

# Extrapair paternity in relation to sexual ornamentation, arrival date, and condition in a migratory bird

A. P. Møller,<sup>a</sup> J. Brohede,<sup>b</sup> J. J. Cuervo,<sup>c</sup> F. de Lope,<sup>d</sup> and C. Primmer<sup>b,e</sup>

<sup>a</sup>Laboratoire de Parasitologie Evolutive, CNRS UMR 7103, Université Pierre et Marie Curie, 7 quai St. Bernard, Case 237, F-75252 Paris Cedex 05, France, <sup>b</sup>Department of Population Biology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden, <sup>c</sup>Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Calle General Segura 1, E-04001 Almería, Spain, <sup>d</sup>Departamento de Biología Animal, Universidad de Extremadura, E-06071 Badajoz, Spain, and <sup>e</sup>Department of Ecology and Systematics, P.O. Box 17, FIN-00014 Helsinki University, Finland

We tested the novel hypothesis that arrival date in migratory birds represents a reliable indicator of male quality that can be used by females as a cue in extrapair mating decisions. Secondary sexual characters are often condition-dependent, and competition for early arrival leads to condition-dependent migration. Hence, both secondary sexual characters and arrival date are predicted to be condition-dependent indicators of male phenotypic quality. We studied the relationship between expression of a secondary sexual character, arrival date, and condition, respectively, and extrapair paternity in a Spanish population of barn swallows, *Hirundo rustica*. By using microsatellite markers to determine paternity, we showed that 17.8% of all offspring ( $N = 674$ ) and 32.4% of all broods ( $N = 170$ ) were due to extrapair paternity. Quasi-parasitism (in which the male nest owner fathered the offspring, but the eggs were laid by another female) occurred in 2.6% of all nestlings and 2.9% of all broods. Individuals were consistent in the frequency of extrapair paternity among first, second, and third broods. Males with long outermost tail feathers, arriving early and in prime body condition, had little extrapair paternity in their nests. This was also the case when controlling for the confounding effects of male age. Partial correlation analysis was used to investigate the direct and indirect effects of tail length, arrival date, and body condition on extrapair paternity. Body condition accounted for most of the variance in extrapair paternity, whereas tail length and arrival date accounted for a smaller proportion of the variance. Body condition was strongly correlated with tail length and arrival date. However, because females cannot directly assess condition or arrival date (males arrive before females), females may obtain an indirect measure of condition and migration ability from tail length and other phenotypic traits of males. This suggests that extrapair paternity depends on the effects of condition, through its indirect effects on arrival date, tail length, and other variables. **Key words:** barn swallow, condition-dependent migration, condition-dependent secondary sexual character, *Hirundo rustica*. [*Behav Ecol* 14:707–712 (2003)]

Many secondary sexual characters are condition-dependent because only males in prime condition are able to produce the most extravagant phenotypes (Andersson, 1994). The generality of such condition dependence has been substantiated by the observation that males with the most extreme secondary sexual characters have a higher probability of survival than do males with less extreme characters (for review, see Jennions et al., 2001). This observation provides evidence for such males being in better condition after development of their secondary sexual characters. The prevalence of condition-dependent secondary sexual characters allows females access to indirect information about the quality of potential partners in terms of their condition. Many studies of animals have shown that males in prime condition, indeed, have better mating success (Andersson, 1994; Johnstone, 1995). Not only social mating success but also the ability of males to sire offspring is related to the expression of secondary sexual characters. For example, studies of extrapair paternity in birds have shown that the expression of secondary

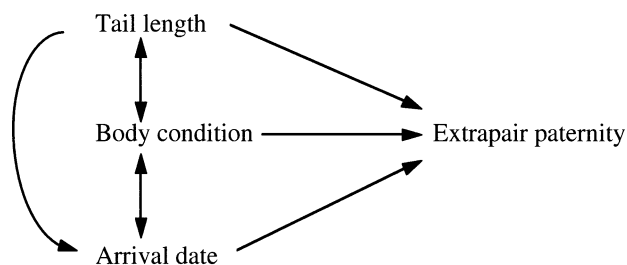
sexual characters is the single-most important predictor of the frequency of extrapair paternity (Møller and Ninni, 1998).

