

Individual differences in protandry, sexual selection, and fitness

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Protandry is the difference in arrival date between males and females, with competition among males for access to preferred territories (the rank advantage hypothesis) or mating success (the mate opportunity hypothesis) supposedly driving the evolution of protandry. The fitness costs and benefits of protandry accruing to individuals differing in degree of protandry (arrival date of a male relative to the arrival date of his partner) have never been quantified. We analyzed the fitness consequences of sex differences in arrival date in the barn swallow *Hirundo rustica*, in which arrival date can be precisely estimated and the fitness of pairs differing in degree of individual protandry assessed. Early arriving males had greater mating success than late arriving males. The number of extrapair offspring in own nests decreased with increasing degree of individual protandry, whereas the number of offspring fathered by a focal male was unrelated to individual protandry. There was directional selection on individual protandry as shown by pairs with a larger than average degree of protandry reproducing early and, hence, supposedly producing more recruits. There was also stabilizing selection on individual protandry as shown by pairs with an intermediate degree of protandry reproducing early. Annual production of fledglings increased with early arrival of males, but not with early arrival of females, once the effect of laying date had been considered, with no additional effect of individual protandry. Neither male nor female survival was significantly related to degree of individual protandry. These findings are consistent not only with the mate opportunity hypothesis but also with a sexual conflict hypothesis, suggesting that males and females differ in their optimal timing of arrival due to sex-specific fitness costs and benefits. **Key words:** barn swallow, extrapair paternity, *Hirundo rustica*, optimal arrival time, sex ratio. [*Behav Ecol* 20:433–440 (2009)]

The earlier emergence at the site of reproduction by males is termed protandry, occurring in migratory salmonids and birds, emerging insects, male and female flowers, and hermaphroditic animals (review in Morbey and Ydenberg [2001]). Such sex differences arise from sex-specific selective advantages that individuals of the 2 sexes acquire from a given arrival or emergence schedule. For example, whereas males enjoy a greater mating advantage from early arrival than females in monogamous birds (Fisher 1930), resulting in protandry, it is the opposite in polyandrous species such as phalaropes (Myers 1981). Individuals of both sexes may enjoy an advantage from early arrival, but there are also costs associated with precocial arrival. Male barn swallows *Hirundo rustica* increased their mating success from early arrival, but such early individuals sometimes died because they encountered inclement weather (Møller 1994a, 1994b). Such fitness costs and benefits of early arrival may depend on individual quality because early arriving males that died had smaller condition-dependent secondary sexual characters than survivors (Møller 1994a, 1994b), and the benefits of early arrival in terms of mating success also differentially favored the most attractive males (Møller 1994a, 1994b).

Morbey and Ydenberg (2001) reviewed the different hypotheses that account for the evolution of protandry. Two different hypotheses have in particular been invoked to ac-

count for protandry in migratory birds and fish, whereas the other hypotheses appear to be less relevant. First, the rank advantage hypothesis suggests that early arriving males benefit in terms of acquisition of high-quality territories, providing such early males with a selective advantage if territory quality is used by females as a cue in mate choice (Morbey and Ydenberg 2001). However, a similar advantage should also accrue to early arriving females, thereby nullifying the sex difference in benefits that would be required for protandry to evolve (Kokko et al. 2006). Second, the mate opportunity hypothesis suggests that early arrival favors males in particular because such males enjoy a mating advantage by mating early with females in prime body condition or with multiple females (Morbey and Ydenberg 2001). Even in a strictly monogamous mating system, this advantage could result in considerable sex differences in selection because early males on average would acquire fat and hence more fecund females (Fisher 1930). Kokko et al. (2006) recently provided extensive simulation studies of these 2 mechanisms suggesting that protandry only readily evolves from competition among males for mating opportunities, as predicted by the mate opportunity hypothesis.

Empirical assessment of the fitness costs and benefits of individual protandry requires not only information on arrival dates of individual males and females but also information on the fitness consequences of sex-specific arrival schedules. Given natural variation in arrival date of males and females due to stochastic and deterministic reasons (Alerstam 1991; Berthold 2001), we can expect certain males with a given arrival date sometimes to mate with females that arrived early and sometimes with females that arrived late. This will generate variation in degree of individual protandry even among

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individuals that arrived on the same date. If early arriving individuals are in better condition than late arriving individuals (e.g., Møller 1994a, 1994b; Møller et al. 2004), and if early arriving females in prime condition have greater probability of mating with preferred males and for doing so rapidly (Møller 1988), such variation in degree of individual protandry will have fitness consequences due to difference in timing of reproduction (early laying results in much greater probability of recruitment than late laying [Møller 1994a]) and fecundity. Surprisingly, there are no data on individual differences in arrival date and their fitness consequences. This is problematic because it is the relative contribution of these fitness components due to different degrees of individual protandry that eventually will mold patterns of protandry.

