Heritability of arrival date in a migratory bird

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The behaviour of long-distance migratory birds is assumed to partly be under the influence of genes, as demonstrated by selection experiments. Furthermore, competition for early arrival among males may lead to condition-dependent migration associated with fitness benefits of early arrival achieved by individuals in prime condition. Here I present field data on the repeatability and the heritability of arrival date in a trans-equatorial migratory bird, the barn swallow *Hirundo rustica*, and I test for a genetic correlation between arrival date and the expression of a condition-dependent secondary sexual character. The repeatability was statistically significant and the heritability of arrival date was estimated to be 0.54 (s.e. = 0.15). There was no significant evidence of this estimate being inflated by environmental or maternal condition during rearing. Arrival date and migration are condition dependent in the barn swallow, with males with the most exaggerated secondary sexual characters also arriving the earliest. There was a significant genetic correlation between arrival date and tail length in male barn swallows, providing indirect evidence for a genetic basis of this condition dependence. Given the high level of heritability, arrival date could readily respond to selection caused by environmental change.

Keywords: barn swallow; climatic change; condition dependence; *Hirundo rustica*; migration; repeatability

1. INTRODUCTION

Bird migration has been hypothesized to evolve because of intraspecific competition leading to gradual increases in the distance moved between breeding and wintering locations (e.g. Salomonsen 1955; Von Haartman 1968; Alerstam & Enckell 1979; Alerstam & Högstedt 1982; Gauthreaux 1983; Alerstam 1991; Berthold 1996). Eventually, the maximum migration distance will represent a compromise between the fitness benefits and costs enjoyed by migrants relative to residents. The benefits of early arrival are assumed to derive from prior access to prime breeding habitat and access to females in prime condition (e.g. Salomonsen 1955; Von Haartman 1968; Alerstam & Enckell 1979; Alerstam & Högstedt 1982; Gauthreaux 1982; Alerstam 1991; Møller 1994a). However, the net benefits will depend on the costs of early arrival. For example, change in environmental conditions is assumed to affect the advantages of early arrival by migrants. Recent studies of birds and other organisms have suggested that timing of reproduction is associated with change in climatic conditions (e.g. Crick & Sparks 1997; Crick *et al.* 1999; Winkel & Hudde 1997; McCleery & Perrins 1998; Brown *et al.* 1999; Dunn & Winkler 1999). Studies of northern records of species of butterflies have indicated a close link between environmental conditions and range expansion (Parmesan *et al.* 1999). Such records of temporal changes in dates or sites of observation can be interpreted as evidence of an entirely phenotypic or a micro-evolutionary response to selection. Evidence from long-term selection experiments on birds suggest that migration (with components such as the timing, duration and peak of migratory restlessness) is genetically based (Berthold & Pulido 1994; Berthold & Querner 1981; see the review in Berthold 1999).

Long-distance migration is by definition costly in terms of time and energy, and individuals may differ in their ability to cope with such costs. Thus, migration may be condition dependent because certain individuals are better able to cope with the costs of migration. Møller (1994a) has shown with graphical models that migration can become condition dependent, with individuals in prime condition also being the first arrivals. This argument crucially relies on the assumption that early arrival is costly, and that males differ in their ability to sustain this cost. A series of formal models by Kokko (1999) has substantiated these conclusions and determined the conditions under which condition-dependent arrival will evolve. An empirical study on the barn swallow *Hirundo rustica* has shown that males arrive earlier than females, that males have more variable arrival dates than females, and that there is a strong relationship between arrival date and the expression of a secondary sexual character, the length of the outermost tail feathers (Møller 1994a). This study also demonstrated that there is significant viability selection against early arrival in years with adverse weather, since mainly males with short tails died during such a year (Møller 1994a). Arrival was later in years with low minimum temperatures in May, and the variance in male arrival date was influenced by weather conditions at the breeding grounds, with more variable arrival in relation to the tail length of males being recorded in cold springs (Møller 1994a). The extent to which this condition-dependent migratory pattern has a genetic basis remains to be determined.

