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Source: *Journal of Avian Biology*, Vol. 38, No. 1 (Jan., 2007), pp. 58-72
Published by: Wiley on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/30244777
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J. Avian Biol. 38: 58–72, 2007
doi: 10.1111/j.2007.0908-8857.03669.x
Copyright © J. Avian Biol. 2007, ISSN 0908-8857
Received 21 March 2005, accepted 15 December 2005

Genetic and phenotypic associations in morphological traits: a long term study of great reed warblers *Acrocephalus arundinaceus*

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We present estimates of standardized selection (directional and quadratic) differentials via reproductive success on eight morphological traits in a newly founded long-term study population of great reed warblers *Acrocephalus arundinaceus* in Sweden. In order to predict the evolutionary response to selection in these traits we present estimates of heritabilities (h^2), phenotypic (r_P) and genetic (r_A) correlations among the same traits. We also examined the extent of parental effects in the expression of the phenotypic traits. Overall, the population is subject to low levels of directional selection and higher levels of stabilizing selection. This makes us predict that the population is changing very little if anything, even though h^2 in many cases are considerable. Midparent-midoffspring h^2 ranged from 0.14 and 0.94 (mean 0.58) and were significant for seven of eight traits. We found indications of positive maternal effects in tarsus length. Phenotypic correlations between traits ranged from 0.02 to 0.43 (mean 0.15) and showed generally much lower values than the corresponding genetic correlations that ranged between 0.08 and 1.04 (mean 0.46). Overall, the correlation between r_P and r_A was significant, although moderate, but they tended to differ in magnitude, possibly due to overestimation of additive covariance between traits.

The evolutionary response to selection depends on the genetic variances and covariances among traits and the strength of selection. Thus, in order to study the current evolutionary change in a suit of traits we need both good knowledge about the genetic variance/covariance among traits and estimates of selection on the trait mean and variance in the population. There is now substantial amount of studies done on the genetic variability (Merilä and Sheldon 2001) and selection (for references see Kingsolver 2001) on morphological traits in birds. These studies have shown that morphological traits often are highly heritable (Merilä and Sheldon 2001) and sometimes subject to linear selection, typically stronger than on life-history/phenology traits (Kingsolver 2001). High heritabilities are however not necessarily accompanied with high evolvabilities, because heritability depends on both the amount of additive genetic variance as well as environmental variance (Houle 1992, Hansen and Houle 2004).

Studies of genetic change in natural populations become more complicated due to the fact that measured traits are correlated (Hansen and Houle 2004, Merilä and Björklund 2004). Hence, an important factor to take into account when studying evolvability is that the genetic potential for change in a trait that is subject to directional selection, depends on the genetic variability in the trait but also on the change it imposes on other traits (Hansen and Houle 2004). To understand evolutionary processes we therefore not only need to know the characteristics of one isolated trait, but also how this character interacts with other traits. The interaction between traits is estimated through phenotypic correlations (Falconer and Mackay 1996, Lynch and Walsh 1998) that can arise in two main ways. First, the traits share the same environment (i.e. the individual). Second, traits can to some extent share inheritance due to pleiotropy (or linkage disequilibrium). The genetic correlation is the net effect of all

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the segregating genes that affect the characters (Lynch 1999).

We have studied a recently founded natural population of great reed warblers for more than twenty years focusing on questions such as female mate choice (Bensch and Hasselquist 1992, Bensch 1996), male reproductive tactics and success (Hasselquist et al. 1995b, 1996, Bensch et al. 1998, Hasselquist 1998), MHC diversity (Westerdahl et al. 2004a, b), inbreeding (Bensch et al. 1994, Hansson et al. 2004), genetic variability (Hansson et al. 2000), and dispersal (Hansson et al. 2002a, b, 2003a). So far, there is no comprehensive study made on the inheritance and selection on morphological traits in this population (but see Hasselquist et al. 1995a, Hansson et al. 2003b). In the present study, we estimate standardized linear and quadratic selection differentials on eight morphological traits and relate these to the corresponding heritabilities and correlations among the traits. The great reed warbler is a relatively new species on the Scandinavian peninsula that comprises the northernmost population in the geographical range of the species. We therefore might expect directional selection on several traits due to changes in migration distance, climate and food composition the species may have encountered since the beginning of the last century on the Scandinavian peninsula. Heritabilities and the resulting variance components are calculated with parent-offspring regressions. In an earlier study of the heritability of tarsus length and wing length in this population, it was found that maternal inheritance exceeded that of paternal inheritance, indicating that maternal effects acted on morphological traits (Hasselquist et al. 1995a). Here we investigate a much larger data set and more traits to study the general importance of maternal effects in this species. We also calculate phenotypic and genetic correlations between the traits, and investigate if the phenotypic correlations provide good estimates of genetic correlations. In several studies it has been suggested that r_P may be used to approximate the level of r_A (Cheverud 1988, Roff 1995, Reusch and Blanckenhorn 1998, Reale and Festa-Bianchet 2000), whereas other studies suggest that methods based only on r_P are unreliable substitutes for r_A (Willis et al. 1991, Hébert et al. 1994).

Material and methods

Study population

The great reed warbler is a long-distance migrant passerine bird, which breeds in eutrophic lakes and marshes on the Eurasian continent (Cramp 1992). It has a facultative polygynous social mating system (Hasselquist 1998). Since 1983, we have followed a breeding population at Lake Kvismaren (50°10′N, 15°25′E) in south Central Sweden (e.g. Bensch 1996, Bensch et al. 1998, Hasselquist 1998, Hansson et al. 2000). Each breeding season, we have made daily visits to all territories in the study area from beginning of May to mid July. Almost all (>95%) of the territorial males and breeding females have been caught by using mist nets, measured and marked with an individually unique combination of plastic colour rings and an aluminium ring. Since 1985, nearly all nests (>98%) at the study site have been located and followed to the fledgling stage or until nest failure. When nestlings are nine days old, they have been ringed with a unique aluminium ring. We have taken blood samples from all individuals, adults as well as nestlings, in the study area since 1987 and hence established true parentage to all individuals hatched in the area until 1998 (Hasselquist et al. 1995b, Arlt et al. 2004). Hence, more than eighty percent of the offspring in the data set have been successfully assigned to their genetic father. The frequency of cuckoldry is low in the population; ca 3% of the nestlings have been sired by extra-pair males (Hasselquist et al. 1995b, 1996, Arlt et al. 2004). The few offspring that were sired by extra-pair males (N = 20) are included in the analyses together with their genetic fathers.

Data used in the present study was collected between 1983 and 2002. From 1983 to 1989 the population size increased steadily from ca 10 to about 60 individuals. After 1989 the population has fluctuated between 42 and 78 adults. The total reproductive output in the population between 1983 and 2002 is 1680 young, of which 253 young (15.1%) have returned to breed in the area the following years. We have previously estimated that a 15% return rate to the natal site or the nearest marsh (Segersjö 10 km away) represents about half of the number of surviving offspring from each cohort (Bensch et al. 1998, Hansson et al. 2002b). Hence, for a long-distance migratory passerine, an unusually high proportion of surviving juveniles born in the study area also return to breed at their natal site (Hansson et al. 2002b). Most of the remaining juveniles that have survived but not returned to our study site appear to have dispersed to nearby lakes (Hansson et al. 2002b).

The present study includes 524 adult individuals, distributed among 137 families. For most of the families, there is only one returning offspring (64.2%), while 28.5% consists of two, and 7.3% of three to five returning offspring.