Here we analyze extensive, individual-based data on protandry and its fitness consequences for a migratory bird, the barn swallow. We define protandry as the effect of the interaction between male and female arrival date of pairs of barn swallows because this approach allows quantification of the effects of individual protandry "independent" of the effects of arrival date of the 2 sexes. Thus, if male arrival date is M and female arrival date is F , then protandry is defined as $M \times F$. In a full model that includes M and F , by definition, this interaction $M \times F$ is zero when there is no multiplicative effect of male and female arrival date in addition to the effects of M and F .

The objectives of this study were to investigate the relationships between individual protandry and mating success, timing of breeding, fecundity, and viability. In addition, we exploited the unique situation that male tail length is condition dependent, with long-tailed males arriving early and mating rapidly (Møller 1988, 1994a, 1994b), thus providing a direct link between tail length and individual protandry. We predicted that 1) early arriving males would have a mating advantage, as predicted by the mate opportunity and the rank hypothesis (Morbey and Ydenberg 2001), with significant stabilizing selection due to the costs of "too early" arrival (Møller 1994a, 1994b). 2) Extrapair paternity in the nest of a focal individual would decrease, and extrapair paternity in other nests would increase in response to individual protandry if the mate opportunity hypothesis accounted for arrival patterns. The argument, based on simulations presented by Kokko et al. (2006), is that early arrival favors males in particular because such males enjoy a mating advantage by mating early not only with females in prime body condition but also with neighboring females during extrapair copulations. 3) Laying date would not only be affected by arrival date of the 2 sexes, because laying cannot start before arrival, but also differentially by individual protandry if the fitness benefits of early arrival differed between the sexes, as predicted by the mate opportunity and the rank hypothesis. For example, laying is preceded by nest building and mate guarding. Both sexes build the nest, although there is sexual conflict over the relative contribution of males and females (Møller 1994a). Furthermore, males guard their mates intensely for more than 3 weeks, and mate guarding may increase certainty of paternity, but may also be beneficial or costly for females depending on whether females attempt to avoid or seek extrapair copulations (Møller 1994a). The intensity of nest building by males and females and mate guarding by males may depend not only on time since arrival but also on time since arrival by the mate. 4) Survival would be reduced by individual protandry if males, females, or both experienced a viability cost from differences in their own arrival date and arrival date of their partner.

The barn swallow is an approximately 20 g aerially foraging passerine that breeds in temperate and subtropical regions of the northern hemisphere, with European populations wintering south of the Sahara (Møller 1994a). Males and females are morphologically very similar with the exception of the

outermost tail feathers that are considerably longer in males than in females, and such elongated tails are associated with a mating advantage in Denmark, Italy, and Spain (review in Møller 1994a). Males in Denmark arrive on average 4 days earlier than females, and males show significantly greater variance in arrival date than females (Møller 1994a, 1994b). Males and females with long tails arrive early to the breeding grounds, in particular, in years with poor environmental conditions (Møller 1994a, 1994b). In addition, very early arrival is associated with a mortality cost due to bad weather, especially in short-tailed males (Møller 1994a, 1994b). Senescence is associated with a delay in arrival date (Møller and de Lope 1999; Balbontín et al. 2007). There is a significant heritability of arrival date (Møller 2001). The degree of protandry in a Danish population has increased significantly during the last 35 years because males advanced arrival date more than females (Møller 2004). This increased degree of protandry in the Danish population was associated with an increase in the size of a secondary sexual character and an amelioration of climatic conditions during early spring, thereby reducing the costs of early arrival differentially for males (Møller 2004). Less than 10% of all males remain unmated (Møller 1994a). Extrapair paternity accounts for 20–35% of all offspring, with significant effects of male tail length, body mass, and arrival date on the frequency of extrapair paternity (Møller and Tegelström 1997; Saino et al. 1997; Møller et al. 1998, 2003).

MATERIALS AND METHODS

General field procedures

We studied barn swallows in Badajoz (38°50'N, 6°59'W), Southern Spain. The study site consists of open farmland with pastures, cereals, and fruit plantations, and most barn swallows breed in farm buildings. The present study was based on birds captured during 1994–1997, with detailed information on paternity only obtained in 1994.

All birds were provided with aluminum rings and color rings, which allowed identification in the field with binoculars. Barn swallows were assigned to nests by color rings when birds were at their nests. In case of doubt, the bird was excluded from the following analyses.

Arrival date

Barn swallows were captured twice per week by closing all windows and doors in the buildings housing breeding birds, which were captured the subsequent morning in a mist net. F. de Lope measured all birds, which eliminated noise due to interobserver variability. First capture date was assumed to reflect arrival date because of the regular nature of captures, with the precision of arrival dates thus being 3 days (this level of precision is high compared with the range of arrival dates in males of 187 days and in females of 132 days).

