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## Phenotype-dependent arrival time and its consequences in a migratory bird

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**Abstract** Arrival times for migratory animals can be viewed as the result of an optimization process of costs and benefits of early arrival, and when the cost and benefit functions of early arrival depend on phenotypic quality, this will result in phenotype-dependent optimal arrival times. This hypothesis was tested for males of the migratory and sexually size-dimorphic barn swallow *Hirundo rustica*. The major cost of early arrival is poor environmental conditions which resulted in mortality of short-tailed early-arriving males in one year. The major benefits of early arrival are higher mating success, enhanced reproductive success, improved recruitment rates for offspring, and enhanced quality of the mate acquired. Annual variation in male arrival date is related to weather conditions at the breeding grounds, but also to some extent to weather conditions in the African winter quarters. Individual variation in arrival time can be explained by phenotype-dependent cost and benefit functions of early arrival. Male barn swallows with long tail ornaments arrived earlier than short-tailed males. The costs of early arrival should be particularly high under poor environmental conditions and lead to a stronger negative relationship between arrival date and phenotypic quality in years with poor environmental conditions. This prediction was confirmed by a stronger negative relationship between male tail length and date of arrival in years when arrival was relatively late because of poor weather. A female preference for early-arriving males may result in acquisition of good genes for optimal migratory behaviour, if migratory direction and extent have a genetic basis as shown in a number of different bird species.

**Key words** Arrival time · *Hirundo rustica*  
Cost-benefit analysis · Phenotypic quality  
Environmental conditions

### Introduction

Female animals should time their reproduction so that it coincides with optimal conditions for the rearing of offspring (Lack 1954). Males should subsequently adjust their reproductive activities to the breeding schedule of females, and males often appear at the sites of reproduction earlier than females (Lack 1954), apparently because males compete with each other for access to resources essential for reproduction or mate acquisition (e.g. Myers 1981). The optimal arrival time at the breeding sites for males has been modelled several times (Wiklund and Fagerström 1977; Fagerström and Wiklund 1982; Bulmer 1983a,b; Iwasa et al. 1983; Parker and Courtney 1983). The optimal arrival time for males will depend on the costs and benefits of arriving at a particular time. The costs of early arrival include increased maintenance costs and mortality risks due to bad weather, while the benefits of early arrival include acquisition of a high-quality territory and mate, and a resultant high annual reproductive success.

The problem facing males is to arrive at a time in relation to the arrival of females and environmental conditions that maximizes male fitness. The optimality models developed by Wiklund and Fagerström (1977) and Fagerström and Wiklund (1982) predicted that the optimal degree to which males should emerge before females is approximately equal for similar lengths of the emergence periods of the sexes, irrespective of the life expectancy of males. An alternative solution to this optimality problem of emergence times is the evolutionarily stable strategy approach adopted by Bulmer (1983a,b), Iwasa et al. (1983), and Parker and Courtney (1983). Iwasa et al. (1983) determined the optimal time of emergence for males so that males emerging on different days enjoy equal fitnesses. Their approach was to predict the position and the shape of the male emergence curve for any given female emergence schedule. The main result of Iwasa et al. (1983) was that the sex ratio decreases with time during the period when some males emerge, and thus female availability per male increases

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with time as long as males emerge every day. The models of Bulmer (1983a,b) are special cases of that by Iwasa et al. (1983).

Parker and Courtney (1983) also used a game-theory approach to determine the mixed evolutionarily stable strategy for male emergence time so that male fitnesses are equal for all individuals, irrespective of their emergence times. Parker and Courtney (1983) assumed that the fitness gain to an individual on a given day is equal to the number of females available divided by the number of males. When the mortality rate of males is high, the emergence curve of males should closely track the seasonal distribution of females. When the mortality rate is low, the peak of male emergence should occur well before the peak of female availability, and the male emergence curve should be much tighter than that of females. There are three effects on male emergence when the mortality rate decreases: (i) the variance in male emergence time decreases; (ii) the peak in emergence time is shifted towards an earlier date; and (iii) the skewness of male emergence increases despite a normal distribution of female availability. These three effects are also increased when there are hierarchies of male competitors as in the case of males differing in attractiveness. The predictions are thus that (i) males should arrive well before females, and (ii) males of high phenotypic quality should arrive earlier than other males.

There are very few empirical tests of the assumptions and predictions of the models of optimal arrival time (see Parker and Courtney (1983) for one exception). The objectives of this paper are twofold. First, the cost and benefit functions of early arrival are described for males of the migratory barn swallow *Hirundo rustica*. Second, the patterns of arrival of male and female barn swallows are used to test the qualitative predictions about the relationship between individual quality and optimal time of arrival, as suggested by the model by Parker and Courtney (1983).

