AN ANALYSIS OF CONTINENT-WIDE PATTERNS OF SEXUAL SELECTION IN A PASSERINE BIRD

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Abstract.—Patterns of selection are widely believed to differ geographically, causing adaptation to local environmental conditions. However, few studies have investigated patterns of phenotypic selection across large spatial scales. We quantified the intensity of selection on morphology in a monogamous passerine bird, the barn swallow *Hirundo rustica*, using 6495 adults from 22 populations distributed across Europe and North Africa. According to the classical Darwin-Fisher mechanism of sexual selection in monogamous species, two important components of fitness due to sexual selection are the advantages that the most attractive males acquire by starting to breed early and their high annual fecundity. We estimated directional selection differentials on tail length (a secondary sexual character) and directional selection gradients after controlling for correlated selection on wing length and tarsus length with respect to these two fitness components. Phenotype and fitness components differed significantly among populations for which estimates were available for more than a single year. Likewise, selection differentials and selection gradients differed significantly among populations for tail length, but not for the other two characters. Sexual selection differentials differed significantly from zero across populations for tail length, particularly in males. Controlling statistically for the effects of age reduced the intensity of selection by 60 to 81%, although corrected and uncorrected estimates were strongly positively correlated. Selection differentials and gradients for tail length were positively correlated between the sexes among populations for selection acting on breeding date, but not for fecundity selection. The intensity of selection with respect to breeding date and fecundity were significantly correlated for tail length across populations. Sexual size dimorphism in tail length was significantly correlated with selection differentials with respect to breeding date for tail length in male barn swallows across populations. These findings suggest that patterns of sexual selection are consistent across large geographical scales, but also that they vary among populations. In addition, geographical patterns of phenotypic selection predict current patterns of phenotypic variation among populations, suggesting that consistent patterns of selection have been present for considerable amounts of time.

Key words.—Barn swallow, breeding date, Darwin-Fisher theory of sexual selection, fecundity selection, *Hirundo rustica*, sexual dimorphism.

Numerous studies have investigated the spatial and temporal distribution of near neutral loci such as allozymes, minisatellites, and microsatellites (e.g. Endler 1986; Avise 1994). These studies have shown clear patterns of variation with latitude and environmental gradients such as temperature and humidity (e.g., Endler 1986; Bell 1997). Likewise, numerous studies of spatial variation in phenotype such as reflected by Bergman's and Gloger's rule have indicated that there are consistent patterns of spatial variation in size and shape across taxa, albeit with many exceptions (e.g., Brown and Lomolino 1998). These studies indicate that response to local environmental conditions has resulted in local adaptation, due to processes of selection and microevolutionary change as modified by geneflow along a gradient; a process that has been modeled extensively (e.g., Garcia-Ramos and Kirkpatrick 1997; Kirkpatrick and Barton 1997; Peck and Welch 2004).

Many fewer studies have investigated spatial patterns of selection in relation to variation in phenotype, although such patterns of selection together with patterns of gene flow would be expected to be the underlying basis for clinal variation in phenotype. For example, recent studies of climate change have shown consistent spatial patterns of variation in laying date of passerine birds across Europe and advantages of early timing of reproduction (e.g., Both et al. 2004). Likewise, studies of the degree of brood parasitism of the magpie *Pica pica* by the parasitic great spotted cuckoo *Clamator glandarius* across the entire distribution range of the host in Europe have shown how patterns of selection covary with patterns of phenotypic distribution (Soler et al. 1999, 2001). In populations with intense selection from the brood parasite host, resistance as reflected by ejection of foreign eggs is elevated compared to allopatric populations, both due to selection in the population in question but also due to gene flow from other populations (Soler et al. 1999, 2001). However, such large-scale studies are rare, and we still only have

856

a very poor understanding of how patterns of selection covary with patterns of phenotype across continent-wide spatial scales.

Here we investigate spatial patterns of sexual selection in relation to spatial patterns of phenotype, using the barn swallow *Hirundo rustica* as a model system. This model system has the advantage that a large amount of knowledge is available for many different populations for most traits related to reproduction. A range of experimental and observational studies has identified a large number of different components of sexual selection. We concentrated on two components of sexual selection. First, we quantified the classical Darwin-Fisher component of sexual selection in monogamous species arising from benefits of early breeding by the most attractive males (Darwin 1871; Fisher 1930; Kirkpatrick et al. 1990). Fisher (1930) in his classical model of this mechanism assumed that females would differ in body condition for entirely phenotypic reasons, and that females in prime condition would reproduce early, thereby causing the most attractive males to reproduce earlier than less attractive males due to their mates being in prime condition. Because early start of reproduction causes an advantage in terms of probability of recruitment in many different species (e.g., Møller 1994), attractive males would recruit a disproportionate number of offspring to subsequent generations. This mechanism of sexual selection has found empirical support in a few species of monogamous birds (O'Donald 1983; Møller 1988; McGraw et al. 2001), but not in others (Dearborn and Ryan 2002). The intensity of selection on breeding date in relation to male attractiveness can be assessed by quantifying the relationship between the standardized size of the secondary sexual character and the standardized fitness component (breeding date).

Second, attractive males will also gain a sexual selection advantage by producing more offspring when mated to females of superior condition, as suggested by Fisher (1930). This implies that attractive males will have mates that potentially can lay more eggs or lay eggs more frequently than less attractive males. Therefore, this component of sexual selection is qualitatively different from the first component that exclusively relies on benefits acquired due to earliness of reproduction. Again, this mechanism of superior reproductive output produced by females mated to the most attractive males has been demonstrated repeatedly in many different species (e.g., Møller 1988, 1994; review in Møller and Legendre 2001). We can assess the intensity of sexual selection caused by differential access of attractive males to fecund females by quantifying the relationship between the standardized size of the secondary sexual character and the standardized fitness component (annual fecundity). The intensity of selection can be quantified using the approach of Arnold and Wade (1984) and Lande and Arnold (1983), whereby phenotypic traits are standardized to a mean of zero and a variance of one whereas the fitness components are standardized to a mean of one.

The objectives of this study of two components of sexual selection in the barn swallow across an entire continent were (1) to determine whether the phenotypes and the intensity of selection were consistent for particular populations in different years; (2) to determine if patterns of selection on a secondary sexual character and two control characters showed consistent directionality across study populations in Europe and North Africa; (3) to assess whether the intensity of selection was similar in males and females; (4) to quantify whether sexual selection due to breeding date reinforced sexual selection due to annual fecundity; (5) to assess to which extent effects of age were confounding estimates of selection; and (6) to assess whether current patterns of phenotypic variation in morphology and sexual size dimorphism in morphology could be accounted for by current patterns of selection. To this end we investigated sexual and natural selection in over 6000 adults from 22 populations across North Africa and Europe.

