Sex differences in survival selection in the serin, *Serinus serinus*

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Introduction

Natural selection is the most powerful process to shape evolutionary change in the majority of circumstances in nature. Consequently, the details of the process of natural selection have been studied in considerable detail in many species (see review by Endler, 1986). A major pattern is that, given appropriate sample sizes, whenever selection is looked for, indications of selection in some form, is actually found. This means that natural selection is currently acting on local populations and that these populations rarely are on the top of their adaptive peak but are more or less displaced for some reason. There are several, not mutually exclusive, reasons for this: (i) a changing environment, i.e. the position of the peak is moving regularly which means that the population is tracking the moving peak; (ii) conflicting selection pressures by different parts of the phenotype. As selection acts on whole phenotypes, conflicting selection on correlated parts of the phenotype results in unexpected selection forces (Lande, 1979; Lande & Arnold, 1983; Zeng, 1988), which in turn may result in unexpected responses given the genetic architecture of the population (Björklund, 1996); (iii) strong genetic correlation between the sexes for certain traits (Lande, 1980; Reeve & Fairbairn, 1996; Merilä *et al.*, 1998), may force the two sexes to depart from their sex-specific optimum if there are sex-related differences in selection; (iv) selection is acting only on the environmental part of the variation (Alatalo *et al.*, 1990; Van Tienderen & de Jong, 1994).

One major pattern in the morphology of birds is that species within a genus tend to differ almost entirely in terms of size, but not in terms of shape (Björklund, 1991, 1994). At a short-term scale this can readily be explained in terms of genetic correlations among characters. However, as these patterns are found even at higher taxonomic units, like families, which have lasted for millions of years, this explanation loses its power with increasing time (Björklund, 1994; but see Schluter, 1996). This is because the correlations themselves may be subject to selection and thus change over time, and there are theoretical studies showing that even strong genetic correlations are unlikely to last for a very long time (Lande, 1979; Zeng, 1988; Gromko, 1995; Lascoux, 1997). This suggests that the patterns we see are to some extent a result of correlational selection (selection on...
character combinations, Endler, 1986) in addition to selection for changes in mean and variance (Hansen, 1997). This kind of selection has, however, rarely been analysed in natural populations compared with studies of selection on means and variances (Schluter & Smith, 1986; Björklund, 1992; Brodie, 1992; Swain, 1992; Schluter & Nychka, 1994).

Selection can be analysed in many ways in natural populations. The most common way is to measure short-term, or episodic selection, i.e. the selection that acts at one (or a few) selective events. This will give information about the current, short-term, selective forces acting on a population. Fluctuating selection pressures at different episodes will then give a picture of the extent of environmental stochasticity (Grant, 1986). An alternative approach is to look for long-term selection by pooling data over a large number of years. This will then give additional information about the selection that acts consistently on a given population. Significant long-term selection may be the result of long-term environmental changes that may be masked by short-term environmental fluctuations. By extending a selection analysis to include correlational selection, a long-term study can give valuable insights in the relationship between traits. Similarly, consistent long-term selection in one sex suggest that there is opposing selection acting on another correlated trait or on the same trait in the other sex. Thus, by the analysis of long-term selection for different traits and trait combinations, we can get a picture of the relation between the phenotypes and their environments that is over and beyond that from a short-term selection analysis, in particular the extent of possible constraints. This approach identifies the pattern of selection, i.e. the statistical relationship between phenotypes and their environment. Given these patterns the ecological causes of selection can then be identified by proper observational and experimental data.

In this paper we analyse patterns of survival selection in the serin (Serinus serinus), looking for selection not only on means and variances, but also character combinations. By using data gathered over a time period of 13 years we are able to analyse long-term selection patterns to obtain a picture of the long-term fitness surface. In particular, we are interested in the possibility of conflicting selection patterns both between characters, but also between the sexes.