## Methods

### Study species

The barn swallow is a small (about 20 g), monogamous, semicolonial passerine bird feeding on insects caught on the wing (Møller 1994). The sexes are similar in size with the exception of the outermost tail feathers which are considerably longer in males than in females, on average 20% longer in the study population (Møller 1991a). Effects of age on male tail length are weak, and phenotypic correlations between male tail length and other morphological characters are also weak (Møller 1991a). Males arrive from the African winter quarters in April and May, before the females, and establish a small breeding territory of a few square meters within which the nest is later built (Møller 1994). Females visit a number of potential mates and make their mate choice based on the length of the outermost tail feathers of the males (Møller 1988, 1990, 1994).

After pair formation the male and the female build a nest, and the female subsequently lays a clutch. Incubation, which is entirely by the female, lasts c. 14 days. Nestlings are fed by both parents for c. 3 weeks before fledging, and fledglings are cared for by adults for another week. Most pairs have two clutches per season.

Adult barn swallows leave the nest site between August and October. Danish barn swallows spend the winter in South Africa as revealed by recoveries of ringed birds (Møller 1994). The single complete annual molt takes place on the wintering grounds.

### Study site

I studied barn swallows during 1970–1992, but mainly 1984–1992, and usually from May to September, at Kraghede (57°12'N, 10°00'E), Denmark. The study area is open farmland with scattered plantations, ponds, and hedgerows. The barn swallows breed on farms either solitarily or in colonies of up to 50 pairs. A detailed description of the study site and the barn swallow population can be found in Møller (1994).

### General field procedures

Barn swallows were captured in mist nets at the breeding sites shortly after arrival during 1984–1992. The first day an individual was observed was recorded as its arrival date. A few barn swallows were captured with sweep nets at night while roosting within their breeding territories. All birds were provided with a numbered aluminium ring and most with an individual combination of two colour rings. Many birds in larger colonies with more than 15 pairs were provided with an individual combination of colour markings on their belly feathers using stamp ink. More than 98% of all individuals were captured as determined by the frequency of unringed birds at the breeding sites.

Individuals were sexed by the presence (females) or absence (males) of a brood patch and by the shape of the cloacal protuberance, which is considerably larger in males than in females (Svensson 1984). I recorded several standard morphological measurements, including the length of each of the two outermost, elongated tail feathers (to the nearest mm, hereafter tail length, using a ruler).

During 1970–1992 all nestlings were banded with an aluminium ring when aged 15 days. The exact age of banded recruits could therefore be determined. All other barn swallows either had not bred previously in the study area (yearlings), or had done so at least once (2 years or older). Because the breeding dispersal of barn swallows in the study area is very limited (Møller 1994), birds being caught for the first time were assumed to be yearlings. This assumption was supported by recaptures of all recruits first occurring when they were yearlings (Møller 1994). A fraction of the nestlings was measured during 1984–1992. The tarsus length of nestlings was measured with a digital calliper to the nearest 0.01 mm when 15 days old, an age when the tarsus has reached adult, full-grown size (Stoner 1935; own observations). Nestling body mass was simultaneously recorded to the nearest 0.1 g on a Pesola spring balance.

Mating success of male barn swallows was determined from the presence or absence of a female within the territory of a male during my regular visits to the breeding sites during 1984–1992. More than 98% of all pairs subsequently built a nest and reproduced, although a few pairs never built a nest, or did build a nest but never laid eggs.

Breeding activities of barn swallows were recorded during regular visits to all nests throughout the breeding season during 1984–1992. This allowed determination of (i) the breeding date which is the date when the first egg of a clutch was laid; (ii) brood size at fledging which is the number of nestlings present on the last visit before fledging minus the number of dead nestlings present after fledging; (iii) the presence of a second clutch; and (iv) annual number of fledgling which is the number of fledglings in the first and the second brood. Egg and nestling mortality were estimated as the proportion of eggs laid not giving rise to hatchlings and the proportion of hatchlings not giving rise to fledglings.

A territory was assumed to be occupied in 2 years if territories in those years overlapped partially. Territories were mapped carefully during observations of interactions between territory owners and intruders throughout the breeding season of 1984–1992.

## Environmental conditions in the winter quarters and the breeding areas

The foraging conditions in the South African winter quarters are determined by heavy rains which are known to trigger swarming flights of termites and other insects, and these are exploited intensively by barn swallows (Rudebeck 1957; Turner and Rose 1989). The foraging conditions were determined from rainfall records at two meteorological stations within the wintering range of the Danish barn swallow population (Pretoria and Johannesburg). I used the mean amount of precipitation for March, just before barn swallows leave their winter quarters, as a measure of the environmental conditions before the start of migration. These data were obtained from the South African Meteorological Office.

The foraging conditions in the breeding area are determined by temperature since insect populations increase with increasing temperatures (Turner and Rose 1989). I obtained mean and mean minimum daily temperatures for May (the month when most barn swallows arrive) from Tylstrup Meteorological Station, which is located just south of the study area.

