SSD is also expected to be larger because of the natural selection advantage of large male body size, as envisaged by the energetic hypothesis.

In this comparative study, we analyze the correlation between protandry and SSD by using a large data set of 21 trans-Saharan migratory monogamous birds species banded in southern Europe. In addition, we test for a relationship between protandry and SD, which was not analyzed previously (Francis and Cooke, 1986; Kissner et al., 2003). Natural and sexual selection mechanisms may produce partly different patterns of associations between protandry and sexual dimorphism in monogamous migratory birds. Our predictions on the possible association between protandry and SSD or SD stemming from the hypotheses we have briefly reviewed are detailed below and summarized in Table 1.

According to the rank advantage hypothesis, if intrasexual selection for the best territories selects for protandry, we should expect a positive association between protandry and SSD, mediated by selection for large size of early arriving males. However, male ornamentation is unlikely to enhance male survival in adverse environments; therefore, an association between protandry and SD may not be expected under this hypothesis. According to the susceptibility hypothesis, a positive association between protandry and SSD is predicted because individuals of the largest sex can afford arriving earlier. Plumage ornamentation and epigamic coloration are unlikely to affect differentially males and females at early arrival on the breeding grounds, and thus, no association between protandry and SD is expected. A positive association between protandry and SSD or SD is expected under the mate opportunity hypothesis, because the intensity of male-male competition for access to females (including sperm competition) or female preference for early arriving males may favor the concurrent evolution of both protandry and different forms of sexual dimorphism. First, selection for early male arrival mediated by sperm competition may result in a positive correlation between protandry and SD; because early arriving males may benefit from being larger, a positive correlation between protandry and SSD can also be predicted. Finally, female choice for early arriving males should result in a positive correlation between protandry and SSD but not SD, because natural selection is not predicted to favor bright coloration among early arriving males.

Predictions from the above hypotheses are not mutually exclusive, and associations between protandry and sexual dimorphism may be promoted by complex interactions between the suggested mechanisms acting in concert. However, although a positive covariation between protandry and size dimorphism would be consistent with all of the hypotheses, a positive correlation between protandry and color dimorphism would more strongly support the hypothesis that protandry is associated with sexual selection mediated by sperm competition.

The study system

The Palearctic-African migration system is among the most intensively investigated models for the study of migration strategies, both from ecological and ecophysiological perspectives (Biebach, 1990; Biebach et al., 2000; Jenni et al., 2000; Moreau, 1972; Rubolini et al., 2002; Schwilch et al., 2002; Spina and Pilastro, 1998). Briefly, migrants leave breeding grounds in the late boreal summer to spend winter in Africa, where they spread over a vast geographical area and occupy a wide range of habitats (see Moreau, 1972). At the end of the boreal winter, birds return to their European breeding quarters. During spring migration, they are confronted with the ecological barriers represented by the Sahara desert and the Mediterranean sea. Phenology data used in our study were collected on some small islands in the central Mediterranean, along the western coast of southern Italy, and refer to birds in active migration, which land right after having crossed the desert and sea with broad-front movements (see Jenni et al., 2000; Moreau, 1972; Pilastro and Spina, 1997; Pilastro et al., 1998; Schwilch et al., 2001, 2002; Spina et al., 1994). Apparently, the coast of North Africa is not used as a substantial refueling site, as residual fuel stores at arrival in southern Europe are mainly correlated to the distance from the last suitable fueling habitat south of the Sahara (Pilastro and Spina, 1997). The Palearctic-African migration system thus offers a valuable opportunity to test comparative hypotheses on the evolution of migration strategies, thanks to the relative uniformity of ecological conditions during migration among species (see Pilastro and Spina, 1997; Spina and Pilastro, 1998; Spina et al., 1994).

METHODS

The species considered

In our analyses we considered 21 sexually dichromatic species that regularly stopover on the central Mediterranean islands during spring migration (see Appendix; Messineo et al., 2001). These were selected based on the following criteria: (1) trans-Saharan migrants, that is, species breeding in Europe and wintering mainly or partly south of the Sahara (following Cramp, 1998); (2) species with a broad-front spring migration across the desert and sea (i.e., not known to concentrate at particular sites in order to avoid prolonged sea crossings); in this case the small islands of the central Mediterranean are likely to represent their first landing opportunities in southern Europe; and (3) sex identifiable in the hand from plumage characteristics on most individuals. Sex was assigned by well-trained bird-banders based on standard field guides (for passerines, Svensson, 1992; for other species, Baker, 1993). Unsexed individuals and retraps were discarded from all analyses. From a taxonomic perspective, our sample encompassed seven orders of long-distance migrants (after the method of Sibley and Ahlquist, 1990): Galliformes (*Coturnix coturnix*), Upupiformes (*Upupa epops*), Coraciiformes (*Merops apiaster*), Cuculiformes (*Cuculus canorus*), Strigiformes (*Caprimulgus europaeus*), Columbiformes (*Streptopelia turtur*)

and Passeriformes (15 species; see Appendix). All species included in the analyses have monogamy as the prevailing mating system (Cramp, 1998). We could not include sexually monochromatic species that are common during migration at the study sites; although some of them (e.g. *Phylloscopus trochilus*) are slightly sexually dimorphic in size, the extensive size overlap between the sexes, the confounding effect of geographic variability in size, and the unknown geographical origin of migrants captured in southern Europe (Cramp, 1998), prevented us to consider these species.

