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RELATION OF WITHIN-POPULATION PHENOTYPIC VARIATION WITH SEX, SEASON, AND GEOGRAPHY IN THE BLUE TIT

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ABSTRACT.—We analyzed within-population variation of external characters in *Parus caeruleus* and its relation to geography. We examined sexual dimorphism, seasonal variation, and individual variation. Characters were measured on 2,184 museum specimens collected over the species range. Males are significantly larger than females in most characters. Extreme dimorphism in bill length only occurred in samples from localities where no other member of the genus *Parus* co-occurred. We used these data to suggest an ecological explanation for dimorphism. Heterogeneity in character variance was widespread. We identified no geographical trend in variation of character variance. Contribution of season to variance was low and varied according to the character's sensitivity to wear. Seasonal variation in bill length reflected seasonal variation in diet and foraging technique. Received 20 June 1990, accepted 11 March 1991.

MOST studies in geographic variation in birds focus on variation among sample means. Less attention is paid to the components of population variance and how they are affected by geography.

Studies of morphometrics have identified three components of measurement variation within a population—polymorphism, seasonal variation, and variation among individuals within a given morph and for a given season. Sexual dimorphism is the most conspicuous form of polymorphism in birds and in most higher vertebrates (Amadon 1959). Sexual selection (Darwin 1871, Selander 1965, Wilson 1975) or pressures to widen the resource spectrum available to a pair (ecological sexual dimorphism) (Selander 1966, 1972; Slatkin 1984; Shine 1989 for a review) have been proposed as explanations for the existence of sexual dimorphism. Selander (1972) suggests that ecological sexual dimorphism explains the stronger sexual dimorphism observed in vertebrate species in the absence of congeners (see Selander 1966, 1972; Schoener 1965). These species increase the width of their ecological niche in accord with Van Valen's (1965) niche variation theory (see Svärdson 1949). The second component of variation (i.e. season) is related to individual development as well as to physiologically or environ-

mentally induced seasonal variation. In birds, characters such as wing length, bill shape, and color can vary seasonally (Davis 1954, 1961; Packard 1967; Johnston 1977; Gosler 1987). Gosler (1987) showed that bill-shape varied within individuals and between seasons according to the proportion of invertebrates in the diet and to changes in feeding. To be consistent with the existence of polymorphism and seasonal variation, variation among individuals should be considered in homogeneous groups (e.g. individuals of the same sex in the case of a sexually dimorphic species, in identical developmental stages, or collected at the same time). Character mean and variance in a sample usually include these components of variation plus variance due to measurement error. Therefore, careful analysis of their contribution is important to understand total variation.

In the Blue Tit (*Parus caeruleus*), as in most Palearctic species, little attention has been given to within-population variation and the effects of geography. Exceptions are studies of sexual dimorphism in bill and wing characters between European and British birds (Geys 1968a, b). We studied components of within-population variation in 20 external characters in samples that cover the entire range of the Blue Tit. The components include sex, season, among-individual variation, and measurement error. For each component the influence of geography on within-population variation is analyzed. Attention was given to the influence the co-occurrence of congeneric species may have on the

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TABLE 1. Male-female differences (%) for 20 mensural and plumage-pattern characters. Difference = $100 \times [(male - female) \text{ divided by } male]$. Levels of significance of "paired samples" Wilcoxon test: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = not significant. Positive differences indicate larger values in male character. The test was performed for each character across 29 sample pairs. Minimal sample size per sample was 10. Mensural characters: I = bill characters, II = wing characters, III = tail length, IV = hind-limb characters; Plumage pattern: I = white markings, II = belly and breast characters, III = neck characters.

