

# PATTERNS AND SIGNIFICANCE OF GEOGRAPHICAL VARIATION IN THE BLUE TIT (*PARUS CAERULEUS*)

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**ABSTRACT.**—I studied geographical variation in mensural characters and plumage pattern over the breeding range of the Blue Tit (*Parus caeruleus*). In Eurasia body size decreases clinally from north-northeast to south-southwest, and bill thinness and relative tarsal length increase clinally from the northeast to the southwest. This variation is consistent with changes in environmental factors known to affect these characters. Geographical isolates in North Africa vary in size and in bill and tarsus morphology in a way consistent with habitat variation among isolates. Similarities in mensural characters among samples are more consistent with similarities in ecological conditions than with taxonomy. Geographical variation in plumage pattern essentially is clinal in Eurasia but discontinuous in North Africa. On a broad scale, plumage pattern variation is consistent with the population groups defined by taxonomists (Eurasian and North African population groups). Within each population group consistency between variation in plumage pattern and the probable population phylogeny is poor. My results substantiate the importance of the unifying effect of gene flow in adjacent samples even over a large geographical area and the necessity of geographical isolation to foster the appearance of gaps in clinal variation or of markedly different population characteristics. Received 20 June 1990, accepted 11 March 1991.

NUMEROUS authors have stressed the relationships between morphological traits and environmental characteristics (for reviews on ecological inferences from morphological data, see Hespeneheide 1973, Leisler 1980, Leisler and Winkler 1985, James 1982; for relations between bill size or shape with prey size and shape, see Snow 1954b; Betts 1955; Schoener 1965; Johnson 1966; Lack 1971; Grant 1972; Partridge 1976; Herrera 1978, 1981; for relations between tarsus length and perching substrate, see Fretwell 1969, Lack 1971, Grant 1971; and for relations between wing shape and maneuverability in flight, see Nachtigall and Kempf 1971, Hespeneheide 1973, Kokshaysky 1973). The heritability of these morphological traits has been demonstrated (Smith and Zach 1979, van Noordwijk et al. 1980, Dhondt 1982, Boag 1983, Grant 1985, Schluter and Smith 1986, Alatalo and Gustafsson 1988). However, geographical variation in morphology is not always genetically based (James 1983, Zink 1989).

The relation of plumage pattern to environmental features is more poorly documented, al-

though plumage color has been used extensively to study geographical variation in birds and to establish their taxonomy (Mayr 1969; for the Blue Tit, Hartert 1910, 1923, 1932-1938; Vaurie 1957). Climatic variation or variation in quality of food can influence variation in color (Gloger 1933, Snow 1954b, Slagsvold and Lifjeld 1985, Vevers 1985).

Based on this knowledge I undertook a comprehensive analysis of the variation in mensural characters (size and shape of bill, wing, and leg) and plumage (extent of color patches) in the Blue Tit (*Parus caeruleus*) over its entire breeding range (Fig. 1). I attempt to define the principal pattern of geographical variation independent of currently recognized subspecies. I compared patterns of differentiation in isolated versus continuously distributed continental populations subject to greater gene flow under the assumption that geographical isolation allows a better match between the species' morphology and the local environment by reducing gene flow (Slatkin 1981, 1987; Rockwell and Barrowclough 1987). For this, I first identified patterns of geographical variation in the selected characters. I then searched for congruence of these patterns with geographical vari-

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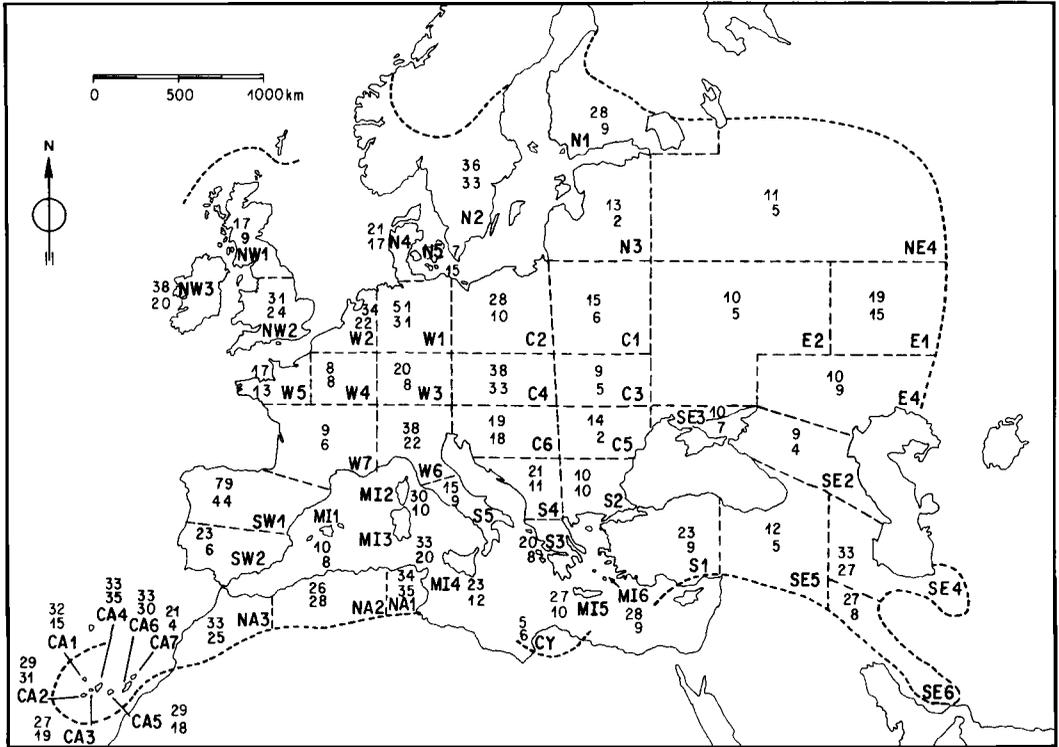


