

SELECTION OF BILL SIZE PROPORTIONS IN THE COMMON ROSEFINCH (*CARPODACUS ERYTHRINUS*)

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ABSTRACT.—This study analyzed the multivariate morphological differences between survivors and nonsurvivors over winter in three years in the Common Rosefinch (*Carpodacus erythrinus*). In addition to the standard selection techniques commonly used, a number of multivariate analyses were employed. Differential survival could not be accounted for by differences in trait means. The variance-covariance matrices of survivors and nonsurvivors were highly significantly different, indicating differences in character relationships between the groups. A principal-components analysis of each matrix revealed that character correlations on the first vector from each matrix differed. Among survivors all characters were positively correlated to the first vector, whereas among nonsurvivors the first vector described bill width in relation to bill length. Therefore, these two characters were chosen and used in a full-quadratic regression model. This analysis showed a positive relationship between survival and the combination of bill length and bill width, resulting in increased variance in bill width. In particular, survivors were characterized by a positive relationship between bill length and bill width, whereas nonsurvivors were characterized by either too broad, or too narrow a bill in relation to bill length. Possible causes behind this variation in bill proportions may be recently altered selection pressures as a consequence of a new habitat, and/or the particular conditions encountered during ontogeny (a purely environmental effect). Received 13 June 1991, accepted 19 February 1992.

PHENOTYPES DIFFER in survival and reproduction as a result of their properties (selection) and by chance (Sober 1984). This differential survival can result in evolutionary change in characters depending on their genetic variance and covariance with other characters (Lande 1976, 1979, Lande and Arnold 1983). Differential survival can be studied in two different ways (Crespi and Bookstein 1989, Crespi 1990): (1) in terms of the sorting process as such (Vrba 1989) to see whether differential survival is a result of the properties of the phenotypes (i.e. selection), or whether it is only a chance process with regard to phenotypic appearance; and (2) in terms of the evolutionary results of selection (i.e. changes in character means over time as the result of selection; Lande and Arnold 1983, Arnold and Wade 1984, Endler 1986).

Despite our limited knowledge of genetic variances and covariances in natural populations, numerous studies of the possible evolutionary effects of selection have been done during the last decade (see Endler 1986), while less attention has been devoted to the sorting process itself. This is unfortunate because a thorough comparative analysis of the properties of the surviving and nonsurviving individuals, respectively, can give insight into the properties of phenotypes, the functional relationships

among parts of the phenotype, and the relationship of phenotypes with the environment (Endler 1986, Mitchell-Olds and Shaw 1987, 1990, Wade and Kalisz 1990).

An analysis of the sorting process can be performed in two basically different ways. First, one can use the standard procedure to analyze the occurrence of selection of character means and resulting changes in variance (Lande and Arnold 1983, Arnold and Wade 1984). Second, a search can be made for differences in phenotypic appearance between survivors and nonsurvivors by analyzing the phenotypic variance-covariance patterns among these two groups to see whether particular trait combinations are related to differences in survival (Lande and Arnold 1983, Phillips and Arnold 1989). If the phenotype acts as an integrated whole, partitioning into different traits is more or less arbitrary (Gould and Lewontin, 1979), and multivariate assessment of differences among groups is necessary.

In this paper, I will use these methods to analyze three years of overwinter-survival data in the migratory cardueline finch, the Common Rosefinch (*Carpodacus erythrinus*). Since adult male mortality each year is about 50% (Björklund 1989a), there is ample opportunity for selection. Since nothing is known about genetic

variances and covariances of characters in this species, the selection analysis will be restricted to methods for the detection of phenotypic correlates of differential survival in adult male Common Rosefinches.

METHODS

The field work was carried out in Rättvik, Central Sweden (60°52'N, 15°6'E) from 1985 through 1988. For a detailed description of the species and the study area, see Björklund (1989b). Birds (males only) were caught in mist nets upon arrival, measured, and individually banded. The following measurements were taken: wing length (flattened); tail length; tarsus length (measured as the distance between the extreme bending points at the intertarsal joint and the toes); bill length (from tip of the upper mandible to an inflexion point just behind the nostrils); bill depth; and bill width (this and previous character measured at the front of the nostrils). Body mass was not used since it is known to change considerably even within a breeding season (Stjernberg 1979). Males have a high site fidelity between years (Stjernberg 1979, Björklund 1990), and their rates of disappearance (ca. 50%) are very close to those for other similar-sized European species (Dobson 1987). Therefore, I am confident that the main cause of disappearance from one year to the next was mortality rather than dispersal. Although numerous nestlings (ca. 150) were banded over the years, none of these became part of the breeding population. This means that the breeding population consists of birds born elsewhere. All males used in the analysis sang in the area until they were paired, at which time some males moved out to breed somewhere else (Björklund 1990). Thus, there is a very little chance that some males were migrants on their way elsewhere. I define survivors as males that were banded in one year and were seen in the area the next, whereas nonsurvivors were males that were not seen in a later year. This allows for pooling the data over the years, since each male only occurs once in the analysis.