We studied barn swallows for which a large number of observational and experimental studies of sexual selection have been performed for the last 18 years (Møller 1994; www.hirundorustica.com). This bird is on average a 20-g migratory passerine that winters in tropical, subtropical, and temperate climates of the Old and New World, although reproduction takes place in subtropical and temperate climates in the Northern Hemisphere. Males and females are similar in phenotype except for the outermost tail feathers being longer in males than in females, ranging from an average difference of 5% in Northern Africa to over 20% difference in Scandinavia (Møller 1994). Males arrive at the breeding ground before females, where they establish a small breeding territory inside a building. Males subsequently attempt to attract a mate by singing and displaying their tail feathers (Møller 1994). Once a mate has been acquired, males and females build a nest of mud, in which the female will lay a clutch of usually five eggs that in the Old World are incubated entirely by the female for two weeks. Males and females feed the nestlings for three weeks, and depending on latitude a second or a third clutch can be reared the same season.

Tail length of males in Europe is condition dependent as revealed by parasite loads, radiation, senescence, and tail length manipulation causing a reduction in tail length following the molt in Africa (Møller 1989, 1990a, 1993a, 2002; Møller and de Lope 1999). Likewise, environmental conditions in Africa affect tail growth (Saino et al. 2004). Long tails provide males with a number of different sexual selection benefits in terms of mate acquisition, timing of reproduction, fecundity of mates, differential parental investment by females, extrapair paternity, maternal egg effects, and reduced risks of infanticide (Møller 1988, 1990b, 1994; de Lope and Møller 1993; Saino et al. 1997a, 2002a,b; Kose and Møller 1999; Kose et al. 1999). In contrast, manipulation of the length of tails in female barn swallows has shown no evidence of sexual selection related to tail length (Cuervo et al. 1996), whereas females pay fitness costs of experimentally elongated tails by reduction in fecundity the subsequent year (Cuervo et al. 2003). Tail length has been hypothesized to provide males with a natural selection advantage (e.g., Evans and Thomas 1997), although no study has so far provided any evidence of associations between flight properties derived from the tail and fitness (Møller et al. 1998a). Male tail length increases slightly from yearlings to middle aged birds, decreasing again at old age (Møller and de Lope 1999).

FIG. 1. Populations involved in the present study of geographical variation in selection on morphology in barn swallows.

MATERIAL AND METHODS

Study Areas

We investigated 22 study populations across Europe and North Africa (Fig. 1): Jyväskylä (62°15′N, 25°44′E), Finland (J. Kilpima, studied in 1998); Häädemeeste (58°24′N, 24°30′E), Estonia (M. Kose, 1996); Skierniewice (51°57′N, 20°05′E), Poland (P. Matyjasiak, 2004); Szypliszki (54°15′N, 23°05′E), Poland (P. Matyjasiak, 2003); Kraghede (57°12′N, 10°00′E), Denmark (A. P. Møller, 1984–2004); Chernobyl (51°10′N, 30°05′E), Ukraine (A. P. Møller, 1990, 1996); Kanev (49°04′N, 33°19′E), Ukraine (A. P. Møller, 1990, 1996); Balmazújváros (47°37′N, 21°21′E), Hungary (P. L. Pap, 1999–2003); Baulmes-Giez (46°48′N, 6°34′E) 1997–2003; Buus (47°30′N, 7°52′E) 1997–2003; Dompierre (46°51′N, 6°59′E) 2000; Egerkingen (47°19′N, 7°47′E) 2000; Jura (47°15′N, 7°15′E) 1997–2003; Pays d'Enhaut (46°28′N, 7°07′E) 1999–2003; Pläviggin (46°55′N, 9°46′E) 1998, Riviera (46°15′N, 9°01′E) 1997–2003; Sarganserland (47°03′N, 9°25′E) 1997–2003; Vaulruz (46°37′N, 6°59′E) 1999–2003, Switzerland (Swiss Ornithological Institute); Milano (45°28′N, 9°10′E), Italy (N. Saino, 1993–1996, 1998); Badajoz (38°50′N, 6°59′W), Spain (F. de Lope, 2001–2004); Sevilla (37°11′N, 6°16′W), Spain (J. J. Cuervo, 1997); and Annaba (36°50′N, 7°55′E), Algeria (Y. Chabi and R. Sakraoui, 2002–2004). A total of 22 populations will allow a reasonable statistical power of statistical tests, although a

better coverage could have been advantageous. Most populations only provided data for one or a few years, with the Danish population being an exception. However, the large number of estimates from Denmark is likely to have caused any statistical tests to be conservative because a dramatic recent increase in male tail length by 1.3 standard deviations during a period of 20 years (Møller and Szép 2005) has caused an amount of variation in that population that is larger than several of the differences among populations reported here. We were able to obtain information for a total of 3161 males and 3334 females.

All populations were located in farmland habitat where barn swallows mainly bred inside barns, but also other buildings.

Phenotypic Measurements

Upon capture we measured length of tail, wing, and tarsus in a standardized way. APM instructed how measurements should be recorded in all populations, with the exception of the Swiss populations. The barn swallow project in Switzerland was directed by the Swiss Ornithological Institute with the help of a large number of amateurs. In the present study we used the length of the outermost tail feathers and the length of the flattened wing, measured to the nearest mm with a ruler and tarsus length was measured with a caliper to the nearest 0.1 mm. All measurements at each site were made by as few measurers as possible (usually one) to avoid problems of errors among measurers. Repeated measurements of the same individuals the same season have revealed that these characters were measured highly repeatably with repeatabilities (Falconer and Mackay 1996) exceeding 94% (Møller 1991, 1994; F. de Lope, M. Kose, P. L. Pap, N. Saino, unpubl. data). We had information on measurements of 114 individual barn swallows measured by APM and another co-author for four different populations (M. Kose; Estonia; P. Pap, Hungary; N. Saino, Italy; and F. de Lope, Spain). Analyses of variance with measurement as the dependent variable and measurer (a dichotomous factor with two levels: APM or another person), population, and measurer by population interaction as factors only revealed highly significant effects of population, but no significant effect of measurer or population by measurer interaction for the three characters (Table 1). This implies that variation among populations was much greater than variation among measurers, and that there was no significant difference in precision of measurements in populations as revealed by the small measurer by population interaction (Table 1). This justifies the use of the available data, under the assumption that the populations from which

TABLE 1. Analyses of variance of size of three morphological characters in relation to measurer, population, and measurer by population interaction. Values are sums of squares. Sample size is 114 individuals measured by two different measurers (APM and another co-author).