The main aims of the present study were (i) to determine the additive genetic basis of arrival date in the migratory barn swallow; and (ii) to determine the genetic correlation between arrival date and tail length in male barn swallows. Such a positive correlation would be predicted if both arrival date and tail length are condition-dependent character under the influence of the same underlying condition factor. This was done using a long-term database with information on arrival date of fathers and their sons and information on additional phenotypic characters.

2. MATERIAL AND METHODS

The data were collected at Kraghede (57°12′ N, 10°00′ E), Denmark, in May to September 1984 to 1999. The study site consists of open farmland with scattered plantations, ponds and hedgerows. The main crops on dairy farms are grass, beets and wheat, while other farms that have abandoned dairy farming mainly have barley, wheat, potatoes, and rape. The total study area covered was originally $30\,km^{-2}$, but was increased in 1987 to $45\,km^{-2}$ to increase the population size as the population has been declining. A detailed description of the study site and its breeding population of barn swallows is given in Møller (1994b).

Barn swallows were captured at farms within the study area. Mark–recapture estimates have revealed that *ca.* 98% of all adults were captured during these events (A. P. Møller and T. Szép, unpublished results). Upon capture, each individual was measured and weighed using standard techniques. For the present study only tail length was used in the analyses. Tail length was defined as the mean length of the two outermost tail feathers. Only individuals with undamaged tail feathers were recorded, and tail damage could be unambiguously determined from broken barbs at the end of the rounded outermost feathers. Arrival date was recorded in years when adults were captured at least twice weekly from the start of the breeding season (1986–1999). Arrival date was defined as the date of the first capture. Each individual only appeared once in the data set. Hence, there was no pseudoreplication.

For the analyses of maternal and common enviroment effects I used information on reproductive events. Nests were visited at least weekly, and usually daily around the predicted time of laying, hatching and fledging. Laying date was defined as the date of laying of the first egg, assuming that one egg is laid daily, as is almost always the case. Clutch size was defined as the number of eggs in the clutch on the first day when clutch size had not increased. Brood size at fledging was the number of nestlings present in the nest at day 12, when nestlings were ringed. After fledging, the nest was visited the subsequent day, and the number of mites in the nest was scored by placing a hand for 10 s on the rim without movements and subsequently scoring the number of haematophagous mites *Ornithynussus bursa* as 0, 10, 100, 1000 or 10 000. This estimate is strongly positively correlated with the number of extracted mites from a sample of nests (Møller 1991a).

Barn swallows are extremely faithful to their nest site once chosen, and only three out of more than 2500 adults have ever moved to a new farm to breed, and then always the nearest neighbouring farm (Møller 1994b). The age of breeding females was estimated assuming that they were one year old in the year of first capture. This is a reliable estimate given the high probability of capture of adults and the high degree of breeding philopatry. There was no significant temporal change in arrival date ($r = 0.104$, $p = 0.30$).

Repeatability of arrival date of the same males in different years can be estimated from a one-way analysis of variance with male identity as a factor (Falconer & Mackay 1996). Natal dispersal is strongly female biased, and the sample of females was therefore very small. Hence, this analysis is based on only the 98 pairs of sons and their fathers. The heritability can be estimated by determining the relationship between the phenotypic character of the offspring and a single parent, since the heritability is twice the slope of this relationship (Falconer & Mackay 1996). This estimate of heritability will include the influence of common environment effects and maternal effects. Some of these can be controlled statistically by determining the relationship between the phenotypic character of interest and the environmental conditions experienced by the offspring (and the parent) during rearing. I determined the relationship between offspring arrival date and laying date for the first egg of the clutch from which the offspring hatched, the size of this clutch, the size of the brood, the age of the mother when rearing the offspring (since older mothers in the barn swallow show signs of senescence; Møller & de Lope 1999), and the intensity of infestation of the nest with the mite (this mite is known from observations and experiments to negatively impair the development, growth and survival of barn swallow offspring; Møller 1990a, 1994c).