## Statistical procedures

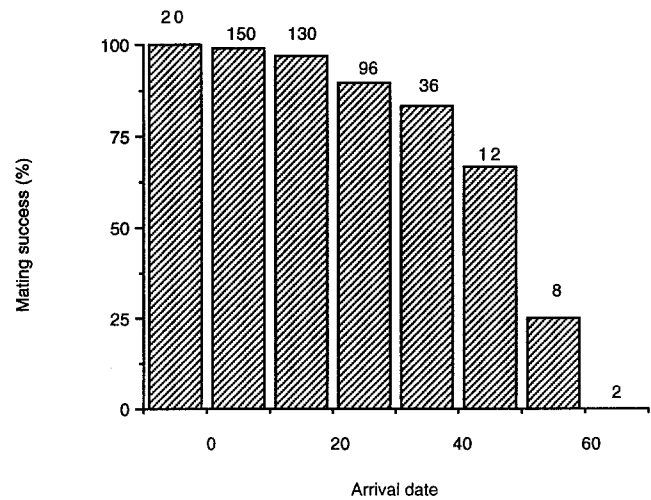
Barn swallows were captured repeatedly during their life span and a randomly chosen observation of an individual was used in the analyses in order to avoid pseudo-replication. I was unable to obtain estimates of all variables for all individuals every year, and sample sizes may therefore differ between analyses. I used parametric or non-parametric statistics as determined by the frequency distribution of the data, which were tested for deviations from normality in Kolmogorov-Smirnov tests. Analyses were performed according to Sokal and Rohlf (1981) and Siegel and Castellan (1988). All statistical tests are two-tailed. All values reported are means (SE).

## Results

### Costs and benefits of early arrival

The single most obvious cost of early arrival in an insectivorous migratory bird is that environmental conditions for survival are worst at the beginning of the arrival season. Twenty-two male barn swallows were reported dead by farmers and myself during a cold spell early in the 1987 breeding season (which was the coldest during the years 1984–1992), and two of these males weighed only 15 g, which is a quarter less than the normal body mass. The tails of males that survived the cold spell were significantly longer than that of males found dead [survivors: 115.7 mm (4.5),  $n = 7$ ; non-survivors: 100.7 mm (0.7),  $n = 22$ ;  $t$ -test:  $t = 5.41$ ,  $df = 27$ ,  $P < 0.001$ ]. There was no relationship between survival and age (Mann-Whitney  $U$ -test:  $z = 0.21$ , NS). I never found mortality caused by bad weather conditions during any of the other years 1984–1992. This suggests that susceptibility to adverse weather conditions is related to tail length in male barn swallows.

Six types of benefit of early male arrival were investigated: (i) mating success; (ii) the presence of a second clutch; (iii) seasonal reproductive success; (iv) recruitment of offspring; (v) mate quality; and (vi) territory quality. First, since there is an excess of males in the barn swallow population, a fraction of males remain

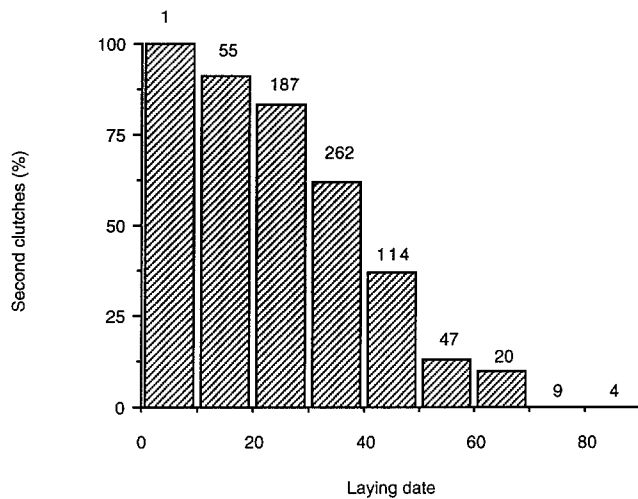


**Fig. 1** Mating success of male barn swallows in relation to their arrival date during 1984–1992. Dates are days since 30 April. Numbers are numbers of males

bachelors (Møller 1994). If male mating success depends entirely on their time of arrival, only the latest-arriving males will be unable to acquire a mate. However, male tail length is also an important determinant of mating success. There is a negative relationship between male mating success and arrival date (Fig. 1; Kendall  $\tau = -0.31$ ,  $n = 454$ ,  $P < 0.001$ ), and this effect remained even after controlling statistically for male tail length (Kendall partial  $\tau = -0.29$ ,  $n = 454$ ,  $P < 0.001$ ) and male tail length and age (Kendall partial  $\tau = -0.30$ ,  $n = 454$ ,  $P < 0.001$ ). Statistically significant negative relationships were found in all years 1984–1992 (Kendall  $\tau = -0.24$  to  $-0.53$ ,  $P < 0.05$ ). Early-arriving males therefore have a higher probability of acquiring a mate than late-arriving males.