Factor	Tail length	Wing length	Tarsus length	df
Measurer	1959.53	0.18	0.37	1
Population	14,598.52***	1217.74***	18.51***	3
Measurer × population	6619.60	0.16	1.30	3
Residual	629,382.40	1612.64	140.23	220

*** $P < 0.0001$.

repeat measurements were unavailable (Finland, Poland, all populations in Switzerland, Sevilla, Spain, and Algeria) did not differ from populations with such measurements or populations that were measured by APM (Estonia; Denmark; Ukraine; Hungary; Italy; Badajoz; Spain). There is no reason to believe that this assumption should have been violated, given that all measurers were instructed in a similar way. The data from Switzerland only consisted of measurements of the length of the outermost tail feathers, and these measurements were made in a consistent way. Again, all measurers were instructed beforehand how to make the measurements, and trials have shown a very high degree of consistency.

The justification for using length of tail, wing, and tarsus as important phenotypic variables is that tail length is a secondary sexual character involved in sexual selection (e.g., Møller 1988). Wing length is an important character that directly relates to the ability to fly, and males with long tails tend to have longer wings, as a means of reducing the aerodynamic costs of exaggerated tail feathers (Møller et al. 1995a). Tarsus length is a measure of skeletal body size, and inclusion of this variable in the selection analyses allows control for any effects of allometric variation on tail length.

All individuals involved in experiments with the exception of untreated controls were excluded from the analyses. Because treatments were assigned randomly, this cannot have caused any bias. Individuals receiving a noncontrol treatment in any given year only involved a small fraction of individuals.

Because barn swallows breed indoor, all reproducing adults can readily be captured in mist nets that are placed across windows and doors. Capture-mark-recapture analyses have shown that the recapture probability exceeds 80% in Switzerland (L. Schifferli and J. von Hirschheydt, unpubl. data) and 95% in the other populations (Møller and Szép 2002; Pap et al. 2005, and unpubl. data). Because all adults were provided with aluminum and color bands (the latter in all populations with the exception of Switzerland) upon capture, subsequent observations were used to assign birds to nests. These observations also allowed quantification of capture efficiency, showing in all populations that more than 95% of all adults had color bands at the end of the breeding season. This ensured that subsequent estimates of selection were unlikely to be biased due to the inability to include a significant proportion of individuals in the analyses.

Summary statistics are reported in Appendix 1 available online at: http://dx.doi.org/10.1554/05-665.1.s1.

Reproductive Variables

All potential breeding sites were visited regularly to record reproductive events. Laying date was defined as the date when the first egg of a clutch was laid, assuming that one egg was laid daily, which generally is the case with the exception of rare laying breaks (Møller 1994).

Brood size at fledging was defined as the number of nestlings present at the last nest check before fledging (which always happened after day 12 of the 20 days nestling period). Nestling mortality during the last week of the nestling period is less than 1% (A. P. Møller, F. de Lope, and N. Saino,

unpubl. data). We recorded laying date and brood size for second and third clutches as described above. Annual fecundity was defined as the number of fledglings per pair in all three broods combined.

Summary statistics are reported in Appendix 2 available online at: http://dx.doi.org/10.1554/05-665.1.s2.

Age

We estimated age in all populations where we worked intensively to catch all adults during a number of years by assigning an age of one year to birds that had not been banded previously. This criterion is reliable because only one of more than 375 local recruits was ever captured at an age older than one year. The single exception was captured as two years old (A. P. Møller, F. de Lope, and N. Saino, unpubl. data). Because laying date, annual fecundity, and tail length mainly change from yearlings to two year old individuals (Møller and de Lope 1999), we classified adults as yearlings (assigning them a value of 0) or older birds (assigning them a value of 1) for the following selection analyses. Information on age was only available for 13 populations.

Selection Analyses

We analyzed selection using the approach developed by Lande and Arnold (1983) and Arnold and Wade (1984). Briefly intensity of directional selection can be estimated from linear regression models. The dependent variable in this approach is a standardized measure of fitness, in which fitness is divided by mean fitness to obtain a relative estimate of fitness with a mean value of one. Phenotypic characters before selection are standardized to a mean of zero and a variance of one. Estimated intensities of directional selection provide estimates of selection acting on the trait, with the standardized selection differential reflecting the change in fitness for a unit change in phenotype estimated in standard deviation units. Directional selection differentials were estimated as the regression coefficient of standardized fitness on standardized phenotype, as described above (Arnold and Wade 1984). Partial selection differentials (selection gradients), controlling for indirect selection on a trait due to selection on other traits (here wing and tarsus length) that are correlated with the trait in question, were estimated using multiple linear regression with the standardized fitness component as the dependent variable and the standardized phenotypic characters as independent variables (Lande and Arnold 1983; Arnold and Wade 1984). Again, the selection gradient provides an estimate of the change in phenotype in standard deviation units for a unit change in fitness. Statistical significance of selection differentials and gradients is inappropriate as a measure of effect size, because it will depend strongly on sample size. Many of the linear selection differentials (and gradients) were statistically significant. Therefore, many statisticians recommend use of measures of effect size rather than reliance on null hypothesis testing as an approach to evaluation of hypotheses (e.g., Burnham and Anderson 1998). Hence, we used selection differentials and selection gradients as estimates of effect size because they have properties of standardization similar to Hedges' d in meta-analysis (e.g., Hedges and Olkin 1985; Rosenthal 1991,

1994). Even without statistical significance, such a standardized measure of effect size will provide the best estimate of the strength of a relationship.

The selection in relation to the fitness components considered here are as follows: (1) Breeding date selection, which represents the classical Darwin-Fisher mechanism of sexual selection in monogamous species for which fitness was considered to be the date when the first egg was laid. Because recruitment to the local breeding population decreases linearly with breeding date (Møller 1994 for Denmark; F. de Lope, and N. Saino, unpubl. data), early breeding constitutes an important component that affects overall fitness. (2) Fecundity selection was quantified with respect to the total number of fledglings produced in a year as a second fitness component, with more offspring produced signifying greater fitness.

The use of total number of fledglings per year as a fitness measure requires justification for male barn swallows, because approximately 30% of all nestlings are extrapair offspring in Denmark and Italy (Møller and Tegelström 1997; Saino et al. 1997a) and 20% in Spain (Møller et al. 2003). Hence, it is possible that estimates of selection based on simple counts of number of offspring may be biased. However, Saino et al. (1997a) have shown that there is a strong positive correlation between the number of offspring fathered in the own nest and the number of offspring fathered in other nests. This demonstrates that male barn swallows losing paternity in their own nest do not simply gain paternity elsewhere, thereby compensating for the loss of paternity in their own nest. These arguments suggest that the overall magnitude of fecundity selection in males may be biased downwards, because extrapair paternity seems likely to increase the variance in fitness derived from a simple count of the number of nestlings in the own nest.

We redid all selection analyses by including the dichotomous age variable as another independent variable in the regressions. This allowed us to obtain estimates of selection differentials and gradients that were adjusted for age.

Mean selection differentials and gradients are reported in Appendix 2.