Fig. 1. Range of the Blue Tit (stippled line) and definition of the 54 sampling units. Letters represent 9 main geographical areas of Eurasia (NE = northeast; E = east; SE = southeast; N = north; C = central; S = south; NW = northwest; W = west; and SW = southwest), 6 Mediterranean islands (MI1 = Majorca; MI2 = Corsica; MI3 = Sardinia; MI4 = Sicily; MI5 = Crete; and MI6 = Greek islands), a sample from Cyrenaica, Libya (CY), samples from the Maghreb (NA), and samples from the Canary Islands (CA). The number attached to letters (e.g. CA2) identifies sampling unit within each geographical area. Numbers within each sampling unit refer to sample sizes (male value above female value).

ation in the species' environment; for example, climatic variation or habitat variation (vegetation structure and composition, feeding resources). Finally, I analyzed the relation between the presence of geographical barriers to dispersal of individuals and the amount of phenotypic geographical variation. I followed many of the recommendations of Zink and Remsen (1986) for improving the study of geographical variation.

I demonstrated that geographical variation in mensural characters is consistent with variation in environmental factors known to affect the characters under study. Variation is strongly enhanced in geographical isolates. The type of variation observed in isolates changes with the habitat type used by species. The consistency of morphological similarity with population systematics is poor. Broad patterns of plumage variation seem best explained by history. On a

more local scale, consistency between sample similarity in plumage pattern and recognized subspecies was weak.

MATERIAL AND METHODS

The Blue Tit occupies most of the western Palearctic (Fig. 1). It inhabits deciduous broad-leaved forests (Snow 1954a, Lack 1971, Perrins 1979) except in the Mediterranean region where it inhabits a variety of deciduous and evergreen habitats distributed in a mosaic pattern (Blondel 1985, Blondel et al. 1987, Isenmann 1987). In contrast to the northern part of its breeding range, the hot dry Mediterranean summer probably is the season when it is most difficult for birds to obtain food and water (see Blondel et al. 1987). As the high number of overwintering birds from the north implies (Blondel 1969), the wet and mild winter is more benign than the central European winter (see Blondel et al. 1987). On the Canary Islands, where the Blue Tit is the only member of the genus *Parus*, it breeds in *Tamarix* woodlands on the

two dry easternmost islands (Bannerman 1963, Ballado 1976), and is more or less restricted to pine forests on the five outer islands (Lack and Southern 1949, Cullen et al. 1952, Hemingsen 1963, Grant 1979).

Vaurie (1957) distinguished two subspecies groups. The first, *caeruleus*, includes all Eurasian populations. The second, *teneriffae*, includes all populations from North Africa (Maghreb and Cyrenaica), the Canary Islands, and Pantelleria (a small Italian island lying off the Tunisian coast) (Brichetti and Violani 1986). Vaurie (1957) recognized 8 subspecies in the *caeruleus* group and 6 subspecies in the *teneriffae* group primarily on the basis of color.

Differences in coloration within the *caeruleus* group are slight and clinal. The southern and westernmost forms are darker and more brightly colored than the northern and easternmost forms (see Snow 1954b, 1955). In the *teneriffae* group, the ground color of the back is slate gray instead of olive green, as in *caeruleus*, and the head cap is of dark ultramarine blue instead of light blue; the light gray neck ring is absent (Etchecopar and H ue 1964). In contrast to the *caeruleus* group, the six subspecies of the *teneriffae* group are well defined by unambiguous color characters. The geographical range of each of them is clearly identified, corresponding to one or several adjacent geographical isolates (Vaurie 1957, Etchecopar and H ue 1964 for the illustration).

*Characters studied.*—I measured 13 mensural and 9 plumage-pattern characters of museum specimens (see Appendix). Most characters were measured with dial calipers accurate to 0.02 mm. The length of the tarsus was measured with dividers and a ruler, the length of wing was measured with a ruler, and three plumage-pattern characters were quantified according to charts. I estimated (a) the proportion of the green wash on the back (1 = less than 1%, 2 = 2–5%, 3 = 6–20%, 4 = 21–50%, 5 = 50–100%), (b) the importance of the black patch on the belly (1 = absent, 2 = small, 3 = large, 4 = very large) and (c) the proportion of white (versus yellow) on the belly and chest (1 = less than 1%, 2 = 2–10%, 3 = 11–40%, 4 = 41–80%, 5 = 81–95%, 6 = 96–100%).

The sex of each specimen, its age (1 = juvenile, 2 = one-year-old adult, 3 = older than one-year-old adult), and the extent of plumage wear (3 classes) were recorded. The collection date and the geographical coordinates of the locality were noted. I examined skins of 2,184 Blue Tits.

*Data analysis.*—I divided the breeding range of the Blue Tit into 54 units on the basis of a latitude-longitude grid (Fig. 1). Geographical isolates (in general islands) were always considered as distinct sampling units.