Many other important aspects of the life of animals are condition-dependent. For example, that is the case for life history (Roff, 1992; Stearns, 1992), immune function (Chandra and Newberne, 1977; Gershwin et al., 1985), and migration (Kokko, 1999; Møller, 1994b). Thus, it is not surprising that condition as the common underlying basis makes many of these phenotypic traits interrelated. Bird migration is a case in point. Because early arrival provides individuals of the chosen sex with advantages in terms of sexual selection, there is often intense competition among males for early arrival (Møller, 1994b). This results in strong relationships between body condition and condition-dependent characters, respectively, and early arrival. As an example, male barn swallows, *Hirundo rustica*, arrive earlier than do females, they have more variable arrival dates than females, and there is a strong positive relationship between arrival date and the expression of a secondary sexual character, the length of the outermost tail feathers, which is a condition-dependent character (Møller, 1994a). Furthermore, there is significant selection against early arrival because of adverse environmental conditions, and this natural selection cost is particularly experienced by short-tailed males (Møller, 1994a). The fact that there is consistent strong selection for early arrival in different species of migratory birds (Lozano et al., 1996;

Address correspondence to A. P. Møller. E-mail: amoller@snv.jussieu.fr.

Received 16 January 2002; revised 18 November 2002; accepted 18 December 2002.

© 2003 International Society for Behavioral Ecology



**Figure 1**  
Hypothetical relationships between condition, tail length, arrival date, and extrapair paternity of male barn swallows.

Lundberg and Alatalo, 1992; Møller, 1994a) sets the scene for the evolution of condition-dependent migration (Kokko, 1999; Møller, 1994b). Male tail length and male arrival date have significant heritabilities, and there is a strong genetic correlation between the two variables (Møller, 1991, 2001a). Because female migratory birds generally arrive later than do males, females obviously cannot use male arrival date as a cue to mate choice. However, they can use other phenotypic traits correlated with arrival date, such as breeding stage, as indirect cues to male arrival date.

Given that both the expression of secondary sexual characters and migration are condition-dependent, what is the relative importance of multiple characters in determining reproductive success? We suggest the following novel hypothetical scenario. Because both these characters will be influenced by condition, this factor will be the underlying determinant of reproductive success (Figure 1). However, if secondary sexual characters are costly to produce and maintain, as has often been assumed and demonstrated (Andersson, 1994), then the expression of the secondary sexual character will have a negative effect on arrival date because the cost of producing a secondary sexual character detracts from early arrival (Figure 1). Thus, there will be both direct and indirect effects of the secondary sexual character and arrival date on mating success (Figure 1).

The aim of the present study was to test the novel hypothesis that arrival date is a condition-dependent indicator of male quality used by females to assess potential extrapair partners. We did this by determining the relative importance of direct and indirect effects of condition on arrival date and expression of a secondary sexual character in a study of extrapair paternity of a transequatorial migratory passerine, the barn swallow. The reason for using extrapair paternity as a component of sexual selection is that this is one of the most important factors contributing to variance in success among males (Møller, 1994b; Saino et al., 1997). Previous studies of extrapair paternity in birds and other organisms have generally only considered one or several independent predictors (for review, see Møller and Ninni, 1998), but have often neglected correlations between these variables. Here we attempt to account for such potentially confounding effects. Obviously, a correlational study as the present one does not allow any inference concerning causation. However, such correlational studies may give rise to new predictions that can be tested in future correlational or experimental studies.

The barn swallow is an approximately 20-g passerine, migratory bird that feeds on flying insects captured on the wing. Males and females are generally similar in phenotype, with the exception of the outermost tail feathers, which are considerably longer in males than in females (Møller, 1994b). This sex difference in tail length increases from 5% in Northern Africa to more than 20% in Northern Scandinavia (Møller 1995). In contrast, mean wing length only differs

between the sexes by less than 1% (Møller, 1994b). Neither wing nor tail length is related to skeletal body size or body mass (Møller, 1994b). Males arrive at the breeding grounds from the African winter quarters before females, and in the Spanish study, population barn swallows arrive from several weeks to more than 2 months before the start of breeding. Males usually attract a single mate with sexual displays, and both partners build a nest, whereas the female in the Palearctic incubates the clutch single-handedly (Møller, 1994b). Both sexes contribute to food provisioning of the offspring, and a second or even a third clutch can be reared during a season. Long-tailed male barn swallows enjoy sexual selection advantages in terms of mating success, latency to mating, female parental investment, and extrapair paternity (Møller, 1994b; Møller and Tegelström, 1997; Saino et al., 1997). Extrapair paternity is more common in the nests of short-tailed males, and long-tailed males sire more offspring in neighboring nests (Saino et al., 1997). In addition, male song rate and breeding synchrony independently affect the rate of extrapair paternity (Møller et al., 1998; Saino et al., 1999). The relationships between extrapair paternity, arrival date, expression of secondary sexual characters, and condition have never been investigated in barn swallows or any other species.