Materials and methods

Field data

The field data has been collected by JCS, 1985–97 at an orchard outside Barcelona, Spain. In total 4967 individuals were individually marked, with 6967 recaptures. Captures were carried out about once every week all year round (for details see Conroy et al., 1999). Birds were sexed and aged according to Svensson (1992). In the analysis birds were included only if first captured before 1991 (4265 birds), because at present a certain proportion of the latest captured birds are still alive and including them will bias survival estimates downwards for these birds. Birds were included only if they were recaptured after 10 days or more to exclude migrants (Buckland & Baillie, 1987; Peach et al., 1990). The population receives an unknown number of migrants during winter. Most migration of serins in Europe occurs in November (Asensio, 1985). However, only about 4% (n = 11934) of the total captures occur at this time in the study area which strongly suggests that the migrants in this area are few compared with the local population. In addition, the migrants show a high degree of winter site fidelity, birds returning the next winter to the same area (JCS, unpublished PhD thesis, Barcelona University), so that survival is not masked by the effect of permanent emigration. We only used data on birds in adult plumage and thus excluded all data on juvenile birds (EURING age 3J) to avoid any bias as a result of dispersal. We used several trapping methods to reduce possible age bias in trapping (Domènech & Senar, 1997). Analyses are presented separately for males and females to avoid bias because of the absolute difference in survival between the sexes (Conroy et al., 1999). Recapture rates did not differ according to sex or age (Conroy et al., 1999).

The following traits were measured: wing length (maximum chord), tail length, bill length (from the tip to the anterior edge of nostrils), beak depth, beak width, tarsus length, body mass. For details of the measurements including information about measurement error see Senar & Pascual (1997) and Borras et al. (2000). Body mass was excluded from the analyses because of large within-individual variance. All measurements were not taken all years, which causes sample size to differ among traits.

Basic statistical analyses

All traits were checked for normality using ln-transformed data within each sex and individual values larger than ±3 SDs were deleted. We then checked for possible outliers by calculating Hotelling’s T²-scores for all individuals (males and females separately) using ln-transformed data (Morrison, 1990). Individuals beyond ±3 SDs were deleted. None of these procedures resulted in any major reductions in the sample size as the ‘faulty’ values were generally very few (around 1%) and could in most cases be interpreted as a result of simple typing errors at data gathering. The means and standard deviations for each trait and sex are given in Table 1, and the phenotypic correlations among the traits for each sex is given in Table 2.

Analysis of selection – the Lande–Arnold approach

All traits were then standardized (zero mean, unit variance) before selection analyses. Fitness was defined as the
number of days between first and last capture. Thus, the fitness component studied in this paper is survival only. Relative fitness was calculated as absolute fitness divided by mean fitness. All analyses were performed on the sexes separately. The univariate directional selection gradients, $\beta_i$, following the terminology by Arnold & Wade (1984), were calculated as the regression of relative fitness on the standardized trait values. The univariate quadratic selection gradient $C$ was calculated as the regression of relative fitness on the squared trait values. This will generate a negative slope if there is stabilizing selection and a positive slope if there is disruptive selection. Quadratic selection affects variance (increase or decrease) but so also does directional selection. Thus, when calculating directional and quadratic selection coefficients they were both entered into the regression, thus the quadratic selection gradient is the amount of quadratic selection gradient taking directional selection into account and vice versa. The opportunity for selection ($l$) is defined as the relative change in relative fitness caused by selection and is estimated as the variance in relative fitness. Thus, the opportunity for selection measures how much scope there is for selection to act in general, rather than the actual selection itself, i.e., a theoretical upper limit to selection (Lande & Arnold, 1983).

Multivariate directional ($\beta_i$) and stabilizing selection gradients ($\gamma_{ij}$) could not be calculated using all traits as the matrix became singular. Therefore, we had to search for character complexes to reduce the number of parameters in the model. This was performed by means of factor analysis for each sex separately. Based on these results, we used bill depth and bill width as one compound character and wing length and tail length as another, whereas the remaining traits seem to have little connection with each other or the compound traits. In addition to the directional and stabilizing components we also estimated the correlational selection coefficients ($\gamma_{ij}$) as the crossproducts of trait $i$ and trait $j$. Thus, the full regression model within each trait group involved two directional selection, two quadratic selection and two correlation selection coefficients, at most six coefficients. Significance of all the coefficients (univariate and multivariate) was assessed by a weighted delete-one jackknife procedure (Wu, 1986; Mitchell-Olids & Shaw, 1987) to avoid bias as a result of heteroscedastic variances. To account for multiple tests, a simultaneous $100(1 - z)$ confidence interval was calculated as $\hat{\beta}_i \pm \sqrt{r+1} F_{r+1, n-r-1}(z)$, where $r$ is the number of variables and $n$ is the number of observations (Johnson & Wichern, 1988). Note that in the univariate case $r$ was chosen to be 12 (six traits x two coefficients) to account for the number of tests on the same data set. As we could not remove the heteroscedasticity of the variances significance tests of the difference in selection coefficients between the sexes had to be in terms of analysing the confidence intervals of unbiased regressions (see above). Non-overlapping confidence intervals were taken as evidence that the coefficients differed between the sexes. This procedure is likely to be conservative.