Symbol	Character	Difference	P
Mensural characters			
I BILL	Bill length	-0.19	NS
BILH	Bill depth	+4.38	***
II WINL	Wing length	+3.24	***
GCWT	Greater covert tip to wing tip	+2.77	***
GCP1	Greater covert tip to first primary tip	-1.72	*
PR1L	First (outermost) primary length	+1.79	NS
P1P2	First primary tip to second primary tip	+4.43	***
P2WT	Tip of second primary to wing tip	+5.35	***
III TAIL	Tail length	+3.43	***
IV TARS	Tarsus length	+2.47	***
MTON	Length of middle toe nail	+4.62	**
HTOE	Length of hind toe	+3.48	**
HTON	Length of hind toe nail	+1.99	***
Plumage pattern			
I FHPT	Width of forehead white patch	+6.36	***
WBAR	Width of wing bar	+8.29	**
SWPA	Width of the white patch on tail tip	+10.35	***
II BBEL	Size of the black patch on belly	+17.50	***
WBEL	Proportion of white breast & belly	-9.34	**
III GNEC	Width of gray neck ring	-3.63	NS
BNEC	Width of black neck ring	+3.89	NS

amount of sexual dimorphism. Geographic variation among populations is discussed in Martin (1991).

MATERIAL AND METHODS

Background.—The Blue Tit's range covers most of the western Palearctic (see Martin 1991: 821). The species almost exclusively inhabits broad-leaved woodlands over a wide range of ecoclimatical conditions (Snow 1954a, Lack 1971). Exceptions are found in some parts of the Mediterranean region (Corsica and North Africa) where the species also breeds in shrublands (Snow 1952; Blondel 1981, 1985; Martin 1982), and in the middle and outer Canary Islands where it is common in pine woods (Lack and Southern 1949, Bacallado 1976). Vaurie (1957 after Hartert 1910, 1932–1938) recognized two main subspecies complexes: the *caeruleus* complex includes all populations from Eurasia, and the *teneriffae* complex includes all North African and Canary Island populations plus the birds on Pantelleria, a small Italian island off the coast of Tunisia (Brichetti and Violani 1986). The Blue Tit occurs in syntopy with one to three other *Parus* species over all its breeding range except in the Canary Islands and in Cyrenaica where the Blue Tit occurs exclusively (Lack 1971).

Measurements.—We studied 2,184 specimens of *Par-*

us caeruleus, from 27 museum collections. Only adults were used. Sampling units (54) were defined on the basis of a latitude-longitude grid (see Martin 1991: 821). Geographical isolates (in general islands) were always considered distinct sampling units. Fifteen mensural and plumage-pattern characters (see list in Table 1) were measured with dial calipers (to ± 0.02 mm). Five additional characters included (1) wing length measured with a ruler; (2) tarsus length, measured with a divider and a ruler; (3) the extent of green on the back; (4) the extent of the black belly patch; and (5) the proportion of white on the belly. Green on the back was scored as follows in order to describe as accurately as possible the variation across the species range: 1 = $\leq 1\%$, 2 = 2–5%, 3 = 6–20%, 4 = 21–50%, 5 = 51–100%; extent of black on belly: 1 = no black patch, 2 = small, 3 = large, 4 = very large; extent of white on belly and breast: 1 = $\leq 1\%$, 2 = 2–10%, 3 = 11–40%, 4 = 41–80%, 5 = 81–99%, 6 = 100%.

Mean and variance were calculated for each character and for each sex separately within each sampling unit (SAS 1985, PROC NEANS).

Sexual dimorphism.—We used the Wilcoxon non-parametric test for paired samples (Conover 1980) to analyze differences between male and female character means across the samples by the formula $[100 \cdot (male - female) / male]$. Sampling units with ≤ 9 specimens were omitted from the analysis. Geographic

variation in the degree of sexual dimorphism in 29 samples with ≥ 10 specimens was studied more carefully for bill length and bill depth (both related to prey size and shape; Snow 1954b; Betts 1955; Schoener 1965; Johnson 1966; Lack 1971; Grant 1972; Partridge 1976; Herrera 1978, 1981) and wing length (to represent overall size; Snow 1954b). Bill characters were chosen because of their relation to foraging behavior; wing length was chosen because of its relation to overall size. Bill size and shape in species or populations of tits greatly vary accordingly to habitat (Snow 1954b, 1955; Lack 1971; Perrins 1979; Alatalo 1982). Male-female differences were plotted against male character mean for each geographic sample and levels of dimorphism were compared among samples. Means of male-female differences in bill length between the samples from the Canary Islands, and the remaining samples were compared by Student's *t*-test.