A major determinant of reproductive success of mated male barn swallows is the number of broods reared per season rather than the number of nestlings per brood (Møller 1990). The probability of raising two broods per season decreases as the season progresses (Fig. 2). While all early breeding male barn swallows rear two broods, the frequency of second broods drops to zero for late breeders (Kendall  $\tau = -0.39$ ,  $n = 699$ ,  $P < 0.001$ ). This effect remained after controlling for the effect of male age (Kendall partial  $\tau = -0.32$ ,  $n = 699$ ,  $P < 0.001$ ). Statistically significant negative relationships were found in all years 1984–1992 (Kendall  $\tau = -0.26$  to  $-0.48$ ,  $P < 0.05$ ). Late arrival therefore involves a cost in terms of reduced opportunities for raising a second brood.

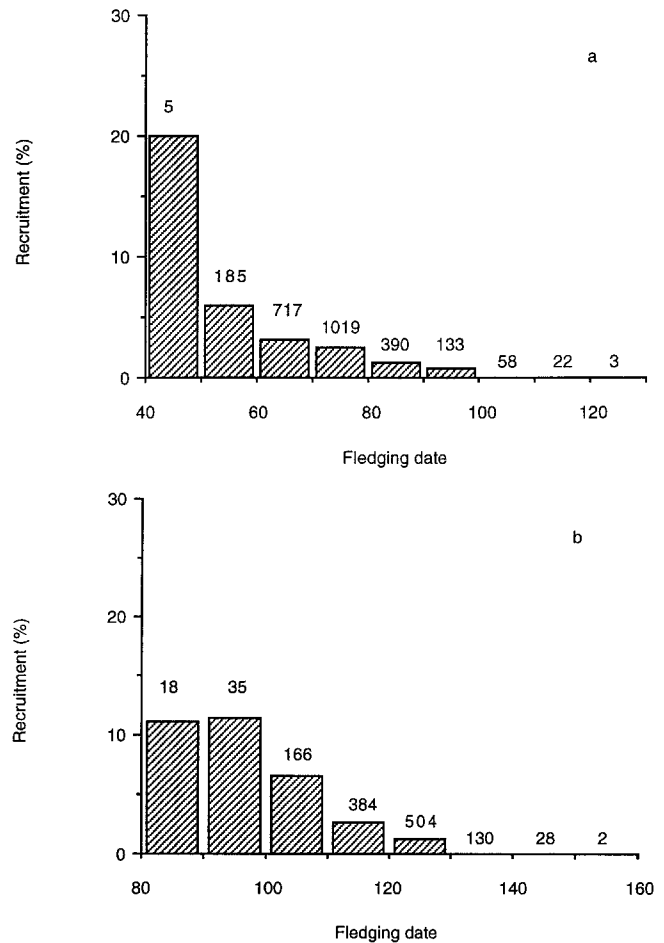
As the probability of raising two broods decreases during the breeding season, so do the conditions for successful reproduction. Nestling mortality, but not egg mortality of second clutches, increased as the season progressed (egg mortality: Kendall  $\tau = 0.04$ ,  $n = 473$  broods, NS; nestling mortality: Kendall  $\tau = 0.07$ ,  $n = 473$  broods,  $P < 0.01$ ). Statistically significant rela-



**Fig. 2** The relative frequency of second clutches (% of pairs having two clutches) in relation to start of laying of the first clutch for barn swallows during 1984–1992. Numbers are numbers of pairs

