NATURAL SELECTION ON BEAK AND BODY SIZE
IN THE SONG SPARROW

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Abstract.—We documented temporal patterns of natural selection on beak and body traits in a song sparrow population. We looked for evidence of selection in association with reproduction and overwinter survival in order to identify the conditions under which size in beak and body traits is adaptive. We also attempted to identify the specific traits most closely associated with fitness under these conditions.

Selection was observed in association with both survival and reproduction. Patterns of selection differed between the sexes. Selection on males was weak and stabilizing in association with overwinter survival. Selection on females was strong, was both stabilizing and directional, and was associated with both survival and reproduction. In females, traits that enhanced juvenile survival also reduced reproductive success; i.e., there was a trade-off between survival and reproduction.

Patterns of selection in the song sparrow parallel those reported for the Galápagos finch, *Geospiza fortis*. However, in song sparrows, selection occurred mainly on tarsus length and beak length, and not on beak depth or width as in *G. fortis*. This difference may occur because most North American sparrows partition food resources by habitat, while most Galápagos ground finches partition food by seed size.

Field measurements of natural selection are invaluable (review in Endler, 1985). One general use is to demonstrate and quantify the existence and importance of adaptation (e.g., Charlesworth et al., 1982). A second use for measurements of selection, of interest to the ecologist, is to test specific ecological hypotheses (Lande and Arnold, 1983).

An example of where field measurements of selection are useful is in studies of the evolution of resource use. Much empirical work in this area has involved comparison of morphology and diet of bird species among communities differing in species composition or food supply (Pulliam, 1973; Cody, 1975; Karr and James, 1975; Grant et al., 1976; Keast, 1976; Ricklefs and Travis, 1980). However, environments are variable, and diets may fluctuate greatly in time (Karr, 1976; Wiens, 1977; Smith et al., 1978; Wiens and Rotenberry, 1980; Schluter, 1982). In variable environments, one cannot be certain that the period over which diet is measured corresponds to the time when natural selection on traits determining feeding is occurring. Identifying this critical period is thus important, particularly for birds, because community composition itself may vary from breeding to nonbreeding seasons.

In this paper, we document temporal patterns of natural selection on beak and body traits in a resident population of song sparrows (*Melospiza melodia*) over a five-year period. Our view is that a study of selection in these traits will aid in indicating the ecological conditions under which morphology

is adapted to exploiting food. A second pur-
pose is to identify the individual traits most
strongly associated with fitness under these
conditions. Most of the traits we use are
heritable (Smith and Zach, 1979; Schluter
and Smith, unpubl.); hence selection can
have evolutionary consequences.

We assume that in the song sparrow, vari-
ation in traits measured is related to feeding,
though this has not yet been demonstrated.
This assumption is probably valid for beak
traits (Abbott et al., 1977; Schluter and
Grant, 1984a, 1984b), and may be valid
also for body traits (e.g., tarsus length; Grant,
1966; Fretwell, 1969; Miles and Ricklefs,
1984). However, body traits are also likely
to be influenced by other factors, such as
mating success (Price, 1984a), or climate
(James, 1970).

In each year of the study, we examined
data for evidence of selection at three life
stages: juvenile overwinter survival, adult
overwinter survival, and adult breeding
success. Analysis of several years' data thus
reveals 1) how often selection occurs and its
strength; 2) whether selection is associated
with summer breeding, overwinter surviv-
al, or both; 3) whether selection in one year,
season, or life stage opposes or reinforces
selection at another; 4) whether selection is
generally stabilizing or directional; and 5)
the traits on which selection is usually fo-
cused. We also consider the possibility that
sexual selection reinforces or opposes nat-
ural selection (e.g., Price, 1984a).