Measurements

We have considered the following eight morphological traits: 1) wing length; the length of a flattened and

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straightened right wing, measured from the carpal joint to the tip of the longest primary feather with a ruler (Method 3, Svensson 1992), 2) wing projection; the distance between the tip of the first secondary and the longest primary feather of a folded wing; measured with a ruler, 3) tail length; the length between the lower base of a tail feather and its tip, measured with a ruler (Svensson 1992), 4) bill width; the width of the bill at the anterior edge of the nostril measured with callipers, 5) bill height; the height of the bill at the anterior edge of the nostril measured with callipers, 6) bill length; the length between the anterior edge of the nostril and the tip of the bill measured with callipers, 7) skull length; in the field a measurement is taken of the length between the tip of the bill and the back of the skull using callipers; by subtracting this measurement from bill length we get a measurement of the length of the skull plus the posterior part of the bill and 8) tarsus length; the length between outer bending points of the posterior tarsus-tibia joint and the anterior inter-tarsal joint at the right tarsus (Alatalo et al. 1984), measured with callipers. All measurements taken with a ruler are measured to the nearest 1 mm and all measurements taken with callipers to the nearest 0.1 mm.

Age and sex

Effects of age were calculated by using individuals that were measured as 1-year (1Y) and 2-year (2Y) old birds, of which a subset also where measured at least once as older than 2Y using paired t-test. The evaluation of age dependence was made for both sexes separately. The difference between age classes sometimes showed significant deviations from a normal distribution when tested with a Kolmogorov-Smirnov test with Lilliefors correction. Therefore, Wilcoxon signed rank test was performed in addition to the paired t-test for some variables. However, the two tests always provided similar results and we therefore only report statistical data from the paired samples t-test. Significant age effects were found in wing length (Hasselquist et al. 1995a), tail length (males; 1Y − 2Y: $t = -4.557$, $df = 23$, $P < 0.001$; females; 1Y − 2Y: $t = -2.366$, $df = 21$, $P = 0.028$), and bill depth (males; 1Y − 2Y: $t = -2.522$, $df = 25$, $P = 0.018$). In the following analyses, we use age-standardized values by adding the mean difference between earlier age classes and the last age class (older than 2Y) to recalculate all data to the age class older than 2Y. Hence for all male 1Y-birds we added 1.852 mm to the wing length, 1.833 mm to the tail length and 0.065 mm to the bill depth, and for 2Y-birds we added 0.395 mm to the wing length. For all female 1Y-birds we added 1.674 mm to the wing length and 1.182 mm to the tail length, and for 2Y-birds we added 0.296 mm to the wing length.

The variation due to sex differences in phenotypic values will add to the phenotypic variance of the trait. If this is not corrected for we may underestimate heritabilities and trait correlations (Schluter and Smith 1986). All traits (including the values standardized for age), except bill width, showed differences between the sexes. In all traits, males were significantly larger than females. Unless stated otherwise, we use measures that are standardized for sex by subtracting the mean difference (wing length 4.32, wing projection 1.01, tail length 4.73, bill depth 0.104, bill length 0.203, skull length 1.03 and tarsus length 1.21) between the sexes from the male's values. The phenotypic variance of the trait measurements V_P did not differ between the sexes after standardization (Levene's test for equality of variances based on F-statistics; all $P > 0.175$).

Repeatabilities

When estimating the reliability (r^2) of our measurements we have chosen to do analyses separately for males and females based on measurements before sex-standardization, to avoid inclusion of extra variance due to the pooling the sexes. Any form of variation in measurements taken from one individual, caused by measurement error or phenotypic plasticity in characters that develops repeatedly, will add to the phenotypic variance V_P of that trait. This inflation of the phenotypic variance may result in an underestimation of heritabilities and genetic correlations, that both have the phenotypic variance (or covariance) in the denominator.

We assessed the variance in measurements within individuals (that is not due to age) by calculating repeatabilities (Lessells and Boag 1987) for all traits. The dataset used for calculating repeatabilities is based on measurements of individuals that have been measured in more than one year. Thus only one measure per individual and season is included. For individuals measured several times in one season we have selected the measurement taken by the most experienced ringer.

The effect of ringers is tested on measurements taken between 1991 and 2001, during which totally 20 ringers contributed with measurement data. Earlier measurements are not included in the analysis since these are not associated with ringer identity in the current files. Between 1983 and 1990, caught individuals were only measured for wing length. Multiple regressions, with the trait as dependent variable and individual bird and ringer identity as random factors, were run. Significant effects of ringers were found for wing projection ($F_{18,169} = 1.83$, $P = 0.025$), bill depth ($F_{18,169} = 2.32$, $P = 0.003$), bill width ($F_{18,167} = 4.05$, $P < 0.001$), bill length, ($F_{18,174} = 3.21$, $P < 0.001$) and skull length ($F_{17,130} = 2.00$, $P = 0.015$). No ringer was

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consistently different from the other ringers in any of the traits. There are several reasons why we would not expect a high bias due to the effect of ringer. First, most of the measures are taken by rather few ringers; 80% (95%) of the data has been collected by 5 (10) ringers only. Second, the uncertainties of individual phenotypic values are reduced by the fact that between 33% and 46% of the individuals have been measured more than once for the trait and measures used are then means of all measures taken.

Assortative mating

Positive assortative mating may inflate heritability estimates because it increases the homozygosity level of trait genes and causes positive covariance between alleles at different loci (Lynch and Walsh 1998). Correspondingly, negative assortative mating may deflate the estimate of heritability. The degree of assortative mating is defined by the correlation between the phenotypic values of mates in a population. We therefore calculated Pearson correlation coefficients between traits of pair-mates.

Heritabilities

We calculated three estimates of the heritability h^2 for every trait by regressing the phenotypic value of recruited offspring (; mid-offspring values were used when >1 recruit was included) on father, mother and mean phenotypic value of the parents (i.e. mid-parent value). The heritability was estimated both from: (1) twice the slope of single-parent regression, and (2) the slope of mid-parent regression (Falconer and Mackay 1996).

We calculated the coefficient of variation of traits based on heritability estimates from midparent-midoffspring regression, where the additive variance was defined as $V_A = V_P h^2$, the coefficient of additive genetic variation as $CV_A = 100\sqrt{V_A}/X$, and the residual coefficient of variation as $CV_R = 100\sqrt{(V_P - V_A)}/X$ (Houle 1992), where X is the average value of the trait.

Phenotypic and genetic correlations

We calculated phenotypic and genetic correlations on a balanced data set, thus containing only individuals that were measured for all traits. Phenotypic correlation r_P is the correlation of the phenotypic values of two traits (X and Y) in the same individual (Lynch and Walsh 1998), here estimated with Pearson correlation coefficients (Sokal and Rohlf 1995).

In order to estimate the heritability of more general measures of size and shape (Grant 1983, Merilä and Gustafsson 1993), we used principal component analysis (PCA). Eigenvectors and individual PC-scores for each principal component were extracted from the non-rotated phenotypic correlation matrix. The PC-scores of parents and offspring were used to calculate heritabilities in the same fashion as described above.