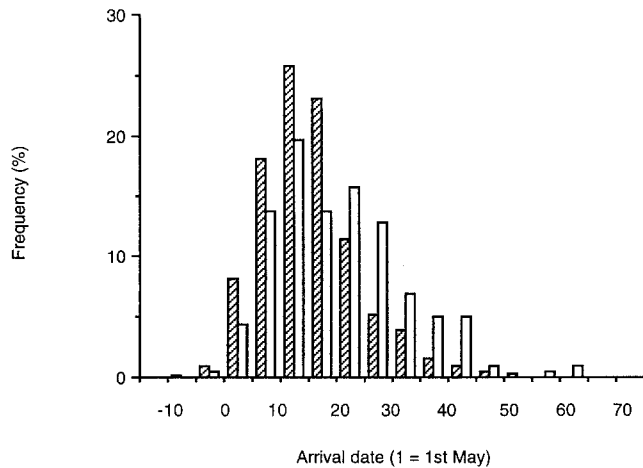
tionships were only found for nestling mortality in three of the years 1984–1992 ( $P < 0.05$ ). The decreasing seasonal favourability for reproduction is also reflected in the decreasing body mass and tarsus length of nestlings as the breeding season progresses (first brood: body mass:  $r = -0.33$ ,  $t = 4.89$ ,  $n = 198$  broods,  $P < 0.001$ ; tarsus length:  $r = -0.35$ ,  $t = 5.00$ ,  $n = 181$  broods,  $P < 0.001$ ; second brood: body mass:  $r = -0.29$ ,  $t = 2.62$ ,  $n = 77$  broods,  $P < 0.02$ ; tarsus length:  $r = -0.25$ ,  $t = 2.00$ ,  $n = 62$  broods,  $P < 0.05$ ). These effects still remained significant after controlling for male age (partial correlation analyses,  $P < 0.05$ ). Statistically significant results were also obtained in several cases when analyses were done for single years (partial correlation analyses controlling for male age; first brood: body mass: 8 of 9 years 1984–1992, sign test,  $P < 0.05$ ; tarsus length: 9 of 9 years, sign test,  $P < 0.05$ ; second brood: body mass: 4 of 9 years, sign test, NS; tarsus length: 2 of 9 years, sign test, NS). For a number of different bird species the probability of recruiting into the breeding population is known to be positively related to nestling body mass (Magrath 1991). Late fledglings had lower recruitment rates than early fledged barn swallow nestlings (Fig. 3; first brood: Kendall  $\tau = -0.96$ ,  $z = 3.59$ ,  $n = 9$  periods of 10 days,  $P < 0.001$ ; second brood: Kendall  $\tau = -0.87$ ,  $z = 3.01$ ,  $n = 8$  periods of 10 days,  $P < 0.001$ ). A partial correlation analysis revealed that this effect remained after controlling for nestling body mass (first brood: Kendall partial  $\tau = -0.78$ ,  $z = 2.94$ ,  $n = 9$  periods of 10 days,  $P < 0.01$ ; second brood: Kendall partial  $\tau = -0.76$ ,  $z = 2.65$ ,  $n = 8$  periods of 10 days,  $P < 0.01$ ). Significant negative relationships were also found when analyses were done for single years during 1984–1992 (first brood: 5 of 9 years; second brood: 4 of 9 years).

Early-arriving male barn swallows may acquire mates of the highest quality, while later arriving males



**Fig. 3** The probability of recruitment of barn swallow nestlings reared at different times of the breeding season for **a** first and **b** second broods during 1970–1992. Numbers are numbers of nestlings that fledged in a specific 10-day period. Dates are days since 30 April

have to mate with the remaining unmated females. If early-arriving males acquire mates of higher quality, their mates should be more likely to survive than mates of later-arriving males. There was a highly significant relationship between both male arrival date and male pairing date, respectively, and female survival prospects (male arrival date: Kendall  $\tau = 0.21$ ,  $n = 519$ ,  $P < 0.001$ ; male pairing date: Kendall  $\tau = -0.23$ ,  $n = 519$ ,  $P < 0.001$ ). This effect also remained after controlling for the effect of male tail length (male arrival date: Kendall partial  $\tau = -0.18$ ,  $n = 519$ ,  $P < 0.001$ ; male pairing date: Kendall partial  $\tau = -0.20$ ,  $n = 519$ ,  $P < 0.001$ ) and male age (male arrival date: Kendall partial  $\tau = -0.19$ ,  $n = 519$ ,  $P < 0.001$ ; male pairing date: Kendall partial  $\tau = -0.18$ ,  $n = 519$ ,  $P < 0.001$ ). Statistically significant results were also found when relationships were calculated for single years (male arrival date: 7 of 9 years 1984–1992, sign test,  $P < 0.05$ ; male pairing date: 8 of 9 years, sign test,  $P < 0.05$ ). It is therefore likely that early-arriving males consistently acquired mates of higher phenotypic quality.



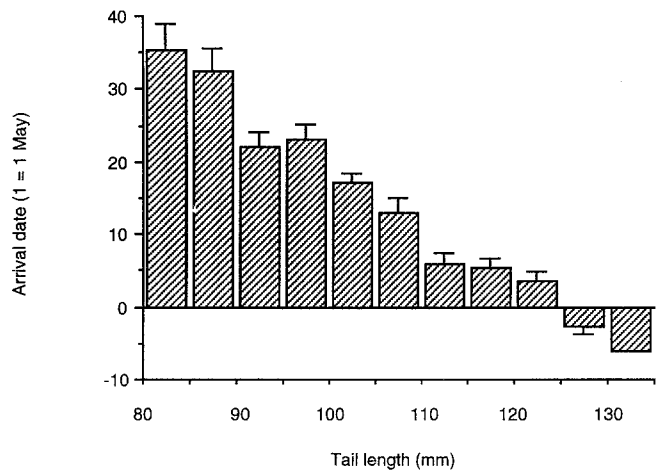
**Fig. 4** Arrival dates for male (shaded columns) and female (open columns) barn swallows during 1978–1992. Sample sizes are 697 and 211, respectively

Finally, early-arriving males may be able to acquire territories of superior quality because their choice is unconstrained by the choice of previously established males. The order of occupation of the same territory differed between years (Kendall  $\tau = -0.22$  to  $0.26$ ,  $n = 10$ –82 territories per year,  $n = 10$  pairs of years, all NS). This suggests that territory quality was not an important factor affecting the order of settlement by males.