The same six morphological traits used
here have been measured in the Galápagos
finches, where selection has also been re-
corded (Grant et al., 1976; Boag and Grant,
1981; Grant and Price, 1981; Price, 1984a,
1984b; Price and Grant, 1984; Price et al.,
1984; Grant, 1985; Schluter et al., 1985).
Our results thus permit a comparison of pat-
terns of selection in two different environ-
ments, one tropical and the other temperate.

MATERIALS AND METHODS

Field Study. — The study was carried out
on the resident song sparrow population on
Mandarte Island, British Columbia, Cana-
da. Tompa (1964) describes the island in
detail. From 1974 to 1979, nearly all song
sparrows on the island were captured in mist
nets, measured, and individually color-

banded. From 1975 to 1979, territories and
nests of breeding pairs were located, and
reproductive success, the number of young
raised to independence, was recorded. Nest-
lings were banded about six days after
hatching. The nestlings were later mea-
sured when captured as independent juve-
niles or adults.

Repeated sightings of banded birds
through each year indicated that disappear-
ances occurred primarily during fall and
winter. Annual spring censuses therefore
determined the fate of individual birds
through the previous fall and winter (here-
after, "overwinter"). Disappearance of ju-
venile sparrows from Mandarte results from
both emigration and mortality (Tompa,
1964). The effects of each process on the
Mandarte population cannot be distin-
guished, and for convenience we refer to the
combination as "mortality." Adults are not
known to disperse: more than 40 juveniles
born on Mandarte have dispersed to the
neighboring Halibut Island (1.3 km distant),
but no breeding adult has yet done so (Tom-
pa, 1963; P. Arcese and J. N. M. Smith,
unpubl.). We therefore assume that the dis-
appearance of adults resulted mainly from
mortality. Immigration to the island was
rare: only four immigrants, all juvenile fe-
males, were recruited between 1975 and
1979.

Three experimental perturbations were
carried out on Mandarte between 1975 and
1979, with possible consequences for selec-
tion. In the first, in 1978, 24 clutches of eggs
and broods of newly-hatched young were
exchanged between parents (Smith and
Dhondt, 1980). Exchanged clutches were
similar in size and age, and so we measured
breeding success of foster parents as the
number of adopted young raised to inde-
pendence. We observed no selection asso-
ciated with breeding in 1978, and this result
is unchanged when we used just the number
of unfostered young raised.

In the second perturbation, supplemental
food was provided to half the population
during winter 1978–1979 (Smith et al.,
1980). The experiment coincided with rel-
atively high overwinter survival in the en-
tire population, mitigating the effects of
added food. Adult survival did not differ in
the two halves of the population, though

supplemental food increased juvenile survival slightly. The winter of 1978–1979 was the only one of three for which sample sizes were adequate to test for selection, yet selection on juveniles was not observed. Thus we cannot rule out an effect of food addition on selection. The experiment had no apparent effect on the number of offspring raised in the subsequent breeding season.

In the third perturbation, in 1979, 10 males were temporarily removed from their territories after their first brood of young had hatched (Smith et al., 1982). These birds were excluded when analyzing reproductive success that year. All the females to which they were paired continued to raise the young. Excluding these females did not alter the results.

Morphology.—Six morphological traits were measured on captured individuals, as described in Smith and Zach (1979). The six traits are weight (in g), wing length, tarsus length, beak length, beak depth, and beak width (all in mm). Most measurements were from late summer or early fall, minimizing effects of seasonal variation in dimensions. Occasional measurements from birds exhibiting obvious wear (e.g., of feathers) were discarded. We used measurements from birds at least 8 weeks old, i.e., birds essentially full-grown (Smith and Zach, 1979). To account for subsequent slight growth and shrinkage, individual measurements obtained from birds at different ages were corrected to a standard age, as described in Schluter and Smith (unpubl.) Age-correction was necessary, since not all birds were measured at the same age. Also, age-correction allowed us to lower measurement error in traits by using the average of measurements taken from the same bird at different ages. Generally, two or three measurements were available per bird. Finally, age-correction allows us to rule out an indirect effect of age when an association is observed between morphology and fitness (i.e., selection). Measurement repeatabilities are given in Smith and Zach (1979).

