

SELECTION INTENSITY IN COMMON EIDERS *SOMATERIA MOLLISSIMA* (AVES: ANATIDAE)

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Abstract

Selection intensity in Somateria mollissima in the White Sea was studied on the basis of the data gathered by Bianki and Bojko (1979). Selection intensities between the young full grown birds and adult ones on the following characters were tested: (1) wing length; (2) tail length; (3) culmen length; (4) tarsus length; and (5) length of the middle toe. It seems probable that selection intensity in that time span depends above all on the variability of the given character in the before selection group. The more variable a character is the higher the selection intensity. Regardless of this association the selection intensities on the wing length were found to be markedly higher than the ones for other characters under study. The possible explanation of this fact was strictly discussed, but it remains doubtful for as long as the functional anatomy in connection with ecological aspects shall be exactly studied.

Introduction

Measuring the selection intensity in wild populations is of great importance for the study of the process of evolution. Only very few concrete data, however, are available on this topic till now (see e.g. Cook 1971, and Wilson 1980 for review). In birds only two papers on *Passer domesticus* have been published till now (O'Donald 1973, Lowther 1977). In the present paper the selection intensity in Common Eiders *Somateria mollissima* will be analyzed.

Material

The data gathered by Bianki and Bojko (1979) were used to study the selection intensity occurring in the ontogeny of *Somateria mollissima*. All the birds were measured in the Kandalakša reserve on the western shore of the White Sea (Carelian district, USSR). Wing length, tail length, culmen length, tarsus length, and length of the middle toe were measured. For concrete methods of measuring the birds see Bianki and Bojko (1979). Sex and three age classes were distinguished: one-year, but full grown birds; older, but not mature birds, and adult birds. In the present study only young (i.e. one-year) and adult birds have been taken into consideration.

Methods

For measuring the selection intensity the method provided by O'Donald (1968, 1970) has been applied using the proportionate change in fitness, $\Delta\bar{\omega}/\bar{\omega}$, as a measure of selection intensity. From this model, O'Donald (1970) showed that if a character x is normally distributed, then $\Delta\bar{\omega}/\bar{\omega} = (\bar{x}' - \bar{x})^2/\sigma_x^2 + 1/2 ((\bar{x}' - \bar{x})^2 + (\sigma_x' - \sigma_x^2))/\sigma_x^2$, where \bar{x} and σ_x^2 are the initial mean and variance of the character x , and \bar{x}' and $\sigma_x'^2$ are these values after some period of selection (O'Donald 1970, 1973).

This method, however, cannot be directly applied on our case because it is possible that in *Somateria mollissima* the characters under study change their values even after the growth of the body has ceased, because all of them are (at least partly) epidermal structures. But if coefficients of variation (C 's) are used in O'Donald's model instead of variances, and the directional component of selection is excluded from consideration (see Appendix), his model may be simplified as follows: $\Delta\omega/\omega = (C_x' - C_x)^2/2C_x^2$, where C_x and C_x' are coefficients of variation of the character x before and after some period of selection (= Eq. 2a of the Appendix). This model is independent of the absolute values of the character x , and measures changes of the coefficient of variation, i.e. the intensity of centripetal/centrifugal selection, only. Since O'Donald's model combines effects of centripetal/centrifugal and directional selections, and is allometrically dependent on $(\bar{x}' - \bar{x})$, in the present study selection intensity is measured with the model presented here.

Results and discussion

The data of Bianki and Bojko (1979) are summarized in the Tables 1 and 2. The calculated selection intensities are presented in the Tab. 3.

Table 1.

Measurements of 5 characters in male *Somateria mollissima* (from Bianki and Bojko 1979). \bar{x} , \bar{x}' in mm; C_x , C'_x in %.

character	adults			young		
	\bar{x}'	C'_x	n	\bar{x}	C_x	n
wing length	295.5	2.5	136	271.0	4.3	26
tail length	97.5	3.5	145	86.0	3.4	29
culmen length	55.6	4.1	156	53.3	4.1	27
tarsus length	55.0	3.2	155	54.4	4.2	28
length of the middle toe	80.4	3.2	155	78.8	3.4	28

Table 2.