#### Annual variation in arrival time

Barn swallows arrive during a prolonged period in spring (Fig. 4). Males arrive between 23 April and 2 July, on average 16 May (SE = 0.48,  $n = 697$ ), while females arrive slightly later, between 26 April and 1 July, on average 20 May (SE = 0.80,  $n = 211$ ). This sex difference in mean arrival date is highly significant ( $t$ -test based on  $\log_{10}$ -transformed data,  $t = 5.86$ ,  $df = 806$ ,  $P < 0.001$ ) and this is also the case when comparisons are made in single years (all years 1984–1992,  $P < 0.05$ ).

There is considerable annual variation in average male arrival date which may vary from 10 to 24 May. The annual variation in arrival date is large and highly significant (one-way ANOVA based on  $\log_{10}$ -transformed data:  $F = 11.21$ ,  $df = 14,786$ ,  $P < 0.001$ ). These annual differences in arrival may be due to environmental conditions in the winter quarters, during migration, or in the breeding areas. I analysed whether male spring arrival at the breeding grounds was related to precipitation in the African winter quarters, which is known to affect availability of swarming insects (e.g. Rudebeck 1957). The relationship between mean arrival date of male barn swallows and precipitation was statistically non-significant during the period 1984–1992 (mean precipitation in March:  $F = 0.43$ ,  $df = 1,7$ , NS, using annual means as data points). However, the variation in arrival date of males measured as the coefficient of variation was positively related to precipitation in the South



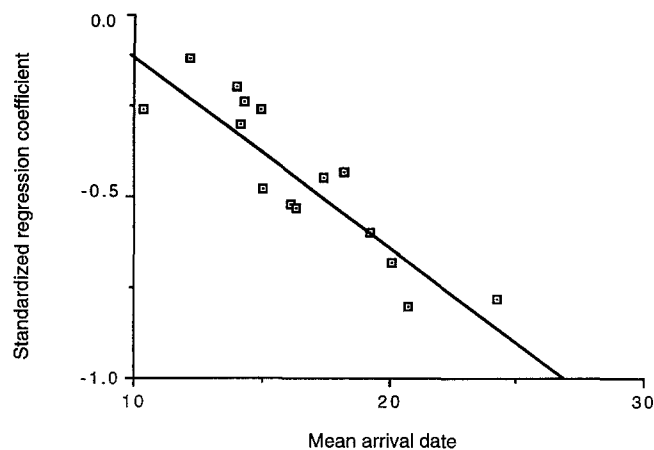
**Fig. 5** Arrival date of male barn swallows in relation to their tail length (mm) during 1984–1992. Values are means (SE),  $n = 697$

African winter quarters just before spring departure [mean precipitation in March:  $F = 5.15$ ,  $df = 1,7$ ,  $\beta$  (standardized regression coefficient) = 0.71,  $P < 0.05$ , using annual means as data points].

Weather conditions in the breeding areas could also affect the time of arrival if barn swallows, for example, could anticipate weather in the breeding areas. This could be the case if weather conditions were similar on a large geographical scale. Mean arrival date of male barn swallows at the breeding sites was negatively related to mean minimum temperatures in May during 1978–1992 ( $F = 5.50$ ,  $df = 1,13$ ,  $\beta = -0.56$ ,  $P = 0.04$ , using annual means as data points), while mean temperatures were unrelated to mean arrival date (linear regression:  $F = 2.62$ ,  $df = 1,13$ , NS, using annual means as data points).

#### Individual quality and early arrival

The game theory model predicts that high-quality individuals should arrive earlier than individuals of low quality (Parker and Courtney 1983), and arrival date of male barn swallows should thus be negatively related to their tail length, if male tail length is a reliable indicator of phenotypic quality. Early-arriving male barn swallows had longer tails than late-arriving males, with tail length accounting for 35% of the variance in arrival date (Fig. 5;  $F = 126.60$ ,  $df = 1,695$ ,  $P < 0.001$ ). Older males have slightly longer tails than young males (Møller 1991a), and the relationship between arrival date and tail length thus could be due to long-tailed males being older and therefore more experienced. Surprisingly, only tail length accounted for a significant proportion of the variation in arrival date [multiple linear regression:  $F = 67.24$ ,  $df = 2,694$ ,  $P < 0.001$ ,  $\beta$  (male tail length) =  $-0.63$ ,  $P < 0.001$ ,  $\beta$  (male age) = 0.006, NS]. Male barn swallows with long tails therefore arrived earlier than short-tailed males regardless of age.