Because of sexual dimorphism (Geys 1968a, b; Martin 1988), analyses were performed separately for males and females. I excluded juveniles and birds with the heaviest feather wear (class 3). The results were similar for both sexes, but the sample size of males was

larger (Fig. 1). I decided to report only the results for the 1,276 male specimens, with the understanding that they can be generalized to the females.

Standardized (or mean centered) principal component analysis (PCA) was used to analyze the untransformed data (SAS software; for details on the method and its use in biology, see Pielou 1977, Orloci 1978, Gauch 1982). This method is well suited to disclose character sets related to size and shape factors (Morrison 1967), and to elucidate the phenetic groupings of individuals. The calculations were made with the individual male specimens as active elements. However, to get a graphic reduction of the data to manageable proportions, I figured the average coordinates of the individuals collected in a given geographical unit in the principal component space (see Fig. 1 for sample sizes in the 54 sampling units). The analysis of the characters' correlation circles in the PCA plane provides a description of the characters' "position" and "representativeness" on the plane (best for characters placed on the circle's circumference). This allows interpretation of the axes in terms of phenotypic characters.

Cluster analysis was used to get further insight into between-sample similarities on a hierarchical basis. First, I constructed classes of sampling units by "Dynamic Clouds" (Diday and Simon 1976), a method that is an extension of the *k*-means (McQueen 1967). For this I used the mean PCA coordinates of the specimens in the 54 sampling units on components 1–4. The hierarchical organization of the classes of sampling units obtained by "Dynamic Clouds" was built by a hierarchical cluster-analysis procedure using the average PC scores of the sampling-unit classes (CAH procedure in ADDAD software) (Roux 1985; also see Sneath and Sokal 1973).

## RESULTS

### VARIATION OF MENSURAL CHARACTERS

The first two principal components summarize, respectively, 29.2% and 25.6% of the variance (Fig. 2a). Principal components 3 and 4 each summarize <10% of the variance. This percentage drops to <6% for the remaining principal components. Interpretation will concentrate on the first two axes.

*Correlation circle analysis.*—The correlation circle (Fig. 3) defines three main groups of mensural characters. The first one has four characters and is correlated with PC1. The characters are wing length (2 characters: WINL and GCWT, see Appendix), which is the best estimate of individual size for this species (Snow 1954b), tail length (TAIL), and bill depth (BILH). Specimens with high values for these characters have negative scores on PC1.

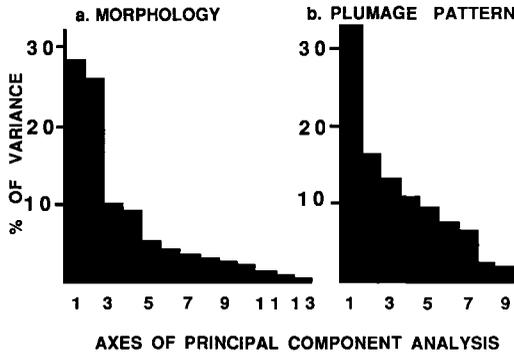


Fig. 2. Percent of variance summarized by the successive principal component axes of the standardized principal component analysis performed on 13 mensural characters (a) and nine plumage pattern characters (b).

The second group of characters is correlated with PC2. The characters are PR1L and GCP1 (see Appendix), both related to the length of the first primary, bill length (BILL), and tarsus length (TARS). Specimens with high values for these characters have negative scores on PC2. Because the length of the first primary is related to the bird's maneuverability in the vegetation (Nachtigall and Kempf 1971, James 1982), all the characters belonging to this second group can be related to foraging behavior. The third group of characters has an intermediate position relative to the two previous groups. It includes three characters related to toe size (MTON, HTON, HTOE; see Appendix). Finally an isolated character, the difference in length between the first and second primary (P1P2), shows high correlations in the plane between PC1 and PC2.

*Between-specimen segregation by PCA.*—Principal component one (Fig. 4) segregates insular sampling units (geographical or ecological islands and most peninsular samples) from continental sampling units. All continental sampling units belong to the Eurasian population complex (negative scores). PC2 segregates the Eurasian geographical isolates (positive scores) from the North African geographical isolates (negative scores).

Seven classes (A to G) are defined by cluster analysis on PC scores (Fig. 4). The hierarchical tree segregates the specimens into two main groups (Fig. 5). The first group (clusters A to D) includes the specimens from Eurasia and from the Maghreb, the second (clusters F to G) in-

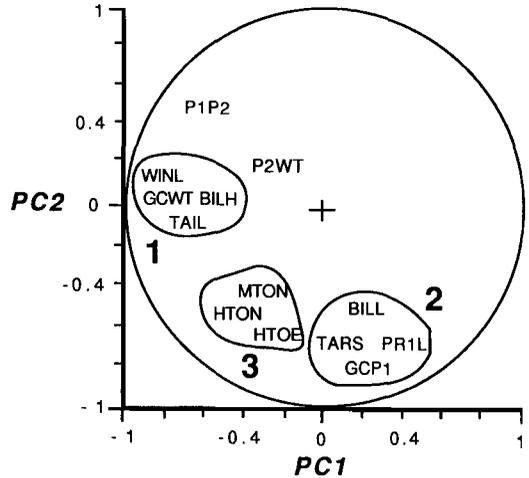


Fig. 3. Coordinates of characters in the PC1-PC2 correlation circle obtained in the standardized principal component analysis on mensural characters. Symbols are defined in the Appendix.

cludes the specimens from Libya and the Canary Islands.

