

Ecological conditions during winter affect sexual selection and breeding in a migratory bird

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Populations of migratory birds have undergone marked declines, although the causes and mechanisms remain unknown. Because environmental effects on population dynamics are mediated by the effects of ecological factors on individuals, understanding changes in individual phenotypes in response to ecological conditions is key to understanding population trends. We show that breeding individuals of a declining population of trans-Saharan migratory barn swallows, *Hirundo rustica*, were affected by environmental conditions, as estimated from the normalized difference vegetation index (NDVI), reflecting primary production, in their winter quarters. The breeding dates of the same individuals in consecutive breeding seasons were advanced and clutch sizes were larger after winters with high NDVI in the winter quarters. Feather moult was also affected by winter conditions, with consequences for male sexual attractiveness. Length of tail ornament was positively correlated with NDVI during the previous winter, and males with large tail ornaments reproduced earlier and had larger clutches. The mean annual breeding date of the population was earlier and breeding success was increased after favourable winters, but this result was mainly determined by a single winter with very low NDVI. Thus, ecological conditions in Africa influence individual performance and productivity in a barn swallow population.

Keywords: carry-over effects; connectivity; migration; normalized difference vegetation index; phenotypic plasticity

1. INTRODUCTION

Migratory birds occupy different areas at different times of the year, but the importance of environmental conditions, particularly during wintering, for reproduction is still largely unknown. Previous studies of population dynamics have shown that ecological factors affect survival and recruitment, the timing of breeding and fecundity at the population level (Baillie & Peach 1992; Szép 1995; Crick *et al.* 1997; Crick & Sparks 1999; Sillett *et al.* 2000; Stevenson & Bryant 2000; Møller & Szép 2002; Hüppop & Hüppop 2003). These studies, however, did not disentangle the effects of natural selection and phenotypic plasticity. Variation in phenotypically plastic traits of migratory species can depend on conditions experienced during winter (Møller 1994a,b) and can affect subsequent performance in three different ways. First, conditions can affect moult during winter and thereby feathers important for flight during spring migration and breeding (Møller 1994b). Second, environmental conditions may affect the expression of condition-dependent secondary sexual characters that influence sexual selection (Møller 1994a). Third, ecological factors may affect body condition with long-term consequences for reproduction during the following summer (Marra *et al.* 1998). We examined the extent to which these different mechanisms affect the performance of a migratory bird, the barn swallow *Hirundo*

rustica, by analysing the phenotypes of the same individuals in different breeding seasons in relation to variation in ecological conditions in the African winter quarters.

Satellite-assisted remote sensing allows investigation of the effect of ecological conditions over large temporal and spatial scales. The normalized difference vegetation index (NDVI) measures photosynthetic activity and reflects the effect of rainfall on distribution and biomass of vegetation (Boone *et al.* 2000; Schmidt & Karnieli 2002). Abundances of birds and their habitats are correlated with NDVI (Maurer 1994; Osborne *et al.* 2001). We used NDVI to investigate the effect of ecological conditions during winter on individual phenotype and breeding performance in the migratory barn swallows that breed in Europe and winter south of the Sahara.

The barn swallow is semi-colonial and socially monogamous, relying on insect prey caught on the wing (Møller 1994a). Plumage is moulted in winter (Møller 1994a). The length of the outermost tail feathers (tail length) of males is a condition-dependent secondary sexual character involved in female mate choice (Møller 1988, 1989a, 1990, 1994a; Saino *et al.* 1997), while the length of the central tail feathers (central tail length) and wing length are sexually monomorphic characters (Møller 1994a; Møller *et al.* 1995). Our study population in northern Italy mainly winters between Ghana and the Central African Republic (see § 2b).

Over a period of 10 years, we related phenotypic values of the same individuals recorded during the breeding seasons of two or more years in Italy to NDVI values

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recorded in the African winter quarters during the winter preceding each focal breeding season. We investigated both short-term effects of NDVI on the phenotypes of individuals, by relating phenotypic values to NDVI values recorded the previous winter, and long-term effects, by relating phenotypic values to NDVI values recorded two winters before the focal breeding season. These analyses were conducted to test for delayed effects of environmental conditions on phenotypic plasticity.

In addition, we analysed temporal variation in breeding performance at the population level by relating mean annual data for the population to NDVI values in the previous winter.