The genetic correlation r_A between two characters expresses the net extent of pleiotropy and linkage disequilibrium that exist genetically between two traits (Lynch and Walsh 1998). We estimated r_A from the covariance between mid-parent and mid-offspring values, $r_A = \mathrm{cov}XY/\sqrt{(\mathrm{cov}XX \times \mathrm{cov}YY)}$, where covXY is the covariance between parental trait X and offspring trait Y or vice versa, covXX and covYY are the "cross-covariances" between parental and offspring traits. Since there are two possible estimates of covXY and consequently two estimates of r_A (r_{A1} and r_{A2}) for each pairwise comparison we present the arithmetic mean of the two estimates r_{A1} and r_{A2} (Lynch and Walsh 1998). The data set used for calculation of r_A consisted of families with mid-offspring and mid-parent values for all traits. We used a resampling procedure (Sokal and Rohlf 1995) to test the significance of obtained r_A values. Offspring values were randomized 9999 times. The level of significance is then given by $(n+1)/(N+1)$, where n is the number of randomized r_A-values equal to or more extreme than the observed value and N is the number of randomizations. A measure of the robustness of the whole r_A-matrix is to compare the r_{A1}- and r_{A2}-matrix, since they are supposed to be equal (van Noordwijk 1984). This was done by calculating an element-wise Pearson product-moment correlation coefficient, tested by using a Mantel test (Smouse et al. 1986, Sokal and Rohlf 1995) based on 9999 randomizations of both matrices.

Previous studies have suggested that r_P and r_A are highly correlated (Cheverud 1988, Roff 1995, Kominakis 2003) whereas some suggest otherwise (Willis et al. 1991, Hébert et al. 1994). We therefore compared our estimates of r_P and r_A as for the r_{A1}- and r_{A2}-matrices above. Since the correlation coefficient is mostly describing the proportionality between the two sets of matrix elements and does not take into account the actual differences between the values (Willis et al. 1991), we also calculated the mean absolute difference (i.e. average disparity; $D = \Sigma|r_{A,i,j} - r_{P,i,j}|/n$) between the matrices, where i and j are the two traits compared in each element and n is the total number of correlations (Roff 1995). A paired t-test was used to evaluate the significance of the difference, $d = r_{A,i,j} - r_{P,i,j}$ and the absolute difference $|d| = |r_{A,i,j} - r_{P,i,j}|$ (Kominakis 2003).

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Selection

Based on the standardized lifetime number of fledged young $\overline{w}$, we quantified the amount of directional selection and the amount of stabilizing/disruptive selection on each trait separately, with standardized linear selection differentials β and quadratic selection differentials γ respectively (Lande and Arnold 1983). To improve normality the lifetime number of produced offspring were square-root transformed before standardization. Although the square-root transformed variable still has a non-normal distribution it will have little affect on the parametric coefficients (Lande and Arnold 1983). The standard error of the parameters may however be affected by the violation of the assumption of normal distribution. The P-values of the selection differentials should therefore be observed with some caution. The γ parameters where estimated with the multiple regression model:

$$\overline{w} = c + \beta z + \beta_2 z^2 (1) \qquad (1)$$

where c is the intercept, z is the standardized trait value, and $\gamma = 2\beta_2$ (Fairbairn and Preziosi 1996). Because of correlations between β and γ values we estimated β from the purely linear model (Brodie et al. 1995). The standardized quadratic selection differential γ is negative when selection is stabilizing and positive when selection is disruptive. All analyses were performed on males and females separately, in order to investigate the existence of antagonistic selection pressures, and the measures are therefore not corrected for sex. Differences in parameter estimates between the sexes were tested by including sex into the model (1). A significant interaction between sex and trait value as a function of fitness would indicate a difference in slopes between the sexes.

The fitness functions of the morphological traits were visualized by using the cubic b-spline method outlined by Schluter (1988). Univariate cubic splines were calculated for all traits using the program glms40 with a widows interface developed by Schluter, freely available at the homepage http://www.zoology.ubc.ca/~schluter/splines.html. The fitness function with the best spline fit is found by searching for the smoothing parameter lambda that minimize the generalized cross-validation score (GCV score). A minimum GCV-score is most often found in the range $-10\lambda 10$. In some cases the GCV score goes towards a constant value as lamda increases. We then chose to use lamda = 10 since the shape of the fitness function is not likely to change above this value. Standard errors of the functions were calculated through 1000 bootstraps employed by the same program.

Results

Means and repeatabilities

The sex-specific mean and variation of the eight morphological traits, after correcting for age, are reported in Table 1. Repeatabilities, for males and females separately, of the traits corrected for age are given in Table 2 and averaged to 0.629 (sexes combined). The range of repeatabilities is large, ranging from 0.23–0.28 in measurements of wing projection to 0.95 in tarsus length. Since skull length is the difference between skull-bill length (with average repeatability 0.822; N = 47 (males) N = 59 (females)) and bill length, it is affected by the measurement error of both measurements which explains its relatively low repeatability.

Assortative mating

There was no significant assortative mating with regard to the eight morphological traits. The Pearson correlation ranged between −0.093 and 0.12 (all $P > 0.1$). Only in wing length and bill length did both parents show non-significant deviation from an expected normal distribution using a Kolmogorov-Smirnov test with Lilliefors correction. However, the estimated coefficients from a Spearman correlation did not differ qualitatively from the Pearson coefficients and none of the Spearman correlations differed significantly from zero.

Principal components

The principal components extracted from the phenotypic correlation matrix (see Table 5) are given in Table 3. We used the first four principal components which together explained 73.3% of the total variance in the correlation matrix. PC1, which represents to a large extent general size, explained 26.0% of the total variance. PC2 explained 20.9% of the total variance and is a shape index consisting of the feather traits against the bill traits. PC3 (14.2% of the variance) consists mainly of skull length and tarsus length while PC4 (12.2% of the variance) contains wing projection to a large extent.

Heritabilities

Estimates from midparent-midoffspring regressions showed significant heritabilities for seven of eight characters, ranging from 0.439 to 0.939 (Table 4; Fig. 1). The only non-significant h^2 was that of bill

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Table 1. Mean values, standard errors and variance components of eight morphological traits, corrected for age, in the great reed warbler. All values except means, standard errors and ranges are corrected for sex. The additive variance components (V_A) are generated from the phenotypic variance components (V_P), the sex-corrected means, and the estimated heritabilities from midparent-midoffspring regression (Table 4) in accordance with formulas in the methods. The residual variances V_R are not reported in the table but can be calculated by subtracting the phenotypic variance with the additive variance. For comparative purposes the coefficient of phenotypic (CV_P) additive (CV_A) and residual (CV_R) variance are also included in the table.

	N	Mean	SE	Range	V_P	V_A	CV_P	CV_A	CV_R
			Males						
Wing length (WL)	244	101.3	0.12	95.8–106.8	3.17	2.20	1.83	1.53	1.01
Wing projection (WP)	171	29.4	0.11	25.0–33.9	2.00	1.00	4.99	3.53	3.52
Tail length (TL)	171	79.5	0.17	71.8–86.8	4.51	2.59	2.84	2.15	1.86
Bill depth (BD)	171	5.2	0.01	5.0–5.8	0.02	0.003	2.96	1.10	2.75
Bill width (BW)	171	5.1	0.01	4.6–5.7	0.03	0.01	3.47	2.30	2.60
Bill length (BL)	173	12.7	0.04	10.9–13.9	0.28	0.26	4.21	4.08	1.04
Skull length (SL)	139	31.7	0.05	29.9–33.0	0.33	0.17	1.87	1.34	1.30
Tarsus length (TR)	170	33.8	0.06	31.7–35.7	0.62	0.45	2.42	2.06	1.26
			Females						
Wing length	264	97.0	0.11	91.7–101.3					
Wing projection	206	28.4	0.10	22.0–32.0					
Tail length	200	74.8	0.14	70.0–80.2					
Bill depth	207	5.1	0.01	4.8–5.7					
Bill width	206	5.1	0.01	4.6–5.7					
Bill length	207	12.5	0.04	10.5–14.2					
Skull length	170	30.6	0.04	29.1–32.1					
Tarsus length	207	32.6	0.06	30.4–34.9					

depth, which also gave non-significant estimates from both singleparent-midoffspring regressions.