Phenology of spring migration across the Mediterranean sea

We used data collected at four Thyrrenian islands (Capri [40°33′–14°15′ E], Ventotene [40°48′ N–13°25′ E], Giannutri [42°15′ N–11°06′ E], and Montecristo [42°14′ N–10°19′ E]) in the period 16 April–15 May, which corresponds to the peak migration period for the majority of the species considered in the analyses (see below and Messineo et al., 2001; Spina et al., 1993). Our data set included more than 87,000 individuals and refers to the years 1988–2001 (although data from some years and sites were missing). After being trapped in mist-nets, birds were marked with individual aluminium bands, processed based on standardized protocols (which included taking some standard biometric measurements, see Spina et al., 1993), and released. Most migrants are caught within a few hours after landing, as they tend to resume the journey as soon as possible, without substantial refueling on the islands (Schwilch et al., 2001). We expressed the difference in migration date between males and females (hereafter, ΔM) as the difference between the median date of capture of females relative to that of males. Thus, great positive values of ΔM indicate an earlier migration date of males compared with females. We chose to use the median value as an index of migration date to be consistent with the ornithological literature on this topic (see Berthold, 1973). We assigned the value one to 1 April. Because we were interested in the relative difference in migration timing between the sexes, and given the unequal duration of the migration period across species, to control for the duration of migration, we corrected ΔM for the estimated overall temporal extent of the migration period for each species, expressed as the difference between the 75th and the 25th percentiles of the migratory distribution for each species (ΔP). The relative difference in migration timing between sexes, corrected for migration spread of each species, was therefore calculated as $\Delta M_C = \Delta M / \Delta P$. In all analyses we used ΔM_C as a measure of the degree of protandry. ΔM and ΔM_C values were strictly and positively correlated ($r = .98$, $n = 21$), and either indexes therefore gave very similar information.

It should be considered that PPI data refer to a period that does not encompass the whole migratory season of the species considered. Although there were data for some years and sites for a more prolonged period, we chose to use this restricted data set in order to avoid having to correct for differential trapping effort between years and sites, which is a difficult task in the absence of detailed information and may thus seriously bias the data (Francis and Cooke, 1986). However, an exploratory analysis revealed that ΔM_C values were strongly and positively correlated with the same index calculated on all available data ($r = .96$, $n = 21$, $p < .001$).

Sexual dimorphism

Size dimorphism
For each species, we obtained the mean wing length and body mass for males and females from our large set of biometric measurements. We calculated an index of body size di-

morphism by regressing male traits on female traits (after $\log_{10}$-transformation) for all the species, and using the standardized residuals as an index of sex dimorphism for each trait (Ranta et al., 1994). To obtain a single index from the two measures of dimorphism, we carried out a principal component analysis (PCA) on the residuals. PCA extracted a single factor, which accounted for 94.5% of the variance. Thus, we used PCA scores in subsequent analyses as an index of body size dimorphism.

Dichromatism
The degree of SD was scored on a scale ranging between zero (a monomorphic species) and 24 (maximum dichromatism). To obtain an accurate index, we combined two scoring methods already described in the literature. Plumage was subdivided into 12 regions, following the method of Gray (1996): crown, forehead, ear coverts, throat, nape, mantle, wing, breast, belly, rump, undertail coverts, and tail. The only difference from Gray's body regions was that we considered forehead instead of eye stripe. To each of these body parts, we assigned a score of relative difference between the sexes, following the scale used by Owens and Bennett (1994) and Dunn et al. (2001): zero, no difference between the sexes; one, difference in shade or intensity; and two, difference in color or pattern. Given that our species were all at least slightly dichromatic, none attained a score of zero. The value used in the analyses for each species was the mean of the total scores from three experienced observers, unaware of our predictions. Scores from individual observers were highly correlated (smallest r was .96, $n = 21$ species). Scores were assigned based on color plates and descriptions taken from Baker (1993), Cramp (1998), Mullarney et al. (1999), and the observers' direct experience of the species considered, and refer to the plumage of adult males and females of the most common subspecies migrating over southern Europe (in case of marked plumage differences between subspecies). We are confident that this index, presented in the Appendix, gives a realistic measure of SD in our species' sample, at least to the human eye.