We have previously considered a number of potential biases in our estimates of arrival dates. Barn swallows may arrive to the breeding areas without entering the actual breeding sites. However, this seems unlikely given intense competition for breeding territories and females. Although 8.7% of all males remain unmated (this study), such males are present in breeding colonies where they establish a breeding territory and attempt to attract a mate (Møller 1988). Thus, even nonbreeders are present in breeding colonies from early spring until the end of the breeding season (Møller 1994a). Barn swallow males and females start roosting within their territories on arrival (Møller 1994a). The precision of our estimate of arrival date was assessed based on data from Denmark in 1985–1990, providing extensive evidence for our estimates based on first

capture being reliable estimates of arrival date for both males and females (Møller et al. 2004). During 6 years adult barn swallows were watched daily with binoculars for 1 h from sunrise, and the identity of all color-banded individuals was recorded. The first observation of each individual in the season provided an estimate of the date of arrival. In addition, mist net captures as described above provided a second estimate of arrival date for each individual. The Pearson correlation coefficient between these 2 estimates of arrival date for each year separately varied between 0.982 and 0.997, $N = 10\text{--}46$, $P < 0.01$, for males, and between 0.983 and 0.998, $N = 5\text{--}44$, $P < 0.01$, for females. A paired *t*-test revealed no significant differences between the 2 estimates for any year or sex (males: $t < 1.23$, $P > 0.22$; females: $t < 0.28$, $P > 0.53$). Thus, our estimates based on first capture provide reliable estimates of arrival date for both males and females. The repeatability of arrival date of male barn swallows among years was statistically highly significant in a Danish sample ($F = 6.12$, degrees of freedom [df] = 22,97, $P < 0.001$; $R = 0.51$) (Møller 2001), despite the fact that young males arrive later than males of intermediate age (Møller and de Lope 1999; Balbontín et al. 2007). Another potential cause of bias in arrival date estimates is that some individuals might have attempted to breed elsewhere before moving into our study sites. We can exclude this possibility because none of the more than 1000 adults ringed in Spain since 1976 ever moved to another farm the same or the subsequent years. Thus, in the remainder of the manuscript, we use first capture date as a proxy for arrival date.

We estimated individual protandry as the product of arrival date of males (M) and females (F), hence $M \times F$.

Measurements of birds

We measured right and left outermost tail feathers with a ruler to the nearest 0.5 mm. Tail length was determined as the mean value of left and right character. Individuals with broken tails were excluded from the analyses, and the rounded tip of undamaged outermost tail feathers clearly reveals whether it is broken. Body mass was recorded with a Pesola spring balance to the nearest 0.5 g.

Age was determined as the number of years present in the study population, assuming that unringed birds are yearlings originating from elsewhere. This assumption is supported by the observation that none of the more than 1000 adults ringed in Spain since 1976 ever moved to another farm the same or the subsequent years. Similarly, all local recruits were captured in their first year of life.

Recording male mating success

Male mating success was assessed on male behavior and presence of a female within a territory. Unmated males display at a high rate, continuously following approaching females (Møller 1994a). Furthermore, once mated a pair spends considerable amounts of time within their territory during early morning and evening and also while roosting together at night.

Recording life-history variables

At least once per week, we systematically searched all buildings for nests and recorded the contents. Nests were visited daily during start of laying and the presumed date of hatching (ca. 14 days "after" laying ceased). Laying date was the date when the first egg was laid, assuming that one egg was laid per day. We recorded annual reproductive success as the total number of fledglings produced by each adult during the 1–3 broods per year.

Survival of adult barn swallows was assessed from presence or absence of an individual during the year following ringing.

Capture probability of adults exceeds 98% according to capture–mark–recapture estimates (Møller and Szép 2002 and de Lope F, Møller AP, Szép T, unpublished data). Therefore, we can use recaptures or lack thereof as simple estimates of individual survival.

Paternity analyses

We determined maternity and paternity by using previously developed microsatellite markers HrU6 (Primmer et al. 1995), HrU9 (Primmer et al. 1996), and HrU10 (Primmer et al. 1996). These markers showed 78, 125, and 66 alleles and heterozygosity values of 0.97, 0.99, and 0.97 (HrU6, HrU9, and HrU10, respectively), making them extremely suitable for parentage testing because males are very different in genotype (for further details, see Møller et al. 2003). Whole blood was treated with Proteinase K, and DNA was subsequently extracted using phenol/chloroform. Polymerase chain reaction (PCR) was performed as described in original reports using fluorescently labeled primers. PCR products were run on an ABI 377 sequencing instrument together with an internal size standard, and alleles were determined with the software GeneScan (PerkinElmer, Waltham, MA). We analyzed all nestlings from 1994, and for each adult, we estimated the number of own offspring in own nest as the sum of the number of own offspring in all 3 clutches. Likewise, the number of extrapair offspring was the total number of extrapair offspring in all 3 clutches.

Statistical analyses

Male and female arrival dates were log transformed because the frequency distributions of arrival dates were skewed (Figure 1). There was missing information for some individuals, resulting in slightly varying sample sizes in different analyses. Individuals were only included once when first recorded.