The father-midoffspring h^2 were significant in five of eight cases and the mother-midoffspring h^2 in six of eight cases. In most traits there was no significant difference between mother- and father-midoffspring h^2. However, there was a substantially higher maternal slope in tarsus length ($F_{1,118} = 4.066$, $P = 0.046$). Also, there are indications of positive paternal effects in bill length, since the father-midoffspring heritability is above unity and the mother-midoffspring heritability is lower than the father-midoffspring heritability, although not to a significant degree ($F_{1,119} = 1.625$, $P = 0.2$).

Table 2. Estimated repeatabilities (r^2) and standard errors (SE) of eight morphological traits in the great reed warbler. The sexes are treated separately.

Trait[2)]	Males			Females		
	r^2	SE[1)]	N	r^2	SE[1)]	N
WL	0.827	0.028	98	0.766	0.035	102
WP	0.232	0.095	60	0.278	0.087	64
TL	0.595	0.072	61	0.587	0.068	66
BD	0.513	0.081	60	0.512	0.074	66
BW	0.482	0.084	60	0.453	0.080	65
BL	0.712	0.055	61	0.619	0.064	65
SL	0.543	0.091	47	0.477	0.084	58
TR	0.949	0.011	62	0.949	0.010	71

1) Standard errors are estimated in accordance to Becker (1984).
2) WL = wing length; WP = wing projection; TL = tail length; BD = bill depth; BW = bill width; BL = bill length; SL = skull length; TR = tarsus length.

Midparent-midoffspring h^2 of PC1-PC4 were significant (mean 0.53; range 0.33–0.70). The singleparent-midoffspring regressions showed significant slopes only for PC1 and PC2. PC1 showed the highest h^2 in the midparent-midoffspring analysis.

To estimate how much additive variance that exists in each trait we calculated the coefficient of additive variation CV_A (Table 1). The average of CV_As was 2.26 (range 1.1–4.1) and the average of CV_Rs was 1.92 (range 1.0–3.5).

The h^2s were similar for feather (average 0.59), bill (average 0.50) and skeletal traits (; skull length and tarsus length; average 0.68; Kruskal-Wallis test $\chi^2_{(2)} = 0.800$, $P = 0.670$). However the range of the bill h^2s was substantially higher (range 0.80) than the other trait classes (range = 0.19 (feather traits); range = 0.22 (skeletal traits)).

Trait correlations

Phenotypic correlations ranged between -0.02 and 0.43, with a mean of 0.15. Genetic correlations ranged

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Table 3. Unrotated PC-loadings for the first four principal components, generated from the phenotypic correlation matrix (Table 5) of the great reed warbler. EIG is the associated eigenvalues.% is the proportion of the total variance accounted for by each eigenvalue.

	EIG.	%	WL[1)]	WP[1)]	TL[1)]	BD[1)]	BW[1)]	BL[1)]	SL[1)]	TR[1)]
PC1	2.077	25.96	0.536	0.399	0.419	0.567	0.544	0.553	0.444	0.577
PC2	1.669	20.86	0.711	0.440	0.548	−0.495	−0.428	−0.447	0.140	−0.152
PC3	1.136	14.20	−0.194	0.169	−0.436	−0.086	−0.356	−0.240	0.612	0.560
PC4	0.978	12.23	0.038	0.703	−0.414	−0.122	−0.062	0.280	−0.461	0.043

1) WL = wing length; WP = wing projection; TL = tail length; BD = bill depth; BW = bill width; BL = bill length; SL = skull length; TR = tarsus length.

between 0.08 and 1.04, with a mean of 0.46 (Table 5). Only 9 of 28 (32%) of r_Ps and 6 of 28 (21%) of r_As were significant after sequential Bonferroni correction (Type I error level = 0.05). The two corresponding genetic correlations r_{A1} and r_{A2} were significantly correlated ($r = 0.441$, $N = 28$, $P = 0.01$).

The correlation between r_A and r_P, as measured with linear regression, was significant and the correlation coefficient was moderately high (Fig. 2; $F_{1,26} = 7.75$, $P = 0.01$, $r = 0.479$). The same conclusion could be drawn from the Mantel test ($P = 0.006$). However, with an average disparity D of 0.33 there are indications that indeed sometimes r_A will differ quantitatively from the corresponding value of r_P (see also Fig. 2). Both the differences d and absolute differences |d| between r_A and r_P were shown to be highly significant (t-test; d: $t = 7.207$, $df = 27$, $P < 0.001$; |d|: $t = 8.854$, $df = 27$, $P < 0.001$).

Selection

Overall, most traits, except bill depth in males and wing length in both sexes, are subject low degrees of linear selection (Table 6). The male fitness function of wing length does also carry a significant quadratic term, but reaches the optima outside the observed range of the trait in the population or at the highest values the trait's range (Fig. 4). The standardized directional selection differentials of wing were positive in males and negative in females and the only differentials that differed significantly between the sexes ($F_{1,438} = 7.405$, $P = 0.007$). This difference coincides with a sexual dimorphism in wing length observed in the population (Table 1). The negative selection on the bill depth does on the other hand not coincide with the observed sex difference, where males tend to be larger than the females.

Table 4. Narrow-sense heritability (h^2) of eight morphological characters and the four first principal components (PC1–4) based on the phenotypic correlation matrix of all the morphological characters, in the great reed warbler. Heritabilities, accompanied with standard error (SE) and sample size (N), are based on midparent-, father- and mother-midoffspring regression

Trait[3)]	Midparent-midoffspring			Father-midoffspring			Mother-midoffspring		
	$h^2 = b$	SE	N	$h^2 = 2b$	SE[1)]	N	$h^2 = 2b$	SE[1)]	N
WL	0.695***	0.095	131	0.654***	0.176	82	0.562**	0.172	89
WP	0.501***	0.144	88	0.226[2)]	0.238	57	0.560**	0.204	66
TL	0.573***	0.119	86	0.644**	0.186	57	0.462**	0.166	65
BD	0.137[2)]	0.162	88	0.183	0.182	57	−0.087	0.168	65
BW	0.439**	0.139	85	0.414[†2)]	0.236	56	0.432*	0.204	63
BL	0.939***	0.114	89	1.086***	0.174	57	0.768***	0.218	65
SL	0.512***	0.140	66	0.486*	0.192	45	0.195	0.284	47
TR	0.729***	0.134	86	0.494*	0.194	57	1.070***[2)]	0.210	64
Mean	*0.576*			*0.519*			*0.521*		
PC1	0.702***	0.13	57	0.564*	0.234	42	0.900***	0.236	44
PC2	0.611***	0.163	57	0.682***	0.190	42	0.518*	0.228	44
PC3	0.327*	0.133	57	0.206[2)]	0.188	42	0.392	0.238	44
PC4	0.487**	0.181	57	0.400	0.256	42	0.278	0.258	44
Mean	*0.532*			*0.463*			*0.522*		

† = $P < 0.1$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.
1) SE of h^2 is twice the standard error of the slope b.
2) Residuals are non-normally distributed (Kolmogorov-Smirnov test with Lilliefors correction $P < 0.05$).
3) WL = wing length; WP = wing projection; TL = tail length; BD = bill depth; BW = bill width; BL = bill length; SL = skull length; TR = tarsus length.