Other variables

Geographic distribution
The distribution range may influence migration dates of migrants (see Francis and Cooke, 1986; Ketterson and Nolan, 1976, 1983; Kissner et al., 2003). This may be true both for breeding and wintering ranges. Thus, for each species, we calculated the mean breeding and wintering latitudes as the mean between the northernmost and southernmost latitudes of breeding and, respectively, African wintering ranges (calculated following the method of Cramp, 1998 and Sibley and Monroe, 1990). Travel distance from the wintering to the breeding areas could have affected the analyses because absolute measures of protandry may be influenced by distance from departure areas, and travel distance is known to be positively correlated with male plumage showiness (Fitzpatrick, 1994, 1998). We therefore calculated this variable as the difference between mean breeding latitude and mean wintering latitude (in centesimal degrees). Moreover, we speculated that if males migrate faster than do females (e.g., if different sexes adopt different migration strategies, with males minimizing the time spent on migration and females minimizing the overall energetic costs) (Alerstam and Lindström, 1990; Lavee et al., 1991; Yong et al., 1998), protandry could be affected by the distance traveled from the northernmost potential fueling site before the crossing of ecological barriers, with species departing from more southern sites showing greater ΔM_C. We therefore included the northernmost wintering latitude (hereafter, N wintering

latitude) in our models. It should be emphasized that distance migrated was not calculated by using N wintering latitude but, rather, mean wintering latitude and therefore was computationally independent of the former. In addition, mean breeding latitude was included because it can affect seasonality of breeding habitats and thus markedly constrain early male arrival (Brown and Brown, 2000; Kokko, 1999; Møller, 1994a; Morbey and Ydenberg, 2001; Slagsvold, 1982). Thus, in the final analysis, we included distance migrated, N wintering latitude, and breeding latitude as potential predictor variables for ΔM_C.

Migration date
The degree of protandry may be correlated with the date of migration of males, with late migrating species showing lower degree of protandry, as shown by Francis and Cooke (1986) for some Nearctic migratory warblers. Thus, we included the median date of male migration on the islands as a possible variable influencing ΔM_C.

Other traits
Although hypothetically a number of other traits can affect the degree of protandry, in the present study we do not consider them further because of the relative homogeneity of our species sample with respect to, for example nest type, coloniality, or parental care. However, exploratory analyses on some of these traits (namely flocking behavior during migration and coloniality) revealed that these variables had no detectable effects on ΔM_C (details not shown).

Comparative method and statistical analyses

In comparative studies, species should not be considered as independent units because they may share characters through common descent rather than independent evolution (Felsenstein, 1985; Harvey and Pagel, 1991). Even though this is widely acknowledged, there has been debate on whether comparative methods that take into account shared evolutionary history should be used or not (Harvey and Rambaut, 1998; Price, 1997; Ricklefs, 1996). Therefore, we present analyses based both on raw species data and on a comparative method that takes into account the phylogeny when examining the relationships between traits (Price, 1997). To control for phylogeny, we used standardized independent linear contrasts that were calculated by means of the CAIC software (Purvis and Rambaut, 1995). Contrasts can be considered as standardized differences in characters at evolutionary independent nodes in the phylogeny (Purvis and Rambaut, 1995). Before entering our variables in CAIC, these were $\log_{10}$-transformed when feasible (plumage scores, date of migration, distance migrated, N wintering latitude, mean breeding latitude), following the method of Felsenstein (1995) and Purvis and Rambaut (1995). Contrasts were calculated by using the CRUNCH algorithm in CAIC, which is suitable for continuous traits. Branch lengths in the phylogeny were set to unity, which is equivalent of assuming a punctuational model of evolution (Purvis and Rambaut, 1995) and which has been demonstrated to be the most reliable evolutionary model in case of incomplete phylogenies (Purvis et al., 1994). Because a complete phylogeny for our species was not available, we based our phylogeny on that of Sibley and Ahlquist (1990), Shirihai et al. (2001), and Figuerola and Jovani (2001) (Figure 1).