The values obtained using the multivariate approach were then used to calculate individual fitness values using the fitness function

$$\hat{w} = \hat{z} + \sum \beta_i \hat{z}_i + \sum \gamma_{ij} \hat{z}_i \hat{z}_j + \sum \gamma_{ij} \hat{z}_i \hat{z}_j$$

(1)

where the summation is over all characters. $\beta$ is the standardized selection gradient, $\gamma_{ij}$ is the quadratic selection coefficient where a negative value indicates stabilizing selection and a positive value indicates disruptive selection, and $\gamma_{ij}$ is the selection coefficient on character correlations. Equation 1 can be written in matrix form as follows:

$$\hat{w} = \hat{z} + \beta^T \hat{z} + \frac{1}{2} \hat{z}^T \gamma \hat{z}.$$  

(2)

This latter form can be used to get a visual interpretation of the selection surface as shown by (Phillips & Arnold, 1989) whose procedure will be followed below. Although the selection gradient vector, $\beta$, describes the direction and length to the nearest adaptive peak, the $\gamma$-matrix contains the information about the shape (orientation and curvature) of the fitness surface. In particular, the signs of eigenvalues of the $\gamma$-matrix contain the information about the shape of the fitness surface, whereas the magnitude describes the curvature of the surface. By taking the derivative of eqn 2 and setting the result equal to zero the stationary point of the fitness surface can be calculated as

$$\hat{z}_0 = -\gamma^{-1} \beta$$

(3)
(Phillips & Arnold, 1989). If all eigenvalues are of the same sign then \( z_0 \) is at a fitness maximum (all eigenvalues negative), or fitness minimum (all eigenvalues positive), and if the signs differ then the fitness surface has a more complicated shape and the equilibrium is unstable. Furthermore, if the eigenvalues are close to zero then the surface is relatively flat, whereas high values indicate a highly curved fitness surface. The confidence interval for the eigenvalues was estimated by the delete-one jackknife procedure.

**Analysis of selection – the nonparametric approach**

The Lande–Arnold approach has been criticized for its dependence on a particular form of the fitness surface, i.e. the quadratic form (Schluter & Nychka, 1994). Instead, Schluter and Nychka proposed a nonparametric analysis which differs in two major ways from the Lande–Arnold approach: it is flexible as no specific mathematical form of the fitness curve is assumed and it is designed to handle non-normal fitness components, like survival. This method uses projection pursuit regression (see Schluter & Nychka, 1994 for details) which is based on a number of univariate cubic splines (Schluter, 1988). In particular, the method tries to find the fitness surface by extracting the cross-sections of the surface that accounts for most of the variance in fitness. Thus, this cross-section defines a new compound trait, \( x \), which is a linear combination of the original traits, \( z \). This procedure is akin to a standard principal components analysis where the parameter space is reduced to only a few new compound characters. This can be formalized as

\[
x_j = \sum_{i=1}^{m} a_i z_i = a^T z
\]

where \( a \) is the constant that relates the trait value to the new compound trait. Thus, a large \( a \) for a trait indicates that this trait has a strong relation to the fitness measure. The \( a \) vector and its standard error was estimated by the program PP by Schluter & Nychka (1994).

**Results**

The mean number of days surviving was 308.4 (SD = 327.1, range 11–1729 days, median = 195) in males and 261.1 (SD = 321.9, range 11–2688 days, median = 135) in females. The opportunity for selection (\( I \)) was 1.12 for males (95% CI = 0.93–1.34, based on 5000 bootstraps) and 1.52 (1.07–2.03) for females. This means that the maximum change was 1.06 and 1.23 standard deviation units for males and females, respectively. The difference between the sexes was not significant as judged from their overlapping confidence intervals.

**Univariate selection**

There was highly significant directional selection for increased size on feather characters (wing length, tail length) in males (Table 3), but not in females (Table 3).

In addition, there was significant stabilizing selection on bill length in females and significant disruptive selection on wing length in males. There were also indications of stabilizing selection on both bill depth and width in males, as the upper 2.5% level for both traits were almost zero (Table 3).