## METHODS

We have studied barn swallows at Badajoz (38°50' N, 6°59' W) in southern Spain since 1976, as part of a long-term project. The study site at Badajoz consists of open farmland with pastures, cereals, and fruit plantations, and most barn swallows breed in barns and other farm buildings. The present study was based on birds captured during 1994.

Barn swallows were captured twice per week by closing all windows and doors in the buildings housing the breeding birds, which were captured the subsequent morning in a mist net. Capture date was assumed to reflect arrival date because of the regular nature of captures. All birds were provided with aluminum rings and color rings, which allowed identification in the field with the help of binoculars. Barn swallows were assigned to nests by reading color rings when birds were at their nests. In case of any doubt, the bird was excluded from the following analyses.

All birds were measured by F.d.L., which eliminated any noise in the data owing to inter-observer variability. We measured beak length, depth and width and length of left and right tarsus with a digital caliper to the nearest 0.01 mm, right and left flattened wing, right and left outermost tail feathers, central tail feathers, and wingspan with a ruler to the nearest 0.5 mm. Tail, wing, and tarsus length was determined as the mean value of left and right character. Individuals with broken tails were excluded from the analyses because the rounded tip of the outermost tail feathers clearly reveals whether it is broken. Body mass was recorded with a Pesola spring balance to the nearest 0.5 g. Body mass of males was weakly, but not significantly, positively related to tarsus length raised to the third ( $F = 2.04$ ,  $df = 1,84$ ,  $r^2 = .024$ ,  $p = .157$ ). Residuals from this regression were used as a measure of body condition. This measure of body condition, which is significantly repeatable among capture events (Møller, 1994b), is a reliable predictor of several fitness components in both male and female barn swallows (Møller, 1994b). The conclusions reached did not change if body mass was used in the analyses instead of residual body mass as a body condition index, as was expected given the small amount of variance explained by the regression.

Age of birds was determined from 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 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. Similar findings have been recorded for 3000 adults ringed in Denmark (Møller, 1994b) and 5000 adults ringed in Italy (Saino N, personal communication).

Tail length of females was manipulated by randomly assigning females to one of three groups if the female was not already mated for details (see Cuervo et al., 1996). The outermost tail feathers were either elongated by 20 mm, reduced by 20 mm, or kept as an untreated control. A total of 16 females had their tails shortened, whereas 14 had their tails elongated and the remaining 56 served as controls. See Cuervo et al. (1996) for further details about this experiment and its results. We also elongated the tails of six and shortened the tails of four randomly selected males. The conclusions presented in the results remain unchanged, when using the treatment of males as a factor in analyses of covariance, or when excluding these males from the 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. 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 by using fluorescently labeled primers. PCR products were run on an ABI 377 sequencing instrument together with an internal size-standard, and alleles were determined by the software GeneScan (Perkin-Elmer).

There was missing information for some of the birds, which resulted in slightly varying sample sizes in the subsequent analyses. We used nonparametric Kendall rank correlation and partial correlation analyses (Siegel and Castellan, 1988) because some variables were not normally distributed. Because the relationship between condition, migration, and tail length and their effect on extrapair paternity hypothetically show both direct and indirect effects (Figure 1), we used partial rank correlation analysis to quantify these effects. We could not use path analysis to investigate the importance of direct and indirect effects because violations of assumptions of normality, even for transformed variables, would make such analyses inappropriate.

We adjusted the significance level of 5% for multiple statistical tests by using sequential Bonferroni correction.