To evaluate multivariate differences between survivors and nonsurvivors, several methods were used. All characters were transformed by natural logarithms. Each character for each group was tested for normality using Shapiro-Wilk's test (Shapiro and Wilk 1965). In no case did the distribution differ significantly from normal. First, I performed a standard selection analysis to estimate the occurrence of selection on character means and variances (Lande and Arnold 1983) using characters standardized to zero mean and unit variance. Selection gradients (i.e. selection on character means after the effect of correlated characters has been removed) were estimated through multiple regression of survival on characters. Selection on character variance (i.e. stabilizing or disrup-

tive) was analyzed by comparing variances before and after selection while correcting for changes in variance due to possible directional selection (see Endler 1986).

Second, to analyze possible selection on character combinations, I tested the homogeneity of covariance matrices by a modified likelihood-ratio statistic (Muirhead 1982). In the case of only two matrices (as in this study), this test is a uniformly most-powerful unbiased test (Muirhead 1982). The test is available in the SAS (1985) statistical package in the DISCRIM procedure. If a comparison of survivors and nonsurvivors reveals that their covariance matrices are heterogeneous, then there is a possibility that they differ in character covariances (probability of survival is not directly related to absolute size of a character, but to its size in relation to other characters).

Third, I performed a principal-components analysis on the survivor and the nonsurvivor groups, respectively, to see which characters and character combinations differ between the groups and if some characters were redundant in the analysis. To analyze how many factors, or principal components, contain important information the following approach was used (adopted from Muirhead 1982:406-420). One wants to find which, k , largest eigenvalues are distinct (biologically relevant) among the total number, t , of eigenvalues. This is a sequential test using the variance-covariance matrix, where the $t - 1, t - 2 \dots$ eigenvalues are tested until we find the number of smallest eigenvalues that are equal and negligible, $q = t - k$. For details the reader is referred to Muirhead (1982).

Fourth, to search for possible selection on character combinations, a full quadratic regression would have been appropriate (e.g. Lande and Arnold 1983, Phillips and Arnold 1989). However, to be able to do such an analysis, the sample size needs to be considerably larger than the number of characters, preferably greater than 100. Therefore, I used the results obtained in the principal-components analysis to reduce the number of characters to be able to run the full regression model. The regression on the remaining characters provides information on the directional selection gradient, β_i , and the quadratic selection gradient (stabilizing versus disruptive selection), γ_i , for character z_i , as well as the quadratic selection gradients for the combination of characters z_i and z_j , γ_{ij} (Lande and Arnold 1983, Phillips and Arnold 1989). I tested the significance of the predictor values in the quadratic regression model by a likelihood-ratio test following Johnson and Wichern (1988:288-289). In short, the model was fitted with and without one of the predictors. The improvement in the residual sum of squares was compared to the residual sum of squares for the full model. This gives an F -value with 1 (if only one predictor is deleted at the time) and $n - r - 1$ degrees of freedom, where r is the number of predictors, and n is sample size.

TABLE 1. Selection differentials (*i*), selection gradients (β), and variance selection coefficients (*j*) for survival in male Common Rosefinches. Critical values are Bonnferroni $\alpha_{0.05}$ levels (*, $P < 0.05$).

| Character | <i>i</i> ^a | β | <i>j</i> ^b |
|----------------|-----------------------|------------|-----------------------|
| Wing length | -0.25 | -0.17 | -0.14 |
| Tail length | -0.01 | 0.08 | 0.08 |
| Tarsus length | 0.14 | 0.13 | 0.49* |
| Bill length | -0.10 | -0.10 | -0.14 |
| Bill width | 0.07 | 0.05 | 0.69* |
| Bill depth | -0.21 | -0.14 | -0.19 |
| Critical value | ± 0.64 | ± 0.59 | ± 0.47 |

^a Selection differential standardized by SD of relative fitness.

