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EVALUATION OF SELECTION ON CLIFF SWALLOWS

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Abstract.—Estimates of the intensity of selection based on measurements of the living and the dead require knowledge of the fraction of the original population dying. We apply recently developed methods (Blanckenhorn et al. 1999) to estimate the intensity of selection in a population of cliff swallows. In this population the fraction of individuals dying was unknown, but certainly high. The inferred selection is very strong and impossible to achieve if the original population is assumed to have followed a normal distribution. We consider several alternative explanations for this result including measurement biases, undetected immigration, and sampling biases. Of these, sampling biases are perhaps the most likely. We conclude that the intensity of selection on the swallows was probably strong, but its absolute magnitude is unknown.

Key words.—Cliff swallows, mortality, natural selection, selection index, selection intensity.

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Over six days in May 1996, severe weather in southwestern Nebraska resulted in massive mortality of cliff swallows, *Petrochelidon pyrrhonota* (Brown and Brown 1998). After the storms, a total of 1856 dead swallows were collected and 1028 living swallows were captured and released. Five traits were measured on each individual (wing length, tail length, tarsus length, culmen length, and culmen width). Morphological differences between the living and the dead were large. The most striking comparison was in tarsus length, which averaged 10.0 mm in the dead and 11.5 mm in the living, a difference of about three standard deviations (Table 1). The differences between the dead and the living suggest very strong selection (for further details, see Brown and Brown 1998). We use recently developed methods (Blanckenhorn et al. 1999) in an attempt to evaluate the strength of that selection.

The measurement of selection on a single trait starts with

the selection differential, s , which is the difference in the mean value of the trait in the population before and after selection. The standardized version of the selection differential is the selection intensity, i ($i = s/\sigma$), where σ is the standard deviation of the trait in the population before selection. A quantitative measure of the selection intensity thus requires estimation of both the population mean and population variance before selection. The mean and variance before selection are not directly observed in samples of the living and the dead. However, they can be estimated as a weighted sum of the means and variances of the living and the dead samples provided the fraction of individuals dying is known (Blanckenhorn et al. 1999).

In the swallow population the mortality rate was unknown, but was clearly high. Based on the number of active nests in 1995 and 1996 the population was reduced by 53% (Brown and Brown 1998). A mark-recapture study of 512 birds caught

TABLE 1. Means and standard deviations for the living and dead swallows. Sample sizes are >1026 for the living and >1794 for the dead (for complete details of sample sizes, see Brown and Brown 1998). All measurements are in millimeters.

	Living		Dead	
	Mean	SD	Mean	SD
Wing length	106.87	2.31	107.53	2.73
Tail length	46.13	1.83	46.65	1.97
Tarsus length	11.52	0.59	10.00	0.47
Culmen length	6.94	0.31	6.33	0.39
Culmen width	6.27	0.37	5.54	0.37

before the event (but not measured) led to an estimate of mortality of 73% (C. R. Brown and M. Bomberger Brown, unpubl. obs.). Because of the uncertainty surrounding the mortality rate, we estimated the selection intensity over a wide range of mortality values using equations (2–4) in Blanckenhorn et al. (1999).

We estimated selection intensity for tarsus length and also for a selection index based on all five traits. The selection index, I , is the linear combination of traits such that if selection acted directly on the index alone the five traits would evolve in the observed directions, with the observed relative magnitudes (see Lande and Arnold 1983, p. 1214). The construction of the index requires an estimate of the covariances between traits before selection (Lande and Arnold 1983), which can be obtained from the covariances and means of the living and dead groups using a modification of equation (3b) in Blanckenhorn et al. (1999). The correlation matrices for the living and dead are given in Table 2. These were used along with the means and standard deviations in Table 1 to reconstruct estimates of the covariances in the population before selection. The variances, covariances, and selection differentials were then combined to calculate the selection intensity on the index, as derived in the Appendix.

The estimated selection intensities on tarsus length and the index as a function of the amount of assumed mortality are shown in Figure 1a. If mortality is assumed to be low, the selection intensity is low because the population before selection is very similar to the living sample. However, if the mortality is assumed to have been high (as appears probable in the cliff swallows), the selection intensity is inferred to have been very high because the population before selection is reconstructed to be very similar to the characteristics of the dead sample.

A useful measure of the strength of selection is the amount of mortality needed to produce an observed selection differential (Lande 1976). The *minimum required mortality* arises when selection is truncation (all individuals one side of the truncation point die, and all individuals on the other side survive). Provided the distribution before selection is approximately normal, the minimum required mortality can be calculated from the selection intensity and tables of the cumulative normal distribution (e.g., Becker 1967, pp. 123–124). The minimum required mortality when selection is acting on more than one trait is calculated using the intensity of selection on the index, and this was our reasoning behind the construction of the index. We also illustrate the consequence of relaxing the assumption of truncation selection, which is unlikely to

TABLE 2. Correlation matrices of traits. Values for dead swallows are above the diagonal and for living swallows are below the diagonal.