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Table 5. Phenotypic (r_P, below the diagonal) and genetic (r_A, above the diagonal) correlations between eight morphological traits in the population of great reed warblers. The phenotypic correlations (N = 287 individuals) and genetic correlations (N = 57 families) were calculated from a balanced data set, where only individuals/families measured for all eight traits were included. Probabilities for r_P were generated from SPSS 11.0 (SPSS Inc.) for Pearson correlations. Probabilities for r_A (below correlations between brackets) were estimated with randomization test. Significant values after sequential Bonferroni-correction are indicated in bold characters.

	WL[1)]	WP[1)]	TL[1)]	BD[1)]	BW[1)]	BL[1)]	SL[1)]	TR[1)]
WL		**0.787**	**0.891**	0.228	**0.661**	0.081	0.418	0.195
		(0.0003)	(0.0001)	(0.27)	(0.0009)	(0.30)	(0.022)	(0.12)
WP	**0.431**		0.494	0.576	**0.864**	0.260	0.212	0.363
	(2×10^{-14})		(0.021)	(0.12)	(0.0008)	(0.11)	(0.23)	(0.055)
TL	**0.549**	0.060		0.182	0.499	0.252	0.585	0.122
	(5×10^{-24})	0.31		(0.33)	(0.010)	(0.070)	(0.004)	(0.26)
BD	−0.023	−0.0001	0.043		0.103	1.036	0.448	0.610
	(0.69)	(1.00)	(0.49)		(0.40)	(0.0007)	(0.17)	(0.052)
BW	0.058	−0.011	0.077	**0.376**		0.518	0.410	**0.748**
	(0.32)	(0.85)	(0.19)	(4×10^{-11})		(0.0024)	(0.054)	(0.0004)
BL	0.036	0.077	0.021	**0.358**	0.363		0.274	0.459
	(0.54)	(0.19)	(0.72)	(4×10^{-10})	(2×10^{-10})		(0.078)	(0.0013)
SL	0.195	0.079	0.109	0.143	0.051	−0.006		0.605
	(0.0009)	(0.18)	(0.064)	(0.0152)	(0.388)	(0.92)		(0.0027)
TR	0.087	0.176	0.011	**0.241**	0.155	**0.240**	**0.330**	
	(0.14)	(0.0027)	(0.85)	(4×10^{-05})	(0.0085)	(4×10^{-05})	(1×10^{-08})	

1) WL = wing length; WP = wing projection; TL = tail length; BD = bill depth; BW = bill width; BL = bill length; SL = skull length; TR = tarsus length.

Both sexes showed significant stabilizing selection for several traits. In males, there was significant stabilizing selection on wing projection and tail length and a tendency to stabilizing selection on bill width. In females, there was stabilizing selection on tail length and bill width and a tendency to stabilizing selection on wing projection. These forces of selection on the trait variation reach their optima roughly at the mean values of each trait.

Discussion

Most of the investigated morphological traits showed high and significant heritabilities (h^2). The wide range of the midparent-midoffspring h^2 (between 0.14 and 0.94) indicates that the traits may show different responses to selection. Some of the variation in h^2s between traits may be due to differences in repeatabilities, since repeatability sets an upper limit to h^2 (Boag and van Noordwijk 1987). However, there is no empirical basis for this claim presented in our paper. Nevertheless, the heritabilities of wing projection and bill length exceeded the repeatabilities of the traits. This can occur whenever there is a source of variation that contributes more variation to the measurements within individuals than to that between individuals, e.g. when there is annual variation in the expression of a trait (Boag and van Noordwijk 1987). However, the low h^2 in bill depth seems not to be due to measurement error alone, since the midparent-midoffspring estimate is much lower than the estimated repeatability. This, together with the comparatively low CV_A (Table 1), indicates that there is little genetic variation in bill depth.

It has been shown that deeper bills are predictors of female social mating status and choice in territories with larger food abundance (Forstmeier et al. 2001). Also, it has been shown that smaller bills correlate positively with a higher vocal performance in medium ground finch *Geospiza fortis* and among Darwin's finches on the Galapagos islands (Podos 2001). Song is important for male reproductive success in great reed warblers (Hasselquist et al. 1996, Hasselquist 1998). It may thus be possible that the low additive variance in bill depth is caused by the negative directional selection observed among males (Table 6), or alternatively that this trait is genetically correlated to another trait that is subject to high selection pressure. If this is the explanation for the low additive variance in bill depth we expect that bill depth indeed is favoured by female mate selection through more attractive song. The alternative explanation for the low heritability is a large environmental variance. There is support for this idea in the comparatively high CV_P and CV_R seen in bill depth (Table 1). One scenario that would explain the low heritability in bill depth would then be that it is determined by a plastic response during its development. In great tits *Parus major* bill character, foremost bill length, show seasonal variation (Gosler 1987). Individuals tend to have longer and deeper bills during the winter season compared to the summer season. Such seasonal variation is not likely to be the reason for the apparent low heritability in great read warblers, since all measurements have been taken during the

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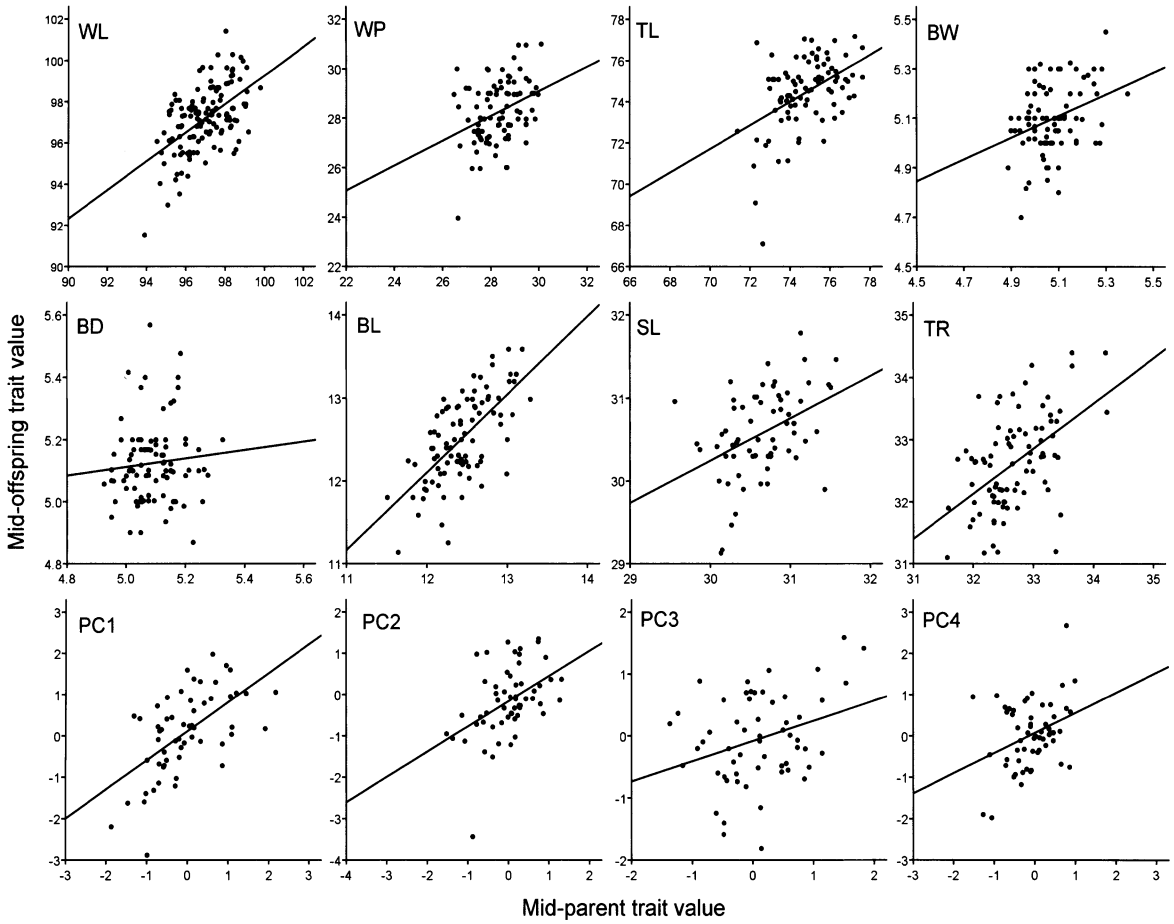