Relationships between contrasts in ΔM_C and contrasts in other predictor variables were tested by simple and multiple linear regressions through the origin (Harvey and Pagel, 1991; Purvis and Rambaut, 1995). Bivariate relationships were inspected for significant outliers in regression residuals (3 SD

or more) (Belsley et al., 1980; Kleinbaum and Kupper, 1978) and in the distribution of variables (by means of Dixon test) (Sokal and Rohlf, 1994). Although no outliers were detected among regression residuals for all variables, a significant outlier datum (Dixon test, $p < .01$) was detected among contrasts in N wintering latitude. This single data point was therefore excluded from subsequent analyses, as regressions depending on one or few outliers can be considered weak (Sokal and Rohlf, 1994). In any case, its inclusion or exclusion did not qualitatively affect the results (see Results). Evolutionary assumptions of contrasts (i.e., that the absolute values of contrasts should be independent of the estimated value of the same trait at the node at which the contrast was calculated) (Purvis and Rambaut, 1995) were not upheld for one variable (migration date of males), for which we were unable to provide an adequate transformation. Thus, we presented the results of the association between ΔM_C and sexual dimorphism with and without controlling for this variable. Associations between ΔM_C and other traits for the raw species data were analyzed through simple and multiple linear regression models. Predictor variables were checked for multicollinearity before being entered in multiple regression models (see Results).

RESULTS

Males of 12 species migrated significantly earlier than did females, whereas in the remaining nine species there was no significant difference in migration dates between the sexes (see Appendix). Overall, there were 16 species in which males migrated before females and five species in which both sexes migrated at the same time or females migrated earlier than did males (binomial test, $p = .027$). ΔM_C across species was significantly greater than zero (one sample t test, $t_{20} = 4.70$, $p < .0001$). Thus, on this enlarged species data set compared with that presented in Spina et al. (1994), we confirm that protandry is a common feature of the spring migration in Palearctic-African migratory birds.

Simple regression analyses on raw species data showed that ΔM_C was strongly and positively correlated with SD, whereas there was no association between protandry and size dimorphism between the sexes (Table 2 and Figure 2). The significant association between raw ΔM_C and dichromatism scores held also in a multiple regression where we included the effects of distance migrated, N wintering latitude and size dimorphism (Table 2). In this analysis, mean breeding latitude was not included due to a strong correlation with distance migrated ($r = .64$, $n = 21$, $p = .002$), to avoid problems of high multicollinearity among predictor variables (see Belsley et al. 1980). However, the results were unaffected when we included mean breeding latitude rather than distance migrated (effect of dichromatism on ΔM_C: b = 0.0240 ± 0.007 SE, $\beta = 0.70$, $t = 3.29$, $p = .005$).

The analyses based on standardized linear contrasts confirmed both a positive association between ΔM_C and dichromatism and the absence of a relationship between protandry and sexual size dimorphism (Table 2 and Figure 3). In a multiple regression model, sexual dichromatism significantly predicted ΔM_C contrasts after controlling for the effects of migration date, distance migrated, and size dimorphism. In this model we did not include N wintering latitude because one contrast was a significant outlier (see Methods). However, the regression models run by including N wintering latitude and either taking or not taking the outlier contrast into account did not qualitatively affect the relationship between ΔM_C and sexual dichromatism ($p < .001$ in all cases; details not shown).
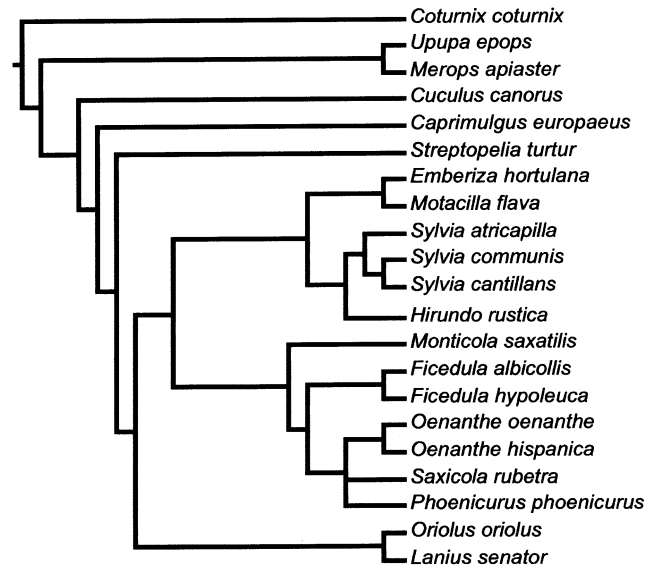
Figure 1
Phylogenetic tree of the 21 trans-Saharan migratory bird species included in the comparative analysis of the association between sexual dichromatism and protandry.

In addition, results were qualitatively unchanged when using mean breeding latitude rather than distance migrated, either including or excluding N wintering latitude (with or without the outlier contrast), as well as when including or excluding date of male migration, which violated evolutionary assumptions and was strongly correlated with distance migrated ($r = .69$, $n = 19$) (see Methods for details) (association between ΔM_C and sexual dichromatism, all $p < .012$ on a total of 12 multiple regression models with different combinations of variables, including the multivariate model presented in Table 2; details not shown).