Three morphological types are defined in the plane between PC1 and PC2. The first type (negative scores on PC1, samples E4 and E1) includes specimens from the easternmost part of the species' breeding range (Figs. 1, 4). They are associated with the characters of group 1 in Fig. 3. They have a large size and a stout bill. The second morphological type includes the specimens from the large Mediterranean islands (Corsica [MI2], Sardinia [MI3], and Crete [MI15]) and those from the southern Iberian peninsula (SW2) (class B of cluster analysis, Fig. 4). These specimens are smaller for all the characters measured (Fig. 3). Finally, the third morphological type is represented by the specimens from the westernmost Canary Islands (La Palma [CA1], Hierro [CA2]; Fig. 4). They are slightly smaller than average (wing and tail length) but have a long, rather thin bill, long tarsus, and long first primaries (absolute and relative length).

The Eurasian samples are distributed along a northeast to southwest geographical cline. They range from large specimens with a stout bill in the northeast (cluster D on Fig. 4) to small specimens with a relatively thinner bill in the southwestern (south of the Iberian peninsula and large isolated Mediterranean islands; cluster B, Fig. 4). Along that cline average distances between means of adjacent sampling units in the

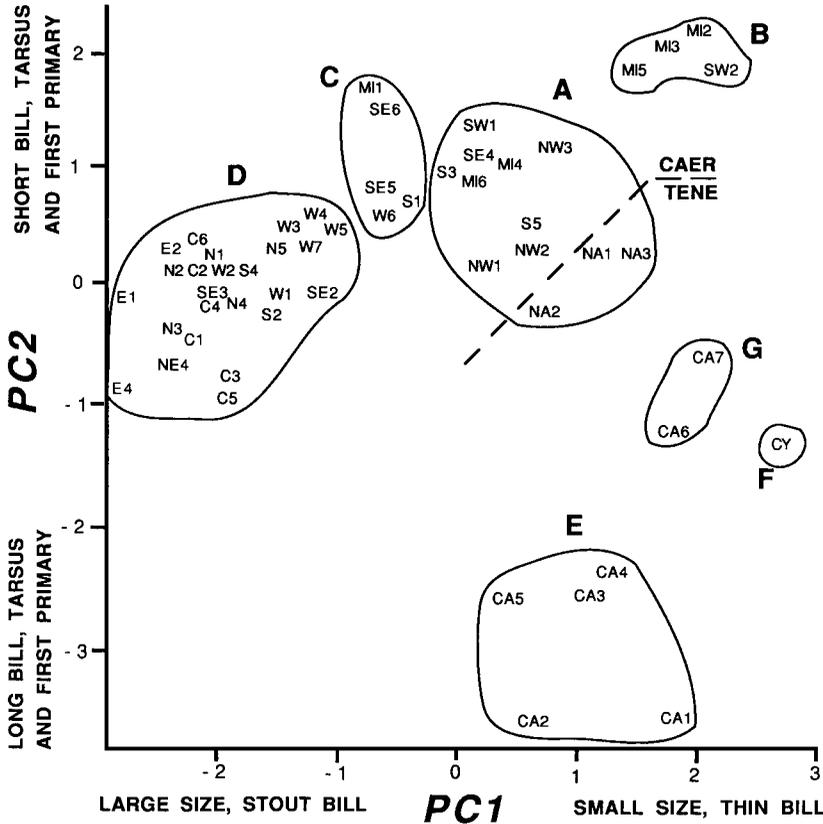


Fig. 4. Mean coordinates of the specimens from the 54 sampling units in the PC1-PC2 plane of the standardized principal component analysis performed on the 13 mensural characters. Symbols are sampling units (envelopes) defined in Fig. 1, letters A-G refer to the sample classes defined by cluster analysis, and the broken line separates the two main population groups defined by Vaurie (1957) (CAER = *caeruleus* group, Eurasia; TENE = *teneriffae* group, North Africa).

PC1-PC2 plane (Fig. 4) are smallest in the central part of the species' range (central, eastern and northern Europe; cluster D, Fig. 4). Overall variation is small despite the huge geographical area. Average distance between sampling unit means tends to increase towards both ends of the cline, especially at the southern and southwestern ends of the species' breeding range (peninsulas and islands, Figs. 1, 4).

The North African sampling units, in marked contrast, show larger average distance between sampling units and gaps between distinct morphological groups (Fig. 4). Specimens from the Maghreb (Algeria [NA1], Morocco [NA2], Tunisia [NA3]; part of cluster A, Fig. 4) are similar to the specimens from the middle part of the Eurasian cline (western pericontinental and south continental specimens, all included in cluster A). Their body size is smaller than average, whereas bill, tarsus, and first primary are

of average size. The North African specimens from Libya (sampling unit CY) and from the two eastern Canary Islands (CA6, CA7; Fig. 6) (clusters F and G on Fig. 4) have a small size, a thin but rather long bill, and rather long tarsus and first primary. Finally, the North African specimens from the 5 western Canary Islands (CA1 to CA5, Fig. 6; cluster E, Fig. 4) are slightly smaller than average, like those of the Maghreb, but are characterized by a long, rather thin bill and long tarsus and first primary.

#### VARIATION IN PLUMAGE PATTERN

The first principal component summarizes 32.9% of the variance (Fig. 2b). There is a marked gap between PC1 and PC2 (15.9% of the variance). The decrease in variance summarized by PC2 to PC7 shows no marked gap.