2. MATERIAL AND METHODS

(a) *Barn swallow phenotypic data*

We studied barn swallows in 18 colonies in northern Italy during 1993–2002. We marked adults and measured the lengths of wings, the two outermost tail feathers and the left innermost tail feather (to the nearest 1 mm), and body mass (to the nearest 0.1 g). Wing and tail length were expressed as the mean of the left and right character. Wing and tail feathers are moulted before arrival at the breeding grounds in 99% of the individuals. Infestation by a chewing louse (*Machaerilaemus malleus*) was estimated by counting the holes they make in tail feathers (Møller 1991). Breeding date was taken as the date of laying of the first egg in the first clutch. Clutch size was the number of eggs at clutch completion.

We considered individuals that were captured during two or more (up to six) breeding seasons and analysed their phenotypic values recorded in each breeding season (breeding season i) in relation to NDVI values recorded in the African winter quarters during the winter preceding breeding season i (hereafter NDVI_i) and also in the previous winter (NDVI_{i-1}).

(b) *Normalized difference vegetation index*

NDVI is recorded by US National Oceanic and Atmosphere Administration satellites. Data calibrated for inter- and intra-sensor degradation can be found at <http://edcintl.cr.usgs.gov/adds/adds.html>. High NDVI indicates high rainfall, green vegetation and thus favourable conditions for swallows. To identify the wintering range of our study population we used recoveries in sub-Saharan Africa of barn swallows ringed in Italy between 15 May and 15 August (mean date, 5 June), when the number of migrating barn swallows is minimal, in an area ranging from 41°30' N to 45°45' N and 7°20' E to 13°53' E. This area includes our colonies centred at 45°20' N, 9°27' E. Out of 19 African recoveries that met these requirements, 18 were from Ghana (6°32' N 1°24' W, one individual), Nigeria (6°17' N 8°55' E, 10 individuals) or Central African Republic (3°59' N 17°19' E, four individuals; 4°18' N 17°25' E, one individual; 4°19' N 17°26' E, one individual; 4°23' N 18°37' E, one individual; the last three locations were averaged). The fact that a large number of barn swallows (more than 300) ringed in other European countries have been recovered in other parts of Africa suggests that the large proportion of recoveries of Italian swallows from the sub-Saharan region we considered was not determined by a small capture effort in other African regions.

We estimated mean winter (December–February) NDVI for a region between 2° N and 8° N and 3° W and 21° E, which includes all Italian recovery locations except the single outlier from Zambia (12°11' S 26°23' E). We first computed the mean

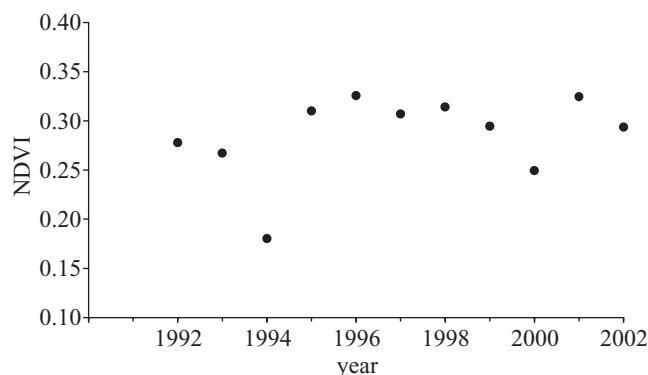


Figure 1. Mean NDVIs for the whole barn swallow wintering area in the winters preceding the breeding seasons of years 1992–2002. Data for 1992 are included because they were used to calculate the long-term effect of NDVI (see § 2a).

NDVIs within 1° latitude \times 2° longitude ‘subareas’. NDVIs estimated for different subareas had high within-year repeatability (ANOVA with year as factor: $F_{9,720} = 43.91$, $p < 0.0001$, $R = 0.371$), implying that among-year variation was significantly larger than within-year variation among subareas. We then estimated mean NDVI by averaging values for subareas. Second, we calculated mean winter NDVI by averaging values in squares located within circles centred on the four recovery locations with radii of 150, 300 or 450 km. Mean NDVI estimates for the entire wintering area (figure 1) were strongly positively correlated with those around recovery locations (correlation coefficient with NDVI always greater than 0.995, $n = 10$, $p < 0.001$). We therefore decided to use NDVI from the entire wintering range in subsequent analyses. NDVI data from consecutive years were not correlated ($r = 0.044$, $n = 10$, $p = 0.90$), implying low temporal autocorrelation of NDVI values.

