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PARASITISM, IMMUNITY, AND ARRIVAL DATE IN A MIGRATORY BIRD, THE BARN SWALLOW

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Abstract. Long-distance bird migration is expensive, and individuals in prime condition are therefore expected to arrive at the breeding grounds earlier than the average individual in the population. We tested whether arrival date during spring migration was associated with low parasite burden and strong T-cell-dependent immune response in populations of the transequatorially migrating Barn Swallow *Hirundo rustica* from Denmark, Italy, and Spain. Male Barn Swallows with heavy infestations of the chewing louse *Hirundoecus malleus* L. arrived later than other males, whereas that was not the case for females. This negative relationship remained after controlling the relationship between parasite load and arrival for tail length. Infection with blood parasites of the species *Haemoproteus prognei* was associated with delayed arrival in the Spanish population, which was the only one with a high prevalence of blood parasites. High intensities of infestation with a commensal feather mite were associated with early arrival by females, but also by males when the independent relationship between tail length and intensity of mite infestation was controlled statistically. Experimental manipulation of nest infestation with the hematophagous mite *Ornithonyssus bursa* Berlese affected the arrival date of adult males, but not of females in the following year, with arrival date being inversely related to the experimental mite population size. Males with strong T-cell responses arrived earlier than males with weak responses, independent of their tail length in two of three populations, but there was no significant relationship in females. These findings are in accordance with predictions based on the hypothesis that bird migration is dependent on condition, with individuals in prime condition arriving early.

Key words: arrival date; Barn Swallow; chewing lice; feather mites; *Hirundo rustica*; immunity; migration; mites; parasitism; sex differences; tail length; T-cell response.

INTRODUCTION

Long-distance bird migration may cover distances of >10 000 km between breeding and wintering sites, and it is therefore costly (Alerstam 1991, Berthold 1996). Many insects, fish, and mammals perform equally extensive annual migrations (Baker 1978). Although fall migration often proceeds slowly, spring migration is usually rapid (Alerstam 1991, Berthold 1996). Early-arriving individuals usually gain access to superior territories, breeding sites, and mates, thereby having much greater reproductive success than the average individual (Møller 1994a, b, Kokko 1999). These benefits are generally greater for males, which usually arrive at the breeding grounds before females (reviews in Alerstam 1991, Berthold 1996).

Competition among individuals, particularly among males, for early arrival at the breeding grounds as reflected by individual differences in cost and benefit functions, sets the scene for the evolution of condition-

dependent migration (Møller 1994a, b, Kokko 1999, Forstmeier 2002). Theory suggests that competition for early arrival will give rise to condition dependence of arrival date (Møller 1994a, b, Kokko 1999). Certain individuals may have superior condition both before and after migration simply because they have more resources available for genetic or environmental reasons. Empirical studies have suggested that males in superior condition indeed arrive earlier than the average male (Radesäter et al. 1987, Piersma and Jukema 1993, Møller 1994a, b, 2001, Piersma et al. 2001). Such males experience a lower probability of mortality due to early arrival than the average male (Møller 1994b). The relationship between male condition and arrival is more pronounced in years when environmental conditions are poor (Møller 1994a, b).

Five different hypotheses may account for optimal bird migration: (1) energy minimization, (2) time minimization, (3) reduction in the risk of predation, (4) minimizing the risk of DNA damage due to free radicals, and (5) minimizing the risk of parasitism (Alerstam and Lindström 1990, Alerstam 1991, Berthold 1996, Alerstam and Hedenström 1998, Jenni and Jenni-Eiermann 1998). The last two hypotheses are novel and

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need some explanation. First, physical activity results in the production of free radicals that can cause temporary or permanent damage to proteins including DNA (Leffler 1993, Ahmad 1995). Free radicals are atoms or molecules with unpaired electrons that arise as by-products of normal metabolism and rapid cell proliferation during immune function, and they may bond with electrons and thereby damage other molecules. If free radicals are not under control, changes in membrane properties (fluidity, flexibility) and functions (intracellular signaling, enzymatic activities) arising through oxidative stress can result in immune system incompetence (Chew 1996). Oxidative stress can arise from inadequate diet-derived antioxidant availability, lack of dietary proteins and inadequate synthesis of metal-binding proteins, excess production of free radicals as a result of toxic compound metabolism, and excessive activation of natural radical-producing systems such as phagocytes in inflammation (Halliwell 1996). These detrimental effects of free radicals can be eliminated through the actions of carotenoids, vitamin A, and vitamin E (Surai 1999, Møller et al. 2000). The fifth hypothesis is that bird migration has evolved to minimize the risks of parasitism. That would be the case if choice of migration routes and wintering sites were to minimize the probability of individuals getting into contact with novel parasites. Antioxidants play an important role in the immune response to parasite infections (Chew 1996, Surai 1999, Møller et al. 2000), and we hypothesize that the common physiological mechanism underlying early arrival and low levels of parasite infection is based on availability, absorption, or efficient metabolism of antioxidants.

Parasitism has been hypothesized to be associated with bird migration because migratory birds may encounter more different parasite faunas than closely related resident species with a similar ecology (Møller and Erritzøe 1998). Therefore, we can predict that migrants have evolved mechanisms to cope with a greater diversity of parasites than resident species. For example, Møller and Erritzøe (1998) found that migrants had significantly larger immune defense organs than closely related residents. Both the bursa of Fabricius and the spleen are critical for different aspects of immune function, and both were enlarged in migratory species compared to residents. Subsequently, Møller and Erritzøe (2001) showed that the timing of regression of the bursa of Fabricius occurred well before the start of breeding, but after exposure to parasites in all parts of the annual range. This allows development of a range of antibodies reflected by the antigens encountered in the breeding area, during migration and in the winter range. This timing of regression may also account for a high degree of site fidelity during these different periods of the year, because immune responses produced during these first encounter subsequently may be stored as memory cells in case of later encounters (Møller and Erritzøe 2001).

The exact mechanisms linking immune function to bird migration may be of several different kinds. Birds in better condition may be arriving early because of their superior body condition or, alternatively, because they have strong immune responses and hence are of superior health status. Immune function has been shown to be strongly condition dependent in numerous studies of wild and domesticated animals including birds (reviews in Chandra and Newberne 1977, Gershwin et al. 1985, Møller et al. 1998). Because it is impossible to be sick and simultaneously do extensive physically strenuous work, we suggest that the link between arrival date for long-distance migrants and immunity arises because individuals with strong immune systems are healthy. However, we are unaware of any empirical studies addressing whether intensity of immune function is associated with arrival date or other measures of migratory performance. Likewise, we are aware of only four studies linking migratory performance to levels of parasitism of individual hosts. These were all based on investigations of a single parasite, and they showed weak or no significant relationships with arrival date (Davidar and Morton 1993, Piersma and Jukema 1993, Rätti et al. 1993, Piersma et al. 2001).

The aims of this study were to determine the relationship between spring arrival date and, respectively, parasitism and immune function. First, we determined the relationship between arrival date and levels of infestation with ectoparasites in adult male and female Barn Swallows (*Hirundo rustica*). Tail length is a condition-dependent secondary sexual character in male Barn Swallows, reflecting their level of parasitism and the strength of their immune system (Møller 1990a, b, c, 1991, 1994a, Saino and Møller 1996, Saino et al. 1997a, Kose et al. 1999, Kose and Møller 1999). However, early arrival may be an additional condition-dependent secondary sexual character under current sexual selection (Møller 1994a). Hence, we predicted that certain males in superior condition would arrive early, independent of their tail length, giving rise to a positive relationship between arrival date and parasitism. Females do not show a similar relationship between tail length, parasitism, and immune response (Møller 1990, 1991, 1994a, Kose and Møller 1998, Kose et al. 1999; N. Saino and A. P. Møller, unpublished data), suggesting that females show less condition dependence of tail length and arrival date than males. Therefore, we did not expect a similar relationship between arrival and parasitism in the two sexes because of differences in underlying condition dependence and intensity of sexual selection. Second, we investigated the relationship between arrival date and the magnitude of a T-cell-mediated response to a challenge of the immune system with a novel mitogen. Here, we predicted a negative relationship between arrival date and immune response because a strong immune response should reflect superior health status. Only individuals in prime

condition were expected to be able to produce a strong response to a challenge with a novel mitogen. Again, females were expected to differ from males because the benefits of early arrival are greater for males than for females. Hence, past selection has resulted in stronger condition dependence of migratory ability in males than in females. We determined these relationships for three populations from Denmark, Italy, and Spain. Third, we determined the direct effect of a hematophagous ectoparasite on arrival date of Barn Swallows by experimentally manipulating nest contents of mites in one year and recording the arrival date of adults associated with these nests in the subsequent year.