Statistical Analyses

We analyzed population differences in phenotype and intensity of selection by using estimates for each year as an independent observation in one-way analyses of variance with population as a factor. These analyses of population differences also revealed the magnitude of the among-year component of variation because a relative large among-year component of variation invariably would imply that differences among populations were small. Therefore, these analyses were restricted to populations for which information was available for at least two years.

Given that we did find significant population effects on phenotype and intensity of selection for populations with multiple estimates (see Results), this explicitly implies that populations are different in terms of the variables under investigation. Comparative analyses of populations, species, or higher level taxa require that the similarity in phenotypic values among the units of analysis due to common descent

be taken into account (Harvey and Pagel 1991). To this end phylogenetic relationships based on neutral genetic markers serve as the basis for comparative analyses, with deviations from this expected neutral pattern reflecting biological phenomena of interest to ecologists and evolutionary biologists. The mechanism accounting for deviations from the null hypothesis of the relationships among populations suggested by the neutral genetic markers is evolution. For studies of populations a first step is to analyze the data for genetic population structure and isolation by distance. If such structure exists, this must be taken into account by using analysis of standardized linear contrasts or Mantel tests to account for the nonindependence of mean phenotypic values of populations (Soler et al. 1999), thereby avoiding any problems of pseudo-replication (Harvey and Pagel 1991). In contrast, if there is no genetic population structure with F_{ST} equal to zero, this implies that nearby populations are as similar to each other as are distant populations, demonstrating that mean phenotypes of populations can be used directly as statistically independent data points in the analyses because all populations can be considered to be equally independent in a statistical sense. J. Ewen, D. Sicard, and A. P. Møller (unpubl. ms.) analyzed seven European populations of barn swallows across a latitudinal range of almost 2200 km (the same populations as used in the present study: Estonia, Denmark, Hungary, Italy, Badajoz (Spain), Chernobyl (Ukraine), Kanev (Ukraine)) at six microsatellite loci to quantify the degree of genetic population structure. There was no evidence of significant population structure with F_{ST} and R_{ST} values being very close to zero (0.002 and -0.002, respectively) and not significantly different from zero. This implies that different populations are similar for neutral genetic markers with no indication of isolation by distance. Therefore, in the remainder of the analyses we used estimates for the different populations as independent data points.

We tested whether directional selection was consistent among populations by using one-sample t-tests to assess whether mean values differed significantly from zero. Separate analyses with nonparametric Wilcoxon matched-pairs, signed-ranks tests revealed similar conclusions. In addition, we tested whether selection gradients for tail length differed from selection gradients for wing and tarsus length using paired t-tests.

Consistency in intensity of selection between sexes was tested using paired t-tests. Kendall rank-order correlations were used to test if selection differentials and gradients were ranked similarly among populations in the two sexes.

We compared selection differentials and gradients before and after correction for age, as described above, by means of paired t-tests and Pearson product-moment correlations.

We tested whether the intensity of selection due to breeding date was reinforced by selection due to annual fecundity by calculating whether selection gradients and selection differentials were acting in the same direction on the different phenotypic traits in the two sexes.

Finally, we tested if current patterns of sexual size dimorphism in tail length among populations could be accounted for by current patterns of selection for breeding date and annual fecundity. We regressed sexual size dimorphism against selection differentials for breeding date and annual

TABLE 2. One-way analyses of variance of phenotypic characters of adult barn swallows within and among populations.

Character	MS (Population)	MS (Residual)	F	df	P
Male tail length	60.17	6.90	8.72	14,73	<0.0001
Male wing length	16.65	0.70	23.81	7,35	<0.0001
Male tarsus length	0.18	0.08	2.25	7,35	0.04
Female tail length	27.78	2.83	9.82	14,73	<0.0001
Female wing length	16.03	0.69	23.34	7,35	<0.0001
Females tarsus length	0.19	0.09	2.11	7,35	0.04
Sexual size dimorphism in tail length	19.13	8.75	2.19	14,73	0.016
Laying date	1682.15	45.44	37.02	14,73	<0.0001
Annual fecundity	4.00	0.64	6.27	14,72	<0.0001

fecundity in the two sexes, using a stepwise procedure to eliminate variables that did not account for significant amounts of variance. Sexual size dimorphism in tail length was quantified as $\log_{10}$(mean male tail length) minus $\log_{10}$(mean female tail length), whereby the log-transformation was used to account for any scaling effects.

Sample sizes differed among tests due to lack of information for some variables. For example, the Swiss data did not include wing length and tarsus length and all analyses of selection gradients were thus only based on the remaining 12 populations. In addition, one sample did not include information on annual fecundity for all individuals, and hence fecundity selection could not be estimated for that population.

RESULTS

Repeatability of Phenotype among Populations

We tested whether estimates of breeding date, total annual fecundity, and morphology provided reliable estimates for particular populations, using one-way ANOVAs with study population as a factor and phenotype as response variables. There were significant differences in reproductive variables and morphology among populations (Table 2). In particular, tail and wing length showed the largest degree of variation among populations implying that annual differences in these characters were small. Likewise, breeding date differed considerably among populations independent of year, although there was much less variation in annual fecundity.

We also tested if these differences were confounded by year by assessing whether estimates from 2003 (the year with data for the largest number of populations) predicted estimates for other years. All analyses showed a high degree of similarity between the two sets of estimates for the 11 pop-

ulations (linear regressions: $F > 6.20$, df = 1, 10, $r^2 > 0.38$, $P < 0.03$).

Effects of Age on Intensity of Selection

We tested for effects of age on estimates of selection differentials, using a partial regression approach that included age as a predictor variable. Using this approach, we found reductions in mean selection differentials by 68 to 81% (Table 3) and reductions in mean gradients by 60 to 75% (Table 3). When analyzed at the level of mean estimates for sites, all these differences were significant for males, but did not reach significance for females (Table 3). When analyzed at the level of single years, all differences were highly significant (results not shown). Thus, correction for age reduced the intensity of selection by 60 to 81%.

Selection differentials and gradients that were corrected for age effects were strongly positively correlated with uncorrected estimates. Pearson correlation coefficients based on the annual estimates ranged from $r = 0.63$, $t = 6.65$, df = 69, $P < 0.0001$ to $r = 0.86$, $t = 9.16$, df = 30, $P < 0.0001$. Likewise, analyses based on estimates for different sites were positively correlated, albeit only significantly for males (results not shown). Thus, selection differentials and gradients that were corrected for age were reduced compared to uncorrected estimates, but showed strong positive correlations. Although age-corrected estimates were only available for a fraction of the populations, we repeated the subsequent analyses using uncorrected and corrected estimates.

Repeatability of Intensity of Selection among Populations

There were highly significant differences in selection differentials for tail length among populations with more than

TABLE 3. Mean (SE) selection differentials and partial selection differentials (selection gradients) on male and female tail length before and after correction for effects of age. Means are compared using paired t-tests. Sample sizes are number of populations. The mean difference (%) is the difference between estimates before and after correction for age.