*Correlation circle analysis.*—Characters GBAK

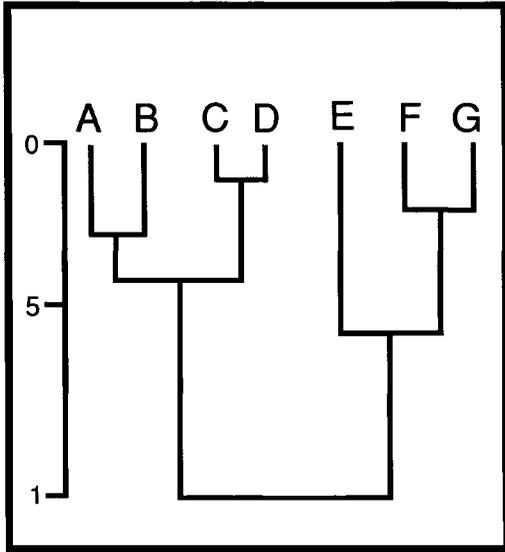


Fig. 5. Hierarchical tree linking the classes of samples defined by cluster analysis. Sample classes are defined in Figure 4.

(amount of green on the back, GNEC (width of the gray neck ring) (see Appendix), WBAR (wing-bar width) and SWPA (width of the white patch on the first secondaries) are correlated with PC1 (Fig. 7).

A second set of characters is correlated with PC2. They are WBEL (the amount of white relative to yellow on the belly), FHPT (the width of the white patch on the forehead), BBEL (the size of the black patch in the middle of the belly) and the size of the white patch on the tail tip (TWPA). One character, BNEC (width of black neck ring), shows low correlations with both PC1 and PC2.

*Between sample segregation by PCA.*—Principal component one (Fig. 8) segregates the 54 sampling units into two distinct subgroups. The first group, with mostly negative scores, includes all Eurasian specimens, characterized by the presence of a gray neck ring, higher values for the proportion of green on the back (close to 100% for all these specimens), and broader wing bars and more white on secondaries. The second group (positive scores on PC1) includes the specimens of all North Africa. They are characterized by the absence of the gray neck ring, little or no green on the back (which is essentially slate gray except for the specimens of Hierro [Fig. 5] for which the slate gray feathers are tipped with green), narrower wing bars, and less white on secondaries.

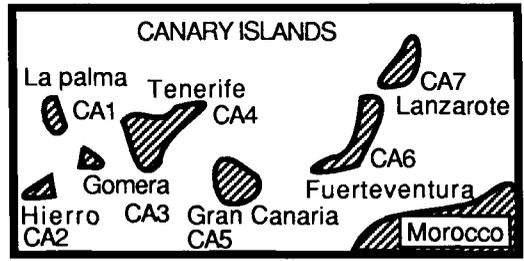


Fig. 6. Map of the Canary archipelago with name and symbol for each island.

Principal component two segregates the Eurasian specimens along a geographical cline going from eastern Europe (negative scores; E1, E2), to southwestern Europe (positive scores; MI2 to MI5, SW2). There is a progressive decrease of the proportion of white on the belly, the size of the white forehead patch and, to a lesser extent, the black markings on the belly, the wing-bar width, and the amount of white on the secondaries from east-northeast towards south-southwest. In the easternmost samples, the tail features are narrowly tipped with white. This clinal distribution has a gap between specimens from continental southern Europe (S3, S5, SW1) and specimens from the large Mediterranean islands (MI2, MI3, MI5) and southern Iberian peninsula (SW2). The four exceptions to this pattern are the specimens from the Balearic islands (MI1; Fig. 1), the Elburz region

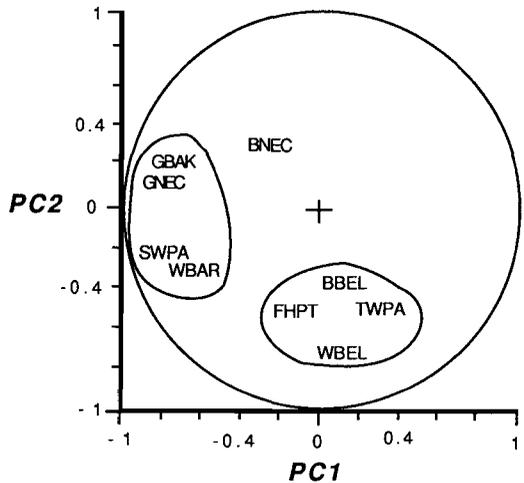


Fig. 7. Coordinates of the plumage-pattern characters on the PC1-PC2 correlation circle obtained in the principal component analysis on plumage-pattern characters. For the definition of the symbols see Appendix.