## RESULTS

The frequency of extrapair paternity was 17.2% in nestlings from first broods, 13.8% in second broods, and 19.0% in third broods of the 86 pairs, with an overall frequency of 17.8% among all nestlings (Table 1). The percentage of broods with extrapair paternity ranged from 19.6 to 31.9% in the three broods (Table 1). A total of 2.6% of all nestlings and 2.9% of all broods had extrapair maternity (Table 1), which involved the nest owner, thus classifying it as quasi-parasitism.

Repeatability of extrapair paternity among broods was high, as revealed by strong positive rank correlations between first and second broods ( $r_s = .46$ ,  $N = 68$ ,  $p = .0002$ ), first and third broods ( $r_s = .47$ ,  $N = 15$ ,  $p = .077$ ), and second and third broods ( $r_s = .69$ ,  $N = 15$ ,  $p = .010$ ). In subsequent analyses, extrapair paternity of each pair was calculated for all broods produced by that pair during the entire breeding

**Table 1**

**Frequency of extrapair paternity and maternity in barn swallows from Badajoz**

	Frequency of nestlings (mean [SE])	N	Frequency of broods	N
Extrapair paternity				
First brood	17.2% (3.3)	354	31.4%	86
Second brood	13.8% (2.9)	264	31.9%	69
Third brood	19.0% (8.0)	56	19.6%	15
All broods	17.8% (2.8)	674	32.4%	170
Extrapair maternity	2.6% (1.4)	674	2.9%	170

season. Analyses for first and second broods separately revealed results similar to those for extrapair paternity across all three broods, and we thus only report findings on extrapair paternity of all broods combined in the following paragraphs.

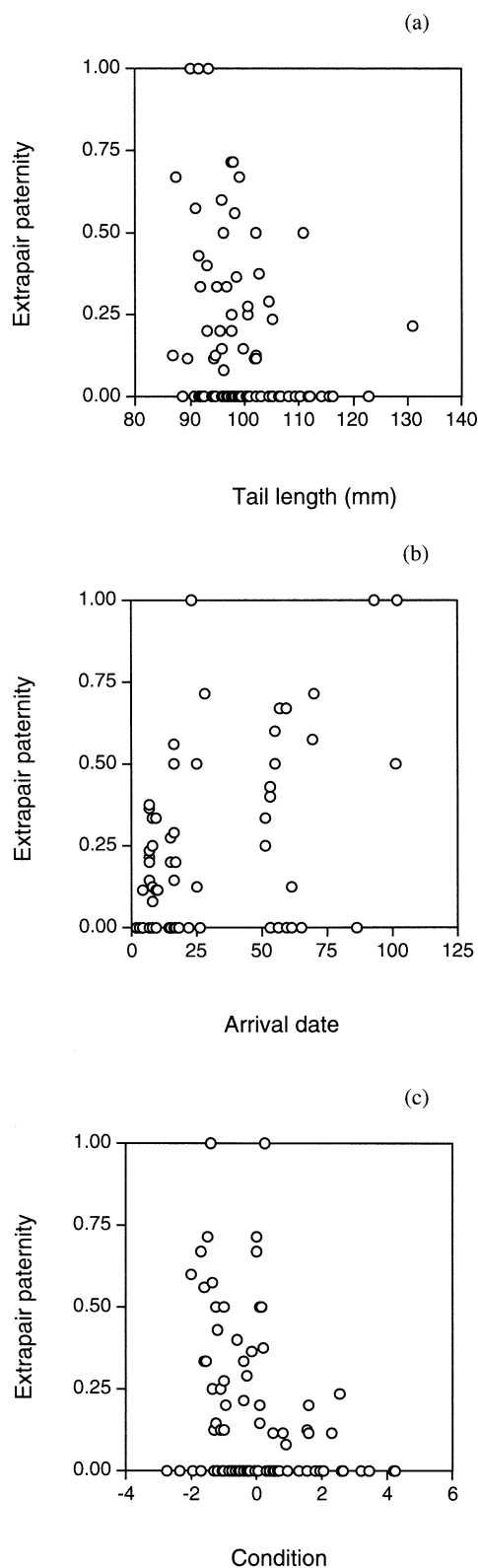
There were three correlates of extrapair paternity in the Spanish barn swallow population (Figure 2). First, males with long tails tended to be more likely to be the fathers of offspring in their nests than were short-tailed males, although not significantly so (Figure 2a and Table 2). Second, male arrival date was a strong predictor of extrapair paternity, with late-arriving males having more extrapair offspring in their nests (Figure 2b and Table 2). Third, male body condition was a predictor of extrapair paternity, with males in prime condition having few extrapair offspring in their nests (Figure 2c and Table 2). This variable accounted for most of the variance. None of the other male phenotypic traits or the female phenotypic traits described in the Methods section accounted for significant relationships with extrapair paternity.