**Multivariate selection – Lande–Arnold approach**

In females, there was a significant directional selection only for increased wing length when selection on tail length was accounted for (Table 4). In males, there were significant directional selection for both wing and tail length, but also significant disruptive selection acting on wing length, and a negative correlational selection between wing and tail length (Table 4).

The selection gradient for tail was significantly larger for males as evident from the nonoverlapping confidence interval. Likewise, the disruptive selection differed significantly from that of females, whereas correlational selection coefficient is not.

The sexes differed considerably with regard to bill traits. In females, there was significant directional selection for both bill traits but in opposite directions: increase in bill width and decrease in bill depth (Table 5). In males, on the other hand, there was significant stabilizing selection acting on bill depth, but no directional selection (Table 5).

These differences can be visualized in terms of fitness surfaces. In the feather traits (wing and tail), there was only one significant eigenvalue of the \( \gamma \)-matrix (Table 6).

### Table 3 Univariate selection gradients and quadratic selection coefficients. Figures in boldface are significantly different from zero as indicated by the 95% confidence interval.

<table>
<thead>
<tr>
<th>Trait</th>
<th>( \beta ) (95% SE)</th>
<th>( C ) (95% SE)</th>
<th>( n )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Males</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wing</td>
<td>0.37 (0.25, 0.49)</td>
<td>0.092 (0.046, 0.18)</td>
<td>496</td>
</tr>
<tr>
<td>Tail</td>
<td>0.29 (0.14, 0.44)</td>
<td>-0.0010 (-0.097, 0.095)</td>
<td>281</td>
</tr>
<tr>
<td>Tarsus</td>
<td>-0.079 (-0.25, 0.089)</td>
<td>0.0091 (-0.13, 0.15)</td>
<td>285</td>
</tr>
<tr>
<td>Bill length</td>
<td>0.059 (-0.14, 0.26)</td>
<td>0.016 (-0.11, 0.14)</td>
<td>202</td>
</tr>
<tr>
<td>Bill depth</td>
<td>0.024 (-0.19, 0.24)</td>
<td>-0.11 (-0.21, -0.0080)</td>
<td>258</td>
</tr>
<tr>
<td>Bill width</td>
<td>-0.013 (-0.17, 0.14)</td>
<td>-0.086 (-0.18, 0.0031)</td>
<td>257</td>
</tr>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wing</td>
<td>0.15 (-0.013, 0.31)</td>
<td>-0.016 (-0.12, 0.089)</td>
<td>352</td>
</tr>
<tr>
<td>Tail</td>
<td>-0.023 (-0.31, 0.26)</td>
<td>0.069 (-0.16, 0.30)</td>
<td>172</td>
</tr>
<tr>
<td>Tarsus</td>
<td>-0.0085 (-0.22, 0.20)</td>
<td>0.029 (-0.14, 0.20)</td>
<td>182</td>
</tr>
<tr>
<td>Bill length</td>
<td>0.12 (-0.15, 0.39)</td>
<td>-0.21 (-0.44, -0.021)</td>
<td>131</td>
</tr>
<tr>
<td>Bill depth</td>
<td>-0.12 (-0.44, 0.20)</td>
<td>-0.038 (-0.21, 0.13)</td>
<td>172</td>
</tr>
<tr>
<td>Bill width</td>
<td>0.11 (-0.14, 0.36)</td>
<td>-0.10 (-0.26, 0.049)</td>
<td>171</td>
</tr>
</tbody>
</table>
This means that the surface is curved in only one direction. This can be seen for males in Fig. 1a where the surface has a valley in the direction of the associated eigenvector (0.79, –0.61), i.e. opposite directions in wing and tail length, whereas the other dimension is (almost) flat. Most individuals are found in the direction of no curvature, i.e. in the fitness valley. In females, the curvature is less pronounced as indicated by the eigenvalue, which is about one-third of the eigenvalue in males (Fig. 1b). The fitness surface has in females a curvature that is different from that in males (–0.23, –0.97), such that the major direction of the curvature is in terms of increasing wing and tail size.

Table 4 Multivariate selection gradients ($\beta$), quadratic selection (diagonal of $\gamma$) and correlational selection coefficients (off-diagonal of $\gamma$) using bill characters only. Figures in boldface are significantly different from zero as indicated by the 95% confidence interval.