The Barn Swallow is an aerially foraging passerine (~20 g) that breeds in temperate and subtropical regions of the northern hemisphere, with European populations wintering south of the Sahara (Møller 1994a). Males and females are morphologically very similar with the exception of the outermost tail feathers, which are considerably longer in males than in females; such elongated tails are associated with a mating advantage (review in Møller 1994a). Males arrive, on average, four days earlier than females, and males show significantly greater variance in arrival date than females (Møller 1994a, b). Males and females with long tails arrive early at the breeding grounds, particularly in years with poor environmental conditions (Møller 1994a, b). In addition, very early arrival is associated with a mortality cost due to bad weather, and this cost is particularly severe for short-tailed males. Senescence is associated with a shortening of tail length, an increase in the abundance of two species of ectoparasites, and a delay in arrival date (Møller and de Lope 1999). Male Barn Swallows with long tails have been shown to have fewer hematophagous mites and feather lice than females (Møller 1990b, 1991, 1994a). In addition, they also have stronger immune responses than males with long tails (Saino et al. 1996, 1997a, 2002), whereas these relationships are absent from females (Møller 1990b, 1991, 1994a, Saino et al. 1997a, 2002; A. P. Møller, F. de Lope, and N. Saino, *unpublished data*).

Chewing lice of the species *Hirundoecus malleus* L. are directly transmitted ectoparasites commonly found on feathers of Barn Swallows (Møller 1991, Kose et al. 1999, Kose and Møller 1999). Although the lice are directly transmitted, individual swallows have highly repeatable infestation levels among years. Genetic offspring resemble the attending male swallow at a nest with respect to parasite load, whereas that is not the case for extrapair offspring (Møller et al., *in press b*). Thus, there are environmental and genetic bases of infestation with this parasite. The commensal feather mite (Astigmata) of an as yet unidentified species is another common, directly transmitted ectoparasite. We have no information on the environmental and genetic determinants of its abundance. None of the ectoparasites is a vector for the blood parasite *Haemoproteus prognei*, which is probably transmitted by a simuliid fly

or a hippoboscid fly. The tropical fowl mite *Ornithonyssus bursa* occurs commonly in Barn Swallow nests. Cross-fostering experiments have shown that infestation levels are partly genetically determined (Møller 1990b). The abundance of all these parasites does not differ significantly between males and females (Møller 1990b, 1991, Kose et al. 1999, Kose and Møller 1999; A. P. Møller, F. de Lope, and N. Saino, *unpublished data*). The T-cell-mediated immune response was estimated using a challenge with a mitogen. This is a standard estimate from poultry studies of the ability to produce a T-cell-mediated immune response (Goto et al. 1978, McCorkle et al. 1980, Parmentier et al. 1993, Dietert et al. 1996). Previous studies of the Barn Swallow have indicated that both environmental and genetic factors contribute to the magnitude of the response (Saino et al. 1997b).

METHODS

Study sites

We have studied Barn Swallows at Badajoz (38°50' N, 6°59' W), southern Spain (since 1976), Milano (45°28' N, 9°10' E), northern Italy (since 1993), and Kraghede (57°12' N, 10°00' E), Denmark (since 1970), 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. The study site at Milano consists of open farmland with pastures, cereals, and hedges; Barn Swallows are mainly restricted to dairy farms, where they breed inside buildings. The study site at Kraghede consists of open farmland with pastures, cereals, potatoes, and rape with mixed plantations, hedges, and ponds; Barn Swallows breed within barns and other buildings. The present study is based on data from 1986 to 1999 from Denmark, 1999 from Italy, and from 1997 to 1998 from Spain.

Capture and banding of birds

Barn Swallows were captured at least weekly, from their arrival in early spring until the end of the breeding season, using mist nets at all entrances to the barns with breeding birds. We terminated capture on a given day when the building did not hold any more Barn Swallows, ensuring that daily capture probability was 100%. Mark-recapture analyses of the data revealed an annual capture probability >97% in Spain and Denmark (Møller and Szép 2002; F. de Lope, A. P. Møller, and T. Szép, *unpublished data*). The capture probability in Milano was presumably equally high, based on the absence of birds without individually numbered aluminum bands at the end of the breeding season (N. Saino, *unpublished data*). The birds that were not captured in a given year were not present in the study area, according to our extensive observations of color-banded birds.

Upon capture, all adults were measured for a large number of phenotypic characters, recorded in a similar,

standardized way in all three populations. In the present study, we only used the mean length of the right and the left outermost tail feathers, measured with a ruler to the nearest millimeter. We measured both left and right characters to calculate asymmetry for other studies. Repeated measurements of the same individuals in the same season revealed that tail length had repeatabilities >94% (Møller 1991, 1994a; A. P. Møller, F. de Lope, and N. Saino, *unpublished data*). Hence, tail length was measured in a highly consistent way.

All birds from Denmark were only included in the data set in the year when they were first captured to avoid any problems of pseudoreplication. Among 165 local recruits from the Danish population, all were captured in their first year of life. Because only three out of >3000 adults were ever recorded breeding in a farm different from that where they were first banded as adults (and then in the nearest neighboring farm), we can safely assume that a Barn Swallow when first captured is one year old. Therefore, we did not control for an effect of age in the Danish sample because all birds were one year old. Birds from Italy and Spain were assigned an age of one year when captured the first time, and age of birds included in the samples analyzed was the number of years since first capture.

Estimating arrival date

Arrival date was recorded in Denmark in 1984–1992 and in 2000, in Italy in 1999, and in Spain in 1997–1998, when adults were captured at least twice weekly from the start of the breeding season. Arrival date was defined as the date of the first capture, although this will provide an underestimate of the true arrival date. It is possible that Barn Swallows may arrive at the breeding areas without entering the actual breeding sites. However, this seems unlikely, given intense competition for breeding territories and females. Although 9.4% of all males remain unmated (A. P. Møller, *unpublished data*), such males are present in breeding colonies, where they establish a breeding territory and attempt to attract a mate (Møller 1988b). Thus, even nonbreeders are present in breeding colonies from early spring until the end of the breeding season (Møller 1994a). The precision of this estimate was assessed based on data from the Danish population in 1985–1990. Barn Swallows spend the night within their small breeding territory, and males sit next to their partner, if mated, during the first couple of hours in the early morning and late in the evening (A. P. Møller, *personal observations*). During the six years of the study, adult Barn Swallows were watched daily for one hour from sunrise, and the identity of all color-banded individuals was recorded with binoculars. The first observation of each individual in the season provided an estimate of the date of arrival. In addition, mist net captures as previously described provided a second estimate of arrival date for each individual. The Pearson correlation coefficient between these two estimates of arrival date

for each year separately was 0.982–0.997, $N = 10\text{--}46$, $P < 0.01$ for males, and 0.983–0.998, $N = 5\text{--}44$, $P < 0.01$ for females. A paired t test revealed no significant differences between the two estimates for any year or sex (for males, $t < 1.23$, $P > 0.22$; for females, $t < 0.28$, $P > 0.53$). Thus, our estimates based on first capture provide reliable estimates of arrival date for both males and females. The repeatability of arrival date of male Barn Swallows among years was statistically highly significant in the Danish sample ($F = 6.12$, $df = 22, 97$, $P < 0.001$; $R = 0.51$; see Møller 2001), despite the fact that young males arrive later than males of intermediate age (Møller and de Lope 1999).

Estimating parasite abundance

We determined the distribution of chewing lice of the species *Hirundoecus malleus* L. from the number of small holes that this species chews in feathers of Barn Swallows (Møller 1991, Kose et al. 1999, Kose and Møller 1999). Previous studies using extraction of live chewing lice and counts of holes in feathers showed a strongly positive correlation between the two estimates of the abundance of lice (Møller 1991). We counted the number of holes in the outermost tail feathers upon first capture, shortly after arrival at the breeding grounds.

We estimated the number of commensal feather mites (Astigmata) of an as yet unidentified species in swallow tail and wing feathers by counting the number of dark spots between barbules of the feathers. The number was counted if there were <20 individuals, and was scored to the nearest multiple of 10 for larger numbers. This estimate of the abundance of feather mites is highly repeatable, as determined from independent estimates for individuals captured on two consecutive days (for repeatability, $F = 274.64$, $df = 52, 53$, $P < 0.001$; $R = 0.99$).