Age was strongly positively correlated with male arrival date (Table 2), but only weakly correlated with male tail length (Table 2), male body condition (Table 2), and extrapair paternity (Table 2). However, the significant relationships between male arrival date and male body condition, respectively, and extrapair paternity remained significant after controlling for age in partial correlation analyses (body condition and extra-pair paternity: partial Kendall  $\tau = -0.234$ ,  $z = 3.187$ ,  $p < .0001$ ; arrival date and extra-pair paternity: partial Kendall  $\tau = 0.175$ ,  $z = 2.387$ ,  $p < .0001$ ), whereas the effect of tail length was no longer significant after controlling for male age (tail length and extra-pair paternity: partial Kendall  $\tau = -0.118$ ,  $z = 1.604$ ,  $p = .110$ ).

We found several significant intercorrelations between body condition and male phenotype. Long-tailed male barn swallows arrived significantly earlier than did short-tailed males (Figure 3a and Table 2). Long-tailed males also had better body condition than did short-tailed males on arrival (Figure 3b and Table 2), and early-arriving males were heavier than late-arriving males (Figure 3c and Table 2).

The correlations between the different indices of male quality and body condition were investigated further in partial correlation analyses. The relationship between tail length and extrapair paternity, after controlling for age, body condition, and arrival date, had a partial correlation coefficient Kendall  $\tau = -0.055$ ,  $z = 0.751$ ,  $p = .453$ . The relationship between arrival date and extrapair paternity, after controlling for age, tail length, and body condition, had a partial correlation coefficient Kendall  $\tau = 0.080$ ,  $z = 1.089$ ,  $p = .276$ . The relationship between body condition and extrapair paternity, after controlling for age, tail length, and arrival date, had a partial correlation coefficient Kendall  $\tau = -0.176$ ,  $z = 2.398$ ,  $p = .016$ .

The effect of female tail manipulation on extrapair paternity was negligible and nonsignificant (Kruskal-Wallis ANOVA,  $H = 0.528$ ,  $df = 2$ ,  $p = .768$ ).



**Figure 2**  
Extrapair paternity (proportion of offspring sired by an extrapair male in own nests) in relation to male tail length (a, in millimeters), male arrival date (b, 1 indicates 15 February), and male body condition (c, residuals from a regression of body mass on [tarsus length]<sup>3</sup>).

**Table 2**

**Kendall rank order correlation coefficients between male tail length, body condition, age, arrival date, and extrapair paternity in barn swallows**

	Condition	Age	Arrival	Extrapair paternity
Tail length	0.225*	0.113	−0.290**	−0.131
Condition		0.180***	−0.424**	−0.252**
Age			−0.344**	−0.134
Arrival				0.209*

All correlations remained significant after sequential Bonferroni correction, with the exception of that between condition and age.

\*  $p < .01$ , \*\*  $p < .001$ , \*\*\*  $p < .05$ .

## DISCUSSION

In this study we tested the novel hypothesis that female birds use arrival date as a cue in their choice of extrapair partners. Females were predicted to do so because arrival date, just like secondary sexual characters, is condition-dependent with males in prime condition arriving to the breeding ground before other males. Barn swallows in the Spanish population arrive well before the start of breeding, with breeders spending from 3 weeks to more than 2 months at the breeding site before starting to reproduce. This also implies that females are not strongly constrained in their choice of extrapair partners or in their possibility of engaging in extrapair copulations because many different potential extrapair males are present simultaneously. Furthermore, because rates of extrapair paternity were highly consistent among broods, females were consistent in their behavior at the start of the breeding season and later on during second and third broods. A weak phenotypic correlate of extrapair paternity in the Spanish population of barn swallows was male tail length (Figure 2a). This effect was confounded by male age in the Spanish population, but not in previous studies of Danish and Italian populations (Møller and Tegelström, 1997; Saino et al., 1997). The negative relationship between extrapair paternity and expression of a secondary sexual character is similar to what has been reported in many other studies of sexual selection (for review, see Møller and Ninni, 1998). The strength of the relationship between tail length and extrapair paternity was relatively weak in the Spanish population (effect size calculated as Pearson  $r = -.225$ ), whereas the similar relationships in Denmark was  $r = -.35$  (Møller and Tegelström, 1997) and in Italy it was  $r = -.35$  (Saino et al., 1997). This implies that the proportion of variance in extrapair paternity explained by male tail length decreased from 12.3% in Denmark and 12.2% in Italy to 5.1% in Spain. This difference in the relationship between tail length and extrapair paternity among populations was matched by similar differences in sexual dimorphism in tail length (Møller, 1995).