(c) *Population-level analyses*

In a survey of a maximum of 131 breeding colonies per year in the same area, we measured mean annual breeding date and fledging success at the population level over 10 years (1993–2002). These data were used to investigate the population consequences of environmental conditions in the winter quarters. We estimated these consequences in terms of the size of the post-breeding population using the mean NDVI value for all years ± 2 s.d.

(d) *Statistical analyses*

We used analysis of covariance of individual phenotypic values (including tail and wing morphology, body mass, infestation by an ectoparasite, breeding date and clutch size; see § 2a) in each breeding season with individual as the main effect and NDVI_i and NDVI_{i-1} (see § 2a) as covariates. To test for an association between breeding date or clutch size and length of male tail ornaments we used analyses of covariance with individual as the main effect and tail length as the covariate. The mean NDVI value of the winter preceding the breeding season of 1994 was exceptionally low (figure 1). To test the stability of our results, we also ran all the analyses while excluding data from the breeding season of 1994. We adjusted the significance level for simultaneous tests on seven phenotypic variables for each sex according to a sequential Bonferroni procedure. Standard errors of parameter estimates from analyses of covariance are given in parentheses.

Table 1. Effect of NDVI values in the winter quarters (covariate) on phenotypic values of barn swallows recorded in Italy during the following breeding season from analyses of covariance where we included individual as the main effect. (*n* is the number of individuals involved in the analyses. The number of data points is *n* + denominator d.f. + 1. Superscript asterisks identify values that are significant after sequential Bonferroni correction for seven simultaneous tests. Superscripts ‘a’ and ‘b’ identify *p*-values that are significant after sequential Bonferroni correction (a: *p* < 0.01; b: *p* < 0.05) in analyses where data from the breeding season of 1994, which followed a winter with extremely low NDVI values, were excluded from the analyses.)

variable	<i>n</i>	coefficient (s.e.)	<i>F</i>	d.f.	<i>p</i>
males					
wing length (mm)	595	4.46 (0.94)	22.59	1,840	< 0.001 ^{*a}
tail length (mm)	584	19.38 (3.62)	28.63	1,817	< 0.001 ^{*a}
central tail length (mm)	594	-2.19 (0.97)	5.14	1,836	0.024
body mass (g)	598	-0.80 (0.70)	1.34	1,842	0.25
chewing-louse infestation	598	-7.59 (12.14)	0.39	1,841	0.53
breeding date	306	-22.52 (19.34)	1.36	1,421	0.24
clutch size	306	4.27 (1.06)	16.20	1,421	< 0.001 ^{*a}
females					
wing length (mm)	527	-0.25 (0.97)	0.07	1,742	0.79
tail length (mm)	511	12.20 (2.59)	22.25	1,723	< 0.001 ^{*b}
central tail length (mm)	523	-3.84 (0.97)	15.55	1,736	< 0.001 ^{*a}
body mass (g)	533	-0.03 (1.48)	0.01	1,742	0.98
chewing-louse infestation	533	-20.91 (13.56)	2.38	1,741	0.12
breeding date	333	-53.79 (18.12)	8.82	1,451	0.003 ^{*a}
clutch size	333	-0.14 (1.02)	0.02	1,451	0.89

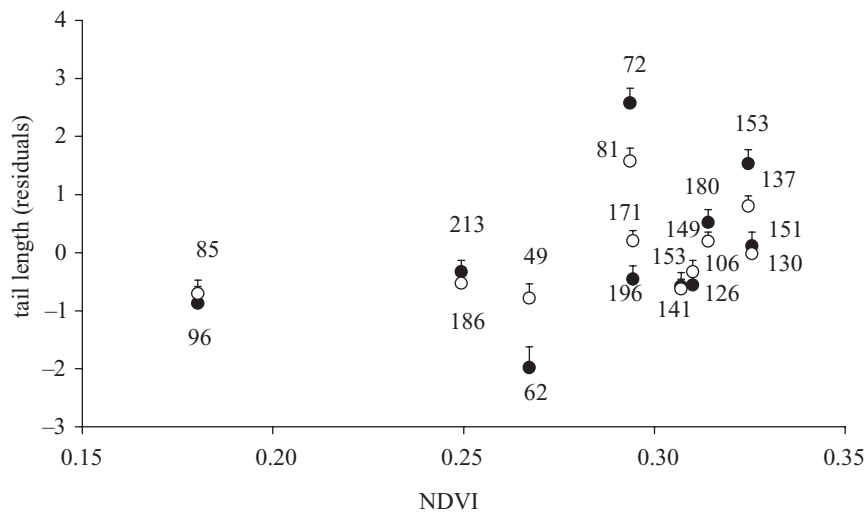


Figure 2. Tail lengths of male (filled circles) and female (open circles) barn swallows captured during two or more breeding seasons in Italy in relation to NDVI in the winter quarters during the winter preceding the focal breeding season. Values are mean (+ 1 s.e.) residuals from an analysis of variance with individual as the main effect. Numbers are sample sizes (see also table 1).