DISCUSSION

In this comparative study of long-distance trans-Saharan migratory birds, we investigated the relationships between sexual color and size dimorphism and the degree of protandry during spring migration. We found a positive relationship between protandry and SD, but not size dimorphism. We relied on a huge bird banding data set, which offers a valuable opportunity to investigate evolutionary correlates of protandry. Indeed, the species considered are homogeneous with respect to migratory strategies. In addition, all data on migration schedules were collected in the same study area and with the same sampling protocol. Of course, our sample did not include sexually monochromatic species, which could not be reliably sexed in the field: the analysis of protandry in these species would require a considerable effort to sex individuals using molecular tools (Ellegren and Sheldon, 1997). The inclusion of monomorphic species in the analyses may produce different patterns of association between protandry, SSD, and SD, owing to different selective pressures acting on dichromatic and monochromatic species. However, in a monochromatic species, the spotted flycatcher (*Muscicapa striata*), there was no difference in median spring migration dates of males and females in the study area (based on a sample size of 65 molecularly sexed individuals banded on the island of Ventotene) (Mabey et al., 2003).

Table 2
Results for simple and multiple regression analyses of factors affecting the difference in migration timing between females and males

Predictors	Simple					Multiple				
	b	SE	β	t	p	b	SE	β	t	p
Raw species data										
Color dichromatism	0.0254	0.005	0.74	4.78	<.001	0.0244	0.007	0.71	3.36	.004
Size dimorphism	0.0150	0.050	0.07	0.29	.769	0.0020	0.046	0.01	0.04	.967
Date of male migration	−0.0090	0.012	−0.17	−0.75	.460	−0.0041	0.014	−0.08	−0.29	.773
Distance migrated	0.0038	0.004	0.22	0.98	.338	0.0017	0.004	0.10	0.41	.685
N wintering latitude	−0.0053	0.005	−0.24	−1.09	.287	0.0006	0.006	0.03	0.11	.913
Breeding latitude	0.0071	0.009	0.18	0.80	.431	—	—	—	—	—
Standardized contrasts										
Color dichromatism	0.4307	0.140	0.59	3.07	.007	0.5560	0.160	0.76	3.47	.003
Size dimorphism	0.0113	0.058	0.05	0.19	.847	0.0442	0.052	0.18	0.85	.407
Date of male migration	−0.0540	2.723	−0.00	−0.02	.984	3.6639	3.464	0.32	1.06	.307
Distance migrated	0.0120	0.277	0.01	0.04	.966	−0.6075	0.376	−0.52	−1.61	.127
N wintering latitude[a]	0.0905	0.082	−0.05	−0.22	.830	—	—	—	—	—
Breeding latitude	0.0230	0.666	0.00	0.03	.973	—	—	—	—	—

Models are presented for raw species values ($n = 21$ species) and for phylogenetically independent contrasts ($n = 19$ contrasts, see Methods). In the case of independent contrasts, values refer to regressions through the origin. In the multiple regressions, values for single predictors are calculated by considering the effect of all other variables simultaneously.

[a] Sample size for this variable was 18 contrasts (one contrast was a significant outlier; for details, see Methods)

Previous comparative studies have demonstrated a positive correlation between SD and high levels of extrapair paternity, possibly arising because of cryptic female choice for brightly colored males as extrapair partners (Møller and Birkhead, 1994; Owens and Hartley, 1998), or polygyny (Dunn et al., 2001). All the species in our sample for which information on social mating system is available have monogamy as the predominant mating system (see Cramp, 1998). If sexual selection is a major determinant of protandry in the species considered, it follows, from current knowledge of the association between different forms of sexual dimorphism and specific mechanisms of sexual selection, that the main fitness benefits of protandry (in terms of male realized reproductive success) should be achieved mainly through extrapair paternity (Birkhead and Møller, 1992, 1998). Such benefits may be obtained in three ways: (1) early arriving males may have larger chances of inseminating early arriving females before egg laying; in fact, among birds, females are known to store sperm for several days, so that eggs can be fertilized by sperm delivered much earlier than egg laying (Birkhead and Møller, 1992). (2) Fewer competitors for fertilization are present at early stages of the reproductive season, thus facilitating extrapair copulations by early arriving males, and (3) early arriving males will be available as extrapair copulation partners later in the season, when they are no longer involved in mate-guarding activities and most females in the population are in their fertile period (Birkhead and Møller, 1992, 1998; see also Langefors et al., 1998). This three-fold advantage in sperm competition for early arriving males may exert strong selection in favor of early mate acquisition and great protandry. The positive correlation between protandry and SD may thus stem from the evolutionary association between sperm competition and dichromatism (Møller and Birkhead, 1994; Owens and Hartley, 1998) and the advantage that early arriving males may acquire in sperm competition. Therefore, intense sperm competition may select for early male arrival and male brightness through separate selection mechanisms (i.e., sperm competition between males and cryptic female choice), resulting in the positive covariation between the two traits. Interestingly, in a few polyandrous shorebirds with sex-role

reversal in parental care (red-necked phalarope [*Phalaropus lobatus*], Wilson's phalarope [*Phalaropus tricolor*], and spotted sandpiper [*Actitis macularia*]) protogynous rather than protandrous arrival to the breeding areas has been documented (Oring and Lank, 1982; Reynolds et al., 1986). The two phalarope species also show reversed SD, females being more colored than males, whereas the spotted sandpiper shows little plumage dichromatism but obvious reversed size dimorphism. These observations support the idea that the evolution of sex differences in arrival patterns at the breeding grounds is associated with sexual selection mediated by competition for mates.