Fig. 1. Regression analyses underlying heritabilities of eight morphological characters and the PC-scores derived from the first four principal components of the phenotypic correlation matrix (Table 5). Trait abbreviations, indicated in the upper left corner of each graph, are as follows; WL = wing length; WP = wing projection; TL = tail length; BD = bill depth; BW = bill width; BL = bill length; SL = skull length; TR = tarsus length. The scale of all morphological measurements is in millimetres.

breeding season and individual repeatability is moderately high. Instead it is more likely that bill depth, at an early age, is affected by environmental factors that set the bill depth for rest of the individual's life.

Parental effects

Some traits showed significant differences between father-midoffspring and mother-midoffspring regressions. This cannot be a result of extra-pair fertilizations as nearly all offspring were assigned to their genetic parents (Hasselquist et al. 1995b, 1996, Arlt et al. 2004). The observed differences may be due to parental effects, i.e. that offspring phenotype is determined by the phenotype or environment of one or both parents (Boag 1983, Falconer and Mackay 1996, Shaw and Byers 1998). Higher maternal inheritance was detected in tarsus length. A prior study on great reed warblers, using a subset of the data included in the present study, detected higher maternal inheritance in both wing length and tarsus length (Hasselquist et al. 1995a). We did not detect any such difference in wing length in our larger data set. Moreover, the magnitude of the maternal effects in tarsus length is not as large as in the previous study, explained by a lower observed maternal inheritance and higher paternal inheritance in the full data set. This could be due to the more powerful analysis provided in this study or that the effects of maternal (or paternal) non-additive inheritance have changed during the last decade. The larger maternal inheritance in tarsus length could be due to differential maternal investment in egg content (e.g. Schwabl et al. 1997) or due to differential investment in feeding. The latter explanation however is not supported by earlier studies of our study population (Sejberg et al. 2000). In bill length and skull length there is seemingly higher resemblance between father and offspring. These differences are however not significant. Paternal effects are rarely observed among birds and have been observed

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Table 6. Sex specific standardized directional (β) and stabilizing (γ) selection differentials with *SE*s of eight morphological traits in the population of great reed warblers. Relative fitness is estimated as square-root lifetime produced fledglings.

Trait[2)]	Males			Females		
	β	SE	N	β	SE	N
WL	0.111†	0.066	225	−0.134*	0.061	264
WP	0.127	0.081	162	0.019	0.074	206
TL	0.045	0.080	162	0.064	0.076	200
BD	−0.173*	0.079	162	−0.004	0.074	207
BW	−0.074	0.079	164	−0.020	0.074	206
BL	−0.104	0.078	164	−0.073	0.074	207
SL	0.076	0.089	131	0.027	0.079	170
TR	0.093	0.079	162	−0.041	0.074	207
Trait[2)]	γ	SE[1)]	N	γ	SE[1)]	N
WL	−0.247**	0.087	225	−0.043	0.091	264
WP	−0.223*	0.097	162	−0.136†	0.082	206
TL	−0.206*	0.095	162	−0.227*	0.106	200
BD	−0.007	0.110	162	−0.139	0.088	207
BW	−0.178†	0.101	164	−0.193*	0.087	206
BL	−0.029	0.113	164	0.055	0.089	207
SL	0.033	0.124	131	−0.172	0.111	170
TR	0.009	0.118	162	−0.075	0.102	207

† = P < 0.1; * = P < 0.05; ** = P < 0.01.
1) SE of γ is twice the standard error of the slope β_2.
2) WL = wing length; WP = wing projection; TL = tail length; BD = bill depth; BW = bill width; BL = bill length; SL = skull length; TR = tarsus length.

mostly in sexually selected traits (Grant and Grant 1996, Griffith et al. 1999, Qvarnström and Price 2001). There are many potential sources of paternal effects on the offspring, since male great reed warblers not only provide a territory but also a substantial amount of parental care in some nests (e.g. Sejberg et al. 2000). It is thus possible that offspring bill length is affected by the quality and quantity of food existing in the territory and that choice of certain territory qualities also show paternal inheritance. Alternatively, the difference in inheritance between mother- and father-midoffspring regressions of bill length is due to a negative effect of the maternal environment. Further study need to be made in order to distinguish between these alternatives.

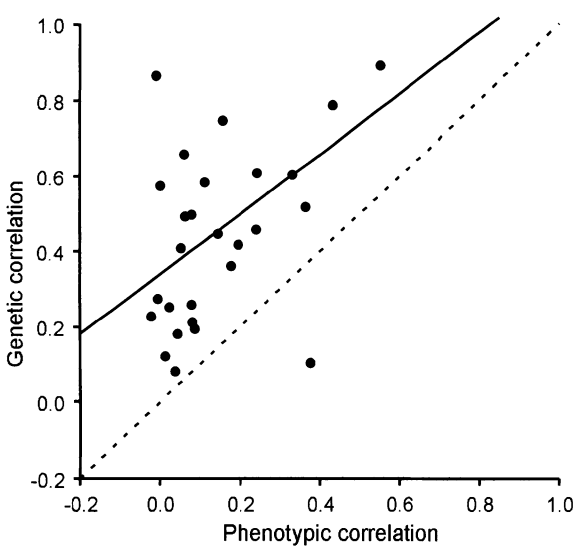

Fig. 2. Association between r_P and r_A in great reed warblers. The solid line represents the regression line (b = 0.797, t = 2.78, df = 26 P = 0.01). The intercept of the slope (i = 0.340) is significantly deviating from zero (t = 5.55, P < 0.001). The dashed line represents the 1:1 relationship and the slope b is not significantly deviating from this relationship (t = 0.711, df = 26, P = 0.48).