Traits were approximately normally-distributed within each sex, and hence all analyses are based on the untransformed data. Log(e)-transformations of morphological traits did not, however, produce significantly different results. Within the sexes,

TABLE 1. The first two principal components based on measurements of all juvenile song sparrows.

Variable	PC1	PC2
Weight	0.46	0.25
Wing length	0.50	0.30
Tarsus length	0.29	0.61
Beak length	0.35	−0.45
Beak depth	0.39	−0.43
Beak width	0.42	−0.29
% variance	42.0	21.5

traits were linearly related to each other, as assumed by standard selection analyses (Price and Boag, 1985).

Data were divided into three sets, relating to each of the three life stages analyzed: juvenile overwinter survival, adult overwinter survival, and adult breeding success. In each set, the number of morphological variables analyzed was reduced to two, by extracting the first two principal components (PC's) from the correlation matrix based on all individuals combined. Components for the juvenile overwinter survival set are shown in Table 1; components were nearly identical for the other two sets. In each set, PC1 and PC2 together accounted for approximately 60% of the total variance among individuals. PC1 is a general size variable (Pimentel, 1979). PC2 measures shape, particularly beak size relative to the three "body size" variables (Table 1).

One reason for reducing the number of variables was to minimize the number of statistical tests performed. A second reason is that our samples were usually too small to test for stabilizing selection on all six original traits. Results for directional selection were similar when all six traits were tested, and when only PC1 and PC2 were tested. For this reason, in most cases we present only the results based on PC's. A third advantage to using the first two principal components is that they exclude much of the measurement error in these traits, if this error is uncorrelated among traits (Gauch, 1982).

Males and females differ in the size of several morphological traits (Smith and Zach, 1979), and so we analyzed the sexes separately. Sex of birds was determined by their reproductive behavior when adults. Juveniles that died during their first winter

were sexed using the canonical discriminant function that maximized separation of those male and female juveniles that survived (Pimentel, 1979). 160 of 170 surviving juveniles (94%) were correctly classified, indicating little overlap along the discriminant function. Finally, when we compared survivors and nonsurvivors, the 10 misclassified juveniles were assigned to their estimated sex rather than to their true sex, to avoid any bias resulting from alternative sexing criteria. Deleting these 10 birds did not affect the results.

Natural Selection.—Natural selection is defined as a nonrandom association between phenotypic variation and a component of fitness (e.g., Arnold and Wade, 1984a). Variance in relative fitness (I) thus places an upper limit on selection intensity, and it is referred to as the "opportunity for selection" (cf. Arnold and Wade, 1984a). In our analysis, survivors are assigned a fitness of 1, and nonsurvivors a fitness of 0. For reproductive data, fitness is the number of offspring surviving to independence. Relative fitness (ω) is fitness divided by the mean fitness of individuals in the comparison. Variance in relative fitness, I, for survival data is estimated as the number of individuals dying divided by the number surviving. This ratio is multiplied by $N/N - 1$, where N is the sample size, to correct for a slight bias. For reproductive data, I is the squared coefficient of variation in offspring number multiplied by $N/N - 1$.

We estimated standardized directional selection differentials S for PC1 and PC2. S is a measure of selection intensity, defined as $S = \text{Cov}(\omega, z)$, where z is the standardized trait (mean = 0, variance = 1) (Lande and Arnold, 1983). We estimated S as the slope of the univariate regression of relative fitness on the standardized characters. For survival data, S is also the difference between means of the characters before and after selection. Though derived from all individuals combined, PC1 and PC2 were only weakly correlated in most subsets of individuals. Hence, partial regression coefficients were similar to the univariate coefficients, S, and in most situations we present only the latter. Stabilizing selection differentials (standardized) are similarly defined as $C = \text{Cov}(\omega, z^2)$ (Lande and Arnold, 1983).