A drop of blood was smeared on a glass slide and air dried to record blood parasites. Blood smears were fixed with ethanol and stained with Giemsa (1/10 volume/volume) for 40 min. Using oil immersion (1000 \times magnification), samples were scanned in search of blood parasites, following the method described in Merino et al. (1997). The abundance of blood parasites was expressed as the number of parasites per 10 000 erythrocytes. This provided a highly repeatable estimate of the abundance of blood parasites.

Ornithonyssus bursa mite loads of nests were experimentally manipulated by randomly assigning nests to one of three treatments during the laying of the first clutch in Denmark in 1988: (1) the eggs were removed and an inoculate of ~50 mites obtained from old Barn Swallow nests was added, and the eggs were replaced in the nest (hereafter mite addition treatment); (2) the eggs were removed and put back again (hereafter control treatment); or (3) the eggs were temporarily removed, the nest was sprayed with a 0.47% pyrethrin

solution (hereafter spray treatment), and the eggs were then put back into the nest. This last treatment has been shown to significantly alter the abundance of mites in active Barn Swallow nests. Adult Barn Swallows were captured in 1988 and handled as previously described, and were recaptured in 1989. Mite loads of adults upon arrival were only estimated in the first year. See Møller (1990a) for further details.

Assessment of T-cell response

T-cell-mediated immune response to a challenge with phytohemagglutinin was used as a measure of one important component of immune function. This is a standard estimate from the poultry literature of the ability to produce a T-cell-mediated immune response (Goto et al. 1978, McCorkle et al. 1980, Parmentier et al. 1993, Dietert et al. 1996). Injection with phytohemagglutinin results in local activation and mitogenic proliferation of T-cells, followed by local recruitment of inflammatory cells and major histocompatibility complex molecules (Goto et al. 1978, Abbas et al. 1994, Parmentier et al. 1998). Adult Barn Swallows were injected with 0.2 mg phytohemagglutinin in 0.05 mL physiological water in one wing web, and with 0.05 mL of physiological water in the other wing web at pre-marked sites indicated by a mark with a waterproof pen. This was done upon capture just after arrival in spring 1998 in a single colony in the Danish population. Because all individuals were living in the same site, this test controlled for any effects of heterogeneity in habitat quality accounting for differences in immune response. In the Italian sample, only males involved in a brood size manipulation experiment in 1999 were injected and therefore included in the present study. These latter males had their brood size either randomly increased or decreased by one nestling at the beginning of the nestling period, using a protocol that ensured that the proportion of nestlings staying in their own nests was the same across treatments (for details, see Saino et al. 1997b). Adults were captured at arrival in 1997–1998 in Spain and tested for response to phytohemagglutinin. The dose of phytohemagglutinin used here is similar to that used in numerous other studies of free-living or captive birds (e.g., Lochmiller et al. 1993, Saino et al. 1997b, Christe et al. 1998, Brinkhof et al. 1999, Merino et al. 2000). We measured the thickness of the patagium injected with phytohemagglutinin and with physiological water before injection and after 12 h (Denmark) or 24 h (Italy, Spain), using a pressure-sensitive caliper with an accuracy of 0.01 mm. Although estimates of T-cell-mediated immune response traditionally have been recorded 24 h after injection, we measured responses after 3, 6, 12, 24, 36, 48, and 72 h in a study of captive House Sparrows *Passer domesticus* (Navarro et al. 2003). We found no significant increase in swelling after 6 h, and the responses at different times post-injection were strongly positively correlated with each other (Navarro et al. 2003). A

similar finding has been reported for chickens (Goto et al. 1978). This justifies the use of T-cell response estimates at 12 h post-injection. The measure of T-cell response has a very high repeatability, as shown by three independent measurements of both wing webs (first measuring the right wing web, then the left wing web, then the right again, etc.; A. P. Møller, *unpublished data*). In the subsequent analyses, we used the increase in the thickness of the wing injected with phytohemagglutinin minus the increase in the thickness of the wing injected with physiological water as a measure of the intensity of the phytohemagglutinin-induced T-cell mediated immune response.

Estimating reproductive success

At least once per week, we systematically searched all buildings for nests and recorded the contents. Nests were visited daily during start of laying and the presumed date of hatching (~14 days after laying ceased). We recorded reproductive success as the total number of fledglings produced by each adult during the 1–3 broods per year. Adults were assigned to nests during regular observation sessions with binoculars while looking for color bands and individual patterns of color markings on the breast feathers. Some of the birds in the Italian samples, after capture, assessment of parasites, and estimation of T-cell response, were assigned to experiments that were predicted to affect their reproductive success. Hence, in the analyses of the relationship between arrival date and reproductive success, sample size for the Italian samples was less than for the analyses of parasites and immune response.

Statistical analyses

Each individual only appeared once in the data set. We analyzed the relationship between arrival date, as a measure of migratory performance, and parasitism and immune response, using the abundance of parasites and T-cell response as independent variables in linear regression analyses. The effects of differences in relationships among years were determined using year as a factor in analyses of covariance (ANCOVA). Condition dependence of tail length could indirectly affect arrival date, and we therefore controlled statistically for the independent effect of any such condition dependence by using tail length as a covariate in ANCOVAs.

We investigated the stability of our conclusions by repeating the analyses using Kendall nonparametric correlation analyses and partial correlation analyses. None of the results changed as a consequence of this procedure, showing that the conclusions were robust to the effects of any outliers.

All tests are two-tailed with a significance level of 5%. The significance of the reported effects did not change after sequential Bonferroni correction to assess the tablewide Type I error rate by adjusting the significance level downward in relation to the number of

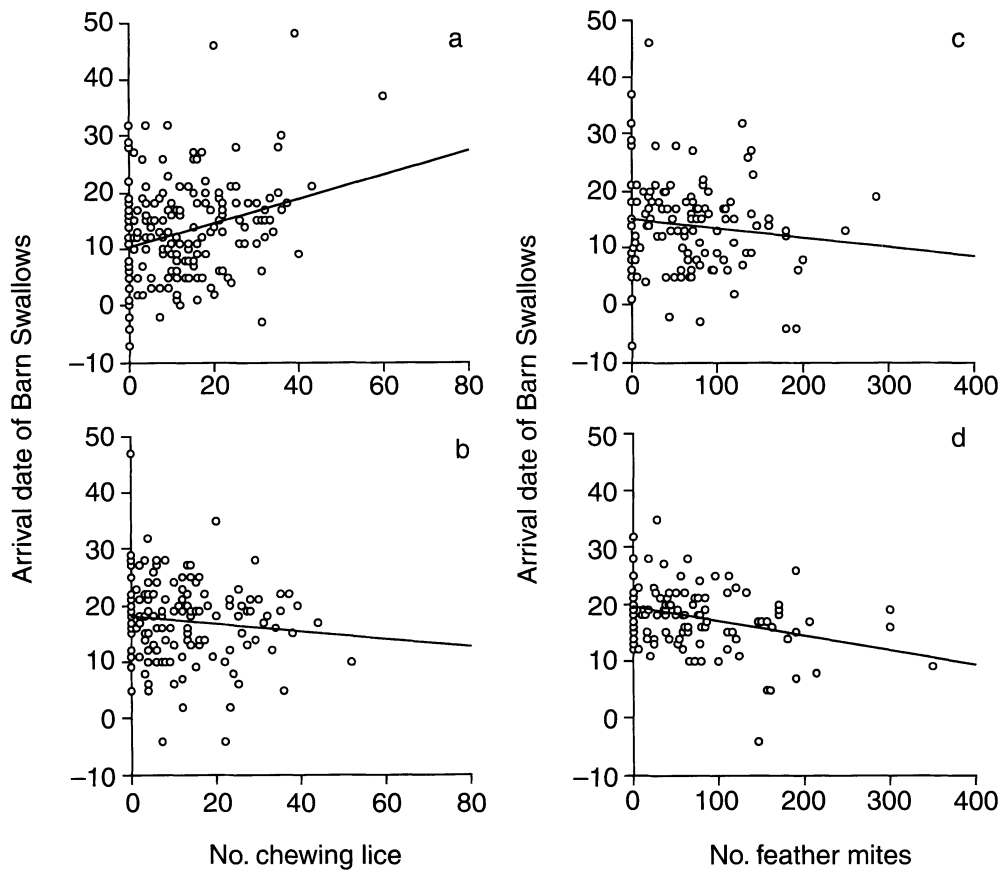


FIG. 1. Arrival date (day 1 = 1 May) of Danish Barn Swallows in relation to parasitism by feather lice in (a) males and (b) females, and by feather mites in (c) males and (d) females. The lines are linear regressions; equations are: (a) $Y = 10.33$ ($SE = 0.89$) + $0.22X$ ($SE = 0.05$); (b) $Y = 18.19$ ($SE = 0.78$) - $0.07X$ ($SE = 0.05$); (c) $Y = 14.998$ ($SE = 1.195$) + $0.016X$ ($SE = 0.013$); and (d) $Y = 19.684$ ($SE = 0.730$) - $0.026X$ ($SE = 0.007$).

tests made (Holm 1979, Wright 1992). Strict application of this method severely reduces the power of tests (Wright 1992), but such sacrificial loss of power can be avoided by choosing an experiment-wise error rate higher than the usually accepted 5%. We used 10%, as suggested by Wright (1992) and Chandler (1995). Values reported are means \pm 1 SE.