	Mean (SE) before control for age	Mean (SE) after control for age	t	P	N	Mean difference (%)
Date selection differential in males	−0.131 (0.018)	−0.025 (0.008)	6.03	<0.0001	13	81
Date partial selection differential in males	−0.081 (0.016)	−0.031 (0.019)	4.22	0.013	5	62
Date selection differential in females	−0.129 (0.059)	−0.036 (0.011)	2.42	0.07	5	72
Date partial selection differential in females	−0.091 (0.017)	−0.036 (0.011)	2.33	0.08	5	60
Fecundity selection differential in males	0.047 (0.016)	0.009 (0.005)	−2.50	0.028	13	81
Fecundity partial selection differential in males	0.069 (0.021)	0.018 (0.005)	−2.94	0.043	5	74
Fecundity selection differential in females	0.044 (0.008)	0.014 (0.012)	−1.85	0.14	5	68
Fecundity partial selection differential in females	0.020 (0.021)	0.005 (0.012)	−1.73	0.16	5	75

TABLE 4.   One-way analyses of variance of selection differentials and partial selection differentials (selection gradients) for phenotypic characters of adult barn swallows within and among populations.

Selection differential	MS (Population)	MS (Residual)	F	df	P
Date selection:					
Male tail length	0.034	0.012	2.83	14,73	0.01
Partial male tail length	0.025	0.006	3.91	7,35	0.003
Partial male wing length	0.003	0.011	0.30	7,35	0.95
Partial male tarsus length	0.015	0.005	2.98	7,35	0.02
Female tail length	0.035	0.013	2.72	14,73	0.003
Partial female tail length	0.067	0.007	9.88	7,35	<0.001
Partial female wing length	0.011	0.006	1.77	7,35	0.12
Partial female tarsus length	0.006	0.005	1.07	7,35	0.40
Fecundity selection:					
Male tail length	0.032	0.008	4.06	14,72	<0.001
Partial male tail length	0.016	0.005	3.57	7,34	0.006
Partial male wing length	0.004	0.008	0.56	7,34	0.78
Partial male tarsus length	0.006	0.007	0.90	7,34	0.52
Female tail length	0.009	0.005	2.00	14,72	0.03
Partial female tail length	0.015	0.010	1.55	7,34	0.19
Partial female wing length	0.004	0.014	0.27	7,34	0.96
Partial female tarsus length	0.004	0.007	0.64	7,34	0.72

a single annual estimate for both males and females with respect to breeding date, although fecundity selection mainly differed among populations in males (Table 4). Likewise, selection gradients that controlled statistically for indirect selection on tail length due to selection on wing and tarsus length also differed significantly among populations for breeding date in both sexes (Table 4). The selection gradient on tail length with respect to annual fecundity was only significantly different among populations for male tail length (Table 4). In contrast, the intensity of selection on wing and tarsus length showed little or no significant difference among populations (Table 4). This means that the strength of selection differed considerably among populations independent of year for tail length, in particular in males, although that was not the case for the two other morphological characters.

We tested whether these differences in selection among

populations were confounded by year by assessing whether estimates from 2003 (the year with data for the largest number of populations) predicted estimates for other years. These analyses showed a high degree of similarity between the two sets of estimates for the 11 populations ($F > 6.44$, df = 1, 10, $r^2 > 0.42$, $P < 0.02$). That was also the case for the populations with information on age-corrected selection estimates ($F > 26.17$, df = 1, 8, $r^2 > 0.77$, $P < 0.0001$).

Second, we tested if the intensity of selection among populations was consistent across populations by determining whether mean selection differentials and selection gradients differed significantly from zero. There was evidence of consistent selection on tail length in both sexes for date selection (Table 5). There was also evidence of consistent directional selection on male wing and tarsus length with respect to breeding date, when correlated selection on the other trait

TABLE 5.   Mean and variance of selection differentials and partial selection differentials (selection gradients) with respect to selection on breeding date and annual fecundity. Also reported is the number of populations and a test of whether the mean estimate of selection differs from an hypothetical value of zero in a one-sample *t*-test.

Selection differential	Mean	Variance	N	t	P
Date selection:					
Male tail length	−0.169	0.015	22	−6.48	<0.0001
Partial male tail length	−0.156	0.018	12	−4.00	0.002
Partial male wing length	0.060	0.007	12	2.46	0.032
Partial male tarsus length	−0.048	0.004	12	−2.75	0.019
Female tail length	−0.172	0.031	22	−4.54	0.0002
Partial female tail length	−0.160	0.037	12	−2.87	0.015
Partial female wing length	−0.003	0.011	12	−0.10	0.92
Partial female tarsus length	0.004	0.002	12	0.26	0.80
Fecundity selection:					
Male tail length	0.080	0.015	21	2.96	0.008
Partial male tail length	0.157	0.043	11	2.51	0.031
Partial male wing length	−0.046	0.022	11	−1.02	0.33
Partial male tarsus length	0.027	0.021	11	0.61	0.55
Female tail length	0.068	0.022	21	2.10	0.049
Partial female tail length	0.045	0.014	11	1.27	0.23
Partial female wing length	−0.046	0.022	11	1.45	0.18
Partial female tarsus length	0.027	0.021	11	0.98	0.35

TABLE 6. Correlations of selection differentials and partial selection differentials (selection gradients) between males and females across populations. Kendall rank-order correlations are reported.

Variable	τ	P
Date selection:		
Tail length	0.67	<0.0001
Partial tail length	0.46	0.004
Partial wing length	0.18	0.41
Partial tarsus length	−0.03	0.89
Fecundity selection:		
Tail length	0.24	0.13
Partial tail length	0.35	0.14
Partial wing length	0.02	0.94
Partial tarsus length	−0.02	0.94

and tail length was controlled statistically (Table 5). Selection favored males with long tails and tarsi, but short wings. In contrast, there was no evidence of consistent directional selection on wing and tarsus length in females with respect to breeding date or annual fecundity (Table 5).

Analyses of selection differentials and selection gradients from 11 populations in 2003 showed similar results as the analyses based on the entire dataset (data not shown), demonstrating that these effects were not confounded by data originating from different years in the overall analyses.

Likewise, analyses of age-corrected selection differentials and selection gradients showed similar results as the analyses based on the entire dataset, with most mean estimates differing significantly from zero ($t > 2.68$, df $= 10$, $P < 0.01$), demonstrating that the effects were not confounded by age.