	Wing length	Tail length	Tarsus length	Culmen length	Culmen width
Wing length		0.375	0.232	0.108	0.122
Tail length	0.301		0.023	0.027	0.052
Tarsus length	0.155	0.058		0.231	0.237
Culmen length	0.056	0.024	0.044		0.579
Culmen width	0.086	−0.007	0.004	0.630	

ever apply in nature, by fitting a Gaussian fitness function to the data. The Gaussian function has two parameters, the optimum and width of the function, which can be estimated from the change in mean and variance of the distribution, assuming the original population is normally distributed (e.g., Bulmer 1980, p. 151). If fitness at the optimum is scaled to be 1.0, the mean fitness based on this function is an estimate of the mortality required to produce the observed selection intensity. The required mortality estimates for truncation selection on the index and for truncation and Gaussian selection on tarsus length are plotted in Figure 1b.

A paradox in our results is that even the minimum amount of required mortality (i.e. truncation selection on the index) is higher than postulated mortality across the whole range of values tabulated in Figure 1. A main assumption underlying the methods used to calculate the required mortality is that the population before selection is approximately normally distributed. In fact, the samples of the living and the dead themselves appear to be more or less normally distributed (e.g., Fig. 2). A mixture of two different normal distributions cannot itself be normal, and if the two distributions are more than two standard deviations apart (as in the case for tarsus length, see Fig. 2), the reconstructed population is not even unimodal. In this case, the reconstructed population is bimodal, with one mode corresponding to the dead and the other corresponding to the living.

There are several possible explanations for these results. One is that measurement techniques differed between the living and the dead, with live birds consistently measured as larger due to effects of specimen shrinkage. Although this is a potential problem for any study of selection based on living birds and specimens (Jenni and Winkler 1989), in cliff swallows there was no difference in measurements for 29 birds processed both alive and dead (Brown and Brown 1998) and thus no apparent measurement bias. Another possible problem with selection studies based on separate samples of living and dead animals is immigration by individuals after the selection event. If the immigrants are morphologically different from the individuals exposed to the event, the intensity of selection will be incorrectly estimated. In the case of the cliff swallows, there clearly was immigration after the severe weather, because the number of breeding pairs later in the summer was greater than expected based on the estimated mortality during the storm. However, the measurements of survivors were taken immediately after the severe weather ended, thus minimizing the possibility of including immigrants among those measured (Brown and Brown 1998). In an explicit test of the immigration hypothesis, we compared live birds measured during the first two days after the storm

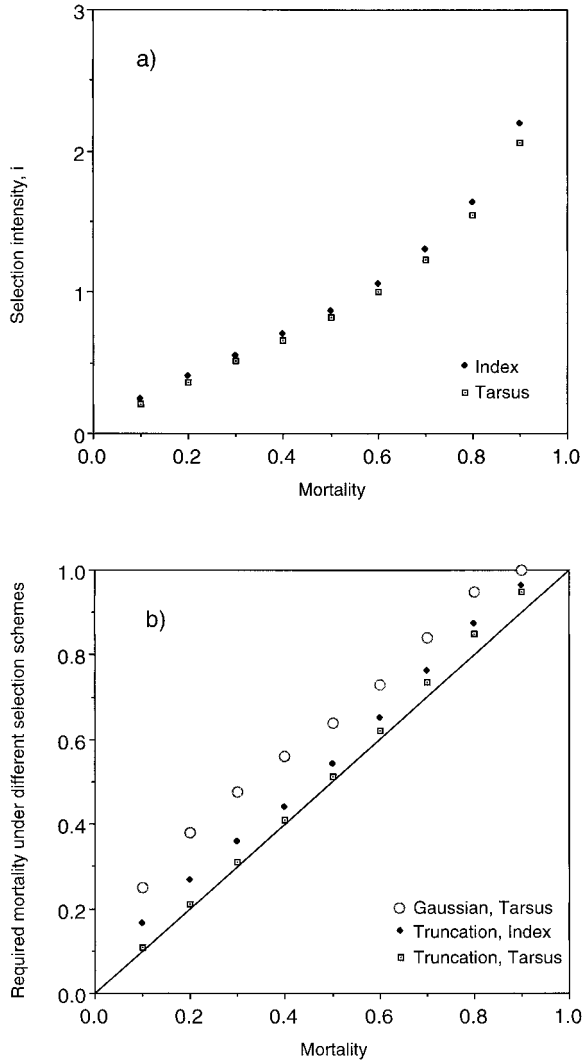


FIG. 1. (a) The selection intensity on tarsus length and an index based on all five traits (see Appendix for derivation) given different amounts of mortality in the swallow population. (b) The required amount of mortality, assuming a normal distribution in the original population, given the selection intensities in the top figure. The x-axis is the same in both graphs. Required mortality under truncation selection for tarsus length and the index is shown, as well as mortality under a Gaussian fitness function for tarsus length (the plotted function is $(\omega^2/(\omega^2 + \sigma^2)) \exp[-(\bar{x} - \theta)^2/(2\omega^2 + 2\sigma^2)]$, where ω^2 and θ are the width and optimum of the fitness function respectively, estimated from the change in mean and variance due to selection). The line is the line of equality between the y and x values.