3. RESULTS

(a) Phenotypic plasticity in relation to environmental conditions in the winter quarters

Wing and tail lengths of individual males were positively related to NDVI recorded in the previous winter (NDVI_{*i*}) (table 1; figures 2 and 3). Among females, a significant positive correlation with NDVI_{*i*} existed for tail length but not wing length (table 1; figure 2). In females, the length of the innermost tail feathers was significantly and negatively related to NDVI_{*i*}, while this relationship was not significant after sequential Bonferroni correction of significance level in males (table 1). NDVI_{*i*} negatively predicted the breeding date of females, implying delayed breeding

following winters with relatively poor conditions in Africa (table 1). In addition, NDVI_{*i*} positively predicted the size of the clutch fathered by individual males (table 1; figure 4). The results of analyses of covariance with individual as the main effect where we excluded the year (1994) that had extremely low NDVI_{*i*} (see §2d) were qualitatively similar to those obtained from the analyses run on the whole dataset (see table 1 for significance of the tests).

We tested for long-term effects of conditions in Africa on phenotype in analyses of covariance where we included individual as the main effect and both NDVI_{*i*} and NDVI_{*i-1*} as covariates. We found positive effects of NDVI_{*i-1*} on the wing lengths of both sexes (males: *F*_{1,839} = 22.48, *p* < 0.001, coefficient = 4.29 (0.90);

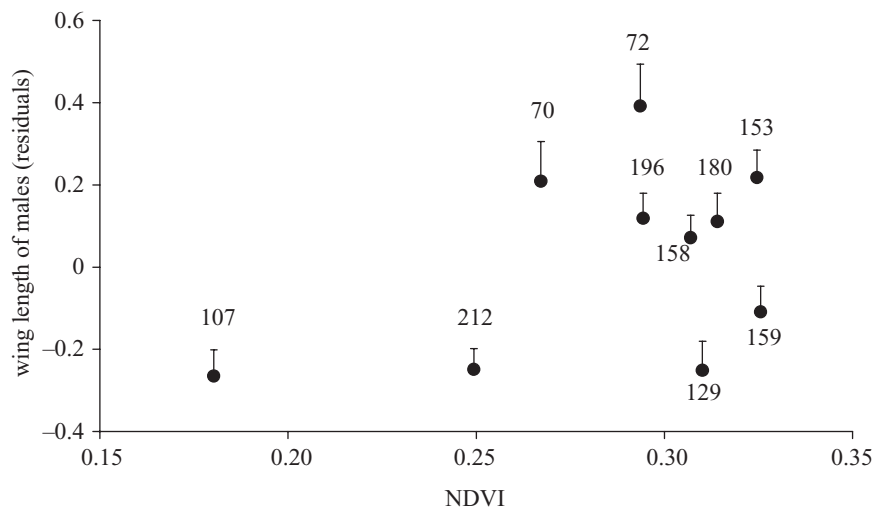


Figure 3. Wing lengths of male barn swallows captured during two or more breeding seasons in Italy in relation to NDVI in the winter quarters during the winter preceding the focal breeding season. Values are mean (+ 1 s.e.) residuals from an analysis of variance with individual as the main effect. Numbers are sample sizes (see also table 1).