Selection gradients for breeding date on tail length were significantly larger than for wing and tarsus length in both sexes (paired t-tests, $t > 2.57$, df $= 10$ or 11, $P < 0.026$). For fecundity selection, selection gradients for tail length in males were larger than selection gradients for wing or tarsus length (paired t-tests, $t > 1.97$, df $= 11$, $P < 0.049$). In contrast, there was no significant difference in selection gradients for fecundity selection in females (paired t-tests, $t < 0.74$, df $= 10$, $P > 0.48$).

Variation in Intensity of Selection between Sexes

We tested whether patterns of selection were similar in males and females. Only one of the mean selection differentials differed significantly between males and females, with the value for fecundity selection gradients for tail length in males exceeding that for females (Table 6; paired t-test, $t = 2.53$, df $= 10$, $P = 0.03$). For selection related to breeding date, selection differentials and selection gradients for tail length in the two sexes were strongly positively correlated (Fig. 2; Table 6). In contrast, there was no evidence of significant covariation in selection differentials or gradients with respect to fecundity selection (Table 6).

Analyses of data from 2003 revealed similar conclusions as the global analysis, with only selection differentials and selection gradients for breeding date reaching statistical significance (Kendall $\tau > 0.80$, $P < 0.01$).

Analyses of age-corrected selection differentials showed that only the results for breeding date reached statistical significance (Kendall $\tau > 0.70$, $P < 0.05$).
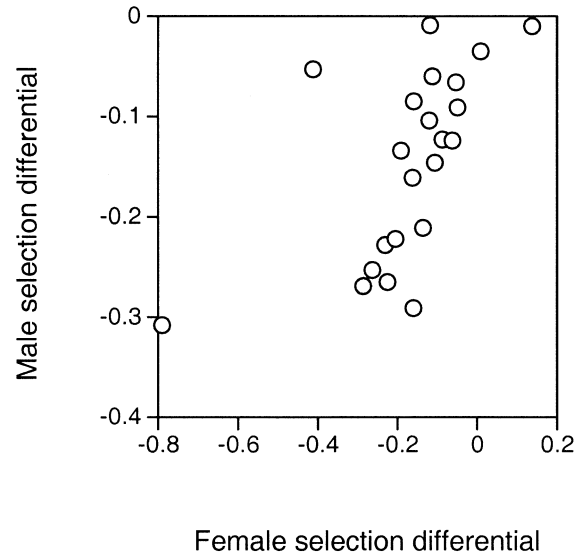

FIG. 2. Relationship between selection differentials with respect to breeding date for tail length in males and females. Individual data points are estimates for different populations.

Consistency in Intensity of Selection between Fitness Components

We tested whether the two different estimates of selection with respect to breeding date and total annual fecundity were correlated. The correlation was significant for selection gradients for tail length in males and for selection differentials and gradients in females (Table 7, Fig. 3). Furthermore, there was evidence of significant correlation of selection gradients on wing length in females for breeding date and fecundity selection, even when using rank-order correlation (Table 7). Thus populations in which selection due to breeding date is strong also experience intense selection due to annual fecundity.

Analyses of selection differentials and selection gradients from 2003 revealed qualitatively similar results as the global analyses (selection gradient for tail length of males: $\tau = −0.50$, $P = 0.01$; selection differential for tail length of females: $\tau = −0.55$, $P = 0.008$; selection gradient for tail length of females: $\tau = −0.66$, $P = 0.009$; selection gradient for wing length of females: $\tau = −0.75$, $P = 0.001$). Likewise, analyses of age-corrected selection differentials and selection

TABLE 7. Correlations between selection differentials and partial selection differentials (selection gradients) for breeding date and annual fecundity with different morphological characters in males and females across populations. Kendall rank-order correlations are reported.

Variable	τ	P
Male tail length	−0.16	0.30
Partial male tail length	−0.49	0.036
Partial male wing length	−0.24	0.31
Partial male tarsus length	−0.42	0.07
Female tail length	−0.45	0.005
Partial female tail length	−0.60	0.010
Partial female wing length	−0.64	0.006
Partial female tarsus length	0.24	0.31

Fig. 4. Sexual size dimorphism in tail length in relation to selection differentials for tail length in males with respect to breeding date. Individual data points are estimates for different populations.
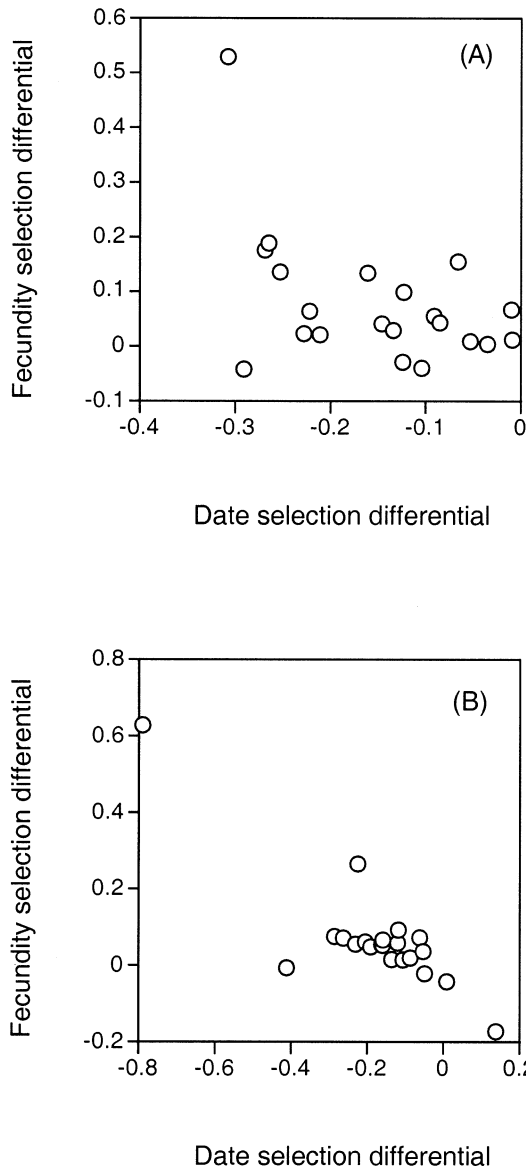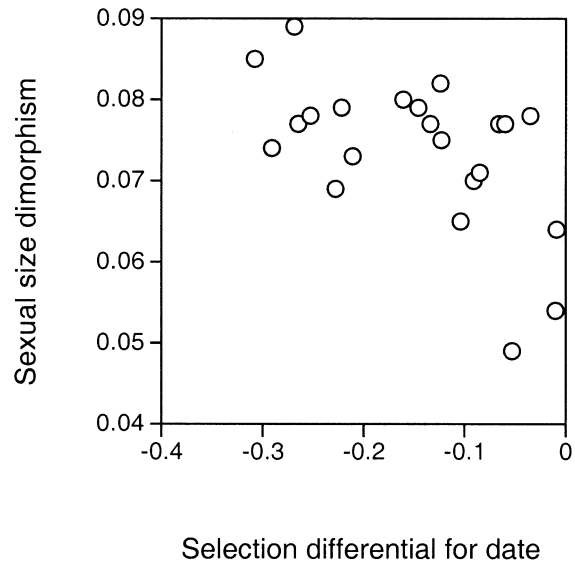

Fig. 3. Relationship between selection differentials for tail length with respect to breeding date and annual fecundity in (A) male and (B) female barn swallows. Individual data points are estimates for different populations.

gradients provided similar conclusions as those reported in Table 7.