Seasonal and individual variation.—Because sexual dimorphism exists in this taxon, we analyzed seasonal and individual variation in males only. We chose males because of the larger sample size. Our unpublished results from analyses of females show similar trends to variation in males. Homogeneity of variance was analyzed across samples character by character. We used Bartlett's test of homogeneity of variance (Sokal and Rohlf 1981). The test was applied to the 33 male samples that exceeded 19 specimens (Table 2).

We used a nested ANOVA with unequal sample size (Sokal and Rohlf 1981; SAS 1985, PROC NESTED) to determine the proportion of variance explained by (1) geography (sampling unit); (2) season (season at which the specimen was collected) (Table 2); and (3) individual variation. Individual variation included both biological variation among individuals and measurement error. The relative importance of measurement error was estimated for each character. We did this by ranking characters according to the coefficient of variation obtained after remeasuring each character 20 times for four randomly selected individuals (see Martin 1988).

We also studied spatial variation in the variance of each character. We constructed scatter plots of the variance by sampling unit for each character.

Estimated seasonal variation in bill shape.—We analyzed seasonal variation in bill shape in order to compare our data with results obtained in other species of *Parus*. We studied changes in mean bill length and bill depth by season. Seasonal variation cannot be studied directly when working on museum specimens. However, variation in mean character values between different subsamples collected in the same area at different seasons will give an estimated seasonal variation. This assumes that the population is sedentary. In the Blue Tit, populations from the Mediterranean are sedentary, while seasonal movements may affect the northernmost Eurasian populations (Mohr 1960, 1962; Linkola 1961; Berndt and Henss 1963).

TABLE 2. Distribution of specimen sampling dates for male samples with more than 19 specimens. For sample codes see p. 821. Spring = April to June; Summer = July to September; Autumn = October to December; Winter = January to March.

Sample	Spring	Summer	Autumn	Winter
C2	9		9	9
C4	5	3	14	17
CA1	8		3	21
CA2			4	25
CA3	17			10
CA4	13		9	10
CA5	5	11	6	7
CA6	5			28
CA7	14		6	
MI2	4		16	10
MI3	18	3	5	7
MI4	3	2	14	4
MI5	16	11		
MI6	6	9		
N1	3	5	6	14
N2	14	4	8	10
N4	5	1	9	6
NA1	16		1	14
NA2	8		4	8
NA3	12	2	3	13
NW2	14	2	1	13
NW3	3		5	30
S1	11		6	5
S3	4	4	4	7
S4	12	2	5	2
SE4	7	4	13	9
SE6	11		7	9
SW1	27	1	20	31
SW2	16		5	2
W1	20	4	11	6
W2	4	3	11	16
W3	10		3	7
W6	8	4	19	4

We pooled some sampling units to increase sample sizes. These units were chosen to maximize the coverage of the species' range. In the North African subspecies complex these units are the Canary Islands (males of Gran Canaria Island) and the Maghreb (females from the Maghreb, samples NA1, NA2 and NA3, see p. 821). In the Eurasian subspecies complex the geographic units are the Iberian peninsula (females from samples SW1 and SW2), Central Europe (males from Germany, Holland and Denmark) and Northern Europe (males from Fennoscandia). Despite these groupings most summer subsamples remain small (Fig. 6). Mean character values of adjacent subsamples were compared by Student's *t*-test.