We estimated C as the slope of the univariate regression of ω on the standardized characters squared. For survival data, and in the absence of directional selection, C is equivalent to the difference between the variances of the standardized characters before and after selection. A negative value of C indicates stabilizing selection, and a positive value indicates disruptive selection.

For survival data, significance of S was tested by comparing survivors and nonsurvivors in mean PC1 and PC2 using two-sample t tests. Significance of C when $S = 0$ was tested for these same traits by comparing variance estimates in the two groups using two-tailed F-tests. Because F tests are sensitive to departures from normality, C values significant at $\alpha < 0.10$ were retested by bootstrapping. This is a resampling procedure used to estimate the distribution of a test statistic when the exact distribution is unknown (Efron, 1982). The test involved drawing n_1 individuals randomly (with replacement) from the survivors, and n_2 individuals from the nonsurvivors, where n_1 and n_2 are the observed numbers of survivors and nonsurvivors, respectively. We then computed the variance of each random sample (x^2 for survivors, y^2 for nonsurvivors), and the difference between these variances ($x^2 - y^2$). This sampling procedure was repeated 500 times. We computed the fraction of differences between variances exceeding zero and the fraction less than zero. The smaller of these two fractions, when multiplied by 2, estimates the two-tailed significance level for rejection of the null hypothesis that $C = 0$. To improve accuracy, significance levels close to 0.050 (± 0.025) were reestimated using 1,000 replications. In the Results, we present only significance levels from the bootstrap procedure.

When S is significantly different from 0, differences in variance resulting from directional selection alone must be accounted for in a test for stabilizing selection. We corrected for the effects of directional selection, as follows. If only directional selection is present, variance in the survivors is $a^2 = \sigma^2 - S^2$, where σ^2 is the variance before selection (Lande and Arnold, 1983 eq. 13a). Similarly, it can be shown that the variance of nonsurvivors is $b^2 = \sigma^2 - S^2(p/1 - p)^2$,

TABLE 2. Standardized directional (S) and stabilizing (C) selection differentials associated with overwinter survival in juvenile song sparrows. The two values separated by a comma refer to selection on PC1 and PC2, respectively. A value of zero indicates no significant selection. I is the variance in relative fitness. N is the sample size, with the proportion dying given in parentheses.

	Males				Females			
Winters	I	N	S	C	I	N	S	C
1975–1976	032	13 (0.30)	0, 0	0, 0	2.94	11 (0.73)	0, 0	0, 0
1976–1977	0.66	36 (0.39)	0, 0	0, 0	1.08	39 (0.51)	0, −0.34*	0, 0
1977–1978	0.78	48 (0.44)	0, 0	0, 0	1.42	43 (0.58)	0, −0.41*	0, 0
1978–1979	0.39	55 (0.27)	0, 0	0, 0	0.69	52 (0.40)	0, 0	0, 0
Combined	0.54	152 (0.35)	0, 0	0, −0.19*	1.05	145 (0.50)	0, −0.30**	0, 0

* $P < 0.05$.
** $P < 0.01$.

where p is the fraction of individuals surviving. Significance of C was thus tested by comparing $a^2 + S^2$ with $b^2 + S^2(p/1 - p)^2$, using the bootstrap. The procedure was the same as when $S = 0$ (above) except that we used $x^2 + S^2$ and $y^2 + S^2(p/1 - p)^2$ in place of x^2 and y^2.

Reproductive data were analyzed similarly: mean and variance in morphology of individuals whose reproductive success was higher than the average for that subset ("survivors") were compared with the individuals below average ("nonsurvivors"), using t tests, F tests, and the bootstrap. We used the average instead of the median because reproductive success is a discrete variable, and the median was often found to be zero. Use of the average in each case divided individuals into two groups of roughly equal number. Note that since reproductive success is a binary variable in this analysis, S must be recomputed when correcting for directional selection in variance comparisons.