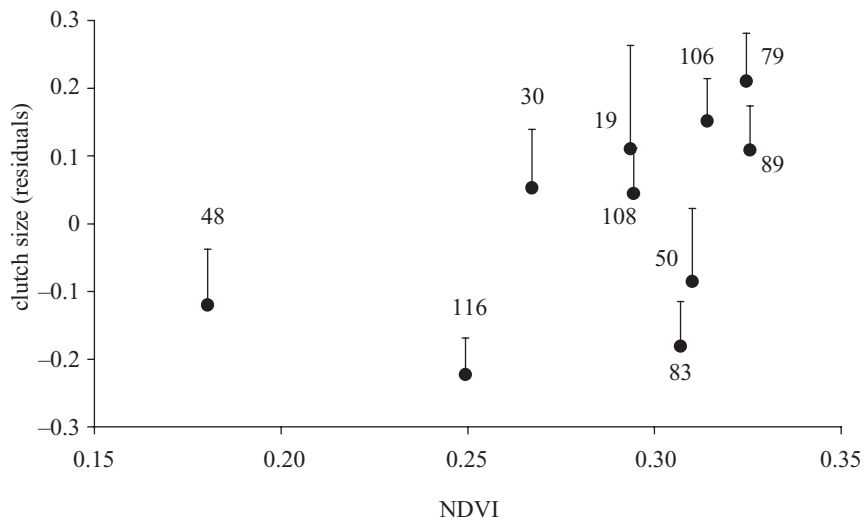


Figure 4. Sizes of the clutches laid by mates of individual males captured during two or more breeding seasons in Italy in relation to NDVI in the winter quarters during the winter preceding the focal breeding season. Values are mean (+ 1 s.e.) residuals from an analysis of variance with individual male as the main effect. Numbers are sample sizes (see also table 1).

females: $F_{1,741} = 37.38$, $p < 0.001$, coefficient = 5.64 (0.92)). In addition, there was a positive effect of $NDVI_{i-1}$ on chewing-lice infestation of males ($F_{1,840} = 13.05$, $p < 0.001$, coefficient = 42.55 (11.78)). In these analyses, the results for the effect of $NDVI_i$ were qualitatively similar to those reported in table 1.

In analyses of covariance with individual as the main effect, tail length negatively predicted breeding date ($F_{1,408} = 159.1$, $p < 0.0001$, coefficient = -2.06 (0.16)), implying that males that had a greater change in tail length between consecutive years bred earlier than males that had a smaller change, and positively predicted clutch size ($F_{1,408} = 38.51$, $p < 0.001$, coefficient = 0.07 (0.01)). The positive covariation between clutch size and tail length persisted in an analysis of covariance where we included breeding date as a covariate (effect of tail length: $F_{1,407} = 9.82$, $p = 0.002$, coefficient = 0.04 (0.01)). This result implies that a larger increase in the size of clutches laid by mates of males that had a larger increase in tail

length did not simply result from an earlier breeding date being associated with increased clutch size ($F_{1,408} = 47.12$, $p < 0.0001$, coefficient = -0.02 (0.002)). These results remained qualitatively similar when data from the breeding season of 1994 were excluded from the analyses (details not shown). Clutch size strongly predicts fledging success in our study population ($F_{1,5485} = 1506.65$, $p < 0.0001$, coefficient = 0.81 (0.11)).

(b) Population consequences of environmental conditions in the winter quarters

After winters with high NDVI, mean first clutch initiation estimated at the population level occurred earlier (regression on $NDVI_i$: $t = -2.342$, d.f. = 1,8, $p = 0.047$, coefficient = -59.49 (25.40), based on $n = 5862$ first clutches) and mean annual fledging success was higher ($t = 2.650$, d.f. = 1,8, $p = 0.029$, coefficient = 3.995 (1.50), based on $n = 6917$ first broods) than after winters with low NDVI. Hence, favourable conditions in winter resulted in

more-productive first broods. The difference in fledging success between first broods in poor years (defined as years when NDVI = mean - 2 s.d. = 0.198) and favourable years (NDVI = mean + 2 s.d. = 0.376) estimated from the slope of the regression of fledging success on NDVI was 0.71 offspring. Earlier first-clutch initiation by *ca.* 11 days in favourable years results in an 11% increase in the frequency of second broods and thus in 0.39 more nestlings produced by second broods in favourable than in poor years, since the average number of offspring produced by second broods in our population is 3.6 nestlings (N. Saino, T. Szép, R. Ambrosini, M. Romano and A. Pape Møller, unpublished data). As a consequence of the combined effects of more-productive first broods and a larger frequency of second broods, the post-breeding population size was *ca.* 15% larger after favourable winters than after poor winters.

However, the relationships between NDVI_t and both breeding date and fledging success were not significant when data from the breeding season of 1994, which had very low associated NDVI_t, were excluded from the analyses (regression of breeding date: $t = -0.15$, d.f. = 1,7, $p = 0.89$; fledging success: $t = 1.41$, d.f. = 1,7, $p = 0.20$). In fact, breeding date in 1994 was significantly later than in the other nine years ($t_8 = 3.07$, $p = 0.015$). In addition, in 1994 fledging success tended to be smaller than in the other years ($t_8 = 1.93$, $p = 0.09$).