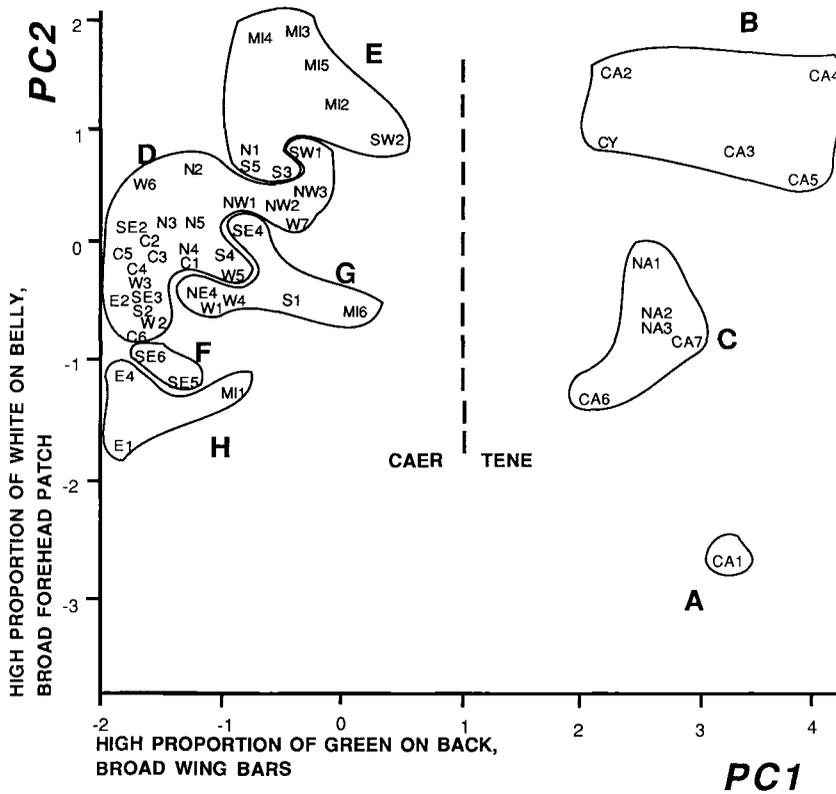


Fig. 8. Mean coordinates of the specimens for each of the 54 sampling units in the PC1-PC2 plane of the principal component analysis performed on the nine plumage-pattern characters. Symbols refer to the sampling units defined in Figure 1; letters A-H refer to the sample classes (envelopes) defined by cluster analysis. The broken line separates the two main population groups defined by Vaurie (1957) (CAER = *caeruleus* group, Eurasia; TENE = *teneriffae* group, North Africa).

(SE4; Fig. 1), the Greek islands (MI6; Fig. 1) and western Turkey (S1; Fig. 1).

In contrast to the Eurasian condition, North African sampling units (positive scores on PC1) were separated into three clear-cut groups by the cluster analysis (Fig. 8). The sample from La Palma (CA1; cluster A) in the Canary Islands represented a phenotypical extreme of extensive white on the belly and white patches on the tail tip. The other phenotypical extreme, cluster B, includes specimens from Hierro (CA2, one of the islands geographically closest to La Palma [CA1]), from Cyrenaica (CY) in Libya (the most distant north African population from La Palma), and from the three central Canary Islands (CA3 to CA5). These specimens have deep yellow bellies with little or no white, and tail tips with very little or no white. The third North African group (cluster C) has an intermediate position and includes the specimens from the

Maghreb (NA1 to NA3) and from the two easternmost Canary Islands (CA6, CA7).

The hierarchical tree (Fig. 9) linking the eight clusters defined by cluster analysis (Fig. 8) segregates the Eurasian (classes D to H) from all except one North African sample (classes B and C; Fig. 9). The exception (class A) is the birds of Palma, which have characters typical of North African populations and characters present in the easternmost samples from the Eurasian group (class H on Fig. 9)

## DISCUSSION

### GEOGRAPHICAL VARIATION IN MENSURAL CHARACTERS

*Variation in body size.*—Clinal size variation among Eurasian samples on PC1-PC2 (Fig. 4) is consistent with Bergmann's (1847) ecoclimatic

rule, which states that homeotherms have an increased body size with increasing latitude. This may be related to heat economy (see maps of temperature isotherms in January, *Times Atlas of the World* 1967). The ecological significance of Bergmann's rule is widely debated (James 1970, McNab 1971, Murphy 1985, Zink and Remsen 1986). James (1970) and Murphy (1985) suggest that intraspecific size variation in homeotherms can be related to a combination of climatic factors that include temperature and moisture. In this case small size is associated with hot humid conditions, larger size with cooler or drier conditions.

Data that fit Bergmann's rule (Snow 1954b, for parids) might also be explained by Geist's hypothesis that relates latitudinal size increase in homeotherms to a latitudinal increase in the seasonal resource peak in phase with the growing period of the offspring (Geist 1987). According to Geist, the seasonal peak increases from 0° to 60° latitude and decreases thereafter. The smaller size of Blue Tits in the Mediterranean is consistent with Geist's hypothesis. Indeed Cramm (1982) and Clamens (1987) have shown that the resource peak used by Blue Tits to raise their young is lower in evergreen Mediterranean broad-leaved forests than in deciduous broad-leaved forests. Together with results of long-term field studies (Blondel et al. 1987, Clamens and Isenmann 1989), this suggests that there is a relationship between the lower spring resource peak in evergreen Mediterranean habitats and the smaller adult size of Blue Tits in these habitats. Adult size decrease is strongest in populations in evergreen habitats geographically isolated from populations living predominantly in deciduous habitats (Martin and Bellot 1990). The smallest Blue Tits are found in the most arid regions of North Africa, which could result from even lower levels of available resources in these habitats. The contribution of environment and genetics to size variation remains an open question.