In a few cases in which directional selection on PC's was observed, relative fitness was regressed on the original six traits combined (standardized), in order to determine the "targets" of selection (Lande and Arnold, 1983). The partial regression coefficients form the standardized directional selection gradient, β. This gradient indicates the intensity of selection acting directly on the individual traits included in the analysis, whereas the selection differentials (S) also include phenotypic responses to selection on correlated traits. An important assumption of the gradient analysis is that there has been no selection on unmeasured traits that are correlated with the traits mea-

sured. Violation of this assumption may lead to biased estimates of β. In the song sparrow, phenotypic correlations between traits are relatively low (Schluter and Smith, unpubl.), and hence our results are less vulnerable to possible selection on unmeasured traits. A similar partial regression was not performed for stabilizing selection, because of the large number of variance and covariance terms.

In our analyses, relative fitness is discrete, invalidating an assumption on which statistical testing of standard regression models is based. However, probit analyses (Finney, 1971) gave essentially identical results. Since regression coefficients are simpler to interpret than the probit results, we present only the former.

Sexual Selection. — Song sparrows are largely monogamous. Nonetheless, opportunity for sexual selection on morphological traits is present in two situations. First, a territory is necessary for breeding, and not all males that survive to breeding age succeed in gaining a territory. Second, not all

TABLE 3. Directional selection (standardized) on the original six traits associated with overwinter survival in juvenile females, all years combined. S is the vector of selection differentials. β is the selection gradient ($R^2 = 0.16$, $N = 145$, $P = 0.0004$).

Trait	S	β
Weight	0.01	0.08
Wing length	0.08	0.08
Tarsus length	−0.32***	−0.32***
Beak length	0.24**	0.18*
Beak depth	0.02	−0.10
Beak width	0.17*	0.08

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

TABLE 4.   Selection on PC1 and PC2 associated with overwinter survival of adults. Symbols as in Table 2.

	Males				Females			
Winters	*I*	*N*	*S*	*C*	*I*	*N*	*S*	*C*
1976–1977	0.10	33 (0.09)	0, 0	0, 0	0.05	20 (0.05)	—	—
1977–1978	0.26	53 (0.21)	0, 0	0, 0	0.14	40 (0.13)	0, 0	0, 0
1978–1979	0.16	77 (0.17)	0, 0	0, 0	0.20	65 (0.17)	0, 0	0, 0
1979–1980	3.45	66 (0.77)	0, 0	0, 0	10.78	58 (0.91)	0, 0	−0.53**, 0

** $P < 0.01$.

males which gain a breeding territory acquire a mate. In each situation, selection differentials were computed and tested as for survival data.

Mating success was also compared with territory size. Territory size here refers to the square root of territory area in spring (late April), measured in the manner described by Smith (1986). When computing selection differentials for all years combined, territory size was standardized within each year, to account for variation in breeding density among years.

RESULTS

Juvenile Overwinter Survival.—Table 2 shows temporal patterns of selection on PC1 and PC2 associated with juvenile overwinter survival. Data from different years are also combined in an overall comparison, since the different years are independent. No selection was observed in males in any year, though stabilizing selction on PC2 is suggested for the four winters combined. Variance in relative fitness was invariably higher in females than in males, resulting from their greater mortality. Correspondingly, selection was observed more frequently on females: strong directional selection on PC2 occurred in two of four years, and the directional trend was identical in the other two years. Selection on PC2 is strong and significant when all years are combined (Table 2).

Table 3 presents the selection differentials and the selection gradient for the six original characters in juvenile females, for all years combined. Pairwise phenotypic correlations between traits are quite low (average $r = 0.12$), and for this reason **S** and β are similar. β values suggest that differences in PC2 scores between surviving and nonsurviving females resulted from direct selection on only two of the original six traits.