We found best-fit generalized linear models, using the software JMP (2000), relying on Akaike's information criterion (AIC) as an estimate of improvement in fit for addition of variables (Burnham and Anderson 2001). Variables were tested for normality, and no significant deviations were found after adjustment for multiple tests. We started out by using full models that included all 2-way interactions and then eliminating factors according to their delta AIC values, using the criterion that a change in AIC of more than 2.00 would be considered biologically meaningful (Burnham and Anderson 2001). The full models for the individual-based data included male (M) and female arrival date (F), the squared arrival dates of both sexes ($M \times M$ and $F \times F$, respectively) (the quadratic selection term as quadratic selection is defined as a significant change in variance in phenotype across a selection episode [Arnold and Wade 1984; Manly 1985; Endler 1986]), the interaction between male (M) and female arrival date (F) ($M \times F$, the protandry term, units in days²), and the interaction between protandry ($M \times F$) and arrival date of the male (M) and the female (F) (the quadratic selection component on protandry). The interaction between male and female arrival date ($M \times F$) represents protandry because a similar effect of arrival date of males (M) and females (F) on fitness components would imply that this product is zero, whereas an interaction different from zero would imply effects of male (M) and female arrival date (F) that deviated from purely additive effects. By including male arrival date (M) and female arrival date (F) in this full model, we controlled any effects of protandry for effects of arrival date per se in the 2 sexes; a requirement for disentangling the effects of protandry from arrival date. In addition, we included tail length and body mass of males and females because previous studies suggested that these variables predict mating success, timing of laying,

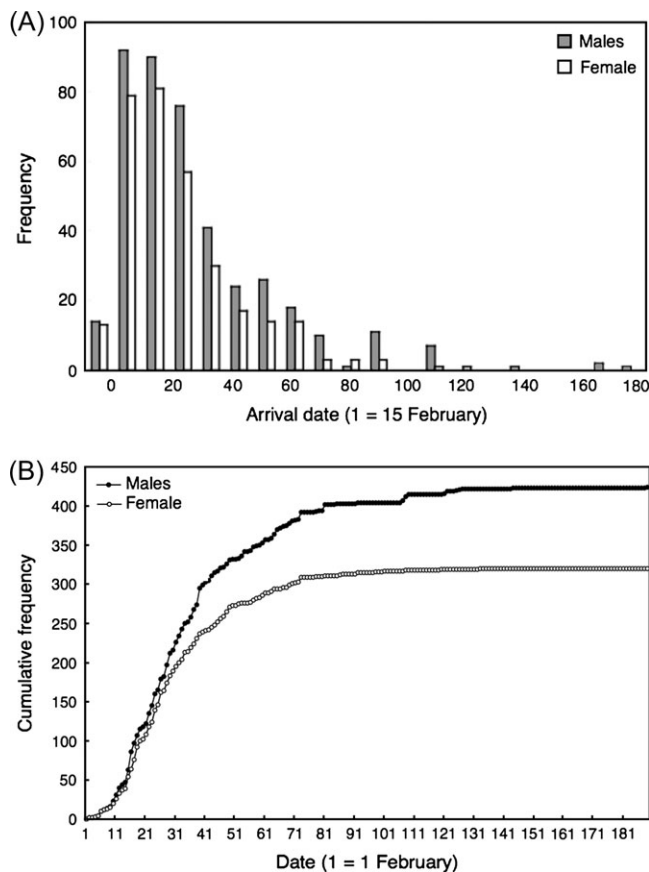


Figure 1
(A) Frequency distributions of arrival dates (1 = 15 February) of male and female barn swallows to Badajoz in 1994–1997.
(B) Cumulative frequency distributions of arrival dates (1 = 1 February) of male and female barn swallows to Badajoz in 1994–1997.

annual fecundity, and survival (Cuervo et al. 1996; Møller 1988, 1994a, 1994b; Møller and Szép 2002; Møller et al. 2003). We also included year as a factor to account for differences among years. In our analyses of annual production of fledglings, we included a second model that also had laying date as an additional predictor variable because the probability of having 2 or 3 clutches per years decreases with advancing laying date (Møller 1994a). Thus, this second model investigated whether annual production of fledglings depended on arrival date and protandry, after having accounted for the effects of laying date.

We analyzed male mating success and survival of both sexes in relation to arrival using logistic regression.

RESULTS

Patterns of arrival in the 2 sexes

Arrival date of male barn swallows in Badajoz 1994–1997 ranged from 8 February to 14 August, with mean = 7 March, median = 8 March, standard error (SE) = 1.43, $N = 414$ (Figures 1–2). Male arrival date differed significantly among years, although only explaining 4% of the variance ($F = 5.72$, $df = 3,410$, $r^2 = 0.040$, $P = 0.0008$).