Genetic and phenotypic correlations

The genetic correlations were all positive and ranged between 0.08 and 1.04. Phenotypic correlations (range −0.02–0.55) were generally lower than corresponding genetic correlations (Fig. 2). The lack of strong and significant negative r_Ps indicates that there are no strong trade-offs among the morphological traits. However, an average r_A of 0.46 and that almost 30% of traits had moderately high correlations ($r_A > 0.6$), indicates that the population might have difficulties to evolve in proportionality, i.e. changing in shape. Traits that are supposedly functionally related, e.g. feather traits (; wing length, wing projection and tail length) and bill traits (bill depth, bill width, and bill length), show only

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very weak indications of being more genetically related. The exceptions are the genetic correlations between wing length and wing projection ($r_A = 0.79$), wing length and tail length ($r_A = 0.89$) and bill length and bill depth ($r_A = 1.03$). Surprisingly, bill width show high genetic correlations with both wing length ($r_A = 0.66$) and wing projection ($r_A = 0.86$). However, the phenotypic correlations clearly show a pattern, where functionally related traits also are phenotypically more correlated. The exception to this is the phenotypic correlation between wing projection and tail length ($r_P = 0.06$), and could be due to the low repeatability observed in wing projection ($r = 0.23$). It is thus possible that non-additive forces determine the observed shape among functionally related characters. It should, however be noted that only seven out of 28 estimates (all $r_A > 0.65$) were significantly different from zero at $\alpha < 0.05$ after sequential Bonferroni correction. Additionally, the correlation between r_{A1} and r_{A2} was only moderate, although significant.

Similarity between genetic and phenotypic correlations

The matrix comparison between r_P and r_A showed a moderate, although significant, correlation. The slope of the regression line was not significantly deviating from the expected 1:1 relationship (Fig. 2). However, the absolute difference $D = 0.33$ and the positive intercept of the regression line between r_P and r_A show that genetic correlations are generally much higher than corresponding phenotypic correlations independent of absolute correlation value. Most studies to date supports Cheverud's (1988) conjecture that phenotypic correlations are reasonably good substitutes for genetic correlations (Cheverud 1988, Roff 1995, Koots and Gibson 1996, Reusch and Blanckenhorn 1998). In our study, r_P were generally lower than the r_A (Fig. 2). We suspect that genetic correlations between the traits are systematically overestimated (Roff 1995, Reusch and Blanckenhorn 1998) since many of the traits show high genetic correlations even though the heritability of one of the characters show low heritability, e.g. that between bill depth and bill length. The reason for this overestimation is that in 11 out of 56 cases the cross-correlation (the correlation between trait A in the offspring and trait B in parents) is higher than the correlation between same trait (A or B) in parents and offspring. This may be due to a large difference in measurement error between the two traits. In most of these cases one of the traits show low repeatability (8 cases with bill depth, 3 cases with wing projection) and there is a tendency to significant correlation between the absolute difference in repeatability and the genetic correlation (Spearman's $\rho = 0.319$, $N = 28$, $P = 0.098$). Cheverud (1988) showed that the effective number of families $N_{es} = h_X h_Y N$ were negatively correlating with the average squared difference between genetic and phenotypic correlations, and he recommended effective sample sizes higher than 40 to estimate genetic correlations. Since the effective sample sizes (based on heritabilities in Table 1) in this study ranged between 11 and 43, we should in some instances be careful to compare the magnitude of r_P and r_A. However, by observing the relationship between the effective sample size N_{es} and the absolute difference between r_P and r_A there seems to be a trend towards more similar estimates of r_A and r_P with increasing N_{es} (Fig. 3). However, based on our data it is impossible to say whether this is an effect the sample size or the heritabilities of the correlated traits.

Selection

Overall, all traits are subject to rather weak selection (all $|\beta| < 0.2$ and all $\gamma > -0.25$) via lifetime reproductive success (Table 6). Low levels of directional selection on morphological traits are commonly observed in passerines both via fecundity and survival (e.g. Björklund and Lindén 1993, Schluter and Smith 1986b, Wiggins 1991, Przybylo et al. 2000) with the exception for Darwin's finches of the Galapagos Islands (Grant and Grant 1989). However, note that the selection analyses in this study of great reed warblers do not include the first year life stage, which due to the high mortality may be a period when selection pressures on quantitative characters are rather strong (e.g. Schluter and Smith

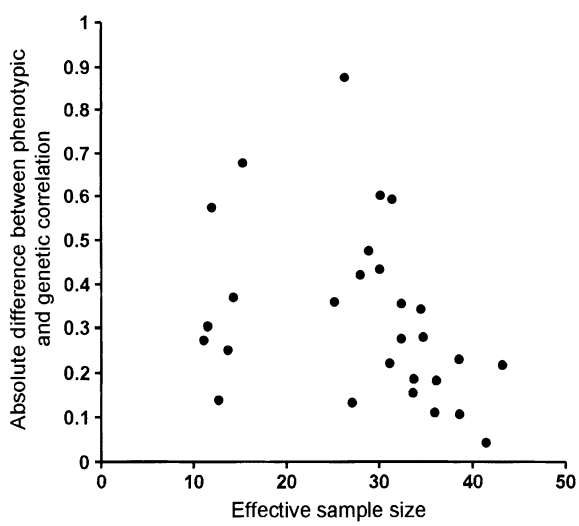

Fig. 3. The absolute difference between r_P and r_A in relation to the effective sample size $N_{es} = h_X h_Y N$, where h_X are h_Y are the squared heritabilities of the traits X and Y (calculated from individuals used in the genetic correlation analyses) and N is the actual sample size.

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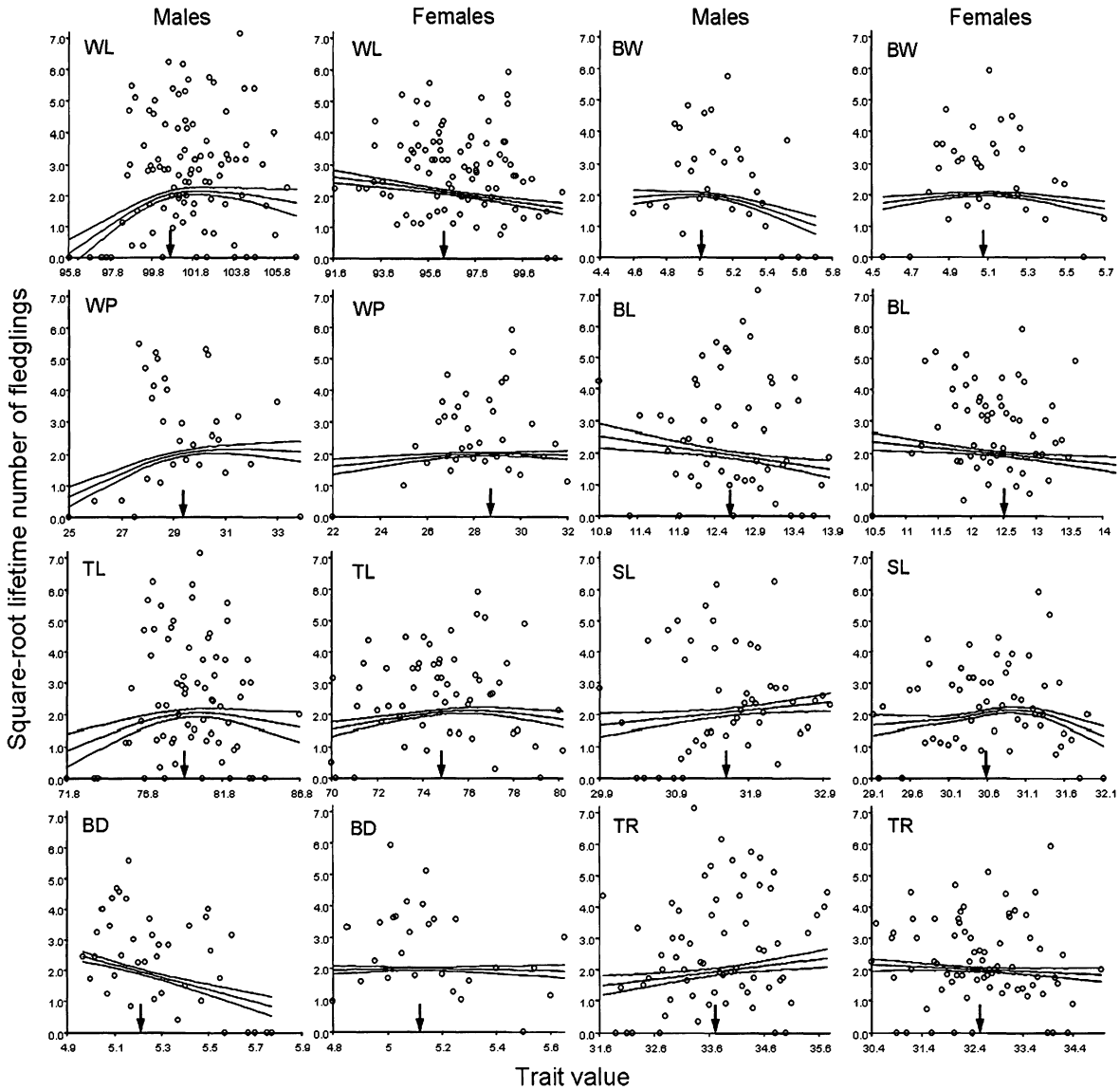