<table>
<thead>
<tr>
<th>Trait</th>
<th>$\beta$ (95% SE)</th>
<th>$\gamma$ (95% SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bill depth</td>
<td>$-0.20 (-0.40, -0.012)$</td>
<td>$-0.0018 (-0.092, 0.089)$</td>
</tr>
<tr>
<td>Bill width</td>
<td>$0.21 (0.050, 0.38)$</td>
<td>$-0.073 (-0.22, 0.076)$</td>
</tr>
</tbody>
</table>

Table 5 Multivariate selection gradients ($\beta$), quadratic selection (diagonal of $\gamma$) and correlational selection coefficients (off-diagonal of $\gamma$) of body traits. Figures in boldface are significantly different from zero as indicated by the 95% confidence interval.

<table>
<thead>
<tr>
<th>Trait</th>
<th>$\beta$ (95% SE)</th>
<th>$\gamma$ (95% SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing</td>
<td>$0.30 (0.14, 0.35)$</td>
<td>$-0.12 (-0.28, 0.028)$</td>
</tr>
<tr>
<td>Tail</td>
<td>$-0.15 (-0.34, 0.029)$</td>
<td></td>
</tr>
<tr>
<td>Wing</td>
<td>$0.22 (0.086, 0.33)$</td>
<td>$0.19 (0.033, 0.32)$</td>
</tr>
<tr>
<td>Tail</td>
<td>$0.18 (0.050, 0.28)$</td>
<td></td>
</tr>
</tbody>
</table>

Table 6 Eigenvalues (95% CI) of the $\gamma$-matrix and values at the stationary point ($z_0$) for each sex. Figures in boldface are significantly different from zero as indicated by the 95% confidence interval.

<table>
<thead>
<tr>
<th>Eigenvalues</th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bill depth and width</td>
<td>$-0.073 (-0.24, 0.09)$</td>
<td>$0.034 (-0.099, 0.17)$</td>
</tr>
<tr>
<td>Wing and tail length</td>
<td>$-0.069 (-0.19, 0.048)$</td>
<td>$-0.20 (-0.25, -0.14)$</td>
</tr>
<tr>
<td>Bill depth and width</td>
<td>$0.11 (-0.24, 0.46)$</td>
<td>$0.35 (0.039, 0.66)$</td>
</tr>
<tr>
<td>Wing and tail length</td>
<td>$-0.13 (-0.23, -0.029)$</td>
<td>$-0.086 (-0.20, 0.029)$</td>
</tr>
</tbody>
</table>

In the two bill traits the difference between the sexes is considerable. In males, there was one significant eigenvalue (Table 6), with the direction of the curvature being influenced by the stabilizing selection on bill depth, whereas the surface is flat in the other possible direction. In females, there was no significant eigenvalue, and the fitness surface is flat and pointing in the direction of the $\beta$-vector (increased bill width and decreased bill depth).

Multivariate selection – nonparametric approach

The nonparametric approach revealed a similar picture as above. In males, the direction that accounted for most of the variation was related to wing length (Table 7) and to a lesser, nonsignificant, degree wing length in relation to tail length. This means that the diverging selection on wing and tail length was also apparent by using this approach.

The univariate spline function for wing length shows an almost linear function of survival and wing length (Fig. 2a).

In females, the only significant trait loading was for bill width, which relates positively to survival (Table 7). The function relating survival to the main projection show a tendency of a peak at intermediate values (not shown), whereas the univariate spline of bill width on survival show an almost linear relationship with increasing survival with increasing bill width below the mean value, but levels off for larger individuals (Fig. 2b).
Discussion

The selection analysis show that in both sexes there was strong directional selection for increased wing length. In addition, males experience strong directional selection for tail length and selection for a negative correlation between wing length and tail length. In females there was strong directional selection for increased bill width and decreased bill depth, contrasting to the pattern found in males with stabilizing selection acting on bill depth.