Female arrival date in Badajoz 1994–1997 ranged from 8 February to 20 June, with mean = 11 March, median = 5 March, SE = 1.18, $N = 316$ (Figures 1–2). The difference in arrival date between sexes for pair members was statistically significant (paired t -test, $t = 4.05$, $df = 293$, $P < 0.0001$). Female

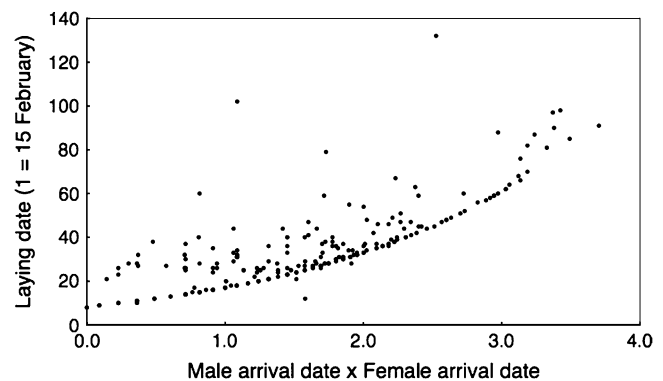


Figure 2
Laying date (1 = 15 February) in relation to degree of protandry (days), estimated as arrival date of male minus arrival date of female of different barn swallow pairs in Badajoz in 1994–1997.

arrival date differed significantly among years, although only explaining 4% of the variance ($F = 4.26$, $df = 3,310$, $r^2 = 0.040$, $P = 0.0057$).

Individual protandry estimated as the difference in arrival date of males minus arrival date of their mates in Badajoz 1994–1997 ranged from 109 days earlier arrival by males than their mates to 51 days earlier arrival by females than their mates, with males arriving on average 3 days before their mates, median = 0, SE = 0.71, $N = 294$. There was no significant difference in individual protandry among years ($F = 1.69$, $df = 3,288$, $r^2 = 0.017$, $P = 0.17$).

There was no evidence of strong collinearity among variables (with the largest variance inflation factor being 1.8). For example, log-transformed male arrival date times log-transformed female arrival date ($M \times F$, the degree of individual protandry) was only weakly related to $\log_{10}$ -transformed arrival date accounting for at most 14% of the variance (M , males: $F = 1.99$, $df = 1,279$, $r^2 = 0.007$, $P = 0.16$; F , females: $F = 43.96$, $df = 1,279$, $r^2 = 0.136$, $P < 0.001$), and the quadratic effect in both sexes only accounted for at most 7% of the variance ($M \times M$, males: $F = 2.39$, $df = 1,278$, $r^2 = 0.009$, $P = 0.12$; $F \times F$, females: $F = 20.97$, $df = 1,278$, $r^2 = 0.07$, $P < 0.001$).

Male mating success and arrival date

Mated males in Badajoz 1994–1997 arrived significantly earlier than unmated males (Table 1). Unmated males arrived on average day 1 May (SE = 3.78), $N = 99$, whereas mated males arrived on average day 8 March (SE = 0.98), $N = 315$. In addition, there was a significant stabilizing effect as shown by the relationship between mating success and quadratic arrival term ($M \times M$, Table 1). Using the equation derived from the model in Table 1 to predict mating success, keeping tail length constant at the mean value of 95 mm, showed that the latter peaked at an intermediate arrival date of 13 April. The model that only included male arrival date and male arrival date squared explained 33% of the variance. In contrast, the effect of male tail length was not significant (Table 1), although tail length has been shown previously to predict mating success in this population (Møller et al. 2006), nor was the year effect significant (Wald $\chi^2 = 2.04$, $df = 1$, $P = 0.56$).

Laying date and protandry

The best-fit model of laying date in Badajoz 1994–1997 accounted for 94% of the variance (Table 2). Laying date was related to arrival date of the 2 sexes (M and F), with a stronger effect of female than male arrival date (t -test for

Table 1

Best-fit model of the relationship between male mating success in relation to tail length and arrival date (M) in barn swallows from Badajoz in 1994–1997

Variable	Wald χ^2	df	P	Slope (SE)
Male arrival (M)	64.72	1	<0.0001	−0.0731 (0.0091)
M ²	7.64	1	0.0057	0.00032 (0.00011)
Male tail length	0.15	1	0.70	−0.00785 (0.02040)

The full model had the statistics $\chi^2 = 143.92$, df = 3, $r^2 = 0.33$, $P < 0.0001$.