^b Standardized by SD of relative fitness and corrected for effects of directional selection.

Crespi and Bookstein (1989) suggested an alternative method where a general size vector is assumed and the selection coefficients for characters are the differences in adjusted means in an analysis of covariance of the characters and survival with size as the covariate. In addition to the assumption of a general size factor, this method also assumes common slopes for survivors and nonsurvivors. In my data set, several slopes in fact differed. Therefore, this approach was not used.

RESULTS

In total, 29 surviving males and 35 nonsurviving males were used in the analysis. Selection coefficients as well as gradients (Table 1) most often were far from being significant (all values $P > 0.1$), especially when a tablewide α is employed (Rice 1989) of $0.05/6 = 0.008$ (Table 1). Thus, there was no detectable selection for changes in mean values for the measured characters. Similarly, changes in character variances were very low; therefore, further testing was not performed. Hence, there was no detectable stabilizing selection of any of the characters.

The covariance matrices for survivors and nonsurvivors differed significantly ($X^2 = 140.22$, $P < 0.0001$). This means that survival was related to differences in the covariances of traits, since no significant differences in variances were found (Table 1). For survivors, only one vector was unique, whereas the other five were equal (equality of the five smallest eigenvalues; $X^2 = 31.11$, $P = 0.054$); for nonsurvivors two vectors were distinct (equality of the four smallest eigenvalues; $X^2 = 21.22$, $P = 0.4$). Among survivors the first vector accounted for about 55% of the total variance (Table 2), and for nonsurvivors only 37.6% (Table 2). Since only the first

TABLE 2. Correlations of characters with first principal component for surviving and nonsurviving male Common Rosefinches.

| Character | Survivors | Nonsurvivors |
|---------------|-----------|--------------|
| Wing length | 0.03 | -0.19 |
| Tail length | 0.70 | -0.28 |
| Tarsus length | 0.31 | -0.40 |
| Bill length | 0.61 | -0.88 |
| Bill width | 0.95 | 0.70 |
| Bill depth | 0.47 | -0.07 |
| <i>n</i> | 29 | 35 |

vector in the survivor group was biologically relevant, the comparison between the groups was confined to this first vector. The first vectors of the two matrices differed widely in their character loadings, with a vector correlation (r_v) of only 0.13, which corresponds to an angle of 82.5°. In the survivor group all traits were positively correlated to the first vector, indicating a general size vector, but in the nonsurvivors group the first vector was dominated by a high positive correlation with bill width, and an even higher negative correlation with bill length (Table 2). Since these two characters were the only ones that were consistently highly correlated in both groups, the following analysis will be confined to these characters.

To assess possible selection on covariation among bill length and width, a full quadratic regression was performed on these two characters. This included absolute deviations from character means (β_i), squared deviations (γ_i), and cross-products of the absolute deviations for the two characters (γ_{ij}). This kind of analysis is best suited for large sample sizes. When samples are small, as in this case, addition of single individuals may have large effects on the results. This was dealt with in two ways. First, I checked the possible occurrence of outliers; an outlier was defined as having a residual value more

TABLE 3. Jackknifed estimates of quadratic selection coefficients yielding estimates of selection gradients (β), stabilizing/disruptive selection (C_i), and selection on character combinations (γ_{ij}), on survival in male Common Rosefinches.

| Bill character | β | <i>C</i> | γ | <i>P</i> |
|----------------|---------|----------|----------|----------|
| Length | 0.05 | | | 0.72 |
| Width | 0.12 | | | 0.35 |
| Length | | 0.03 | | 0.83 |
| Width | | 0.32 | | 0.023 |
| Length × width | | | 0.34 | 0.024 |

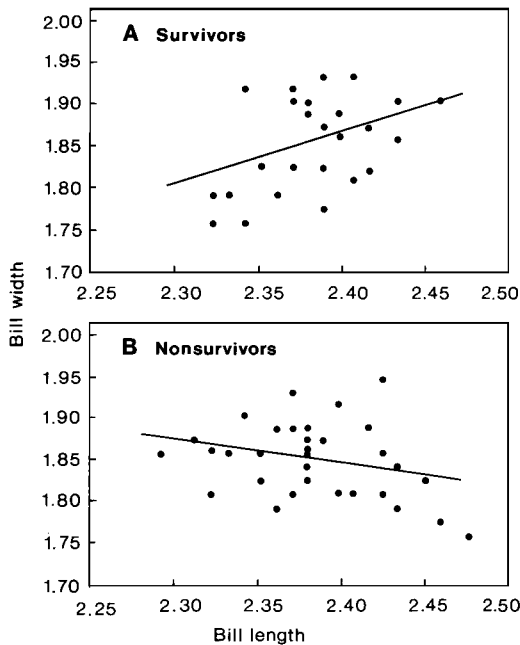


Fig. 1. Regression of bill width on bill length for (A) surviving and (B) nonsurviving male Common Rosefinches.