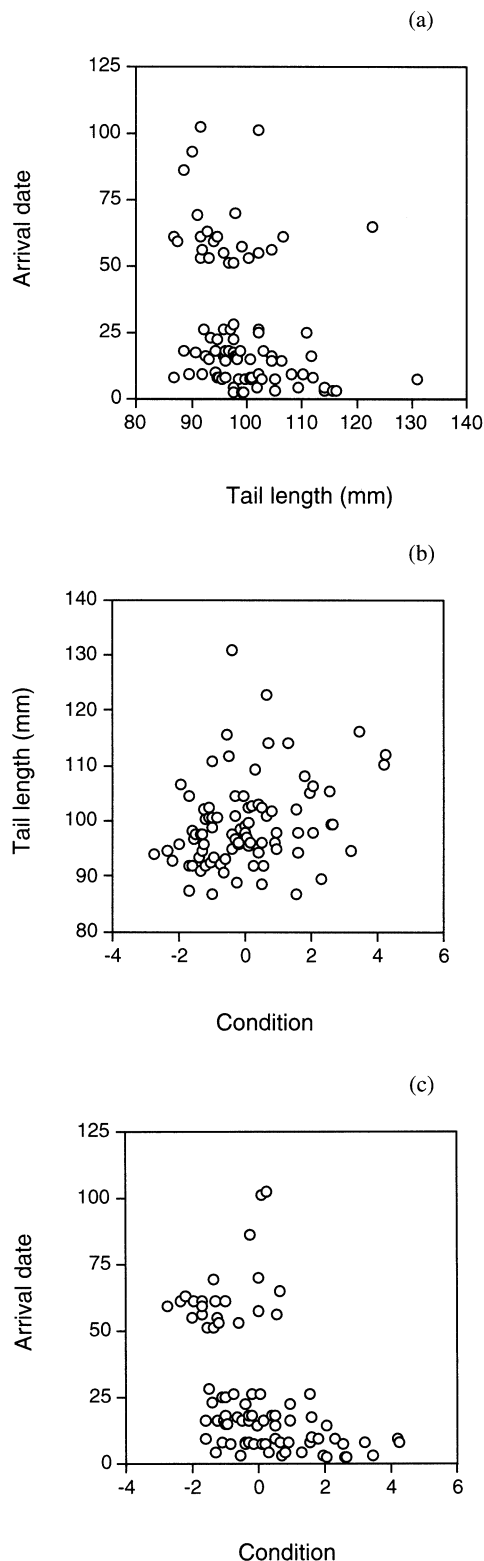
Two factors were found to be significantly correlated with extrapair paternity, male arrival date, and male body condition. Early-arriving males were much less likely to have extrapair offspring in their nests than were late-arriving males (Figure 2b). Furthermore, heavier males were less likely to have extrapair offspring than were males in poor condition (Figure 2c). Both of these effects were independent of male age. These findings suggest that early arrival is beneficial for males. Early-arriving males also had better body condition than did late-arriving conspecifics. This finding is surprising given that insect abundance at the breeding grounds during early arrival in our study site in Spain in December–February is low. Insect abundance also is likely to be low at any stopover site between the West African winter quarters in Nigeria, Ghana, and the

Ivory Coast and Spain. Therefore, body condition of early-arriving males is predicted to be lower than that of late-arriving males, unless early-arriving males are of high phenotypic quality, as indicated by their longer tails.