Measurements of 5 characters in female *Somateria mollissima* (from Bianki and Bojko 1979). \bar{x} , \bar{x}' in mm; C_x , C'_x in %.

character	adults			young		
	\bar{x}'	C'_x	n	\bar{x}	C_x	n
wing length	286.1	2.8	222	246.6	9.3	18
tail length	94.2	3.7	251	83.3	6.1	19
culmen length	52.6	4.2	261	51.2	7.9	19
tarsus length	53.1	3.2	260	52.3	3.9	19
length of the middle toe	77.4	3.3	254	76.3	2.7	18

The selection intensities vary in a remarkable degree (see Tab. 3), so that it is to search for a cause of this variability. It may be assumed that as a character state x deviates from an optimum phenotype, fitness of its bearer decreases. This means that in the course of selection the C 's should be smaller if the initial variation was so great that it caused

Table 3.

Selection intensity measure for 5 characters in *Somateria mollissima*.

character	male	female
wing length	0.0876	0.2442
tail length	-0.0004	0.0774
culmen length	0.0000	0.1097
tarsus length	0.0283	0.0161
length of the middle toe	0.0017	-0.0247

selective deaths of the more deviate individuals. Consequently, it may be assumed that the more variable a group is before the period of selection the more intensive was the selection pressure as measured by the model presented in this paper. The test of this assumption (see Fig. 1) showed that the assumption is true. Without regard to the wing length (see below) the Spearman correlation test proved that the correlation shown in the Fig. 1 is significant at least by $p = 0.01$. Regression for this data set is the following: $C_x = -8.99 + 2.60 \pm 0.94$ (selection intensity $\times 100$). Regression quotient for both the data for the wing length is as measured by eye nearly the same as the one for all other data, but the selection intensity is markedly higher in them. This probably indicates that the selection operates on the wing length much more intensively than on other tested characters, which fact again indicates that to have an optimal wing length is much more important for *Somateria mollissima* individuals than to have optimal tail length, tarsus length and length of the middle toe. This assumption is very interesting in regard of the fact that for the foraging behavior hind limbs are much more important than wings in eiders (see e.g. Townsend 1909, Bergman 1939, Madsen 1954, Humphrey 1958, Player 1971). Selection values on all other characters under study, i.e. lengths of tail, culmen, tarsus and middle toe, are equivalent to each other and dependent probably only on the initial variability of the respective character.