**Fig. 6** Relationship between dependence of arrival date on male tail length (standardized regression coefficients) and mean arrival date of male barn swallows. Data points are for different years during 1978–1992. Dates are days since 30 April. The line is the model I regression line with the equation: standardized regression coefficient =  $0.42 - 0.05$  (SE = 0.007) mean arrival date

If environmental conditions differ among years, one should expect the relationship between male arrival date and tail length to differ relative to the net benefits of early arrival. Poor environmental conditions may differentially affect individuals of low phenotypic quality, and low-quality male barn swallows should therefore arrive later than high-quality males in years when good weather comes late. Both male tail length and year, and their interaction, affected male arrival date (ANCOVA:  $F = 16.02$ ,  $df = 15,217$ ,  $P < 0.001$ ; tail length:  $F = 55.69$ ,  $P < 0.001$ , year:  $F = 7.68$ ,  $P < 0.001$ , tail length  $\times$  year:  $F = 6.85$ ,  $P < 0.001$ ). The effect of tail length on arrival date was much stronger in years when males arrived late than in early years (Fig. 6; linear regression:  $F = 50.04$ ,  $df = 1,13$ ,  $P < 0.001$ ). Long-tailed males therefore arrived relatively earlier in years with poor environmental conditions.

## Discussion

### Cost and benefit functions of early arrival

There is relatively little information on the costs and benefits of early arrival by migratory birds despite an extensive literature on bird migration (reviews in e.g. Alerstam 1982; Berthold 1990). The major cost of early arrival for migratory birds breeding at high latitudes is obviously that adverse weather conditions may increase maintenance costs or in extreme situations even result in mortality. For example, many early-arriving males died during an unseasonably cold spell in 1987. There are many other examples of extreme weather conditions sometimes killing large numbers of barn swallows (Fischer 1869; Glutz von Blotzheim and Bauer 1985). The costs of early arrival can therefore sometimes be severe.

Male barn swallows acquire a number of benefits from an early arrival, and a detailed analysis revealed that most of these were of importance even when controlling for year and effects of male age. First, male mating success was clearly related to arrival date at the breeding grounds (Fig. 5). Analysis of the independent effects of male tail length and male arrival date suggests that both play a role in determining mating success [as suggested previously by Møller (1990)].

Second, the majority of barn swallows in my study population raise two broods per season, and the main determinant of annual reproductive success is the number of broods rather than the number of fledglings per brood (Møller 1990). The probability of raising two broods per season decreases rapidly as the season progresses (Fig. 2), and late-arriving barn swallows therefore appear to have a lower probability of becoming double-brooded.

Third, the environmental conditions for breeding in the barn swallow are mainly determined by access to abundant insect prey (Turner and Rose 1989). Flying insects are abundant between May and August in my study area, although conditions deteriorate at the end of the breeding season as revealed by increased nestling mortality. Second clutches are smaller than first clutches (Møller 1994), but offspring quality measured in terms of nestling mass and tarsus length decreased as the season progressed in both first and second clutches. This is important because the recruitment probability of fledgling birds is often determined by nestling body mass (Magrath 1991; in the barn swallow: Møller 1994). The local recruitment rate of barn swallow nestlings was indeed associated with nestling mass and time of fledging. Early-fledged offspring were more likely to recruit than late fledged offspring (Fig. 3). There were no recruits from first broods after day 100 (Fig. 3a), but many in second broods (Fig. 3b). This suggests that early-nesting birds are better at producing fledglings than late-nesting birds.

Fourth, early-arriving male barn swallows may experience a reproductive advantage by acquiring females of high phenotypic quality. Females of high quality may have access to preferred males, and/or high-quality females may invest differentially in the offspring of preferred males (Burley 1986). There is experimental evidence for both these effects in the barn swallow (Møller 1991b, 1994; de Lope and Møller 1993). I used female survival prospects as an indicator of the phenotypic quality of females. Female survival prospects were positively associated with early arrival of their mates, even after controlling for the potentially confounding effects of male tail length and male age. This is a very conservative test because the mates of early-arriving male barn swallows reproduce earlier, lay larger clutches, more often lay two clutches per season and for that reason reproduce at a higher rate than the mates of late-arriving male barn swallows. This suggests that early-arriving male barn swallows indeed acquired mates of high phenotypic quality.

The only resources in the territory of barn swallows are nest sites and perches used for roosting and copulations. Nest predation was only rarely recorded over the whole study period (Møller 1994), and safety from nest predators thus was an unimportant cue for males when choosing a territory. However, other properties of the territory could be important. If females were to employ territory quality as a cue in their mate choice, male barn swallows should use a similar cue when choosing territories. Territories of high quality in one year would also be predicted to be of high quality in subsequent years, since there were no obvious changes in their appearance (Møller 1990). There was no indication that a territory which was preferred and therefore occupied early in one year was also occupied early in subsequent years.