Fig. 1 Fitness surfaces for (a) wing and tail length in both sexes (in SD units), and (b) for bill depth and width in both sexes (in SD units). Fitness values for each individual were estimated using eqn 1. The dots represent individual values. The surface was calculated using a quadratic smooth function.
This means that there is conflicting selection pressures acting on the phenotype in both males and females, in addition to the difference in selection acting on each sex. These findings have several causes and implications. The finding that in both sexes long wings are beneficial can be related to flight agility (Norberg, 1990) as this species is a ground feeder in open areas and thus very vulnerable to predation. In dominance experiments in this species, tail length seems to be the most important factor determining dominance in males, whereas wing length was not important at all (Senar, unpublished). This suggests that wing length is indeed related to agility rather than dominance, as tail length is selected only in males. Interestingly, a negative correlational selection between wing length and tail length was found. In this population, the phenotypic correlation between these two traits is around 0.60 in both sexes (Table 2). The pattern of selection in bill traits also reveals conflicting selection for bill depth and width in females. There was also conflicting selection between the sexes as males experience stabilizing selection on a trait that is directional selection for in females, i.e. bill depth. The phenotypic correlation between bill depth and bill width is positive and high in females (Table 2). If the genetic correlation approximates that of the phenotypic (Roff, 1995) we can expect the rate of evolution in divergent directions for these traits to be constrained by this correlation (Zeng, 1988; Björklund, 1996). The rate of change in the selected direction in the bill is even more constrained by the stabilizing selection on bill depth in males. If there is a high genetic correlation among the sexes, which is reasonable to assume, given the available evidence (Lande, 1980; Reeve & Fairbairn, 1996; Merilä et al., 1998) males will be faced with stabilizing selection as long as they are displaced from the optimum by the directional selection acting on females, whereas females will experience directional selection as long as they are displaced from their optimum by the stabilizing selection acting on males.

The evolutionary consequences of these different selection pressures on the sexes are determined by the genetic variances and covariances between the characters and the sexes. If the genetic correlations between the sexes are high, then the pattern of selection can persist for a long time as the resulting phenotypes will be a compromise between the selection on each sex and thus not be optimal. The same is also true for the correlations between characters within each sex. Here, the magnitude can be assumed to be lower than between the sexes, but the short-term rate at which the adaptive peak can be reached will be hampered by the presence of these correlations. Unfortunately, nothing is known about genetic correlations in this species, so further discussion will be speculative.

The findings in this study have implications for the understanding of the adaptive landscape as estimated by the quadratic approximation to the individual fitness surface. It is clear that different parts of the phenotype are more or less displaced from their optima as a result of conflicting selection acting on different parts and the sexes. This displacement can persist over a considerable ecological time scale, affected mainly by selection and the interrelationship between the traits. As it is the whole phenotype that die or survive at a given time, the result will be a compromise between different selection acting on different parts of the phenotype. This study highlights

### Table 7

The direction of selection in males and females estimated by the projection pursuit regression. Boldface figures are significantly different from zero.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Females (SE)</th>
<th>Males (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing length</td>
<td>0.42 (0.30)</td>
<td>0.77 (0.27)</td>
</tr>
<tr>
<td>Tail length</td>
<td>−0.43 (0.35)</td>
<td>−0.52 (0.30)</td>
</tr>
<tr>
<td>Tarsus length</td>
<td>0.36 (0.41)</td>
<td>0.061 (0.36)</td>
</tr>
<tr>
<td>Bill length</td>
<td>0.18 (0.34)</td>
<td>0.20 (0.35)</td>
</tr>
<tr>
<td>Bill depth</td>
<td>0.095 (0.39)</td>
<td>0.046 (0.36)</td>
</tr>
<tr>
<td>Bill width</td>
<td><strong>0.69</strong> (0.32)</td>
<td>0.16 (0.31)</td>
</tr>
<tr>
<td>ln (a)</td>
<td>−13.57</td>
<td>−13.57</td>
</tr>
</tbody>
</table>

Note. SE determined by 100 bootstraps.
the importance of long-term studies of selection for understanding the curvature of the adaptive landscapes found in nature which can act as a basis for further theoretical studies.

This study also highlights the importance of not only analysing the directional or stabilizing patterns of selection, but also the correlational selection. Unfortunately, this requires considerable sample sizes and even in this large study this may be a problem. The two methods used, the parametric Lande–Arnold approach and the nonparametric approach of Schluter and Nyscha gave qualitatively the same result, even if the result was clearer using the former approach than the latter. Whether this is a result of sample sizes, or the methods for inferring standard error is not known, but it suggests that for medium levels of selection, sample size has to be large. The finding of directional selection for wing length has also been found when survival rates were estimated by capture–recapture data (Conroy et al., in press). This gives strong support for the use of the methods used in this study.

In conclusion, this study illustrates that within a population and given habitat the selection may differ considerably between sexes. This in turn may result in a slow response to selection, but details about that has to await information about genetic correlations between characters and sexes. However, the patterns of selection give rise to several testable predictions about the ecological causes of selection and the relationship between morphology and behaviour which could not have been reached without this kind of analysis.

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