RESULTS

Arrival date and parasitism

Danish male Barn Swallows with more chewing lice arrived later than the average male in the population (Fig. 1a, Table 1). However, that was not the case for adult females from the same population (Fig. 1b, Table 1). The number of feather mites was not significantly related to arrival date in male Barn Swallows (Fig. 1c, Table 1). For females, there was a significantly negative relationship, implying that females with many mites arrived early (Fig. 1d, Table 1). In these samples, arrival date was strongly negatively related to the number of fledglings produced per year (after controlling for year and tail length) in males (partial regression, $F =$

7.851 , $df = 1$, 184 , $P = 0.0056$, slope = -0.099) and in females (partial regression, $F = 6.791$, $df = 1$, 149 , $P = 0.010$, slope = -0.101).

In the Italian sample, males with more chewing lice arrived later than other males (Table 1). There was no significant relationship in females (Table 1). For feather mites, males with more parasites arrived earlier than males with few mites (Table 1). That was also the case in female Barn Swallows (Table 1). In these samples, arrival date was strongly negatively related to the number of fledglings produced per year in males ($F = 9.066$, $df = 1$, 56 , $P = 0.004$, slope = -0.052) and in females after controlling for tail length ($F = 10.511$, $df = 1$, 60 , $P = 0.002$, slope = -0.049).

In the Spanish sample, chewing lice infestation was significantly associated with delayed arrival in males, but not in females (Table 1). In total, 26.3% of Barn Swallows from Spain ($N = 76$ birds) were infected with blood parasites of the species *Haemoproteus prognei*, whereas prevalence was $<2\%$ in the Danish and Italian samples (see also Møller 1994a). Therefore, only the Spanish sample was used to analyze the relationship

TABLE 1. Linear regressions with arrival date as the dependent variable and parasite load and T-cell response as independent variables.

Variable	<i>F</i>	df	<i>r</i> ²	<i>P</i>	Slope (1 SE)
Denmark					
Chewing lice in males	16.24	1, 190	0.079	<0.001	0.215 (0.053)
Chewing lice in females	1.97	1, 159	0.006	0.162	
Feather mites in males	1.57	1, 117	0.005	0.213	
Feather mites in females	12.33	1, 112	0.091	0.0006	-0.026 (0.007)
T-cell response in males	24.21	1, 13	0.624	0.0003	-55.89 (11.36)
T-cell response in females	0.20	1, 7	0.000	0.667	
Italy					
Chewing lice in males	22.50	1, 283	0.074	0.001	0.317 (0.061)
Chewing lice in females	1.55	1, 268	0.006	0.200	
Feather mites in males	17.96	1, 283	0.060	0.001	-0.022 (0.005)
Feather mites in females	9.96	1, 268	0.036	0.0018	-0.016 (0.005)
T-cell response in males	11.53	1, 30	0.278	0.002	-0.164 (0.048)
Spain					
Chewing lice in males	7.05	1, 36	0.140	0.012	-0.246 (0.093)
Chewing lice in females	0.02	1, 35	0.000	0.883	
Haematozoa in males	4.77	1, 37	0.090	0.036	2.500 (1.145)
Haematozoa in females	0.0003	1, 35	0.000	0.986	
T-cell response in males	5.61	1, 37	0.132	0.023	-1.090 (0.460)
T-cell response in females	0.92	1, 35	0.000	0.344	

between blood parasites and arrival date. For males, there was a significant relationship between infection with *Haemoproteus* and arrival date, with infected individuals arriving late (Table 1). That was not the case for females (Table 1). Because three-quarters of Barn Swallows from Spain did not have any blood parasites, we repeated the analyses using Kendall partial rank order correlations. The conclusions remained unchanged with these nonparametric analyses. In these samples, arrival date was strongly negatively related to the number of fledglings produced per year (after controlling for age and tail length) in males (partial regression, $F = 8.642$, $df = 1, 37$, $P < 0.01$, slope = -0.112) and in females (partial regression, $F = 4.764$, $df = 1, 35$, $P < 0.05$, slope = -0.081).

Because Barn Swallows with long tails also arrive early and tend to have fewer parasites than short-tailed birds (Møller 1994a), we performed multiple regression analyses with arrival date as the dependent variable and parasite load and tail length as independent variables. Males from Denmark that arrived early had fewer chewing lice than late-arriving males, independent of their tail length (Table 2). However, that was not the case for females, because the partial regression for the number of chewing lice was not statistically significant (Table 2). For both males and females, arrival at the breeding grounds was earlier for individuals with many feather mites, independent of any effects of tail length (Table 2). Similar patterns were found for the Italian Barn Swallows. Males with more chewing lice arrived late, independent of tail length, whereas that was not the case for females (Table 2). In both males and females from Italy, individuals with many feather mites arrived earlier than individuals with few

mites, independent of their tail length (Table 2). In the Spanish sample, chewing lice abundance was significantly associated with delayed arrival in males, but not in females, even when controlling for tail length (Table 2).

Similarly, *Haemoproteus* was significantly associated with delayed arrival in males, but not in females (Table 2).

Arrival date and T-cell response

Danish males with strong T-cell responses arrived earlier than males with weak responses (Fig. 2a, Table 1). That was not the case for females (Fig. 2b, Table 1). A multiple linear regression controlling for the independent effect of tail length still revealed a significant negative relationship between arrival date and T-cell response for males, but not for females (Table 2). In these samples, arrival date was strongly negatively related to the number of fledglings produced per year (after controlling for tail length) in males (partial regression, $F = 14.578$, $df = 1, 13$, $P = 0.0021$, slope = -0.374) and in females (partial regression, $F = 10.861$, $df = 1, 7$, $P = 0.013$, slope = -0.249).

Among males from Italy, there was a strong negative relationship between T-cell response and arrival date (Fig. 2c, Table 1). No tests were available for females from Italy. This relationship disappeared when tail length of males was controlled statistically (Table 2).

In the Spanish sample, males with strong T-cell responses arrived earlier than males with weak responses (Table 1). However, female arrival date was not significantly related to T-cell response (Table 1). These relationships were independent of tail length (Table 2). In the Spanish samples, arrival date was strongly neg-

actively related to the number of fledglings produced per year (after controlling for tail length) in males (partial regression, $F = 36.385$, $df = 1, 35$, $P < 0.001$, slope = -0.578) and in females (partial regression, $F = 25.725$, $df = 1, 34$, $P < 0.001$, slope = -0.358).

Arrival date in relation to experimental manipulation of parasite abundance

Experimental manipulation of nest contents of hematophagous mites significantly affected the arrival date of male Barn Swallows in the subsequent year (Fig. 3a; $F = 9.47$, $df = 2, 57$, $P = 0.0004$). All three mean arrival dates differed significantly ($P < 0.05$) from each other in Fisher's PSLD (protected least squares difference) tests. Previous analyses have shown that the change in tail length of male Barn Swallows in this experiment during the annual molt was affected by treatment (Møller 1990b), and tail length and arrival date are generally negatively associated in the Barn Swallow (Møller 1994a). Hence, we performed an ANCOVA with arrival date as the dependent variable, treatment as a factor, and tail length as a covariate. This analysis showed independent significant relationships between arrival date and, respectively, treatment and tail length (Table 3). None of the interactions was statistically significant. An analysis of females did not reveal any significant effect of treatment on arrival date (Fig. 3b, $F = 2.31$, $df = 2, 51$, $P = 0.110$). An ANCOVA revealed a significant effect of tail length, but no effect of treatment on arrival by females (Table 3). In this experiment, arrival date was strongly negatively related to the number of fledglings produced per year in males after controlling for tail length (partial regression, $F = 42.602$, $df = 1, 55$, $P < 0.001$, slope = -1.138), but not in females after controlling for tail length (partial regression, $F = 0.604$, $df = 1, 51$, $P = 0.441$).