than ± 2 SDs from the mean. One individual was found outside that range and was deleted from the analysis. Second, I calculated a jackknife estimate of the regression coefficient by deleting six individuals (randomly drawn) from the data set and calculating new regression coefficients. This was repeated 10 times. The results presented in Table 3 are the jackknifed estimates of the regression coefficients. Apparently, the results were robust against addition and deletion of individuals. The quadratic regression model revealed a significant positive selection on the character combination ($F_{1,55} = 6.36$, $P = 0.024$; Table 3) and, as a result, an increase in the variance in bill width ($F_{1,55} = 6.85$, $P = 0.023$). In particular, surviving males were characterized by a positive allometric relationship between bill width and bill length, whereas nonsurviving males generally had either smaller or larger bill width in relation to their bill length compared with the survivors (Fig. 1).

DISCUSSION

My results show that the probability of survival was not related to differences in character

means among individuals but to differences in proportions between characters. Specifically, probability of survival was related to the relationship between bill length and bill width.

Relationships between bill morphology and fitness have been demonstrated in several seed-eating birds. This is particularly the case for Galapagos finches, where it has repeatedly been shown that food and morphology are causally related (for review, see Grant 1986; Grant and Grant 1989), but also is true for other finches (Schluter and Smith 1986, Smith 1990). Unfortunately, nothing is known of the food of the Common Rosefinch in its winter quarters (Bozhko 1980). Therefore, little can be concluded about the causes of natural selection in the Common Rosefinch—only that for the bill to function optimally, bill length and bill width are related to one another in a certain manner. This means that for bill length a wide range of values is possible provided the bill width has an appropriate value, and vice versa. Consequently, selection on character means in any direction is not to be expected and indeed may be constrained through the effects of the other characters and combinations (Burger 1986, Wagner 1988). If this pattern of selection is common and selection for the break-up of covariation in bill design is rare, it becomes easier to understand why phenotypes within a given taxon—for example, cardueline finches—exhibit such a low level of phenotypic variation in relation to the enormous time since divergence (Björklund 1991).

Differences in variance-covariance structure among surviving and nonsurviving individuals can be expected, for example, when populations enter new habitats (Endler 1986), a phenomenon that has been demonstrated (Service and Rose 1985). The Common Rosefinch has rapidly spread westwards in Europe during the last decades, entering many new areas and habitats (Bozhko 1980, Stjernberg 1985). Although relevant data to a large extent are lacking, the findings in this study are at least compatible with the idea of environmental change as a cause of changes and variation in the variance-covariance structure of populations.

An alternative explanation may be that individuals differ as a result of different conditions during ontogeny. It has been repeatedly demonstrated that differences, for example, in food composition and weather factors can strongly affect general body size and the size

of different characters (e.g. James 1983, Murphy 1985, Boag 1987, Richner 1989, Alatalo et al. 1990, Larsson and Forslund 1991). Nonsurviving individuals to a greater extent may have suffered from suboptimal conditions as young, either by pure chance, or as a result of genotype-environment interactions. In that case one would not necessarily see any selection of trait correlations since the origin of the variance that selection has acted upon is not genetic. This means that the phenotypic variance-covariance matrix may be a poor estimate of the genetic variance-covariance matrix, and then selection coefficients may be poor predictors of future evolution (Endler 1986, Mitchell-Olds and Shaw 1987, Willis et al. 1991).

Finally, since the causes of change in character means are the differential reproduction and survival of phenotypes (and not characters), only a thorough study of phenotypic properties including character combinations can give insight into why phenotypes change or do not. Nonsignificant selection coefficients in a standard multivariate selection analysis do not prove that individuals do not differ in survival probability as a result of their phenotypic appearance, only that: there is no selection for a change in the mean of the measured character; such selection is too weak to be detected; selection acts on combinations of characters; or we have been unable to properly identify what constitutes a relevant character.

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