Overall, selection favored females with shorter tarsi and longer beaks. Selection differentials for the other four traits were not significant, or in one case (beak width) resulted from a correlation with tarsus length or beak length (Table 3).

Adult Overwinter Survival.—In each year, mortality of adults was lower than that of juveniles, resulting in lower variance in relative fitness (Tables 2 and 4). Mortality was substantial only during the winter of 1979–1980, and only then was selection on adult morphology observed. Selection on juveniles in this same winter is not reported (Table 2), since virtually all of them died, and most were not measured. Unlike juveniles, selection in females was primarily stabilizing, and was restricted to general size (PC1) (Table 4). Selection in adult females was strong: the standardized coefficient $C = -0.53$ indicates that variance in PC1 was reduced by 53% in 1979–1980. Variance in PC1 was also reduced in adult males in 1979–1980 ($C = -0.22$), but this value is not significant ($P > 0.10$). Analysis of the original characters showed significant stabilizing selection differentials for two traits in females: tarsus length and beak length. Stabilizing selection differentials were significant for none of the original six traits in males.

Sexual Selection.—Most males that fail to acquire a territory in their first breeding season do not gain a territory in subsequent years. We therefore tested for sexual selection by comparing morphology and success in obtaining a territory in first-year males. No selection was observed: 27 of 100 males did not gain a territory in their first season (four years combined, $I = 0.37$), but they were similar in morphology to the remaining 73 males ($P > 0.05$). Results were the same within each year.

Among 99 males of all ages with terri-

TABLE 5. Selection on PC1 and PC2 associated with reproductive success. Analysis of males includes only those that acquired mates. Symbols as in Table 2.

Summers	Males				Females			
	I	N	S	C	I	N	S	C
1975	2.56	11	0, 0	0, 0	1.10	11	0, 0	0, 0
1976	0.72	20	0, 0	0, 0	0.52	10	0, 0	0, 0
1977	0.44	34	0, 0	0, 0	0.35	26	0, 0	0, 0
1978	0.51	40	0, 0	0, 0	0.42	42	0, 0	0, 0
1979	0.79	55	0, 0	0, 0	0.89	57	0, 0.30*	0, 0

* $P < 0.05$.

tories, six did not acquire a mate (all years combined). Mated and unmated males did not differ significantly in morphology ($P > 0.05$). However, mated males had larger territories than unmated males ($S = 0.08$, $P = 0.002$). Territory size was uncorrelated with male morphology (all $P > 0.05$). Territory size varied with male age, and so we repeated this analysis, using instead the standardized residuals from within-year regressions of territory size on male age. The result was similar ($S = 0.06$, $P = 0.03$).

Adult Breeding Success. — Variation in male reproductive success was present in all years (Table 5), but it was not associated with variation in male morphology. In females, however, directional selection on PC2 was observed in 1979, when variance in relative fitness was high (Table 5). The same result was observed within each age cohort of females present in the 1979 sample. Large I in 1979 was associated with high densities of sparrows, low average breeding success, and presumably elevated levels of aggression or competition for food. Variance in relative fitness was also high in 1975, a second year when average breeding success was poor, but the sample size for 1975 is small.

In females, selection on PC2 associated with reproduction was similar in magnitude, but opposite in sign, to selection associated with juvenile overwinter survival (Table 2). This pattern is confirmed when reproductive success is compared with the original six morphological traits (Table 6). As with juvenile survival, selection associated with female reproduction was restricted to only two traits: tarsus length and beak length. Adult females that produced more young had longer tarsi and shorter beaks than other females, but this same combination of traits was associated with reduced survival at the juvenile stage (Table 3). Thus,

in females there was an apparent trade-off between survival and reproduction, as determined by beak and body size.