We used partial correlation analysis to determine the magnitude of the relationships between three different variables (tail length, arrival date, body condition) and extrapair paternity after taking both direct and indirect effects into account. In particular, body condition had a strong effect, through its indirect effect on arrival date and to a lesser extent through effects on tail length, but also a strong direct effect. We hypothesize that this direct effect of condition may act through effects on behavior such as song rate (Møller et al., 1998). Thus, condition appears to be the underlying main factor determining extrapair paternity, either directly (through as yet in this population unmeasured variables such as behavior) or indirectly through its effects on arrival date and perhaps tail length. Because most females cannot assess age, condition, or arrival date of potential mates directly, they must rely on other phenotypic markers of mate condition. We suggest that they use tail length and perhaps behavioral variables as indicators of male condition. Previous studies have shown that nest sites per se are unimportant as cues for female choice, because reproductive success is mainly determined by the quality of the male present rather than the nest site (for review, see Møller, 1994b).

Female barn swallows have considerably longer tails than do juveniles, but on average 5–20% shorter tails than do males, depending on population (Møller, 1994b). The evolutionary forces accounting for this elongation of tail feathers in females may be sexual selection or a correlated response to selection on males (Cuervo et al., 1996; Møller, 1994b). We have previously reported the results of a female tail manipulation experiment from the same year as the present study (Cuervo et al., 1996). In that study, we found no evidence of direct sexual selection on female tail length. Neither did we find any evidence of costs in the year of manipulation by females having experimentally elongated tails (Cuervo et al., 1996). In the present study, we could add yet another piece of evidence suggesting that there are no sexual selection benefits to females. If female tail length was subject to sexual selection, we should expect an effect of tail manipulation on extrapair paternity in females because the experiment should have created a mismatch between the quality of females and their mates. However, female tail manipulation did not significantly affect their level of extrapair paternity. This observation strengthens our previous conclusions that female tail length has evolved as an indirect response to sexual selection on male tails.

The overall frequency of extrapair paternity in this Spanish population of barn swallows was 17.8% of nestlings and 32.4% of all broods (Table 1). These values compare to 28% of nestlings and 33% of broods in a Danish population (Møller and Tegelström, 1997) and 33% of nestlings among unmanipulated males in an Italian population (Saino et al., 1997). The proportion of extrapair nestlings was significantly smaller in Spain than in Denmark and Italy (Kruskal-Wallis ANOVA,  $H = 7.24$ ,  $df = 3$ ,  $p < .05$ ). Thus, there was considerably less extrapair paternity in the Spanish population, although a similar fraction of broods were affected. The reason for this low level of extrapair paternity remains unclear. Because sexual size dimorphism in tail length is much smaller in the Spanish population than in the two other populations (Møller, 1995), we might expect less intense sexual selection based on the general pattern observed in paternity studies of birds (Møller and Ninni, 1998). A smaller degree of sexual size dimorphism and a smaller variance in male tail length in the Spanish population compared with other populations may



**Figure 3**

Arrival date (1 indicates 15 February) of male barn swallows in relation to tail length (millimeters). (b) Tail length (millimeters) of male barn swallows in relation to body condition (residuals from a regression of body mass on [tarsus length]<sup>3</sup>). (c) Arrival date (1 indicates 15 February) of male barn swallows in relation to body condition (residuals from a regression of body mass on [tarsus length]<sup>3</sup>).

make it more difficult for females to use this character to discriminate among males for extrapair copulations. Furthermore, the level of local recruitment is much higher in Spain than in Italy or Denmark (de Lope F, Møller AP, and Saino N, unpublished data). Hence, inbreeding levels may be larger in Spain, and a low level of genetic variation may reduce female genetic benefits of extrapair paternity, as shown by a reduced level of extrapair paternity in populations of birds with little genetic variation (Møller, 2001b).

We found a few cases of extrapair maternity in the Spanish population, which differs from what has been recorded elsewhere. All of these cases were quasi-parasitism, because the attending male was the father of the offspring. Such parasitism has also been recorded in the sand martin, *Riparia riparia* (Alves and Bryant, 1998). We hypothesize that the occurrence of extrapair maternity in this barn swallow population is related to the extremely high density, with most pairs breeding within a distance of less than 2 m from the nearest neighbor.

In conclusion, barn swallows in a Spanish population had relative high levels of extrapair paternity that were determined mainly by the condition of males, through direct effects on paternity and indirect effects on the size of a secondary sexual character and arrival date. These findings support the novel suggestion that arrival date as affected by condition can provide reliable information about male quality, and that this information can be used by females as a cue in extrapair mate choice.