Therefore, our results are more consistent with the mate opportunity hypothesis than with other hypotheses (Table 1). This is different from the prevailing view that protandry in birds evolved mainly as a result of male-male competition for territories (the rank advantage hypothesis) (Morbey and Ydenberg, 2001), which should result in a positive association between SSD and protandry.

Although a sperm competition advantage experienced by early arriving males may explain our results, an alternative mechanism may determine a positive association between protandry and dichromatism. According to parasite-mediated models of sexual selection, male epigamic colorations function as reliable signals of resistance to parasites (Hamilton and Zuk, 1982). Sexual selection for condition-dependent early male arrival is expected to be more intense in species with more virulent parasites because females may have stronger preference for early arriving males if arrival date is associated with low levels of parasite infestation, as shown in single-species studies (for a study on barn swallows, *Hirundo rustica*, see Møller et al., 2004). This could result in a positive association between protandry and SD across species, because species with relatively large parasite burden should show greater dichromatism (Hamilton and Zuk, 1982) and a more advanced arrival of males relative to females. Under this scenario, protandry and male epigamic coloration may function as multiple signals of male quality (Iwasa and Pomiankowski, 1994; Johnstone, 1995; Møller and Pomiankowski, 1993). These signals may convey information on different aspects of male quality, as envisaged by the multiple
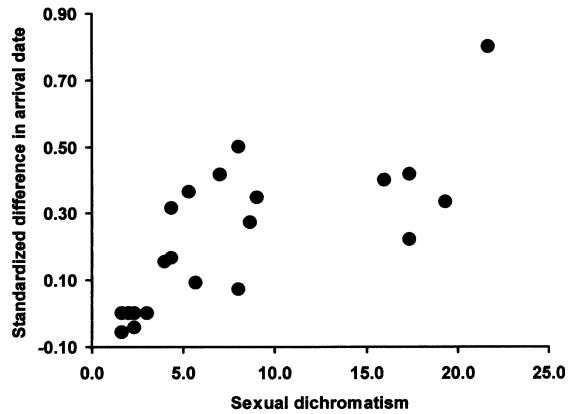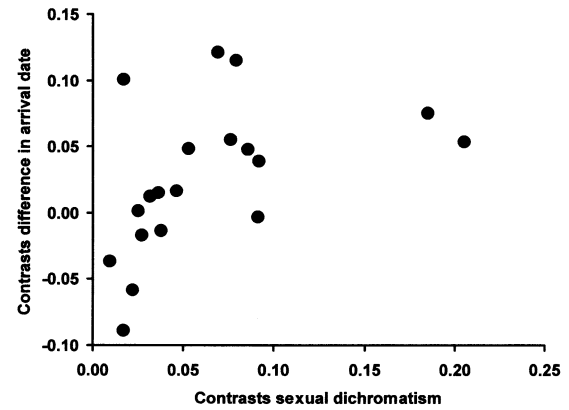
Figure 2
Relationship between standardized difference in migration dates between females and males (ΔM_C) (greater values indicate that males are migrating earlier than females, see Methods for details) and degree of sexual dichromatism (scored on a 0–24 scale) for 21 species of long-distance trans-Saharan migratory birds.

Figure 3
Relationship between contrasts of standardized difference in migration dates between females and males (ΔM_C) (greater values indicate that males are migrating earlier than females) and contrasts in degree of sexual dichromatism (for details, see Methods) for 21 species of long-distance trans-Saharan migratory birds. Sample size is 19 standardized linear contrasts.

message hypothesis (Johnstone, 1996; Møller, 1994b; Møller and Pomiankowski, 1993; Møller et al., 1998; Saino et al., 1997). Plumage coloration may mainly reflect male condition at the time of molt, which occurs in the wintering areas in most of the species considered, whereas protandry may also reflect the speed of migration, which is likely to be condition-dependent, early arriving males being in better state than do late arriving ones (Andersson and Gustafsson, 1995; Arvidsson and Neergaard, 1991; Lozano, 1994; Marra et al., 1998; Stolt and Fransson, 1995). In fact, a link between condition-dependent arrival and plumage ornamentation established at the time of molt is suggested by the observation that species with relatively greater plumage dichromatism tend to molt just before the start of the breeding season compared with species with smaller dichromatism (Figuerola and Jovani, 2001).