DISCUSSION

Natural selection on beak and body size in the song sparrow was surprisingly frequent and intense during the course of this field study. Both directional and stabilizing selection were detected. By comparison, selection has also been observed frequently in the Galápagos finch, *Geospiza fortis* (e.g., Price et al., 1984). But in that case, morphological variability is high (Grant and Price, 1981), and it is less surprising that large differences in size between individuals should be associated with detectable differences in fitness. Morphological variation in the song sparrow is relatively low (Schluter and Smith, unpubl.), as is variability in most other bird populations. Despite this low variability, size in the song sparrow was found to be associated with variation in survival and reproduction. Since the traits are heritable (Smith and Zach, 1979; Schluter and Smith, unpubl.), the results imply significant potential for evolutionary change across a presumably typical five-year period. We doubt that song sparrows are pe-

TABLE 6. Directional selection on the six standardized traits associated with female reproduction in 1979. S is the vector of selection differentials. β is the selection gradient ($R^2 = 0.29$, $N = 57$, $P = 0.007$).

Trait	S	β
Weight	0.20	0.12
Wing length	0.02	−0.14
Tarsus length	0.35**	0.38**
Beak length	−0.23	−0.30*
Beak depth	0.01	0.02
Beak width	0.12	0.24

* $P < 0.05$.
** $P < 0.01$.

Fitness Components   JUVENILE SURVIVAL   ADULT REPRODUCTION

TARSUS LENGTH   BEAK LENGTH

Phenotypic Values

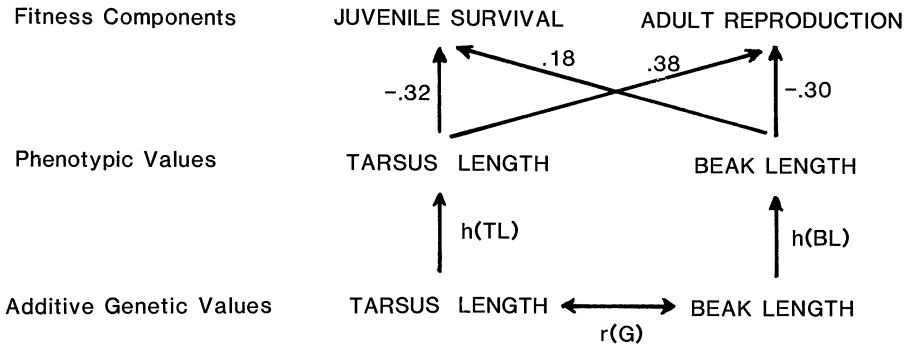Additive Genetic Values   TARSUS LENGTH ⟷ BEAK LENGTH

FIG. 1. Path diagram summarizing relationships between morphological traits and fitness components in female song sparrows. Single arrows link dependent (arrowheads) with independent variables. Positive and negative numbers are partial regression coefficients, elements of β (Tables 3 and 6). h is the square root of the heritability of each morphological trait. Double arrow indicates a possible genetic correlation, $r(G)$ between traits.

culiar in this respect (e.g., Johnson et al., 1980; Johnston and Fleischer, 1981; Arnold and Wade, 1984b; but see Ross and Mc-Laren, 1981). Hence, our results are grounds for optimism that adaptation can be studied directly through measurements of selection in natural populations (Lande and Arnold, 1983).

Selection was sporadic during this study. In numerous cases where sample sizes were adequate, we failed to detect any hint of selection. This pattern supports speculation (Wiens, 1977; Wiens and Rotenberry, 1980) and previous evidence (Price et al., 1984) that the intensity of selection on morphological traits influencing feeding is variable, and related to vicissitudes of the environment. Most selection in the song sparrow occurred overwinter, or during periods of high breeding density, indicating a possible connection between selection intensity and resource scarcity.