RESULTS

Sexual dimorphism.—Sixteen out of 20 characters had significant differences between male

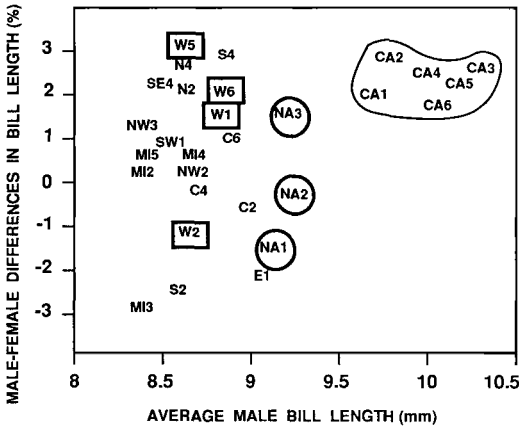


Fig. 1. Sexual dimorphism [$100 \cdot (\text{male} - \text{female}) / \text{male}$] in bill length in relation to male bill length. Symbols defined p. 821. The envelope identifies the samples from the Canary Islands. Neighboring North African samples are circled. Samples from the Western subregion are in rectangles.

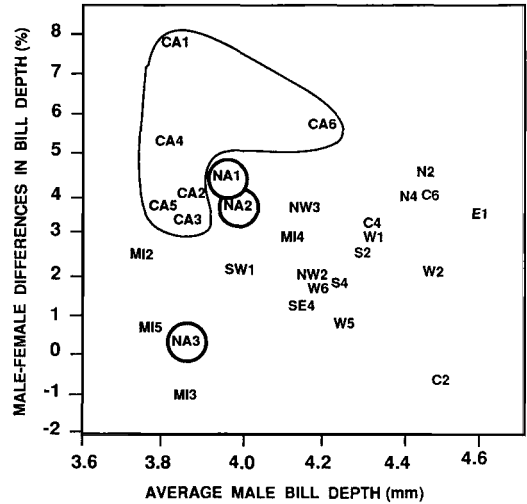


Fig. 2. Sexual dimorphism in bill depth (see legend to Fig. 1).

and female character means across the 29 pairs of samples analyzed (Table 1). Fourteen of 16 characters were significantly larger in males. Male-female differences in bill length and in first primary length are not significant. Difference between the tip of the greatest covert and the tip of the first primary (GCP1) was, on average, significantly smaller in males (Table 1).

Males had significantly larger white markings (forehead white patch width, wing bar width, width of white patches on primary tip), larger black patches on the belly and a smaller proportion of white on the belly. This agrees with differences in coloration between male and female Blue Tits found by Dementiev and Heptner (1932).

Male-female differences in bill length, bill depth and wing length vary over the species' range (Figs. 1–3). However, samples from the Canary Islands had stronger sexual dimorphism (Figs. 2 and 3) than the other samples. Even in absolute bill length (Fig. 1), for which no significant dimorphic trend was diagnosed at the species level, dimorphism was extreme in the Canary Island samples. Indeed, mean sexual dimorphism in bill length for 23 samples from Eurasia and Maghreb equals 0.59% with a standard deviation of 1.69, whereas mean sexual dimorphism for the 6 samples from the Canary Islands equals 2.13% with a standard deviation of 0.39. The difference between these two means is significant ($P < 0.05$, t -test). Geographic vari-

ation in absolute character value (x axis) is discussed elsewhere (Martin 1988, 1991).

Results for wing length (Fig. 3) reflect the observed data for the other wing and leg characters (not shown) which exhibit significant positive differences between males and females.

Seasonal and individual variation in males.—Heterogeneity in character variance is widespread (Table 3), and season is the smallest component of variance for all characters (Fig. 4). The contribution of season varied from character to character. The relative contribution of individual variation and geography to variance varied greatly between characters. We ordered morphometric characters according to decreasing measure accuracy (increasing average coefficient of variation) (Table 4). Character variances fluctuate across the species' range as illustrated for wing length (Fig. 5). Characters do not show an obvious pattern in the spatial distribution of variance. We used plots of wing length variance to illustrate all characters

Estimated seasonal variation in bill shape.—Bill lengths were generally longer in summer and autumn than in winter or spring in all samples studied (Fig. 6). In all instances, except for the samples of north-western Europe, differences between the winter-spring and the summer-autumn period are statistically significant (Student's t -test). For bill depth, there is no seasonal trend similar to the differences found for bill length.