difference in slopes, $t = 5.83$, df = 268, $P < 0.0001$), implying that laying date was later when a female rather than a male arrived late (Table 2). In addition, there was a significant relationship between individual protandry and laying date, as shown by the significant male by female interaction ($M \times F$) (Figure 2; Table 2). The negative sign of this interaction implies that as degree of individual protandry increased (males arrived earlier than their mates), laying was delayed (Figure 2). There was also a significant relationship between squared male arrival date ($M \times M$) and laying date, implying that there was an intermediate optimal arrival date for males (Table 2). Using the equation derived from the model in Table 2, setting female arrival date to the mean value (11 March), showed a minimum in laying date at a male arrival date of 16 February. Likewise, there was a significant relationship between squared female arrival date ($F \times F$) and laying date, implying that there was an intermediate optimal arrival date for females, with the effect of squared arrival date being stronger in males than in females (Table 2; test for difference in slope of the squared term between males and females: $t = 3.33$, df = 268, $P < 0.0001$). Using the equation derived from the model in Table 2, setting male arrival date to the mean value (7 March), showed a minimum in laying date at a female arrival date of 3 January, well outside the range of observed female arrival dates. The protandry effect ($M \times F$) was affected by arrival date of the male (M), as shown by the significant interaction between $M \times F$ and M, with the negative sign suggesting that the protandry effect decreased with later male arrival (Table 2). Finally, the protandry effect ($M \times F$)

Table 2

Best-fit model of the relationship between laying date of the first clutch and male (M) and female arrival date (F) and degree of protandry ($M \times F$) in barn swallows from Badajoz in 1994–1997

Variable	Sum of squares	df	F	P	Slope (SE)
Year	5177.45	3	73.41	<0.0001	
Male arrival (M)	1198.75	1	50.99	<0.0001	0.369 (0.052)
Female arrival (F)	4127.49	1	175.58	<0.0001	0.604 (0.046)
($M \times F$)	622.24	1	26.47	<0.0001	−0.012 (0.002)
M ²	323.62	1	13.77	0.0003	0.008 (0.002)
F ²	508.49	1	21.63	<0.0001	0.003 (0.001)
$M \times (M \times F)$	183.51	1	7.81	0.006	−0.00015 (0.00005)
$F \times (M \times F)$	190.17	1	8.09	0.005	0.00013 (0.00005)
Male age	94.38	1	4.01	0.046	0.716 (0.357)
Error	6323.72	269			

The full model had the statistics $F = 367.92$, df = 11,269, $r^2 = 0.94$, $P < 0.0001$. ($M \times F$) is the term reflecting protandry.

Table 3

Best-fit model of the relationship between total number of fledglings per year and male (M) and female arrival date (F) and degree of protandry ($M \times F$, this latter term was not retained in the model) in barn swallows from Badajoz in 1994–1997

Variable	Sum of squares	df	F	P	Slope (SE)
Year	261.67	3	13.61	<0.0001	
Male arrival (M)	71.37	1	11.14	0.0010	−0.065 (0.020)
Female arrival (F)	111.68	1	17.42	<0.0001	−0.060 (0.014)
M ²	17.90	1	2.79	0.096	0.0008 (0.0005)
Error	1640.94	256			

The full model had the statistics $F = 23.34$, df = 6,256, $r^2 = 0.35$, $P < 0.0001$.

was affected by female arrival date (F), with the positive sign implying that the protandry effect increased with late arrival by the female (Table 2). There was a weak effect of male age but no significant effect of female age (Table 2).

Fledgling production and protandry

A model of annual production of fledglings explained 35% of the variance. Annual production of fledglings differed among years with an additional decrease due to delayed arrival of males and females (M and F) (Table 3). There was a nonsignificant relationship between squared arrival date of males ($M \times M$) and annual production of fledglings (Table 3). The relationship between individual protandry ($M \times F$) and annual production of fledglings did not enter the model ($F = 0.08$, df = 1,255, $P = 0.78$). A second model that also included laying date as a predictor variable showed significant relationships between year, laying date, male arrival (M) and male arrival squared ($M \times M$), and annual production of fledglings, whereas female arrival date (F) and individual protandry ($M \times F$) were not significantly related to annual production of fledglings (results not shown). There was no significant effect of male or female age (Table 3). In conclusion, individual protandry did not significantly affect annual production of fledglings.

Paternity and protandry

We analyzed paternity in 1994 in Badajoz in relation to individual protandry. The total number of offspring produced decreased with delay in female arrival (F) but was not significantly related to male arrival date (M) or individual protandry ($M \times F$) (Table 4A; effect of individual protandry: $F = 0.28$, df = 1,75, $P = 0.60$). There was a strong relationship between total number of offspring and male body mass and a marginally significant effect between total number of offspring and male tail length (Table 4A). There was no significant effect of male or female age (Table 4A).

The number of offspring fathered by focal males in their own nests decreased with delay in both male (M) and female arrival date (F) (Table 4B). In contrast, there was no significant relationship between individual protandry ($M \times F$) and number of offspring fathered ($F = 0.28$, df = 1,75, $P = 0.60$). In addition, there was a positive relationship between male body mass and number of offspring fathered and a marginally significant negative relationship between male tail length and number of offspring fathered (Table 4B). There was no significant effect of male or female age (Table 4B).