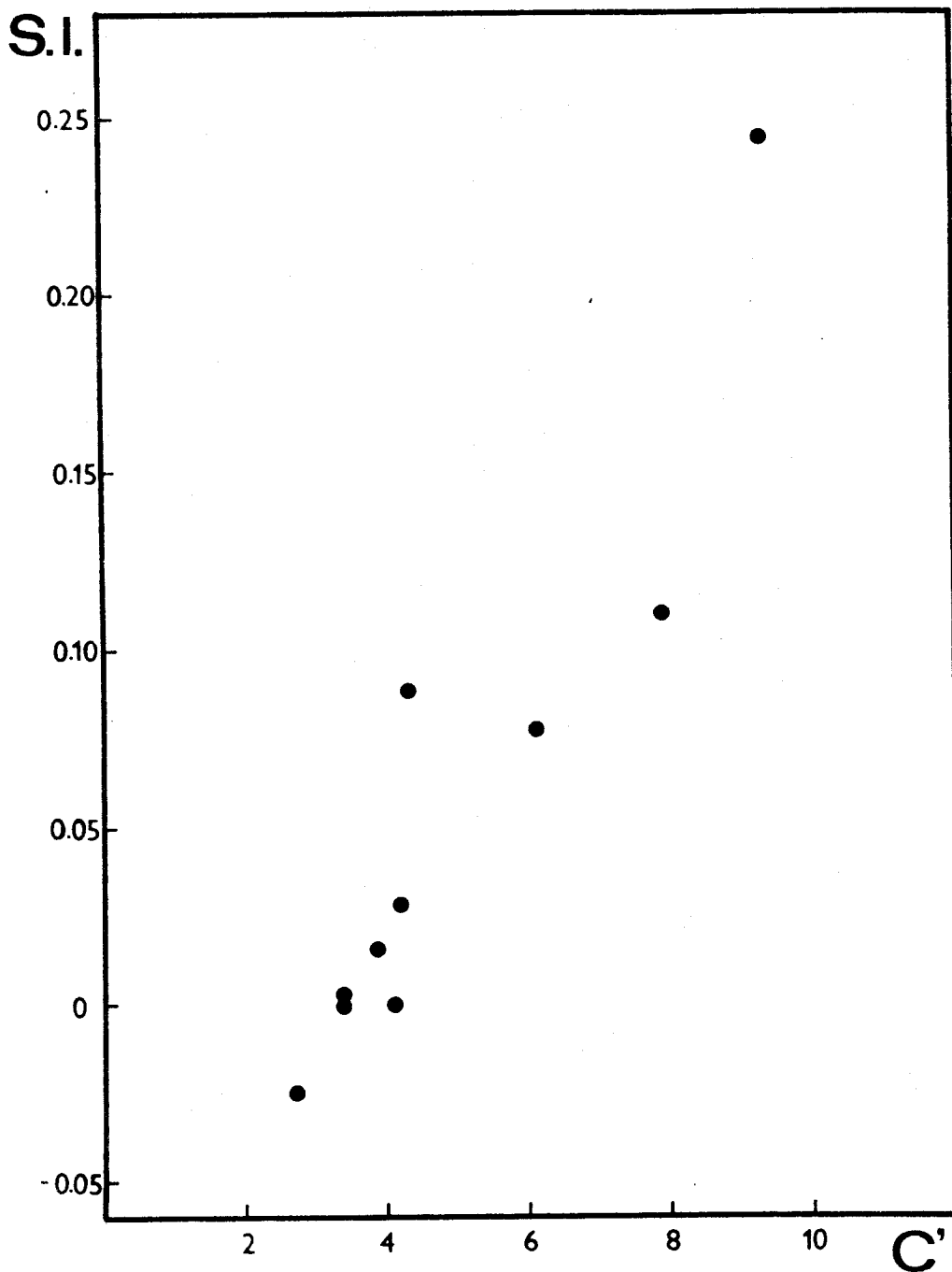


Figure 1.

Correlation between the coefficient of variability of selected characters of young *Somateria mollissima* (C') and the respective selection intensities (S.I.). See text for explanation. For exact data see Tables 1, 2, and 3.

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Appendix: Coefficients of natural selection for metrical characters

All the following coefficients of natural selection are based on the O'Donald's (1970) model which in turn is derived from the genetic measure of fitness (see O'Donald 1968, 1970). O'Donald's coefficient of selection intensity is, however, allometrically dependent on $(\bar{x}' - \bar{x})$. This allometrical effect can be excluded by standardizing $(\bar{x}' - \bar{x})$ by \bar{x} , σ by \bar{x} , and σ' by \bar{x}' (see Eq. 3a). Such a model can be applied on all normally distributed characters, which are mathematically described by their mean values (\bar{x}) and variances (σ). Two kinds of selection quotients may be created: (a) indices not considering time which I will, following O'Donald, call selection intensity (SI), and (b) indices considering time which I will call selection rate (SR). The values \bar{x} and σ are the initial mean and variance, \bar{x}' and σ' are the same values after some period (t) of selection.

O'Donald's (1970) model combines effects of directional and centripetal/centrifugal selection (see Eq 3a, 3b). The directional and the centripetal/centrifugal components may be treated separately (see Eq. 1a, 1b and 2a, 2b, resp.). The disruptive selection cannot be measured by means of the models presented here.

(1) Coefficients of directional selection

The intensity and rate of directional selection are proportionate to the change of \bar{x} , without regarding the change of σ_x .

$$SI = (\bar{x}' - \bar{x})^2 (2\bar{x}\sigma + (\bar{x}' - \bar{x})^2) / 2\bar{x}^2\sigma^2 \quad (1a)$$

$$SR = (\bar{x}' - \bar{x})^2 (2\bar{x}\sigma + (\bar{x}' - \bar{x})^2) / 2\bar{x}^2\sigma^2 t \quad (1b)$$

(2) Coefficients of centripetal/centrifugal selection

The intensity of centripetal/centrifugal selection is proportionate to the change of C_x . The selection is centripetal if SI (or SR) > 0 , and centrifugal if SI (or SR) < 0 . Since it may be assumed that not only the changes of C_x but also the values of C_x themselves are determined by selection, the negative values of S (and SR) may be caused also simply by a decrease of the selection intensity. In this model such a decrease of selection intensity cannot be distinguished from centrifugal selection.

$$SI = (\sigma' - \sigma)^2 / 2\sigma^2 \quad (2a)$$

$$SR = (\sigma' - \sigma)^2 / 2\sigma^2 t \quad (2b)$$

(3) Coefficients of selection in general

The coefficients of selection in general combine the effects of the directional and centripetal/centrifugal selections.

$$SI = ((x' - x)^2 / x\sigma)^2 + ((x'(x' - x)^2 + x(x\sigma' - x'\sigma))^2 / 2x^2x'^2\sigma^2 \quad (3a)$$

$$SR = ((x' - x)^2 / x\sigma t)^2 + ((x'(x' - x)^2 + x(x\sigma' - x'\sigma))^2 / 2x^2x'^2\sigma^2 t \quad (3b)$$