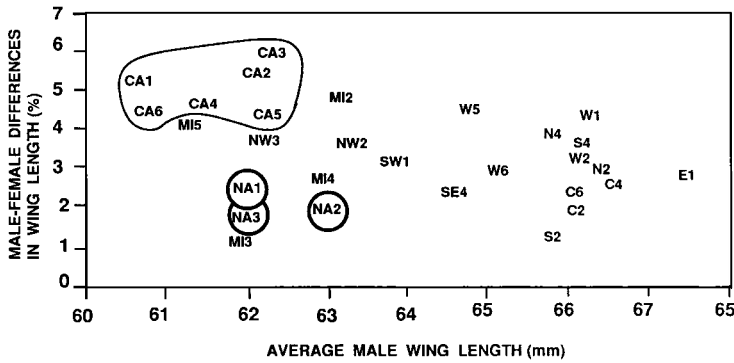


Fig. 3. Sexual dimorphism in wing length (see legend to Fig. 1).

DISCUSSION

Sexual dimorphism in size and shape.—The complexity of interspecific spatial segregation among syntopic *Parus* species has been demonstrated (Gibb 1954, Betts 1955, Lack 1971, Herrera 1981, Alatalo 1982, Laurent 1986, Oksanen 1987). Niche shifts resulting from the absence or the addition of congeners have been documented (Herrera 1978, Alatalo et al. 1985, 1986; Alatalo and Gustafsson 1988, Gustafsson 1988). Gustafsson (1988) and Alatalo and Gustafsson (1988) have shown that the Coal Tit (*Parus ater*) can expand its use of foraging sites and has an increased body size when the larger congener species are missing. In relation to these findings the smaller size of females, as indicated by smaller wing length (Table 1), may imply that females can forage at the tip of twigs of smaller diameter than can males. This might increase the range of foraging sites accessible to a pair

in a way analogous to the way in which between-species size differences affect habitat use. Similar deductions can be made from the larger relative length of the first primary in females which increases flight maneuverability (Nachtigall and Kempf 1971, Kokshaysky 1974).

The lack of dimorphism in bill length does not agree with the smaller wing size of females (Table 1). This result is similar to differences in bill dimensions of the Great Tit. Gosler (1987: fig. 2) analyzed male-female differences in bill length and depth month-by-month over 3 yr for the same individuals. Gosler's results show a constant and marked dimorphism in absolute bill depth, whereas differences between sexes are more erratic and nondimorphic for absolute bill length. Females tended to have slightly longer bills than males in spring and the reverse in late autumn. Snow (1955) found no bill length dimorphism in the Coal Tit, but wing length and tarsus length were significantly larger in

TABLE 3. Bartlett's test on variance homogeneity for mensural characters I-IV in male Blue Tits. Minimal sample size was 20. Null hypothesis is homogeneity of variance. Levels of significance: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = not significant ($df = 32$).

Symbol	Character	χ^2	P
I BILL	Bill length	48.13	*
BILH	Bill depth	77.87	***
II WINL	Wing length	82.45	***
GCWT	Greater covert tip to wing tip	85.98	***
GCP1	Greater covert tip to 1st prim.	86.73	***
PR1L	First (outermost) primary length	67.11	***
P1P2	First primary tip to 2nd primary tip	72.11	***
P2WT	Tip of 2nd primary to wing tip	41.94	NS
III TAIL	Tail length	45.95	*
IV TARS	Tarsus length	44.38	NS
MTON	Length of middle toe nail	129.99	***
HTOE	Length of hind toe	43.90	NS
HTON	Length of hind toe nail	53.51	**

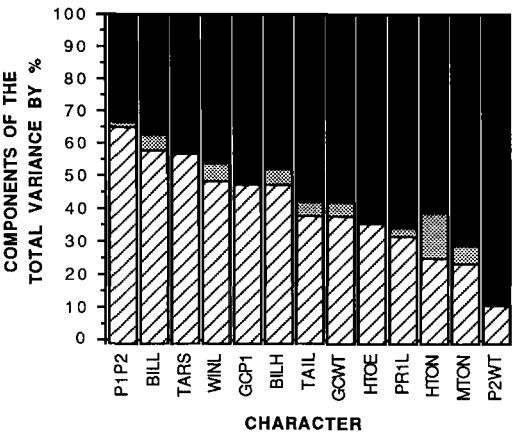


Fig. 4. Contribution of individual variation, season and geography to character variance for male specimens in a nested ANOVA on 33 geographic samples with more than 20 specimens. For character definitions see Table 1. Filled bars = individual; stippled bars = season; striped bars = geography.

males (see also Smith and Zach 1979 for Song Sparrows, *Melospiza melodia*).