But why was size dimorphism not correlated with protandry in the present sample of trans-Saharan migrants, whereas this was the case among Nearctic migrants (Kissner et al., 2003)? Our sample included both Mediterranean and boreal breeding species, whereas Kissner et al. (2003) sampled mainly boreal breeders. Energetic constraints are more likely to apply to boreal breeders, owing to milder conditions in the Mediterranean basin than at boreal Nearctic latitudes in early spring. Furthermore, the species we studied winter almost exclusively in tropical areas, whereas Kissner et al. (2003) considered species which adopt diverse migration and wintering strategies, that is, both transcontinental migrants wintering in the Neotropics and intracontinental migrants wintering in the temperate region, which are known to migrate earlier than do Neotropical migrants (Hagan et al., 1991). Selective pressures on body size may act differently on these two categories of migrants: selection for larger SSD owing to energetic constraints may be stronger in early arriving species wintering in temperate regions than in late arriving species wintering in tropical areas, and this may partly explain the lack of a correlation between protandry and SSD in the present study.

Our results prompt for further studies of the role of sexual selection in the evolution of protandry. First, we interpreted our results based mainly on the assumption that SD is related to extrapair paternity, but a direct comparative test of the mate opportunity mechanism of selection for protandry mediated by sperm competition will be needed to corroborate

our speculation. Such test should provide evidence of a positive correlation between extrapair paternity and protandry across species. Current extrapair paternity estimates available for some species in our sample are compatible with the interpretation of present results: in the European bee-eater (*Merops apiaster*) and the hopooe (*Upupa epops*), which are nonprotandrous species, extrapair paternity is low, whereas it is higher in protandrous species, such as the barn swallow (*Hirundo rustica*), the wheatear (*Oenanthe oenanthe*), and the pied and collared flycatcher (*Ficedula hypoleuca* and *F. albicollis*) (for extrapair paternity estimates, see Currie et al., 1998; Martín-Vivaldi et al., 2002; Owens and Hartley, 1998). Moreover, within-species studies should provide evidence of positive correlations between arrival date, male brightness, male size, and extrapair paternity: brightly colored and larger males should arrive earlier than do dull males and achieve higher paternity. Otherwise, if females select for early arriving, brightly colored males with few parasites, a positive co-variation between protandry and levels of parasite infestation may be expected across species, and both a negative correlation between male brightness and arrival date and a positive correlation between parasite load and arrival date would be expected in within-species studies (Møller et al., 2004). In addition, the mate opportunity hypothesis may be tested in species which vary in the intensity of polygamy: a positive covariation between protandry and number of females acquired would be expected both within and across species (see Hasselquist 1998), and a positive correlation between size dimorphism and protandry is predicted across species, because SSD is related to the level of polygyny (Dunn et al., 2001; Owens and Hartley, 1998). Selection for protandry may also have a correlated response on wintering strategies across species, resulting in latitudinal wintering habitat segregation between the sexes (see Ketterson and Nolan, 1976, 1983; Marra et al., 1998): protandry may therefore be larger in species in which males spend the boreal winter at more northern latitudes compared with females, a hypothesis that could be tested when data on wintering ranges for each sex become available for a sufficient number of species.

Present results may also have broad implications for the study of the evolution of protandry in taxa other than birds, which also show sexual dimorphism (e.g., arthropods, fishes, and amphibians). Although previous studies have demonstrated an association between protandry and SSD (for a study

APPENDIX

Variables considered in the analysis of the association between protandry and sexual dimorphism. All data refer to the period 16 April–15 May, with day 1 = 1 April