DISCUSSION

Early arrival gives male Barn Swallows an enormous advantage in terms of mating success, breeding date, number of broods per year, and paternity in these broods (Møller 1988a, 1990b, 1994a, b, Saino et al. 1997a, Kose et al. 1999, Kose and Møller 1999). For example, a delay in arrival date of just 10 days results in the frequency of second broods dropping from 100% to 0% (Møller 1990b:461). Thus, arrival of certain individuals even a few days earlier than others can have dramatic effects on reproductive success. Male Barn Swallows in Denmark arrive, on average, four days earlier than females (Møller 1994a); this difference has been assumed to arise because of sex differences in patterns of selection. The variance in arrival date by males is significantly larger than the variance in female arrival date (Møller 1994b), and this sex difference in variance arises as a consequence of a greater level of condition dependence in males than in females. Although Barn Swallows are socially monogamous,

males vary considerably more than females in mating success, number of broods per year, and parentage in these broods. These fitness components are all strongly associated with early arrival (Møller 1994a, b, Møller et al., *in press a*). Intensity of selection for early arrival is therefore considerably greater in males than in females. A difference of four days in mean arrival date between the sexes may seem little. However, for a journey of $>12\,500$ km that lasts a minimum of 36–50 days (Glutz von Blotzheim 1985), cutting off four days, or 9.3%, from the total duration may be impossible. That is particularly the case if the birds are already migrating at maximum speed, which is 250–350 km traveled per day for a period of one month, calculated from recoveries of banded birds (Glutz von Blotzheim 1985). This is very fast compared to the maximum speed during foraging in the nestling period (Turner 1980).

The main novel finding of the present study was that arrival at the breeding grounds by a long-distance migratory bird was associated with the abundance of ectoparasites in a sex-specific manner. Males with many chewing lice arrived later than the average male, but that was not the case for females in three different populations. A similar pattern was found for *Haemoproteus prognei* infections in a Spanish Barn Swallow population. Migratory birds may experience serious relapses of hematozoan infections during migration (Valkiunas 1991), but the difference in infection status of early- and late-arriving males suggests that early-arriving males either are less often infected, or they suffer from less severe relapses than late-arriving males. The mean effect size for the relationship between parasitism and arrival date (after controlling for confounding effects), measured in terms of Pearson's correlation coefficient and adjusted for sample size, where $r = \sqrt{t^2/(t^2 + df)}$ (Rosenthal 1991), was 0.24 for males, but only 0.0074 for females. Parasites accounted for 5.8% of the variance in arrival date in males, but $<0.1\%$ in females. Therefore, effect size for males was small to intermediate (*sensu* Cohen 1988), and larger than the mean amount of variance explained by all meta-analyses in biology (Møller and Jennions 2002). Commensal feather mites (Astigmata) provide an interesting control group of invertebrates living on Barn Swallows because they have no known negative effects on host fitness. For this group, the pattern of host arrival in relation to abundance was reversed: hosts with more feather mites arrived early (Fig. 1, Tables 1–2). Finally, males with stronger T-cell-dependent immune responses arrived earlier than males with weak responses, although that was not the case for females (Fig. 2). Mean effect size for the relationship between T-cell response and arrival was 0.38 for males and 0.19 for females, explaining 14.4% and 3.6% of the variance, respectively. Thus, immune response was a better predictor of arrival date than parasite abundance.

TABLE 2. Multiple linear regressions with arrival date as the dependent variable and parasite load, T-cell response, and tail length as independent variables.

Variable, by country	F		df		Slope (1 SE)	
	Males	Females	Males	Females	Males	Females
Denmark						
Chewing lice (males, $F = 26.64$, $df = 7, 184$, $r^2 = 0.370$, $P < 0.001$; females, $F = 191.31$, $df = 9, 149$, $r^2 = 0.170$, $P < 0.001$)						
No. lice	5.63	3.88	1	1	0.099 (0.042)	-0.092 (0.047)
Tail length	113.83	26.62	1	1	-0.519 (0.049)	-0.398 (0.077)
Year	9.38	2.55	5	7		
Feather mites (males, $F = 61.80$, $df = 3, 115$, $r^2 = 0.607$, $P < 0.001$; females, $F = 274.04$, $df = 5, 106$, $r^2 = 0.352$, $P < 0.001$)						
No. mites	4.28	6.77	1	1	-0.017 (0.008)	-0.017 (0.006)
Tail length	181.40	48.92	1	1	-0.661 (0.049)	-0.474 (0.068)
Year	0.02	2.51	1	3		
T-cell response (males, $F = 11.49$, $df = 2, 12$, $r^2 = 0.600$, $P = 0.0016$; females, $F = 1.23$, $df = 2, 6$, $r^2 = 0.054$, $P = 0.358$)						
Response	11.29	0.71	1	1	-62.660 (18.670)	-21.195 (25.279)
Tail length	0.22	2.22	1	1	0.112 (0.240)	-0.631 (0.424)
Italy						
Chewing lice (males, $F = 28.51$, $df = 3, 279$, $r^2 = 0.235$, $P < 0.001$; females, $F = 21.47$, $df = 3, 266$, $r^2 = 0.195$, $P < 0.001$)						
No. lice	12.96	0.19	1	1	0.211 (0.059)	0.025 (0.056)
Tail length	9.55	8.64	1	1	-0.351 (0.102)	-0.454 (0.155)
Age	37.37	41.36	1	1	-5.055 (0.827)	-5.766 (0.898)
Feather mites (males, $F = 33.19$, $df = 3, 279$, $r^2 = 0.274$, $P < 0.001$; females, $F = 24.78$, $df = 3, 266$, $r^2 = 0.218$, $P < 0.001$)						
No. mites	9.77	8.20	1	1	-0.015 (0.005)	-0.013 (0.004)
Tail length	4.30	6.96	1	1	-0.211 (0.102)	-0.404 (0.153)
Age	62.62	43.90	1	1	-6.833 (0.864)	-5.795 (0.875)
T-cell response (males, $F = 5.25$, $df = 5, 26$, $r^2 = 0.503$, $P = 0.002$)						
Response	2.20		1		-0.008 (0.055)	
Tail length	9.54		1		-0.741 (0.240)	
Age	0.61		1		1.112 (1.419)	
Brood size	0.34		2			
Spain						
Chewing lice (males, $F = 3.11$, $df = 2, 34$, $r^2 = 0.105$, $P = 0.057$; females, $F = 0.01$, $df = 2, 34$, $r^2 = 0.000$, $P = 0.985$)						
No. lice	6.10	0.02	1	1	0.296 (0.120)	0.022 (0.149)
Tail length	0.20	0.01	1	1	-0.043 (0.096)	-0.017 (0.182)
Haematozoa (males, $F = 3.96$, $df = 2, 35$, $r^2 = 0.101$, $P = 0.045$; females, $F = 0.005$, $df = 2, 34$, $r^2 = 0.000$, $P = 0.995$)						
Haematozoa	5.81	0.00	1	1	2.795 (1.162)	0.016 (1.544)
Tail length	0.18	0.01	1	1	0.038 (0.091)	-0.017 (0.183)
T-cell response (males, $F = 3.197$, $df = 2, 35$, $r^2 = 0.084$, $P = 0.045$; females, $F = 0.465$, $df = 2, 34$, $r^2 = 0.000$, $P = 0.632$)						
Response	4.28	0.92	1	1	-1.102 (0.534)	-0.502 (0.523)
Tail length	0.01	0.04	1	1	0.011 (0.094)	-0.034 (0.181)

The difference in patterns of ectoparasite abundance in relation to arrival date can best be understood by considering the effects of these parasites on the host. Although chewing lice damage feathers by chewing holes that can result in feather breakage and hence impaired flight (Møller 1991, Kose et al. 1999, Kose and Møller 1999, Barbosa et al. 2002), feather mites can best be considered commensals feeding on the surface of feathers (Blanco et al. 2001). Previous studies of feather mites suggest that their abundance depend on host condition, with hosts in superior condition having larger numbers of mites (review in Blanco et al. 2001). This difference in the effect of the two species

of ectoparasites on host fitness leads to different predictions concerning the relationship between parasite abundance and arrival. For the chewing lice, we would expect a delay in arrival caused by the presence of many parasites, particularly in early-arriving males, whereas we would expect late arrival among adult Barn Swallows with few feather mites because such individuals would be in poor condition. These predictions were clearly borne out (Fig. 1, Tables 1–2).