*Variation in bill and leg dimensions.*—Vegetation structure and prey types are essential elements in the process of morphological adaptation to foraging. In addition to the relationship between bill size/shape and prey size/shape or between wing shape and flight, parids that forage in broad-leaved trees have stouter bills than those in coniferous habitats (Snow 1954a, 1955; Lack 1971). Further, the length of the tarsus relative to body weight is related to the struc-

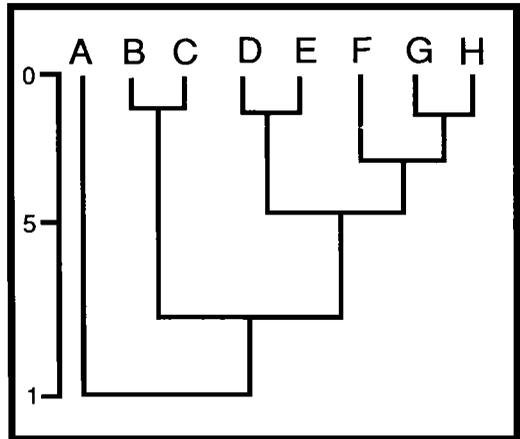


Fig. 9. Hierarchical tree linking the classes of samples obtained by cluster analysis. Classes A-H are defined in Figure 8.

ture of the perching substrate (Grant 1971). A longer tarsus is associated with stable perches, a shorter tarsus with unstable perches.

The thinner bill in Mediterranean Blue Tit populations could be related to the progressive change from habitats dominated by deciduous trees (smooth foraging substrate) in the northeastern part of the species' breeding range to habitats dominated by evergreen trees (harsh foraging substrate) in the southwest of the range (see map of natural vegetation types in *The Times Atlas of the World* 1967). Differences in wing shape, bill dimensions, or tarsus length between North African populations may similarly be linked to differences in the general structure of the habitat (e.g. broad-leaved versus coniferous woodlands). In this context the segregation observed between the different sampling units from the Canary Islands is informative. The specimens from the two driest islands (Lanzarote and Fuerteventura, where the tits nest in semi-arid habitats [Bacallado 1976] and especially in *Tamarix canariensis* woods [Bannerman 1963]) group with those from Libya (Figs. 4 and 5). In Libya, Blue Tits also live in semi-arid habitats dominated by short-leaved trees or bushes (*Juniperus* woods [Bundy 1976] but also historically cypress and pine [Hartert 1923]). In contrast, the Blue Tits from the middle Canary Islands breed mainly in *Pinus canariensis* (a long-leaved pine) and in laurel forests dominated by *Visnea mocanera*. In the outer islands the birds are restricted almost completely to pine woods (Lack and Southern 1949, Cullen et al. 1952,

Hemingsen 1963, Grant 1979). Accordingly, the Blue Tits of the middle and outer Canary Islands have the longest tarsus and the longest and thinnest bills within the species. Indeed, the more a population is restricted to pine the longer the bill and tarsus (PC1, Fig. 4; see also Grant's (1979) analysis of ecological and morphological variation of Canary Island Blue Tits).

Lack and Southern (1949) suggested that the longer and thinner bill of the Blue Tits from Tenerife was the result of convergence towards the morphology of Coal Tits (*Parus ater*). However, Partridge and Pring-Mill (1977) rejected the convergence hypothesis on experimental grounds. Together with Snow (1954a), they attributed the increase in bill and tarsus length in the Canarian Blue Tits to Allen's rule. This rule claims there is a decrease in the extremities of homeotherms as latitude increases, an observation also explained by body temperature regulation. Allen's rule seems an unlikely explanation. Indeed, the increase in bill and tarsus length from mainland North Africa to the outer Canary Islands (Fig. 4) can hardly be related to latitudinal effects because the difference in latitude between the Canary Islands and the nearest African populations is less than 2 degrees, and among the Canarian populations this difference is less than 0 degrees.

The hierarchical tree that links the clusters of sampling units (Fig. 5) displays strong consistency between overall sample similarity and similarity in habitat. Group one (clusters A to D) contains the groups that forage on broad-leaved trees (deciduous or evergreen). All samples from populations that forage in evergreen broad-leaved trees fall in either cluster A or B. Group two (clusters E to G) comprises birds that forage either on narrow-leaved trees such as *Tamarix*, *Juniperus*, and cypress (clusters F and G), or more or less exclusively on long-needled trees (*Pinus canariensis*) (cluster E).

*The role of geographical isolation.*—In both Eurasian and North African population groups, there is a relation between sudden changes in body-part dimensions (gaps on Fig. 4) and geographical isolation. The importance of isolation in the emergence of geographical variation in parids was pointed out by Snow (1954a). He suggested that the range of biotypes used by the Maghreb populations is larger than that of populations of southern Europe because the lack of geographical isolation has prevented the populations from Mediterranean Europe from

fully adapting to Mediterranean biotopes. This interpretation is strengthened by the observed increase in biotopes used by Blue Tits on Corsica where they are common breeders in matorrals (Blondel 1981, 1985; Martin 1982; Blondel et al. 1988).

*Consistency with taxonomy and phylogeny.*—There is little consistency between the classification of the samples based on similarity in mensural characters (Fig. 5) and the classification proposed on the basis of plumage characters (e.g. Vaurie 1957). The dichotomy between Eurasian and North African population groups based on plumage color does not appear in my analysis of mensural characters (Figs. 4 and 5). The specimens from the Maghreb group with these from Eurasia (Fig. 4, cluster A; Fig. 5).