Species	MM	MF	25th	75th	ΔM	ΔM$_C$	DICR	WINM	WINF	BMM	BMF	LATB	LATW	NLAT	DIST	N	PMED
Caprimulgus europaeus	34.2	37.0	30.0	39.0	2.83	0.315	4.3	192.1	194.3	61.4	64.1	47.5	−7.5	14.0	55.0	269	.062
Coturnix coturnix	30.0	30.0	23.4	36.0	0.00	0.000	2.0	111.5	113.1	100.1	100.5	50.3	18.5	37.0	31.8	104	.799
Cuculus canorus	31.0	30.5	24.6	36.0	−0.50	−0.044	2.3	227.3	216.2	91.7	81.7	51.0	−15.0	0.0	66.0	166	.863
Emberiza hortulana	27.0	32.0	23.0	35.0	5.00	0.417	7.0	90.5	85.2	23.2	21.1	51.5	7.5	10.0	44.0	101	.006
Ficedula albicollis	29.0	31.0	25.0	34.0	2.00	0.222	17.3	83.5	81.8	11.1	10.9	48.8	−10.0	0.0	58.8	737	.001
Ficedula hypoleuca	26.0	30.0	23.0	33.0	4.00	0.400	16.0	81.1	79.5	11.1	10.9	59.0	7.5	15.0	51.5	12837	.000
Hirundo rustica	26.0	28.0	21.0	34.0	2.00	0.154	4.0	126.3	123.7	16.6	16.2	49.0	−10.0	10.0	59.0	5878	.000
Lanius senator	29.0	31.0	24.0	36.0	2.00	0.167	4.3	101.8	101.4	32.1	32.0	39.0	9.5	15.0	29.5	3500	.000
Merops apiaster	33.0	32.5	28.4	37.0	−0.50	−0.058	1.7	151.8	147.0	50.4	48.1	42.5	−2.5	15.0	45.0	421	.859
Monticola saxatilis	20.8	32.0	19.0	33.0	11.17	0.798	21.7	126.5	120.8	49.5	47.6	40.5	2.5	15.0	38.0	81	.000
Motacilla flava	26.0	30.0	21.8	33.3	4.00	0.348	9.0	82.9	79.2	14.5	13.5	49.0	−7.5	15.0	56.5	1163	.000
Oenanthe hispanica	22.0	25.0	20.0	31.0	3.00	0.273	8.7	92.0	89.0	17.3	17.1	37.0	13.0	18.0	24.0	625	.000
Oenanthe oenanthe	25.0	26.0	19.0	33.0	1.00	0.071	8.0	96.7	93.9	23.3	22.0	49.0	4.5	18.0	44.5	3131	.316
Oriolus oriolus	33.0	36.0	30.0	39.0	3.00	0.333	19.3	153.5	151.7	59.5	58.0	45.5	−12.0	6.0	57.5	1525	.000
Phoenicurus phoenicurus	27.0	32.0	23.0	35.0	5.00	0.417	17.3	81.3	79.4	13.7	13.4	49.0	7.5	15.0	41.5	5290	.000
Saxicola rubetra	28.0	34.0	25.0	37.0	6.00	0.500	8.0	78.1	76.0	14.8	14.3	56.0	0.0	15.0	56.0	16319	.000
Streptopelia turtur	31.0	31.0	25.0	35.0	0.00	0.000	1.7	178.8	175.1	137.9	131.6	45.5	12.5	15.0	33.0	2230	.571
Sylvia atricapilla	21.0	22.0	17.0	28.0	1.00	0.091	5.7	73.7	73.7	16.5	16.6	48.0	11.0	37.0	37.0	2658	.062
Sylvia cantillans	23.0	23.0	18.0	29.0	0.00	0.000	3.0	61.9	61.1	9.3	9.2	37.0	13.0	15.0	24.0	11765	.051
Sylvia communis	32.0	36.0	28.0	39.0	4.00	0.364	5.3	74.6	73.4	13.7	13.5	48.0	−2.5	15.0	50.5	18116	.000
Upupa epops	22.0	22.0	17.0	29.0	0.00	0.000	2.3	149.8	143.4	64.0	57.1	44.0	16.0	37.0	28.0	410	.707

Species are sorted in alphabetical order. MM indicates median migration date of males; MF, median migration date of females; 25th, 25th percentile date of migration; 75th, 75th percentile date of migration; ΔM, difference between median migration date of females and median migration date of males; ΔM$_C$, standardized difference in migration date (see Methods); DICR, SD score (see Methods); WINM, mean wing length of males (mm); WINF, mean wing length of females (mm); BMM, mean body mass of males (g); BMF, mean body mass of females (g); LATB, mean breeding latitude (degrees of latitude N); LATW, mean wintering latitude (degrees of latitude N); NLAT, northernmost wintering latitude (degrees of latitude N); DIST, distance migrated (in centesimal degrees, see Methods); N, sample size; PMED, *p* value for median test on the difference between median dates of migration of males and females.

on butterflies, see Wiklund and Forsberg, 1991), we are aware of no comparative studies in which protandry has been analyzed in relation to SD either in birds or in other taxa. Moreover, experimental studies may help in clarifying whether timing of male emergence/arrival at the breeding grounds is condition-dependent and whether female preference can select for early male emergence/arrival while controlling for variation in male condition

In conclusion, our comparative study provides indirect evidence that sexual selection may be a major force driving the evolution of sex differences in migration schedules in trans-Saharan migratory birds, resulting in larger protandry among species with large SD. However, further direct tests of the role of sperm competition are necessary, and it remains to be elucidated whether the evolution of protandry is favored by variance in male reproductive success mediated by sperm competition, or protandry is the consequence of direct sexual selection for early arrival through mate choice for reliable indicators of male quality.

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