The genetic correlation between arrival date and tail length was estimated from the correlation between arrival date in the offspring and tail length of the father, and tail length of the offspring and arrival date of the father (following Falconer & Mackay 1996).

3. RESULTS

The repeatability of arrival date of male barn swallows was high and statistically significant ($F = 6.12$, d.f. $= 22,97$, $p < 0.001$; $R = 0.51$). The heritability of arrival date in the barn swallow was statistically significant (figure 1; $F = 13.18$, d.f. $= 1,96$, $r^2 = 0.121$, $p = 0.0005$; slope (s.e.) $= 0.268$ (0.074)). The estimate of the heritability is twice the slope, which equals 0.536 (s.e. $= 0.148$).

There was little evidence of the arrival date of sons being influenced by condition during rearing. The correlation with laying date was very weak and non-significant ($r = 0.043$, $p = 0.73$). This was also the case for clutch size and brood size ($r = 0.030$, $p = 0.81$ and $r = 0.180$, $p = 0.15$, respectively). The mite load of the nest was not significantly correlated with subsequent arrival date of the sons ($r = 0.090$, $p = 0.49$). Finally, the age of the mother when rearing the son was not significantly correlated with the subsequent arrival date ($r = 0.048$, $p = 0.69$).

The genetic correlation between arrival date and tail length was statistically significant (figure 2; arrival of son: tail length of father, $r_A = 0.269$, $p = 0.0071$; arrival of father: tail length of son, $r_A = 0.281$, $p = 0.0051$). This gives an overall estimate of the genetic correlation of $r = 0.275$.

4. DISCUSSION

The main findings of the present study are that spring arrival date of the migratory barn swallow has a large, statistically significant heritability (figure 1). This estimate may be biased to some extent because a number of different factors are associated with early arrival, such as weather conditions, age and tail length. The effect of weather conditions on arrival should only tend to increase the variance in the data set and hence reduce the probability of finding a significant heritability. Furthermore, early arrival is phenotypically (Møller 1994a,b) and genetically correlated with the expression of a secondary sexual character (figure 2). Since the expression of the secondary sexual character in the barn swallow in particular (Møller 1990b, 1991a,b, 1993, 1994a,b), and in other organisms in general (Andersson 1994), is condition dependent, this provides indirect evidence for spring
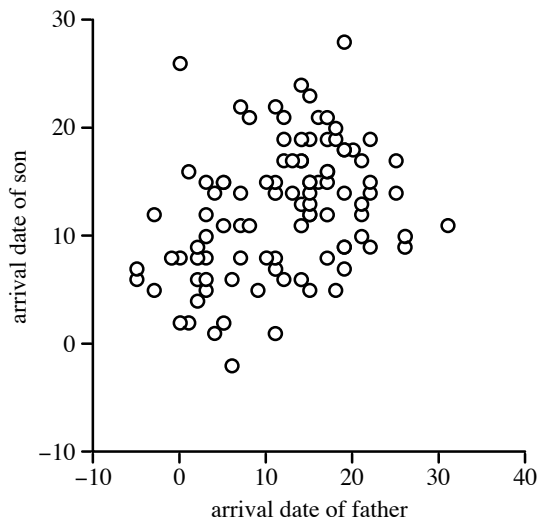
Figure 1. Arrival date of sons in relation to arrival date of their fathers in barn swallows. Date 1, 1 May; $n = 98$.
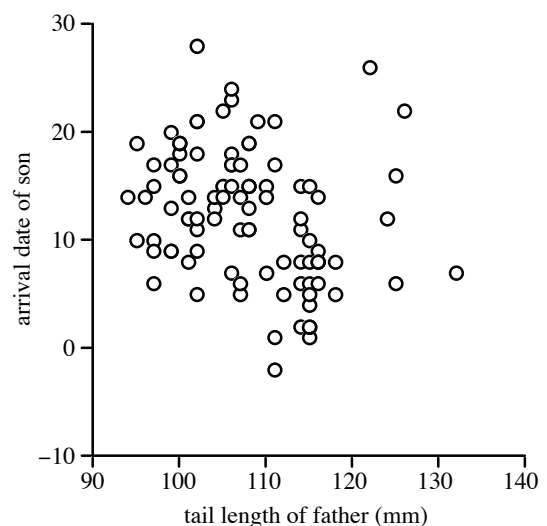