Fig. 4. Sex-specific fitness functions relating the square-root number of fledglings to eight morphological traits in great reed warblers. The functions are visualized with the cubic b-spline method outlined by Schluter (1988). The lines for each graph illustrate the most likely fitness function given a lamda that minimizes the GCV-score (see methods) and standard errors calculated by 1000 bootstraps. The arrows on each graph indicate the sex-specific mean of the traits. Trait abbreviations, indicated in the upper left corner of each graph, are as follows; WL = wing length; WP = wing projection; TL = tail length; BD = bill depth; BW = bill width; BL = bill length; SL = skull length; TR = tarsus length. The scale of all morphological measurements is in millimetres.

1986b). Nevertheless, there is significant directional selection on wing length in females and other (mainly feather) traits are subject to significant stabilizing selection. Furthermore, wing length is subject to antagonistic selection in males and females, and the difference is in concordance with the mean trait differences among the sexes. The great reed warbler is a long distance migrant and in such species feather morphology is an important character, which might determine how well birds can optimize their migratory flight. Positive directional selection on wing length via fecundity was also found in another long distance migrant, the collared flycatcher (Przybylo et al. 2000). A larger wing span would be favoured if there is selection for increased migratory flight speed (Hedenström and Alerstam 1998). Early spring arrival is one of the key predictors of annual pairing success (harem size) and production of offspring in male great reed warblers (Hasselquist 1998). We therefore expect males to be selected for early and/or rapid migration. A positive

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selection on migration speed could thus explain the tendency for positive selection on male wing length. Indeed it has been found in an earlier study that male wing length correlated significantly with harem size (Hasselquist 1998). In the same study, wing length was also correlated with territory occupation date, but may be confounded by an effect of age. In males there is also a significant quadratic term in the fitness function of wing length, indicating that there could be stabilizing selection disfavouring males with the longest wings. However, note that the standard error at larger wing length is large and therefore no clear fitness optimum can be observed within the range of the trait (Fig. 4). Contrary to the males, female great reed warblers are subject to negative directional of selection on wing length. Since females arrive on average 10 days later than males to the breeding grounds (Hasselquist 1998) we could speculate that the negative selection on wing length may relate to other factors rather than migration speed. One possibility is that a shorter wing allows for a better capacity flying and manoeuvring in reed beds, a potentially important quality in great reed warblers that spend a lot of time in the reeds when foraging and escaping predators. This antagonistic selection among the sexes may also account for the relatively high additive variance and heritability in wing length (Table 1 and Fig. 1).

There are significant negative standardized quadratic selection differentials on all feather traits in males (Table 6). This is in contrast to females, where tail length is the only feather trait that has a significant quadratic differential. This may be in concordance with the speculation stated above. The wing and tail morphology may be subject to stabilizing selection since large values have a positive effect on flight speed during migration while small values may have a positive effect on the manoeuvrability in reed. However, since the differentials are calculated from univariate models and the feather traits are phenotypically correlated, we cannot exclude that the general pattern of stabilizing selection in feather traits are due to correlated selection on one of the traits.

Also bill width is subject to significant stabilizing selection in females and nearly so in males. It is likely that this stabilizing selection on bill width is related to food quality and food acquisition. In insectivorous birds bill width and bill depth correlates with the pressure that the force that the bill can exert on an object (Lederer 1975). Wider and deeper bills seem thus better at handling bigger and harder prey while a longer and more slender bill is better at capturing fast moving prey since mandible speed is then improved (Lederer 1975). It has been found that female great reed warblers that have a secondary mating status feed their young less frequently but with larger prey than females with a primary mating status (Sejberg et al. 2000). These two strategies may reflect the use of a bill that is slender enough to capture small and fast prey but strong enough to handle large prey. This may be the cause of stabilizing selection bill width in great reed warblers.

From the fitness functions it seems that all effects of stabilizing selection coincides with selection towards the population mean, suggesting that we expect a change in variance rather than a change in means of many morphological traits, in the population. One exception might be wing length, which in both sexes are subject to directional selection. However, we can not exclude that the selection differentials that we have observed in the population are acting mainly on the environmental deviation of the traits (Alatalo et al.1990), which if true would not result in any change in the heritable variation in the traits due to selection.

Conclusions

Our study population of great reed warblers shows significant heritabilities in most morphological traits. These data together with the significant heritability of the first principal component make us expect rapid evolutionary responses when these traits are subjected to (differential) directional selection. But considering the sometimes very high genetic correlations and moderate phenotypic correlations we expect a lower response to selection on shape, especially among functionally related traits. This has been observed in a previous study of a passerine bird, the collared flycatcher *Ficedula albicollis* (Merilä and Gustafsson 1993). Also, considering the rather low strengths of directional selection, in combination with several traits being subject to significant stabilizing selection, we expect low or no evolutionary change in any of the investigated morphological characters that we have studied in this paper. One exception might be wing length, which is subject to antagonistic directional selection between the sexes. However, stabilizing selection on correlated characters such as tail length and wing projection might hamper such an evolutionary change. Furthermore, our results suggest that only when the mean heritability of two traits is above 0.65, phenotypic correlations are good substitutes for genetic correlations. The general pattern is that genetic correlations exceed the values of the phenotypic correlations irrespective of the magnitude of the correlation.

Acknowledgements – We thank all the field assistants (in particular Bo Nielsen) for their invaluable efforts in the field. Bengt Hansson gave helpful comments on the manuscript and Erik Svensson and Fabrice Eroukhmanoff helped out with the studies on selection. The work was supported by grants from the Swedish Research Council (VR), the Swedish Council for Environment, Agricultural Sciences and Spatial Planning

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(FORMAS), the National Swedish Environment Protection Board, the Carl Tryggers stiftelse, the Royal Swedish Academy of Science (J.A. Ahlstrand and Hierta-Retzius Foundations), the Lunds Djurskyddsfond, the Magnus Bergvalls Stiftelse and the Crafoordska Stiftelsen. This is report no. 141 from Kvismare Bird Observatory.

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