4. DISCUSSION

Analyses of phenotypic plasticity in the barn swallow showed that ecological conditions during winter influence phenotypic traits, including a secondary sexual character of males, parasitism and breeding performance of individuals. This study relies on the assumption that African recoveries reflect the wintering areas of barn swallows breeding in Italy, an assumption that cannot be directly verified at present. However, its validity is supported by the fact that almost all recoveries of Italian swallows are from the sub-Saharan region we considered, despite a large capture effort in other African regions.

The present results thus provide evidence that individuals of a migratory bird are affected by environmental conditions many months later, when the migratory barn swallows are in a different continent. We found evidence of several mechanisms of carry-over effects from the winter quarters to the breeding areas. First, breeding performance was associated with environmental conditions during wintering. In addition, we found evidence of plumage being affected by environmental conditions during moult in the winter quarters. Tail and wing lengths in males and tail length in females were positively correlated with NDVI, whereas central tail length in females was negatively correlated with NDVI. These findings suggest that not all characters are affected similarly by changes in environmental conditions, and that these differences among characters depend on the sex of the individual. Such sex dependence suggests that both natural and sexual selection may have been important in shaping the reaction norms of the phenotype in relation to environmental conditions.

Models of sexual selection posit that male secondary sexual characters are condition-dependent traits that

reveal the quality of signallers (Heywood 1989; Iwasa *et al.* 1991; Andersson 1994). Female barn swallows prefer long-tailed males and adjust clutch size to male ornamentation (Møller 1988, 1989*a*, 1990, 1994*a*; Saino *et al.* 1997). We have shown that ecological conditions during winter predict the expression of a male secondary sexual character. Individual males had longer tails after favourable winters, and males with large sexual ornamentation advanced their breeding dates more and had larger clutch sizes than males with small ornamental tails. Clutch size predicts fledging success in our study population. Hence, NDVI predicted the expression of a male secondary sexual character that affected female reproduction, thereby increasing male breeding success. However, females delayed breeding after adverse winter conditions. Therefore, ecological conditions during winter affected the breeding successes of the two sexes through different mechanisms.

We investigated both long-term and short-term effects of ecological conditions on phenotype and found evidence that both effects were operating. Wing lengths of both sexes depended on NDVI two winters before each focal breeding season. Likewise, there was a long-term positive effect of NDVI on the abundance of chewing lice in males. To the best of our knowledge, this is the first empirical evidence of long-term effects of environmental conditions in the winter quarters of a migratory bird on phenotypic plasticity. The mechanisms generating long-term links between ecological conditions and phenotype remain to be elucidated. Insect prey may show a delayed response to variation in primary productivity, so that favourable conditions during one winter have positive effects on insect abundance the following winter. The positive long-term effect of NDVI on chewing-lice infestation may result from the effects of humidity on demographic trends in chewing lice (Moyer *et al.* 2002), which however may show a delayed population response to ecological conditions.

Individual phenotypic responses to changes in environmental conditions may affect future population size through the different effects of the environment on different individuals. We estimated the population consequences of NDVI by determining the effects of poor and good conditions on post-reproduction population size. Using mean NDVI \pm 2 s.d. as the two extreme environments, we found that this range of environmental conditions resulted in a considerable variation in population size of 15%, which may have demographic consequences, since population size in the breeding season is strongly correlated with the post-breeding population size in the previous year (Møller 1989*b*).

The significant associations between NDVI and both breeding date and fledging success at the population level, but not at the individual level, appeared to be produced by a year (1994) with very low NDVI (table 1). The breeding date was delayed in the spring following this winter compared with other years, suggesting that very bad conditions in the winter quarters can affect the phenology of breeding at the population level.

Climatic change such as that affecting the desertification of the Sahel is thought to be caused by global warming, and results in reduced primary production (Wickens 1997). Barn swallow populations breeding in

several European regions have undergone a marked decline in the last decades (e.g. Møller 2001; but see Robinson *et al.* 2003). Any future deterioration of the ecological conditions experienced by barn swallows that winter in this African area would reduce the productivity of their populations. This effect will be partly mediated by a reduction in the expression of a condition-dependent secondary sexual character produced during the winter, affecting female reproductive decisions half a year later. However, concomitant effects of ecological conditions during migration or in the breeding quarters, such as changes in animal farming practices in the breeding quarters (Møller 2001; Ambrosini *et al.* 2002), may exacerbate the current negative trends of barn swallow populations in Italy and other European regions. The present results prompt future studies aimed at establishing the generality of our results in other species.

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