The trend towards similar absolute bill length in both sexes may indicate similarity in prey size (for review of the relation between prey size and bill size, see Betts 1955, Lack 1971, Partridge 1976). Thinner bills in females may be related to increased foraging efficiency by the sexes at the micro-site exploited on the plants. Similar interpretations of sexual dimorphism in passerines are given by Johnson (1980) and by Selander (1966) (for a theoretical discussion see Slatkin 1984).

TABLE 4. Character rank according to the average coefficient of variation (CV) obtained by remeasuring each character 20 times, nonconsecutively, on four individuals chosen randomly (after Martin 1988).

Symbol	Character	CV
WINL	Wing length	0.4
GCWT	Greater covert tip to wing tip	0.5
TARS	Tarsus length	1.1
P1P2	First primary tip to 2nd primary tip	1.2
TAIL	Tail length	1.2
BILH	Bill depth	1.3
BILL	Bill length	1.4
PRIL	First (outermost) primary length	1.7
MTON	Length of middle toe nail	1.8
GCPI	Greater covert tip to 1st prim. tip	1.9
HTON	Length of hind toe nail	1.9
HTOE	Length of hind toe	2.0
P2WT	Tip of second primary to wing tip	2.7

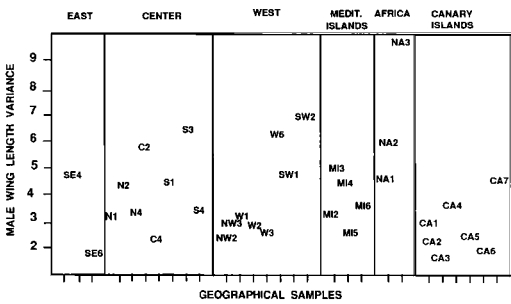


Fig. 5. Variance in male wing length for geographic samples with >20 specimens. Eurasian specimens are grouped from left to right into Eastern, Central, Western Europe and Mediterranean Islands respectively (see legend p. 821). North African samples are grouped into western Maghreb and Canary islands.

However, selection for larger males can also result from territorial interactions (Selander 1972). But our results (Figs. 1-3 and Table 3) strengthen the hypothesis of dimorphism as an evolutionary response to intraspecific selective pressures that tend to increase the range of resources utilized by a pair. This is ecological sexual dimorphism in the sense of Selander (1972). Indeed, only in samples from areas where the Blue Tit is the only species of the Paridae guild are bills sexually dimorphic (Fig. 1). Dimorphism in other characters is also highest in these samples (Figs. 2 and 3). This implies that direct or diffuse interspecific pressures control sexual dimorphism in plurispecific parid guilds, and that the absence of the other members of the guild is accompanied by increased intraspecific morphological differentiation (see Svärdsön 1949). Further, that bill length is, in a congeneric species assemblage, more strongly influenced by interspecific direct or diffuse interactions related to resource partitioning among species than are other characters.