Figure 2. Arrival date of sons in relation to tail length (mm) of their fathers in barn swallows. Date 1, 1 May; $n = 98$.

arrival being condition dependent as well. Condition-dependent arrival has been predicted to evolve because the cost of early arrival depends on the phenotypc quality of the individual (Møller 1994b; Kokko 1999). I have previously shown that males with long tails are better able to survive adverse conditions during arrival than short-tailed males (Møller 1994a). This provides direct evidence for among-individual differences in the ability to cope with the costs of early arrival. Since early arrival is associated with a dramatic fitness benefit for the barn swallow, because of access to females in prime condition and a higher probability of rearing two broods in a given breeding season (Møller 1994a,b), and for other migratory bird species (e.g. Lundberg & Alatalo 1992; Lozano et al. 1996), there is consistent strong selection for early arrival among migratory birds. This selection pressure is the basis for the condition-dependent nature of competition for early arrival (Kokko 1999).

Quantitative genetic parameters can be seriously biased by common environment or maternal effects (Falconer & Mackay 1996; Mousseau & Fox 1998). In particular early maternal effects such as those experienced during early life stages can have dramatic effects on the expression of the phenotype (Falconer & Mackay 1996; Mousseau & Fox 1998). I investigated the relationship between arrival date and a number of different components of the rearing environment. However, there was no significant evidence of common environment or maternal effects due to clutch or brood size, breeding date, maternal age and parasite load of the nest. Since maternal age is correlated with tail length and intensity of infestation of nests with haematophagous mites (Møller & de Lope 1999), we can conclude that maternal effects are weak or absent despite these negative effects on maternal phenotype. Similarly, previous studies have indicated that the abundance of the haematophagous mite directly affects the expression of the secondary sexual character in male barn swallows (Møller 1990b, 1991a). Again, there was no evidence of an effect of mites on arrival date in the present sample of barn swallows.

The estimates of quantitative genetic parameters presented here will be biased if extra-pair paternity is common. Extra-pair paternity in the barn swallow has been shown to be around 30% in several independent studies (Saino et al. 1997; Møller & Tegelström 1997; Møller et al. 1998). Such high levels of extra-pair paternity will cause a downward bias in heritabilities and genetic correlations because foster fathers and their extra-pair offspring will resemble each other less than fathers and their offspring. This has been demonstrated in analyses of heritability of a range of phenotypic characters based on all parents and their presumed offspring and heritability of the same characters after excluding extra-pair offspring (N. Saino, M. Martinelli and A. P. Møller, unpublished results). Hence, we can expect the estimates reported here to be underestimates of the true heritability.

Recent studies have indicated that the mean spring temperature has increased significantly in the northern temperate zone during the past century, with particularly dramatic changes in recent decades (e.g. Easterling et al. 1997). This increase in spring temperature should reduce the cost of early arrival by migratory birds. Hence, we can predict a gradual change towards early spring arrival. Consistent with this prediction, recent observations of breeding date of several birds have shown earlier start of reproduction in recent years (Crick & Sparks 1997; Crick et al. 1999; Winkel & Hudde 1997; McCleery & Perrins 1998; Brown et al. 1999; Dunn & Winkler 1999). Similarly, northernmost observations of thermophilic butterflies have been recorded consistently further towards the north in recent years (Parmesan et al. 1999). Whether spring observations of migratory birds also have become earlier as the spring temperature has increased in temperate Europe remains to be determined. Given that the heritability of arrival date in the barn swallow is high, we can predict a strong response to selection due to climatic change. Such rapid changes in migratory performance have been documented for the blackcap *Sylvia atricapilla* (Berthold et al. 1992; Berthold 1999). Thus, we can expect that changes in migration behaviour across generations will reflect microevolutionary changes rather than phenotypic responses to increased temperatures.

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