The number of extrapair offspring in nests of focal males increased with delay in male arrival (M) and decreased with

Table 4

Best-fit models of the relationship between measures of offspring production and male (M) and female arrival date (F), degree of protandry, male and female age, and male and female tail length and body mass in barn swallows from Badajoz in 1994

Variable	Sum of squares	df	F	P	Slope (SE)
(A) Total offspring					
Female arrival (F)	173.95	1	23.72	<0.0001	-0.050 (0.010)
Male tail length	25.99	1	3.54	0.064	-0.086 (0.046)
Male body mass	98.18	1	13.39	0.0005	0.863 (0.236)
Error	550.05	75			
(B) Fathered offspring					
Male arrival (M)	36.82	1	4.27	0.042	-0.036 (0.018)
Female arrival (F)	35.59	1	4.13	0.046	-0.026 (0.013)
Male tail length	29.92	1	3.47	0.067	-0.094 (0.051)
Male mass	117.45	1	13.62	0.0004	0.993 (0.269)
Error	638.16	74			
(C) Number of extrapair offspring					
Male arrival (M)	27.31	1	12.23	0.0008	0.0282 (0.0081)
Female arrival (F)	12.94	1	5.79	0.018	-0.0155 (0.0065)
M × F	9.03	1	4.04	0.048	-0.0004 (0.0002)
Error	183.16	82			

The full models had the statistics (A) $F = 16.88$, $df = 3, 75$, $r^2 = 0.40$, $P < 0.0001$; (B) $F = 4.95$, $df = 3, 82$, $r^2 = 0.15$, $P = 0.0033$; and (C) $F = 12.28$, $df = 4, 74$, $r^2 = 0.40$, $P < 0.0001$.

delay in female arrival (F) (Table 4C). In addition, there was an additional independent, significant relationship between individual protandry ($M \times F$) and the number of extrapair offspring, with the latter decreasing with degree of individual protandry (Table 4C). There was no significant effect of male or female age (Table 4C).

Survival rate and protandry

Female survival in Badajoz 1994–1997 was not significantly related to arrival date (F), individual protandry ($M \times F$), tail length, body mass, age, or number of fledglings produced (effect for protandry: Wald $\chi^2 = 0.31$, $P = 0.58$), whereas survival differed among years (Wald $\chi^2 = 16.38$, $P = 0.0009$). Likewise, male survival was not significantly related to arrival date (M), individual protandry ($M \times F$), tail length, body mass, age, or year (effect for protandry: Wald $\chi^2 = 0.02$, $P = 0.88$), whereas males that produced many fledglings survived well (Wald $\chi^2 = 9.72$, $P = 0.0018$, slope [SE] = 0.017 [0.005]).

DISCUSSION

The main findings of this study were that differences in arrival date between pair members had important fitness consequences, independently of the arrival schedule of each member of a pair. Although arrival date affected mating success including paternity of offspring and annual fecundity, the degree of individual protandry affected timing of breeding and hence recruitment success. There was extensive evidence of a stabilizing component on the fitness benefits of early arrival, especially in males. Furthermore, this stabilizing component of selection depended on arrival date of the partner. We briefly discuss these findings and their implications.

The classical advantage of early arrival is the increase in mating success or quality of the mate acquired (e.g., Fisher 1930; Lundberg and Alatalo 1992; Lozano et al. 1996). A couple of comparative studies of birds have also indicated that protandry at the population level is associated with sexual selection

(Rubolini et al. 2004; Coppack et al. 2006). Here we confirmed the previously reported mating advantage for early arriving males in a Spanish population of barn swallows. In addition, we showed significant stabilizing selection on male arrival date associated with mating success, implying that there is an optimal timing of arrival to the breeding site. Previously, Møller (2004) has shown how protandry increased as spring temperatures at the breeding grounds ameliorated and as tail length of males (a condition-dependent secondary sexual character [Møller 1988, 1994a]) increased across generations. Although Kokko et al. (2006) predicted that male-biased sex ratios should produce protandry, we found little evidence consistent with this prediction. This suggests that it is not only the fitness benefits in terms of mating success that affect the evolution of individual protandry but also the sex-specific costs of protandry as shown by males being more affected by inclement weather during spring than females (Møller 1994a, 1994b, 2004, 2007).

Males of socially monogamous species may experience increased variance in reproductive success through extrapair copulations and hence extrapair paternity (Birkhead and Møller 1992). Here, we confirmed the previously reported finding not only that early male arrival is advantageous in terms of number of offspring fathered in own nest (Møller et al. 2003) but also that there is an independent effect of female arrival date (Table 4B). The number of extrapair offspring in own nest was predicted by both male and female arrival date but in an antagonistic fashion (Table 4C). Late arriving males and early arriving females had more extrapair offspring in their nests. In addition, there was an independent significant effect of individual protandry as shown by the negative interaction between male and female arrival date, implying that the number of extrapair offspring in focal nests was larger when males arrived before their mates (protandry) but smaller when males arrived after their mates (protogyny). These findings are consistent with the mate opportunity hypothesis of protandry (Morbey and Ydenberg 2001).