(which were unlikely to have had time to immigrate to the study area) with birds measured eight days later (ones more likely to have had time to immigrate). We found that the birds measured earlier were actually larger than those measured later. For example, mean (\pm SD) tarsus length for birds on days 1–2 was 11.63 mm (\pm 0.58, $N = 176$) and on day 8 was 11.37 mm (\pm 0.58, $N = 107$) mm. (Wilcoxon test, $P < 0.001$). Thus, in this case, immigration during the time period that measurements were taken was unlikely to have contributed to the morphological patterns observed.

Perhaps the most likely possibility is that the dead birds salvaged for measurement may have been a nonrandom sub-

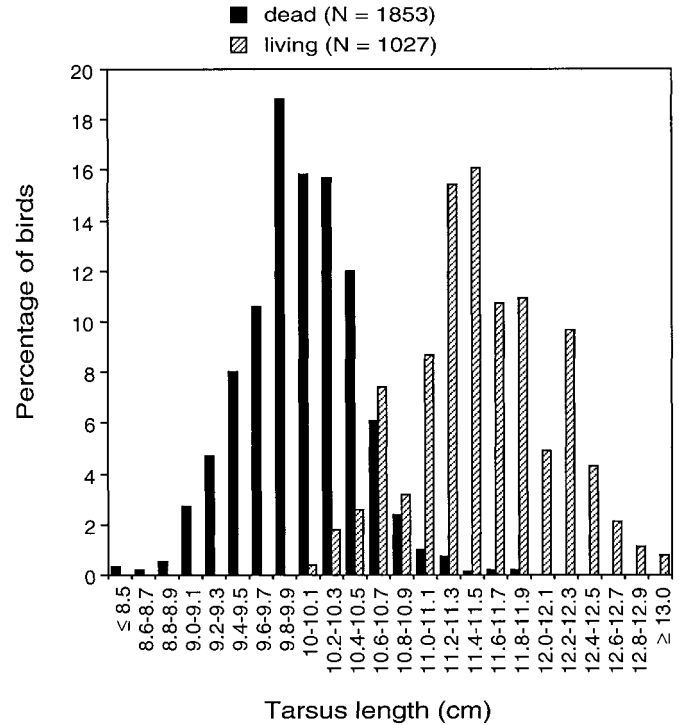


FIG. 2. Distribution of tarsus length among the dead ($N = 1853$) and living ($N = 1027$) swallows. The distributions are separately scaled to 100%.

set that included only the smallest. Most of the dead birds collected were ones found on the ground below nests or on nearby sandbars. These birds either fell out of nests or never had nests. Thousands more birds died inside nests, and we could not retrieve those. Perhaps only the smallest birds were apt to be found dead on the ground, only the largest ones survived, and the intermediate sized birds were those that died in nests. This might be the case if the smallest birds were unable to secure nesting sites prior to the severe weather and were thus more exposed to the elements. Their smaller legs also might have influenced their ability to cling to protected substrates (such as the eaves of bridges), causing them to be more likely to fall to the ground, die, and be represented in our measurements. While this does not change the conclusion that the population was subject to intense selection on body size, it prevents us from accurately quantifying the strength of that selection.

Our results highlight the difficulties of obtaining random samples in studies of selection. These difficulties are not restricted to methods based on comparisons of samples of individuals. Thus, although it is possible to apply regression methods to the well-known dataset of Bumpus (1899), the sample of house sparrows Bumpus studied across a storm is certainly a highly biased sample of all the sparrows that experienced the storm (Price and Yeh 1999). Any study of selection needs to be accompanied by a consideration of potential biases in the dataset (Blanckenhorn et al. 1999).

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APPENDIX

The numerical value of the index for an individual bird is defined as $I = (\mathbf{P}^{-1} s)^T z$, where \mathbf{P} is the phenotypic variance-covariance matrix before selection, s is the vector of selection differentials for the traits, z is the vector of trait measurements for that individual, and superscript T indicates transpose (Lande and Arnold 1983, p. 1214). Using the result that the covariance of a character with relative fitness (w) is the selection differential on that character (Price's theorem) we calculate the selection differential on the index as

$$\begin{aligned} s_I &= \text{cov}(I, w) = \text{cov}[(\mathbf{P}^{-1} s)^T z, w] = (\mathbf{P}^{-1} s)^T s \\ &= s^T \mathbf{P}^{-1} s. \end{aligned} \quad (\text{A1})$$

The covariance of I with z is $\text{cov}(I, z) = (\mathbf{P}^{-1} s)^T \mathbf{P} = s$ (Lande and Arnold 1983). Substituting I for z in this formulation shows that the variance in I equals its selection differential, $\sigma_I^2 = s_I$. The definition of the selection intensity on I is the selection differential divided by the standard deviation $s_I/\sigma_I = \sigma_I = \sqrt{s_I}$. Using this and (A1), we find the selection intensity for I to be $\sqrt{(s^T \mathbf{P}^{-1} s)}$. It is this value that is plotted in Figure 1. The use of a similar formula to estimate minimum intensities of selection in retrospective studies of selection (based on the genetic variance-covariance matrix) is discussed briefly by Lande (1979, p. 408).