Both male and female Barn Swallows with long tails arrive at the breeding grounds before short-tailed individuals (Møller 1994a, b). This is the case, independent of age (Møller 1994b). Similar patterns of asso-

TABLE 2. Extended.

<i>t</i>		<i>P</i>	
Males	Females	Males	Females
2.37	1.97	0.019	0.051
10.67	5.16	0.0001	0.0001
		0.001	0.017
2.07	2.60	0.041	0.011
13.47	6.99	0.0001	0.0001
		0.882	0.063
3.36	0.84	0.0057	0.434
0.47	1.49	0.650	0.187
3.60	0.44	0.0001	0.66
3.09	2.94	0.002	0.004
6.11	6.43	0.0001	0.0001
3.13	2.86	0.002	0.005
2.07	2.64	0.039	0.009
7.91	6.63	0.0001	0.0001
1.48		0.15	
3.09		0.005	
0.78		0.44	
		0.72	
2.47	0.15	0.019	0.885
0.45	0.09	0.659	0.926
2.41	0.01	0.022	0.992
0.42	0.09	0.680	0.925
2.07	0.96	0.046	0.344
0.12	0.19	0.905	0.851

ciation between arrival date, parasites, and breeding plumage have been reported in the Bar-tailed Godwit *Limosa lapponica* at an intermittent stopover site, showing that healthy individuals are ahead already during mid-migration (Piersma and Jukema 1993, Piersma et al. 2001). Male Barn Swallows with long tails generally have fewer chewing lice and other ectoparasites than short-tailed males, but that is not the case for females (Møller 1991, 1994a, Saino and Møller 1996, Kose et al. 1999, Kose and Møller 1999). Thus we must determine the association between arrival date and parasitism, independent of tail length. The patterns of arrival in relation to parasitism, independent of tail

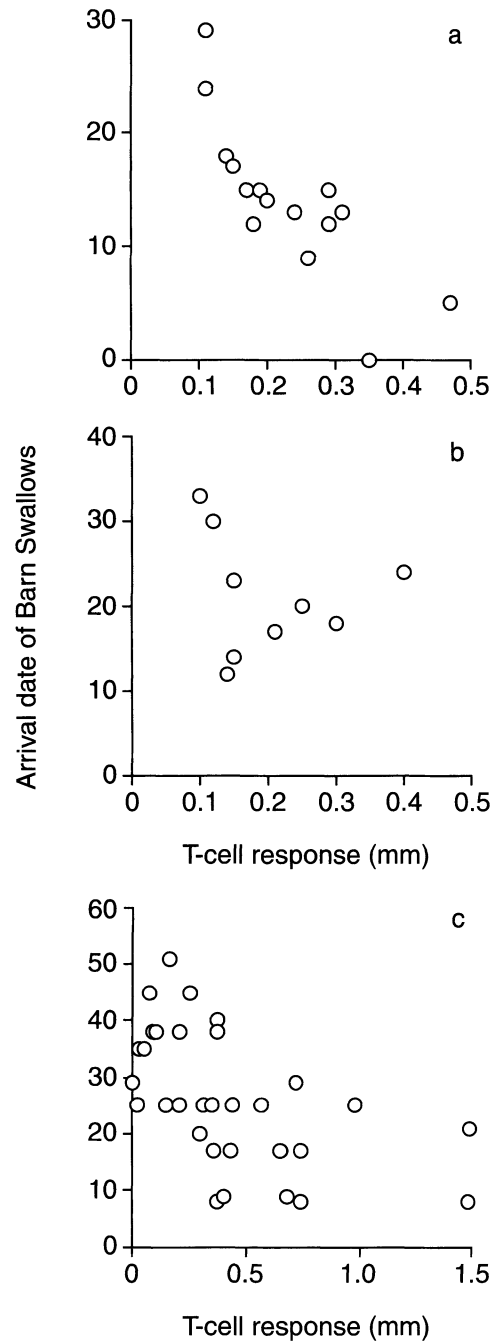


FIG. 2. Arrival date (day 1 = 1 May) of Barn Swallows in relation to T-cell response in (a) males from Denmark, (b) females from Denmark, and (c) males from Italy.

length, as revealed by multiple linear regressions (Table 2). The correlation between tail length, arrival date, and parasitism in the Barn Swallow can be hypothesized to be due to an underlying condition effect. Thus, we expect condition to be the underlying factor accounting for the positive covariation between parasitism and arrival date. Adult males are often more sus-

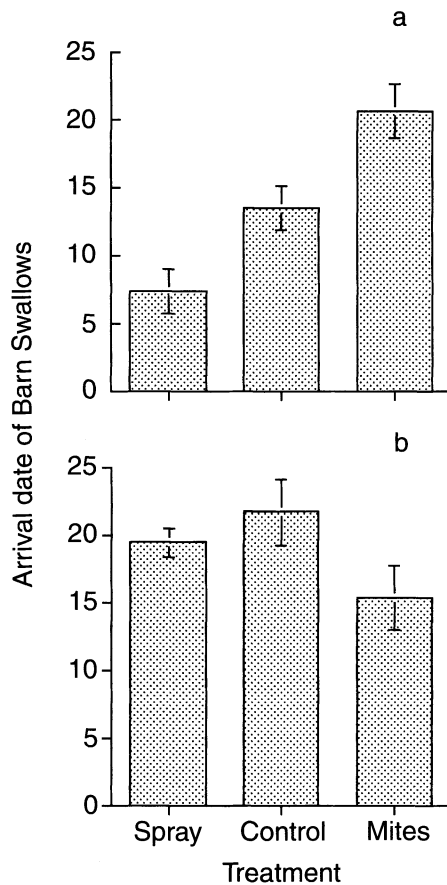


FIG. 3. Arrival date (day 1 = 1 May) of adult Danish (a) male and (b) female Barn Swallows in relation to mite treatment of their nests in the previous year. Values are means \pm 1 SE.

ceptible to parasitism than females (Alexander and Stimson 1989, Zuk 1990, Poulin 1996, Schalk and Forbes 1997, Sheridan et al. 2000). Adult males also tend to have weaker immune systems than females (Grossman 1989, Hazarika and Gupta 1989, Nigam et al. 1997, Møller et al. 1998). We did not find any sex differences in parasite prevalence or in immune response in this study, and more extensive studies of T-cell response across species of birds have reached a similar conclusion (Møller et al. 2003). However, even if levels of defense are similar in the two sexes, males may still be more susceptible to parasites than females, because they compete more intensely for mates. Although higher susceptibility of males to parasitism is inconsistent with males arriving earlier than females, it may explain why males show greater variability in arrival date than females (Møller 1994b). Male Barn Swallows experience stronger selection for early arrival than do females, and males are therefore expected to trade early arrival against survival differently than females. The generally stronger relationships between parasitism, immune response, and arrival date in male

vs. female Barn Swallows may arise as a consequence of arrival date, parasitism, and immune function of males being more strongly condition dependent than the same characters in females.

Although correlations between parasite abundance and arrival date cannot provide information about the causal relationship, we used experimental manipulation of nest contents of the tropical fowl mite *Ornithonyssus bursa* to investigate how parasite abundance directly affects subsequent host behavior. Manipulation of mite numbers affected host reproduction during the year of manipulation (Møller 1990a), but also affected subsequent molt in the African winter quarters (Møller 1990b) and arrival date at the breeding grounds in the following spring (Fig. 3). Because increased mite abundance reduced the tail length of males (Møller 1990b), and because long-tailed males arrive earlier than short-tailed males (Møller 1994a, b), the relationship between mite treatment of nests and arrival date (Fig. 3) may be a consequence of condition being affected by treatment. However, experimental treatment affected the arrival date of males independent of tail length (Table 3), suggesting that tail length only partly reflects changes in condition, and that arrival date provides an independent measure of change in condition. Effect size for treatment in males was 0.88, accounting for 77% of the variance in arrival date, whereas effect size was only 0.18 for females, accounting for 3.4% of the variance. This demonstrates that parasites (or the ability to cope with the effects of parasites) are a major determinant of arrival date in male, but not in female, Barn Swallows.

Arrival date of males was also predicted by a measure of T-cell-mediated immune response to a challenge with a novel mitogen, phytohemagglutinin (Fig. 2). This association between arrival date and immune response only occurred in males, and it was independent of any association between T-cell response and tail length, with the exception of the Italian sample (Table 2). Therefore, we can conclude that early arrival is associated with low abundance of parasites, but also with a measure of the ability of hosts to cope with

TABLE 3. Analysis of covariance with arrival date of adult male and female Barn Swallows as the dependent variable, nest treatment as a factor, and tail length as a covariate.