N. Saino kindly counted the leukocytes. F. de Sande kindly made the analyses of immunoglobulins. This study was supported by grants from the Spanish Ministry of Science and Technology BOS2000-0293 and Junta de Extremadura IPR00A021 for FdL. J.J.C. was supported by a postdoctoral grant from the European Union (Human Capital and Mobility Program).

## REFERENCES

- Alves MAS, Bryant DM, 1998. Brood parasitism in the sand martin, *Riparia riparia*: evidence for two parasitic strategies in a colonial passerine. *Anim Behav* 56:1323-1331.
- Andersson M, 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.
- Chandra RK, Newberne PM, 1977. Nutrition, immunity, and infection. New York: Plenum Press.
- Cuervo JJ, de Lope F, Møller AP, 1996. The function of long tails in female barn swallows (*Hirundo rustica*): an experimental study. *Behav Ecol* 7:132-136.
- Gershwin ME, Beach RS, Hurley LS, 1985. Nutrition and immunity. Orlando, Florida: Academic Press.
- Jennions MD, Møller AP, Petrie M, 2001. Sexually selected traits and adult survival: a meta-analysis of the phenotypic relationship. *Q Rev Biol* 76:3-36.
- Johnstone RA, 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biol Rev* 70:1-65.
- Kokko H, 1999. Competition for early arrival in migratory birds. *J Anim Ecol* 68:940-950.
- Lozano GA, Perreault S, Lemon RE, 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. *J Avian Biol* 27:164-170.
- Lundberg A, Alatalo RV, 1992. The pied flycatcher. San Diego: Academic Press.
- Møller AP, 1991. Sexual selection in the monogamous barn swallow (*Hirundo rustica*), I: determinants of tail ornament size. *Evolution* 45:1823-1836.
- Møller AP, 1994a. Phenotype-dependent arrival time and its consequences in a migratory bird. *Behav Ecol Sociobiol* 35:115-122.
- Møller AP, 1994b. Sexual selection and the barn swallow. Oxford: Oxford University Press.
- Møller AP, 1995. Sexual selection in the barn swallow (*Hirundo rustica*), V: geographic variation in ornament size. *J Evol Biol* 8:3-19.
- Møller AP, 2001a. Heritability of arrival date in a migratory bird. *Proc R Soc Lond B* 268:203-206.
- Møller AP, 2001b. Sexual selection, extra-pair paternity, genetic variability and conservation. *Acta Zool Sin* 47:2-12.
- Møller AP, Ninni P, 1998. Sperm competition and sexual selection: a meta-analysis of paternity studies of birds. *Behav Ecol Sociobiol* 43:345-358.
- Møller AP, Saino N, Taramino G, Galeotti P, Ferrario S, 1998. Paternity and multiple signaling: effects of a secondary sexual character and song on paternity in the barn swallow. *Am Nat* 151:236-242.
- Møller AP, Tegelström H, 1997. Extra-pair paternity and tail ornamentation in the barn swallow *Hirundo rustica*. *Behav Ecol Sociobiol* 41:353-360.
- Primmer CR, Møller AP, Ellegren H, 1995. Resolving genetic relationships with microsatellite markers: a parentage testing system for the swallow *Hirundo rustica*. *Mol Ecol* 4:493-498.
- Primmer CR, Møller AP, Ellegren H, 1996. New microsatellites from the pied flycatcher *Ficedula hypoleuca* and the swallow *Hirundo rustica*. *Hereditas* 124:281-283.
- Roff DA, 1992. The evolution of life histories. New York: Chapman and Hall.
- Saino N, Primmer CR, Ellegren H, Møller AP, 1997. An experimental study of paternity and tail ornamentation in the barn swallow (*Hirundo rustica*). *Evolution* 51:562-570.
- Saino N, Primmer CR, Ellegren H, Møller AP, 1999. Breeding synchrony and paternity in the barn swallow (*Hirundo rustica*). *Behav Ecol Sociobiol* 45:211-218.
- Siegel S, Castellan NJ Jr, 1988. Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill.
- Stearns SC, 1992. The evolution of life histories. Oxford: Oxford University Press.