Intensity of Selection and Mean Phenotype

We tested if estimates of selection could account for variation in sexual size dimorphism among populations. A stepwise multiple regression with estimates of sexual size dimorphism in tail length as the dependent variable and selection differentials for tail length in males and females for date selection and fecundity selection as predictor variables revealed a significant model that accounted for 31% of the variance. Selection differentials for breeding date in males accounted for variation in sexual size dimorphism in tail length among populations (Fig. 4; $F = 8.38$, df $= 1, 19$, r^2

$= 0.31$, $P = 0.009$, slope (SE) $= -0.045$ (0.016)). An analysis based on Kendall rank-order correlation gave a similar result (Kendall $\tau = 0.35$, $z = -2.28$, $P = 0.022$). An analysis based on data from 2003 provided a similar conclusion ($F = 16.96$, df $= 1, 10$, $r^2 = 0.63$, $P = 0.002$, slope (SE) $= -0.031$ (0.007)). Furthermore, an analysis based on age-corrected selection differentials also revealed a strong negative relationship ($F = 11.69$, df $= 1, 8$, $r^2 = 0.59$, $P = 0.009$, slope (SE) $= -0.193$ (0.056)). In contrast, there was no significant effect for females, or for fecundity in either sex (results not shown). Finally, sexual size dimorphism in wing length or tarsus length among populations was not significantly related to selection on either sex (results not shown). These analyses suggest that current patterns of sexual size dimorphism in tail length across populations of barn swallows is predicted by current patterns of selection for early breeding in males.

DISCUSSION

The main finding of the present study of continent-wide selection on a secondary sexual character and two other characters was consistent patterns of mean phenotype and intensity of directional selection for particular populations in different years. Directional selection consistently favored males and females with long tails with respect to early breeding and it favored long-tailed males with respect to annual fecundity. The intensity of directional selection on tail length in males with respect to breeding date was strongly positively correlated with the intensity of selection on tail length in females across populations, although a similar pattern was absent for fecundity selection. The intensity of directional selection on tail length across populations was consistently stronger in males than in females for annual fecundity. Adjustment of selection differentials and gradients for age effects reduced estimates by 60 to 81% on average, although corrected and uncorrected estimates were strongly positively

correlated. Selection differentials and selection gradients for the two fitness components were strongly correlated for tail and wing length in females among populations, but only weakly for selection gradients in males. Variation in sexual size dimorphism in tail length among populations was predicted by selection for early breeding in males, but not by other kinds of directional selection in either sex.

Before discussing these findings we consider (1) bias in estimates, and (2) the relative importance of the two fitness components. Most individuals in the populations investigated were captured as shown by high recapture rates (Møller and Szép 2002, unpubl. data). Likewise, the proportion of adults without color bands at the end of the breeding season was less than 5%, suggesting that we caught most individuals. Thus, the estimates obtained provide information that is representative of the populations sampled, without serious bias due to the noncaptured fraction of the population. A second cause of bias in studies of selection is that selection gradients do not control for effects of indirect selection on other traits. We included two potentially confounding variables in the selection analyses. Wing length is a morphological character of great importance for flight efficiency, with wing length covarying with tail length as an adaptation to reduce the aerodynamic costs of exaggerated tail feathers in males (Møller et al. 1995a). Tarsus length is a measure of skeletal body size. Hence, inclusion of these two variables would control for potentially important components of indirect selection due to selection for flight efficiency and selection on body size. Inclusion of these two variables in analyses of selection provided selection gradients that did not differ significantly from selection differentials. In general, the analyses based on selection differentials and gradients provided similar conclusions.

There are many different fitness components relating to sexual selection (Møller 1994). Components other than the two analyzed here include mating success, extrapair paternity, differential parental investment, and infanticide (Møller 1988, 1990b, 1994; de Lope and Møller 1993; Saino et al. 1997a, 2002a,b; Kose and Møller 1999; Kose et al. 1999). The conclusions of our study would rely on sexual selection advantages of early reproduction and attraction of fecund females not being nullified or reversed by selection on other fitness components. Here, we briefly discuss the relationship between selection on breeding date and fecundity of mates in relation to other components of sexual selection. The fraction of unmated male barn swallows rarely exceeds 10% and is usually less than 5% (Møller 1994). Importantly, this component of mating success is strongly related to male tail length, with unmated males having much shorter tails than mated males (Møller 1994; Saino et al. 1997b), suggesting that this component of selection will reinforce the components analyzed here. Polygyny is extremely rare with only single cases having been documented in Denmark, Italy and Spain, suggesting that this component of fitness is unlikely to affect estimates of overall selection. Likewise, infanticide is a minor component contributing to overall selection (Møller 1994). Probably, extrapair paternity is the most important fitness component not considered in the present study. Three previous studies of extrapair paternity along a latitudinal gradient have shown level of extrapair paternity in own nests of 28.0% in Denmark (Møller and Tegelström 1997), 34.0% in Italy (control nests only; Saino et al. 1997a; Møller et al. 1998b), and 17.8% in Spain (Møller et al. 2003). All three studies showed strong negative relationships between male tail length and level of extrapair paternity in own nests. A study of extrapair paternity that experimentally manipulated the target of selection (tail length) showed a significant positive correlation between number of offspring sired in own nests and number of offspring sired in other nests (Saino et al. 1997a). In addition, early reproducing males sired more offspring in their own nest that late reproducing males in all broods (Møller et al. 2003), showing that this finding is an effect of differences in male quality on paternity maintained across broods. Therefore, the two fitness components considered here are among the most important ones, and other fitness components such as mating success or extrapair paternity will enhance rather than nullify or reverse the effects reported here.

There was significant consistency in morphology for different populations among years. Populations differed the most in breeding date, with a smaller difference among populations in annual fecundity. Therefore, the among-year component of variation is small relative to the among-population component. These results are consistent with previous studies of latitudinal clines in phenotype in the barn swallow (Møller 1995; Møller et al. 1995a). The latitudinal cline in wing and tail length is not caused by a latitudinal cline in body size because tarsus length does not increase with latitude (Møller 1995; Møller et al. 1995a). The latitudinal cline in tail length and sexual size dimorphism in tail length is apparently due to clinal differences in costs and benefits of large secondary sexual characters (Møller 1995; Møller et al. 1995a), as revealed by field experiments (Møller et al. 1995b). Consistent differences in laying date among populations are most likely due to clinal variation in timing of spring migration and resultant variation in start of reproduction.