Seasonal and individual variation in males.—The contribution of season to character variance (Fig. 4), is low on average, but highest in characters affected by wear or in characters which vary according to season in other members of the genus *Parus* (as bill length, Gosler 1987). The contribution of season to variance is smallest in characters least sensitive to wear such as tarsus and toe length or in differences between characters affected by wear (Fig. 4). We suggest that heterogeneity in character variance among samples could partly result from differences in

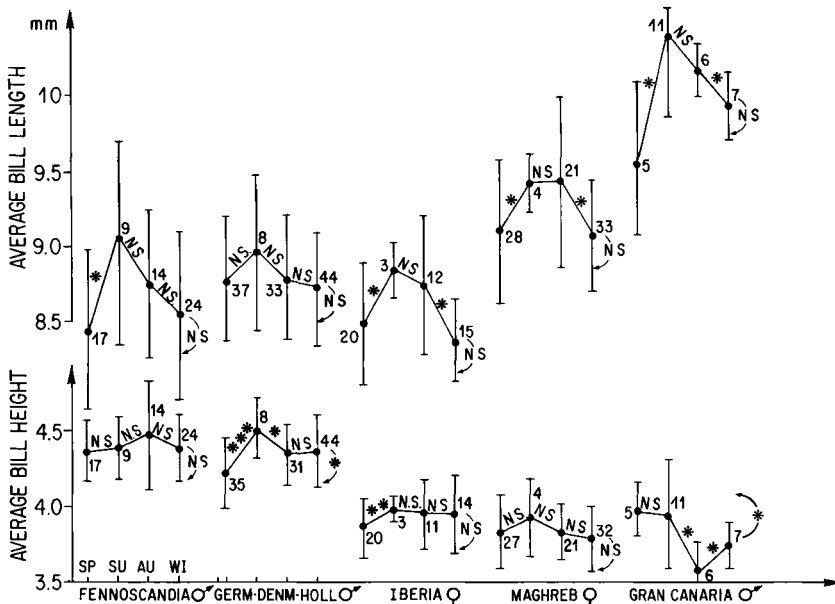


Fig. 6. Seasonal changes in mean values of bill length and depth for 5 selected samples. Standard deviations are given for each seasonal value as well as significance of *t*-test on differences in mean values between adjacent values. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = not significant. Numbers on the graphs refer to seasonal sample size. SP = spring; SU = summer; AU = autumn; WI = winter.

the distribution of sampling dates in the samples (Table 2). Indeed, equal sampling according to season is impossible to obtain from museum collections without deleterious effects on sample size. In a sample with specimens all collected at the same time, the part of variance due to differences in collecting dates is minimized. In a sample with collecting dates spread all over the year, it is maximized. Comparison (Table 2 and Fig. 5), however, does not show consistency between uniform distribution of specimens among seasons and higher character variance.

The ranking of characters according to increasing contribution of individual variation to variance (Fig. 4) is consistent with their ranking according to accuracy in character measure (Table 4). Among the seven characters with the lowest contribution of individual variation to the variance, six are ranked among the seven most accurate characters (Fig. 4, Table 4). Therefore, measurement accuracy seems to be an important part of individual variation for some characters. Best estimates of the contribution of true individual variation (as opposed to measurement error) to variance should thus be obtained for "accurate" characters. In these characters, 30–40% of the total variance results from

among-individual variation, 0–10% from seasonal variation and 50–65% from among-sample (geographical) variation (Martin 1991). But neither sampling dates nor geography seem to be determinant in among-sample heterogeneity in variance (Fig. 5).

Seasonal variation in bill shape.—Data on seasonal variation of bill dimensions in the Great Tit (Gosler 1987) suggest that the pattern of seasonal variation observed in bill length (Fig. 6) results from seasonal changes in the diet. Bills are always longest in summer when the proportion of insects in the diet or when foliage gleaning are highest. In Eurasia maximal bill length tends to be limited more strictly to the summer in the northernmost populations and to extend into the autumn in the southern (Mediterranean) populations (Fig. 6). This may be related to a later shift towards probing in warmer climates. The amplitude of the variation does not seem to be affected by latitude.

Variation in bill length can result from variation in rate of bill wear or from variation in rate of bill growth. Gosler (1987) considers that changes in bill length were selective. Selection may act on genetically controlled seasonal variation in rate of bill growth. Individuals with

lower winter bill growth rates may be at advantage when the proportion of seed in the diet and frequency of probing are high. Their lower bill length to bill depth ratio will increase their feeding efficiency when compared to individuals with higher winter bill growth rates.

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