Variable	MS	df	F	P
Males				
Treatment	558.54	2	13.91	<0.0001
Tail length	1285.35	1	32.01	<0.0001
Residual	40.15	56		
Females				
Treatment	91.90	2	1.76	0.190
Tail length	842.67	1	16.14	<0.0001
Residual	52.21	50		

Note: Nests were randomly subjected to anti-mite treatment, inoculation with mites, or control manipulation.

parasites, as reflected by their T-cell-dependent immune function.

We will briefly discuss these associations between arrival date, parasitism, and immune function in the light of condition-dependent migration. Condition dependence evolves when competition among individuals selects for greater expression of a character among individuals of superior quality (Andersson 1994, Møller 1994a, Kokko 1999). Thus, as condition dependence evolves, a larger number of metabolic and other pathways will affect the expression of the trait, providing a mechanism for expressing the overall condition of an individual in the trait. Only individuals in prime condition will be able to produce the most exaggerated version of the trait; other individuals will not be able to cheat, simply because poor condition does not allow production of extreme traits. As concerns condition-dependent migration, we can assume that long-distance displacement across ranges of >10 000 km only allows individuals in prime condition to arrive early. This test of endurance as a measure of condition is reflected in the correlation between male tail length and arrival date in the Barn Swallow, particularly in years with poor environmental conditions (Møller 1994a, b). In the present study, we have shown that the abundance of four species of parasites (in different ways) is associated with early arrival, even when controlling statistically for any independent effect of condition as reflected by tail length. Similarly, the association between arrival date and T-cell immune response is negative in adult male Barn Swallows, but not in females (Fig. 2). Again, this observation is consistent with predictions from condition-dependent migration theory. The mere fact that arrival date correlates independently with the expression of a secondary sexual character, parasite abundance, and a component of immune function is consistent with the suggestion that arrival date is condition dependent, as reflected by different condition-dependent traits. Currently, we do not know whether early arrival by long-tailed male swallows is due to early start of migration or more rapid migration. Recoveries during the winter period of birds banded in the European breeding areas do not suggest a difference in wintering grounds between males and females (A. P. Møller, unpublished data, based on analyses of all European recoveries). Similarly, long-tailed males depart on fall migration from the breeding grounds later than short-tailed males, simply because long-tailed birds more often have a second (Denmark, Italy) or a third brood (Spain; Møller 1990c, 1994a; A. P. Møller, F. de Lope, and N. Saino, unpublished data). Finally, long-tailed birds do not start molting earlier in the winter quarters than short-tailed males, although the speed of molt is more rapid in long-tailed males (Møller et al. 1995). However, this latter effect cannot possibly compensate the delay in migration departure in the fall by long-tailed males due to their higher frequency of mul-

tle broods. Hence, it seems likely that long-tailed males migrate more rapidly than short-tailed males.

How are migratory birds that face different parasite communities during their annual cycle able to cope with impacts of parasites? One answer to this question is that migrants invest more in immune function than residents, in terms of larger bursa of Fabricius and spleen (Møller and Erritzøe 1998). Because both the bursa and the spleen are enlarged in migratory species, we can infer that migratory species have evolved mechanisms to cope with elevated parasite impact even before the first fall migration starts, as revealed by their enlarged bursa.

In conclusion, spring arrival in the Barn Swallow was associated with levels of parasitism and a measure of T-cell-dependent immune response, particularly in males. We found stronger associations in males than in females between arrival date and, respectively, parasitism and immune function. These are consistent with the hypothesis that migration is highly dependent on condition in male Barn Swallows, but less so in females, because males compete more intensely for early arrival than do females.

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LITERATURE CITED

- Abbas, A. K., A. H. Lichtman, and J. S. Pober. 1994. Cellular and molecular immunology. Saunders, Philadelphia, Pennsylvania, USA.
- Ahmad, S. 1995. Oxidative stress and antioxidant defenses in biology. Chapman and Hall, New York, New York, USA.
- Alerstam, T. 1991. Bird migration. Cambridge University Press, Cambridge, UK.
- Alerstam, T., and A. Hedenström. 1998. The development of bird migration theory. *Journal of Avian Biology* 29:343–369.
- Alerstam, T., and Å. Lindström. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pages 331–351 in E. Gwinner, editor. Bird migration: physiology and ecophysiology. Springer-Verlag, Berlin, Germany.
- Alexander, J., and W. H. Stimson. 1989. Sex hormones and the course of parasitic infection. *Parasitology Today* 4: 1891–1893.
- Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, New Jersey, USA.
- Baker, R. R. 1978. The evolutionary ecology of animal migration. Hodder and Stoughton, London, UK.
- Barbosa, A., S. Merino, F. de Lope, and A. P. Møller. 2002. Effects of feather lice on the flight behavior of male barn swallows. *Auk* 119:213–216.
- Berthold, P. 1996. Vogelzug. Wissenschaftliche Buchgesellschaft, Darmstadt, Germany.
- Blanco, G., J. L. Tella, J. Potti, and A. Baz. 2001. Feather mites on birds: costs of parasitism or conditional outcomes? *Journal of Avian Biology* 32:271–274.
- Brinkhof, M. W. G., P. Heeb, M. Kölliker, and H. Richner. 1999. Immunocompetence of nestling great tits in relation to rearing environment and parentage. *Proceedings of the Royal Society of London B* 266:2315–2322.