The timing of arrival by male barn swallows at the breeding grounds was affected by conditions both at the wintering and the breeding grounds. Food availability for barn swallows in the Southern African wintering grounds is positively affected by precipitation. Heavy rains immediately induce swarming behavior by Isoptera and Hymenoptera, and these are readily exploited as a food source by barn swallows (Rudebeck 1957; Turner and Rose 1989; own observations). Over-winter survival of my barn swallow population is positively related to precipitation during December–March in the winter quarters (Møller 1989a) as in other Palearctic migratory birds wintering in Africa (review in Baillie and Peach 1992). Heavy rains in South Africa in March just before the start of spring migration reduced the variance in male arrival. When precipitation is abundant and food therefore is readily available, most barn swallows may be in prime body condition and for that reason arrive more synchronously than during a very dry year.

There was also an effect of weather conditions at the breeding grounds on the time of arrival by male barn swallows. Spring arrival of migratory birds is often related to weather conditions at the breeding grounds (e.g., Alerstam 1982; Berthold 1990). The limiting factor for early arrival by male barn swallows appears to be low minimum temperatures in early spring. Low temperatures are likely to delay or depress population growth of insects exploited as food by barn swallows, and extremely low temperatures resulted in mortality among male barn swallows during at least one year. The negative correlation between mean date of male arrival and mean minimum temperatures may thus result in an increased probability of survival.

#### Arrival time and phenotypic quality

Observational and experimental evidence suggests that tail length of male barn swallows is a reliable indicator of phenotypic quality (Møller 1989a, 1991c, 1994). For example, long-tailed males are more likely to survive than short-tailed males, irrespective of the size of other morphological characters and age (Møller 1991c). It

may therefore not be surprising that the date of arrival at the breeding grounds for male barn swallows is strongly positively related to their tail length (Fig. 5). This result remained even after controlling for the potentially confounding effects of male age and year which surprisingly were relatively unimportant. This result is consistent with the model of Parker and Courtney (1983) of phenotype-dependent arrival time. Earlier studies of other bird species have also shown that early-arriving males have a mating advantage (Alatalo et al. 1984; Arvidsson and Neergaard 1991), and that males in bright plumage arrive earlier than others (Piersma and Jukema 1993).

Female barn swallows may obtain mates of high phenotypic or genotypic quality by mating with early-arriving individuals. There is considerable evidence in favour of a genetic benefit (Møller 1994). An unnoticed genetic benefit to choosy females arises from the fact that migratory behavior in birds has a genetic basis both with respect to direction and duration of migratory restlessness (e.g. Berthold and Querner 1981; Berthold 1990; Helbig 1991). Females that choose early-arriving males may thus produce offspring with an appropriate genetic setup for optimal migration. This mechanism also provides a solution to the problem of how genetic variance can be maintained despite strong directional sexual selection. Migratory behavior changes continuously in response to environmental changes, and such changes reflect genetic changes in the population (Berthold et al. 1992). Similar genetic benefits may be envisaged in other organisms that regularly move short or long distances, for example, between sites used for reproduction and wintering. A similar argument may be raised for optimal dispersal distance and direction.

Male barn swallows of high phenotypic quality may be able to develop a long tail ornament and also arrive early despite the increased energy costs of flight caused by the drag of long tail feathers. A large feather ornament directly increases the costs of flight by inducing drag (Balmford and Thomas 1992; Thomas 1993), and this results in increased difficulty in capturing agile insect prey (Møller 1989b; Møller and de Lope 1994). The length of the outermost tail feathers of adult barn swallows exceeds the aerodynamical optimum. The reason is that the outermost tail feathers extend beyond the aerodynamically functional triangular tail shape when the feathers are spread during manoeuvring (Thomas 1993). Tail length and arrival date may therefore both be reliable indicators of male quality (Zahavi 1975; Andersson 1986; Heywood 1989; Iwasa et al. 1991). Thus, it is not surprising that both early-arriving and long-tailed male barn swallows experience higher mating success than late-arriving and short-tailed males. A strong effect of male arrival date on mating success has also been reported in other species (e.g. Alatalo et al. 1984).

The relationship between male arrival date and tail length differed among years, and this could potentially be caused by differences in environmental conditions for survival. Early arrival is costly under adverse weather

conditions as determined by occasional mortality, and this mortality cost appears to be particularly high for male barn swallows of poor phenotypic quality (i.e. short-tailed individuals). Poor environmental conditions thus differentially affected individuals of low phenotypic quality, and low-quality male barn swallows should therefore arrive later than high-quality males in years when the spring is cold and favourable environmental conditions come late. The negative relationship between male phenotypic quality as measured by tail length and arrival date was thus more pronounced in cold springs with a late arrival of the barn swallow population (Fig. 6). This observation is consistent with the prediction of the model by Parker and Courtney (1983). Arrival time should depend on phenotypic quality because only individuals of high quality would have a high probability of survival under poor conditions.

In conclusion, male barn swallows with different tail lengths appeared to adjust their arrival at the breeding grounds to the conditions for survival. Short-tailed males arrived relatively later in years with adverse weather conditions for survival, and early arrival by short-tailed males in such years was indeed associated with an increased risk of mortality.

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