Protandry implies that males and females differ in arrival, and protandry has implications for mating success and timing of breeding because early arriving individuals have different opportunities than late arriving conspecifics. We have shown that timing of breeding (for the first clutch and hence also for subsequent clutches) depends not only on arrival date of both sexes but also on individual protandry, the degree of stabilizing selection on arrival, and how this stabilizing selection component is affected by the arrival date of the partner. Like other temperate zone passerines, barn swallows have high recruitment rate from early broods with the proportion of fledglings subsequently recruiting to the breeding population declining from more than 10% among early breeders to none among late breeders (Møller 1994a), implying that there is a considerable selective advantage from early start of reproduction. We have shown here that both males and females start reproduction earlier when arriving early, although this benefit was greater for females than for males (Table 2). In addition, we found a significant effect of individual protandry on laying date. Furthermore, there was an effect of stabilizing selection on arrival date affecting breeding date in both sexes (the quadratic terms of arrival date in Table 2). Finally, the stabilizing effect of arrival date on timing of breeding depended on the arrival date of the partner in both sexes with opposing selection pressures. These results suggest that advantages of both earliness and averageness in arrival time for a focal individual depended on when the partner arrived.

Protandry may have repercussions for survival because climatic conditions during early spring can be perilous (Møller 1994a, 1994b). We found no evidence of adult survival being affected by arrival date or the degree of individual protandry

in either sex. Our sample sizes were 414 males and 316 females, implying a reasonable power even if the true effect was only small. These findings contrast with a study of sex-specific viability and fecundity selection on arrival date in Danish barn swallows (Møller 2007) with sex differences in viability selection among years predicting the degree of population protandry. The Danish population is 2000 km further north than the Spanish population, and it winters in Southern rather than Western Africa. The longer migration distance of the northern population should a priori produce more intense viability selection.

Arrival date is usually considered to be under strong directional selection, with less emphasis on stabilizing selection. We are only aware of a single study explicitly investigating stabilizing selection on arrival date. Møller (1994a, 1994b) showed not only that there were benefits in terms of mating success arising from early arrival but also that individuals may arrive too early. Early arrival may coincide with adverse weather conditions, with early arriving individuals suffering from significant mortality, albeit depending on body condition (Møller 1994a, 1994b). For the first time, we have here explicitly tested for stabilizing selection by inclusion of quadratic terms of arrival date as predictors of fitness components. There were significant effects of stabilizing selection on laying date for both male and female arrival date, with the effect being significantly stronger in males than in females (Table 2). Likewise, there was a significant stabilizing effect of male arrival date on mating success. In contrast, there was no evidence of such stabilizing effects on paternity or survival in either sex. These results suggest that the intensity of stabilizing selection, and hence the extent to which individuals attempt to optimize their arrival date, is larger in males than in females, mainly relating to timing of breeding.

Morbey and Ydenberg (2001) reviewed hypotheses of protandry in animals and plants with the rank advantage hypothesis and the mate opportunity hypotheses receiving support from studies of birds and salmonids. Kokko et al. (2006) suggested based on modeling that only advantages from mating success for early arriving individuals can account for the evolution of protandry, supporting the mate opportunity rather than the rank advantage hypothesis. Here we found evidence consistent with the mate opportunity hypothesis with early arriving males enjoying an advantage in terms of mating success, timing of breeding, and annual fecundity. We documented significant sex differences in advantages of early arrival of pair members. These findings suggest not only that males and females differ in evolutionary interests with respect to arrival date and individual protandry but also that the extent of quadratic selection on arrival date depends on the arrival date of the partner, resulting in sexual conflict over arrival date. Sexual conflict arises from the fact that the optimal arrival date is not identical for the 2 sexes and that the fitness benefits of degree of individual protandry differ between males and females. We suggest that current hypotheses attempting to explain the evolution of protandry would benefit from explicitly considering such sexual conflict. Given that the fitness benefit due to early arrival of one pair member depends on the behavior of the partner, the evolutionary dynamics and the evolutionary stable strategies will require adoption of game theory to determine the coevolutionary stable strategies of both males and females. Thus, theoretical analyses of protandry may benefit from considering the fact that not only sex-specific fitness benefits from early arrival but also sex-specific costs will play a role in determining the degree of protandry.

In conclusion, we have shown that the fitness consequences of individual protandry arise from sex-specific differences in costs and benefits of early arrival. Although early arrival pro-

vides similar benefits to males and females in terms of fecundity, there are large sex differences in terms of fitness benefits due to mating success and timing of breeding. Males and females also differ in terms of stabilizing selection on arrival date, with stronger stabilizing selection in males than in females, implying that individual protandry arises as a consequence of differences in patterns of selection.

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