- Chandler, C. R. 1995. Practical considerations in the use of simultaneous inference for multiple tests. *Animal Behaviour* **49**:524–527.
- Chandra, R. K., and P. M. Newberne. 1977. Nutrition, immunity, and infection. Plenum Press, New York, New York, USA.
- Chew, B. P. 1996. Importance of antioxidant vitamins in immunity and health in animals. *Animal Feed Science and Technology* **59**:103–114.
- Christe, P., A. P. Møller, and F. de Lope. 1998. Immunocompetence and nestling survival in the house martin: “The tasty chick hypothesis.” *Oikos* **83**:175–179.
- Cohen, J. 1988. Statistical power analysis for the behavioral sciences. Second edition. L. Erlbaum, Philadelphia, Pennsylvania, USA.
- Davidar, P., and E. S. Morton. 1993. Living with parasites: prevalence of a blood parasite and its effects on survivorship in the Purple Martin. *Auk* **110**:109–116.
- Dietert, R. R., K. A. Golemboski, H. Kwak, R. Ha, and T. E. Miller. 1996. Environment–immunity interactions. Pages 343–356 in T. F. Davison, T. R. Morris, and L. N. Payne, editors. Poultry immunology. Carfax, Abingdon, UK.
- Forstmeier, W. 2002. Benefits of early arrival at breeding grounds vary between males. *Journal of Animal Ecology* **71**:1–9.
- Gershwin, M. E., R. S. Beach, and L. S. Hurley. 1985. Nutrition and immunity. Academic Press, Orlando, Florida, USA.
- Glutz von Blotzheim, U. N., editor. 1985. Handbuch der Vögel Mitteleuropas. Volume 10. AULA-Verlag, Wiesbaden, Germany.
- Goto, N., H. Kodama, K. Okada, and Y. Fujimoto. 1978. Suppression of phytohaemagglutinin skin response in thymectomized chickens. *Poultry Science* **57**:246–250.
- Grossman, C. 1989. Possible underlying mechanisms of sexual dimorphism in immune response, fact and hypothesis. *Journal of Steroid Biochemistry* **34**:241–251.
- Halliwell, B. 1996. Antioxidants in human health and disease. *Annual Review of Nutrition* **16**:33–50.
- Hazarika, L. K., and A. P. Gupta. 1989. Variation in hemocyte populations during various developmental stages of *Blattella germanica* (L.) (Dictyoptera, Blattellidae). *Zoologica Scientiae* **4**:307–313.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* **6**:65–70.
- Jenni, L., and S. Jenni-Eiermann. 1998. Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology* **29**:521–528.
- Kokko, H. 1999. Competition for early arrival in migratory birds. *Journal of Animal Ecology* **68**:940–950.
- Kose, M., R. Mänd, and A. P. Møller. 1999. Sexual selection for white tail spots in the barn swallow in relation to habitat choice by feather lice. *Animal Behaviour* **58**:1201–1205.
- Kose, M., and A. P. Møller. 1999. Sexual selection, feather breakage and parasites: the importance of white spots in the tail of the barn swallow. *Behavioral Ecology and Sociobiology* **45**:430–436.
- Leffler, J. E. 1993. An introduction to free radicals. Wiley, New York, New York, USA.
- Lochmiller, R. L., M. R. Vestey, and J. C. Boren. 1993. Relationship between protein nutritional status and immunocompetence in Northern Bobwhite chicks. *Auk* **110**:503–510.
- McCorkle, F., Jr., I. Olah, and B. Glick. 1980. The morphology of the phytohemagglutinin-induced cell response in the chicken’s wattle. *Poultry Science* **59**:616–623.
- Merino, S., A. P. Møller, and F. de Lope. 2000. Seasonal changes in cell-mediated immunocompetence and mass gain in nestling barn swallows: a parasite-mediated effect? *Oikos* **90**:327–332.
- Merino, S., J. Potti, and J. A. Fargallo. 1997. Blood parasites of passerine birds from Central Spain. *Journal of Wildlife Diseases* **33**:638–641.
- Møller, A. P. 1988a. Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature* **332**:640–642.
- Møller, A. P. 1988b. Infanticidal and anti-infanticidal strategies in the swallow *Hirundo rustica*. *Behavioral Ecology and Sociobiology* **22**:365–371.
- Møller, A. P. 1990a. Effects of parasitism by the haematophagous mite *Ornithonyssus bursa* on reproduction in the Barn Swallow *Hirundo rustica*. *Ecology* **71**:2345–2357.
- Møller, A. P. 1990b. Effects of an haematophagous mite on the barn swallow (*Hirundo rustica*): a test of the Hamilton and Zuk hypothesis. *Evolution* **44**:771–784.
- Møller, A. P. 1990c. Male tail length and female mate choice in the monogamous swallow *Hirundo rustica*. *Animal Behaviour* **39**:458–465.
- Møller, A. P. 1991. Parasites, sexual ornaments and mate choice in the barn swallow *Hirundo rustica*. Pages 328–343 in J. E. Loye and M. Zuk, editors. Ecology, behavior, and evolution of bird–parasite interactions. Oxford University Press, Oxford, UK.
- Møller, A. P. 1994a. Sexual selection and the barn swallow. Oxford University Press, Oxford, UK.
- Møller, A. P. 1994b. Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology* **35**:115–122.
- Møller, A. P. 2001. Heritability of arrival date in a migratory bird. *Proceedings of the Royal Society of London B* **268**:203–206.
- Møller, A. P., C. Biard, J. D. Blount, D. C. Houston, P. Ninni, N. Saino, and P. F. Surai. 2000. Carotenoid-dependent signals: indicators of foraging efficiency, immunocompetence or detoxification ability? *Poultry and Avian Biology Reviews* **11**:137–159.
- Møller, A. P., J. Brohede, J. J. Cuervo, F. de Lope, and C. R. Primmer. *In press a*. Extrajoint paternity in relation to sexual ornamentation, arrival date and condition in a migratory bird. *Behavioral Ecology*.
- Møller, A. P., P. Christe, J. Erritzøe, and J. Mavarez. 1998. Condition, disease and immune defence. *Oikos* **83**:301–306.
- Møller, A. P., and F. de Lope. 1999. Senescence in a short-lived migratory bird: age-dependent morphology, migration, reproduction and parasitism. *Journal of Animal Ecology* **68**:163–171.
- Møller, A. P., and J. Erritzøe. 1998. Host immune defence and migration in birds. *Evolutionary Ecology* **12**:945–953.
- Møller, A. P., and J. Erritzøe. 2001. Dispersal, vaccination and regression of immune defence organs. *Ecology Letters* **4**:484–490.
- Møller, A. P., J. Erritzøe, and N. Saino. 2003. Seasonal changes in immune response and parasite impact on hosts. *American Naturalist* **161**:657–671.
- Møller, A. P., and M. D. Jennions. 2002. How much variance can be explained by ecologists and evolutionary biologists? *Oecologia* **132**:492–500.
- Møller, A. P., K. Magnhagen, A. Ulfstrand, and S. Ulfstrand. 1995. Phenotypic quality and moult in the barn swallow *Hirundo rustica*. *Behavioral Ecology* **6**:242–249.
- Møller, A. P., R. Martinelli, and N. Saino. *In press b*. Genetic variation in infestation with a directly transmitted parasite. *Journal of Evolutionary Biology*.
- Møller, A. P., and T. Szép. 2002. Survival rate of adult Barn Swallows *Hirundo rustica* in relation to sexual selection and reproduction. *Ecology* **83**:2220–2228.
- Navarro, C., A. Marzal, F. de Lope, and A. P. Møller. 2003. Dynamics of an immune response in house sparrows *Passer*

- domesticus* in relation to time of day, body condition and blood parasite infection. *Oikos* **101**:29–298.
- Nigam, Y., L. Maudlin, S. Welburn, and N. Ratcliffe. 1997. Detection of phenoloxide activity in the hemolymph of tsetse flies, refractory and susceptible to infection with *Trypanosoma brucei rhodensie*. *Journal of Invertebrate Pathology* **69**:279–281.
- Parmentier, H. K., G. de Vries Reilingh, and M. G. B. Nieuwland. 1998. Kinetic immunohistochemical characteristics of mitogen-induced cutaneous hypersensitivity responses in chickens divergently selected for antibody responsiveness. *Veterinary Immunology and Immunopathology* **66**:367–376.
- Parmentier, H. K., J. W. Scharma, F. Meijer, and M. G. B. Nieuwland. 1993. Cutaneous hypersensitivity responses in chickens divergently selected for antibody responses to sheep red blood cells. *Poultry Science* **72**:1679–1692.
- Piersma, T., and J. Jukema. 1993. Red breasts as honest signals of migrating quality in a long-distance migrant, the Bar-tailed Godwit. *Condor* **95**:163–177.
- Piersma, T., L. Mendes, J. Hennekens, S. Ratarison, S. Groenewold, and J. Jukema. 2001. Breeding plumage honestly signals likelihood of tapeworm infestation in females of a long-distance migrating shorebird, the Bar-tailed Godwit. *Zoology Analysis of Complex Systems* **104**:167.
- Poulin, R. 1996. Sexual inequalities in helminth infections: a cost of being a male? *American Naturalist* **147**:287–295.
- Radesäter, T., S. Jakobsson, N. Andbjør, A. Bylin, and K. Nyström. 1987. Song rate and pair formation in the willow warbler, *Phylloscopus trochilus*. *Animal Behaviour* **35**:1645–1651.
- Rätti, O., R. Dufva, and R. V. Alatalo. 1993. Blood parasites and male fitness in the pied flycatcher. *Oecologia* **96**:410–414.
- Rosenthal, R. 1991. *Meta-analytic procedures for social research*. Sage, New York, New York, USA.
- Saino, N., A. M. Bolzern, and A. P. Møller. 1997a. Immunocompetence, ornamentation and viability of male barn swallows (*Hirundo rustica*). *Proceedings of the National Academy of Sciences (USA)* **94**:549–552.
- Saino, N., S. Calza, and A. P. Møller. 1997b. Immunocompetence of nestling barn swallows in relation to brood size and parental effort. *Journal of Animal Ecology* **66**:827–836.
- Saino, N., M. Incagli, R. Martinelli, and A. P. Møller. 2002. Immune response of male barn swallows in relation to acute stress, parental effort and sexual ornamentation. *Behavioral Ecology* **13**:169–174.
- Saino, N., and A. P. Møller. 1996. Sexual ornamentation and immunocompetence in the barn swallow. *Behavioral Ecology* **7**:227–232.
- Schalk, G., and M. R. Forbes. 1997. Male biases in parasitism of mammals: effects of study type, host age, and parasite taxon. *Oikos* **78**:67–74.
- Sheridan, L., R. Poulin, D. Ward, and M. Zuk. 2000. Sex differences in parasite infections among arthropod hosts: Is there a male bias? *Oikos* **88**:327–334.
- Surai, P. 1999. Vitamin E in avian reproduction. *Poultry and Avian Biology Reviews* **10**:1–60.
- Turner, A. K. 1980. The use of time and energy by aerial feeding birds. Dissertation. University of Stirling, Stirling, Scotland, UK.
- Valkiunas, G. 1991. The role of seasonal migrations in the distribution of Haemosporidia of birds in North Palaearctic. *Ekologija* **1993**(2):57–73.
- Wright, S. P. 1992. Adjusted *P*-values for simultaneous inference. *Biometrics* **48**:1005–1013.
- Zuk, M. 1990. Reproductive strategies and sex differences in disease susceptibility: an evolutionary viewpoint. *Parasitology Today* **6**:231–233.