In females, selection occurred in both the breeding and nonbreeding seasons, in association with reproduction and survival, respectively. Figure 1 summarizes the results of directional selection on females in a path diagram. For simplicity, the diagram assumes that genetic and phenotypic correlations between adult and juvenile values for a given morphological trait are 1. This assumption is probably valid, since post-juvenile growth is slight. The figure shows that reproductive success of adult females was enhanced by the same combination of traits that reduced survival of juveniles. This

trade-off between adult reproductive success and juvenile survival has an important consequence. Since tarsus length and beak length are heritable, the contributions of these traits to survival and reproduction are negatively genetically correlated. Additionally, if tarsus length and beak length are the major heritable determinants of juvenile survival and adult reproduction in females, then this correlation is equivalent to a negative genetic correlation between the fitness components themselves (Price and Grant, 1984). Note that if the genetic correlation between survival and reproduction were negative, as determined by morphology, this would not imply that the phenotypic correlation between these fitness components is also negative, since there may be common environmental influences on survival and reproduction. A previous study of this song sparrow population indicated that the phenotypic correlation between adult survival and reproductive success was positive (Smith, 1981).

The genetic correlation between the morphological contributions to survival and reproduction can be estimated as

$$r = \beta_1'\mathbf{R}\beta_2/\sqrt{(\beta_1'\mathbf{R}\beta_1)(\beta_2'\mathbf{R}\beta_2)}, \qquad (1)$$

with ′ indicating transpose. β_1 and β_2 are directional selection gradients for juveniles and adults, respectively, and $\mathbf{R}$ is the genetic variance-covariance matrix of the standardized morphological traits. In the case of Figure 1, $\mathbf{R}$ is a matrix with heritabilities

$h^2(\text{TL})$ and $h^2(\text{BL})$ along the diagonal, and the term $r(\text{G})[h(\text{TL})h(\text{BL})]$ off the diagonal. The relevant genetic parameters are estimated in Schluter and Smith (unpubl.): heritabilities are 0.49 and 0.44 for tarsus length and beak length, respectively, and the genetic correlation between them, $r(\text{G})$, is 0. Using Equation (1), we estimate $r = -0.99$.

Two comparable cases of opposing selection pressures on a heritable character at different life stages have been suggested in the Galápagos finch, *G. fortis*: small adult females bred earlier but survived more poorly than large females (Price, 1984*b*); and small birds of both sexes survived more poorly when adults but possibly better when juveniles (Price and Grant, 1984).

Since selection was associated with both survival and reproduction, it is necessary to estimate the relative importance of both classes of events as determinants of mean morphology in the song sparrow. Comparison of patterns of selection in males and females suggests that overwinter survival may be more important in determining absolute beak and body size, and hence diet. Selection in males was associated only with overwinter survival of juveniles. No directional selection was observed, suggesting that male morphology may be near an optimum for overwinter survival. This conclusion is supported by the observations that overwinter mortality in males was usually less than in females and that survival selection was directional as well as stabilizing in females. Hence, the primary effect of opposing selection pressures associated with survival and reproduction may be to adjust female size relative to male size (i.e., to influence sexual dimorphism) rather than to determine species size per se.

Selection in the song sparrow was most often associated with tarsus length and beak length. This pattern is not a simple artifact of differences among traits in measurement repeatability. Relative measurement error is roughly equal in all traits, excepting body weight, which has low repeatability (Smith and Zach, 1979; Schluter and Smith, unpubl.). This pattern of selection in the song sparrow contrasts with the Galápagos finch, *G. fortis,* where selection occurred more often on beak depth and width. The reason for this difference is not clear, and a more

detailed study of feeding in song sparrows is warranted. Part of the contrast may result from differences in the types of resources utilized in the two situations. *G. fortis* is a habitat generalist, and it is differentiated from most closely-related species in the size and hardness of seeds consumed, as determined by beak depth and width (Abbott et al., 1977; Schluter and Grant, 1984*a*; Price et al., 1984). Sparrows in general are differentiated more by their use of habitat than food size (Pulliam and Mills, 1977; Pulliam, 1983). Tarsus length especially should be related to habitat use, through foraging mode (e.g., Partridge, 1976; Fretwell, 1969; Miles and Ricklefs, 1984).

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