A condition for divergence in phenotype among populations is consistent patterns of directionality and intensity of selection among years. We are unaware of previous tests investigating such consistency, and whether the degree of consistency differs predictably among populations. There was consistency in intensity of directional selection on tail length among years in different populations for breeding date selection and fecundity selection in males, and for breeding date selection in females. In contrast, there was little or no evidence of consistent directionality and intensity of selection on wing and tarsus length. Thus, selection was more consistent on tail length compared to other traits. Analyses of mean intensity of selection revealed persistent selection on tail length with respect to breeding date in the two sexes and with respect to fecundity in males. Intensity of selection was 0.16 and 0.16 for the two selection gradients on tail length in males and 0.05 and 0.16 for the same character in females, which are strong compared to other estimates of intensity of sexual selection (Gontard-Danek and Møller 1999; Kingsolver et al. 2001). Intensity of selection on wing length was 0.003, 0.046, 0.046, and 0.060 for the four selection gradients, which are by all means weak (Kingsolver et al. 2001). The same can be said about the selection gradients of 0.004, 0.027, 0.027, and 0.048 for tarsus length. Therefore, intensity

of selection on tail length was stronger and more uniform than selection on wing and tarsus length.

We tested for differences in patterns of selection among sexes. If mutual sexual selection by the two sexes is at work, we could expect significant selection on the same trait in males and females (review in Amundsen 2000), whereas female mate choice would cause greater selection on males. Fecundity selection as estimated from the selection gradient was the only estimate that was significantly stronger on tail length in males than in females. Patterns of selection in males and females were similar with respect to breeding date, and estimates for the two sexes in the different populations were consistent. Apparently, both long-tailed males and females enjoy an advantage from early breeding. In males, tail length manipulation has consistently shown that experimentally long-tailed individuals enjoy an advantage from early breeding (Møller 1988, 1992; F. de Lope and A. P. Møller, unpubl. data). We suggest that the effect in females arises from females with long tails tending to be in prime condition (Møller 1993b). Accordingly, experimental manipulation of tail length in females failed to advance laying date (Cuervo et al. 1996), suggesting that natural variation in female tail length reliably reflects female condition, causing experimental elongation of tail length to reduce condition (Cuervo et al. 2003). This suggests that selection on females through timing of breeding acts on the environmental component of tail length. Finally, a selection differential of 0.1 in males is larger in absolute terms than a similar selection differential in females. Because mean standard deviation for tail length in males across 22 populations is 10.04 mm, but 6.65 mm in females (data in Appendix 1), a similar intensity of selection in the two sexes will cause a response to selection that is 50% greater in males than in females. This effect will be further exacerbated if selection on the environmental component of variation differs between the sexes.

The size of secondary sexual characters often depends on age, and females may obtain information on age of potential partners from the expression of secondary sexual characters (Trivers 1972; Manning 1985; Hansen and Price 1995; Proulx et al. 2002). That is also the case in the barn swallow because tail length of males increases from yearlings to two years old birds, followed by a decrease when males reach an age of five–six years (Møller and de Lope 1999). We adjusted selection differentials and gradients for age effects and found a reduction in mean estimates by 60 to 81%. We are unaware of any other study that has compared estimates of intensity of selection with and without adjusting for age effects across populations. Although intensities of selection were weaker after adjusting for effects of age, they still showed a similar geographical pattern as before adjustment. Therefore, effects of age did not confound the conclusions.

Many components of sexual selection can act on the phenotype, with net intensity of selection determining response to selection (Andersson 1994). Few studies have assessed whether different components of selection reinforce each other, or whether they are divergent. Selection on tail length in the two sexes acted in the same direction because selection gradients and selection differentials were correlated across populations. Selection gradients were more strongly correlated with each other than selection differentials, suggesting

that covariation in intensity of selection was partly obscured by indirect selection on other traits. In female, but not in male barn swallows there was evidence of consistent directionality of selection on wing length across populations for the two components of selection. Because females are more involved in reproduction than males, due to only females laying eggs and incubating these, the intensity of selection on females should be stronger and more consistent for different components of selection than on males.

Consistent patterns of selection across generations may result in microevolutionary change in phenotype provided that the trait in question has an additive genetic basis, that strong negative genetic correlations do not prevent a response to selection, that selection acts on the genetic component of a trait, and that the microevolutionary change is not masked by change in environmental conditions. There is ample evidence for heritability of morphology in the barn swallow, including similarity in phenotype between adults and nestlings depending on whether they are within-pair or extrapair offspring (Møller 1990a, 1991, 1994; Saino et al. 2003). Sexual size dimorphism evolves over very long time spans due to divergent selection on the two sexes (Lande and Arnold 1985). Population differences in sexual size dimorphism in tail length imply that patterns of selection are consistently different for the two sexes among populations (Table 5), and that the gene flow is insufficient to eliminate such differences. Geographical variation in sexual size dimorphism in tail length was related to variation in selection on males related to breeding date. Populations with a high degree of sexual size dimorphism in tail length were characterized by large selective benefits for long-tailed males from early start of breeding. There was no similar relationship for selection differentials for female tail length. This sex difference is consistent with the interpretation that while selection on males for breeding date acts on the genetic component of phenotypic variation, selection on females acts on the environmental component. The relationship between intensity of selection on tail length in males and sexual size dimorphism in tail length also suggests that patterns of selection remain consistent among populations across generations. Otherwise sexual size dimorphism would not evolve and be maintained. This example is one of only a few studies showing covariation between patterns of selection and patterns of sexual size dimorphism (for another example, see Badyaev et al. 2002).

There are several consequences of this study. First, although there is an absence of genetic population structure based on neutral microsatellite markers (J. Ewen, D. Sicard, and A. P. Møller, unpubl. ms.), there is significant evidence of population differentiation in the additive genetic variance-covariance matrix (Roff et al. 2004). The present study suggests that patterns of selection are consistent among years and populations facilitating differentiation among populations. Second, a corollary of this difference between neutral and additive genetic variation is the question why populations show consistent differences in morphology that are maintained across generations. The answer to that question is that patterns of selection within populations are sufficiently strong to swamp any effects of gene flow among populations. The fact that populations are particularly differentiated with respect to wing and tail length, but not with respect to tarsus

length, and that the same characters differ in intensity of directional selection, is consistent with that suggestion. Third, the relative role of natural and sexual selection in differentiation of populations can partly be deduced from the findings of the present study. For example, the magnitude of sexual size dimorphism for tail length was only significantly related to selection on tail length in males with respect to breeding date, but not to any of the other selection differentials in either sex, suggesting that it is sexual selection on males that is the main cause of divergence in phenotype between the two sexes.

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Corresponding Editor: M. Webster