Further, mensural character similarity can be greater between geographically distant populations that face similar ecological conditions than between geographically close populations subject to different ecological conditions (Chernoff 1982, Dillon 1984). The resemblance between the Maghreb birds and populations from southwestern Eurasia, despite their probable different phylogenetic history, is an example. The similarity of the birds from Cyrenaica to the geographically distant specimens from the inner Canary Islands is another example of apparent morphological convergence. The hierarchical classification of the sampling units (Fig. 5) splits the sample into two main groups of clusters according to environmental similarities and independent of the probable phylogeny.

#### GEOGRAPHICAL VARIATION IN PLUMAGE PATTERN

In Eurasia geographical plumage-pattern variation (Fig. 8) is consistent with the known variation in plumage color (Snow 1954b, 1955). Snow (1954b) evoked climatic variation to explain geographical variation in plumage coloration in the Blue Tit (and in parids in general). In arid climates with cold winters birds are paler and grayer on the back and have less yellow pigmentation. They are darker and of brighter color in warm wet climates. In accord with this explanation the extent and purity of white markings increases from wet warm climates to arid climates with cold winters. The peculiarities of the Elburz specimens (SE4) could be related to the wetter climate of this area. Variation in plumage pattern in Eurasia is essentially clin-

al and no gaps appear (Fig. 8) that relate to the subspecies defined by Vaurie (1957).

The question whether geographical variation is adaptive or the consequences of nutritional factors on the process of pigmentation remains open. For example, Mediterranean Blue Tits reared in captivity have reduced yellow pigmentation (pers. obs.). Nongenetic variation in plumage color in relation to habitat and diet has also been documented for the Great Tit (*Parus major*) (Slagsvold and Lifjeld 1985). Changes in coloration have also been reported due to increased bleaching of the carotenoid pigment in the tropical magpie *Cissa* living in open habitats when compared with populations of dense forests (Vevers 1985).

In the North African populations (*teneriffae* group; Vaurie 1957), the basic color pattern follows the general trend of darker birds in the southwest of the species range (Gloger 1933). However, the change in plumage-color pattern across the Strait of Gibraltar is dramatic and is not paralleled by any equivalent change in ecological conditions.

Among North African populations various isolates differ in such characters as the presence or absence of white wing bars, the presence or absence of white on the belly, or the presence or absence of a green wash on the back. Each geographical isolate or group of adjacent isolates is characterized by certain features used by taxonomists to identify subspecies. These features appear independent of those observed in neighboring populations and unrelated to climatic or environmental determinants. For instance, cluster analysis groups specimens of the driest Canary Islands with those from the Maghreb. Alternatively the specimens from very dry Cyrenaica are more similar to those from the wetter middle and outer Canary Islands (except for Palma). Clusters A, B, and C (Fig. 8) include sampling units that belong respectively to one subspecies (CA1), two subspecies (NA1, NA2, NA3 and CA6, CA7) and three subspecies (CY; CA2; and CA3, CA4, CA5).

I believe that plumage-pattern variation shows that the general differences observed between North African and Eurasian samples directly reflect phylogeny (i.e. they are due to the divergence of two genetically isolated population groups). Secondly, variation within the Eurasian group is essentially linked with clinal change in local conditions. Differences may rest on genetic differences or result from different

responses of similar genotypes to different environments. Such variation may be enhanced in its genetic component by geographical isolation (on the large Mediterranean islands for instance). Finally, variation within the North African group is mainly linked to genetic drift within each of the isolates or group of adjacent isolates. Similarities in coloration on the basis of phylogenetic relationships alone seem unlikely because of the lack of consistency between geographical proximity and similarity in plumage pattern (Figs. 8 and 9).

#### RELEVANCE TO BIOSYSTEMATICS

In theory, two biosystematical interests can be served by this kind of study. One is to diagnose phylogenetic relationships between populations. The second is to use the analysis of the present variation as a pattern to illuminate the geography of speciation. Principal components analysis of mensural characters shows that the data presented better reflect ecology than population phylogeny. Principal components analyses of plumage pattern could do no more than substantiate phylogenetic segregations that were already clear from the general differences in coloration between North African and Eurasian populations. More satisfactory answers in phylogeny will necessitate biochemical analyses (reviews of Zink and Remsen 1986, Hillis 1987).

More positively, my results substantiate the importance of the unifying effect of gene flow between adjacent nonisolated samples even over a large geographical area. Its corollary that geographical isolation is necessary to make possible the appearance of gaps in clinal variation or of markedly different population characteristics was strongly supported. Such studies, especially if supplemented by knowledge of the biology of the species, can lead to a better understanding of the evolutionary implications of a species' population structure and of its geographical, environmental, and historical determinants.

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APPENDIX. Definition of the mensural and plumage pattern characters measured. 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 definition
<b>Mensural characters</b>	
I BILL	Bill length
BILH	Bill depth
II WINL	Wing length
GCWT	Greater covert tip to wing tip
GCP1	Greater covert tip to 1st prim. tip
PR1L	First (outermost) primary length
PIP2	First primary tip to 2nd primary tip
P2WT	Tip of 2nd primary to wing tip
III TAIL	Tail length
IV TARS	Tarsus length
MTON	Length of middle toe nail
HTOE	Length of hind toe
HTON	Length of hind toe nail
<b>Plumage pattern</b>	
I FHPT	Width of forehead white patch
WBAR	Width of wing bar
SWPA	Width of the white patch on tail tip
II BBEL	Size of the black patch on belly
WBEL	Proportion of white breast & belly
III GNEC	Width of gray neck ring
BNEC	Width of black neck ring