

INTRASPECIFIC GEOGRAPHICAL VARIABILITY OF BEHAVIOR: AN EVOLUTIONARY REVIEW

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ABSTRACT - This paper aims to show that not only genetically determined characters, but also characters inherited at behavioral and social levels have geographical distribution, that their distributional patterns and histories have certain regularities, and that they may be studied by methods developed in biogeography. Relevant terminology is discussed and examples are given.

KEY WORDS: Biogeography, Behavior, Distribution of Behavior

INTRODUCTION

There are many kinds of intraspecific variability, and most of them have been carefully studied by evolutionary biologists and systematists during last decades (see, e.g., Rensch 1929, Lukin 1940, Mayr 1963, Endler 1977). The reasons for such an interest consist apparently in difficulties which the phenomenon of intraspecific variability has been causing to the current paradigm in the theory of biological species (see Mlíkovský and Zemek 1983), which is one of the key points of evolutionary biology.

The study of intraspecific variability is, as any study of course, influenced by the respective underlying theory, which has been the so-called synthetic theory of evolution (neo-Darwinism) in this case. Due to the reduction of evolutionary phenomena to the population-genetic level in this theory, most of the pertinent research was devoted to the study of the genetically, or supposedly genetically, determined characters. Recent advances in genetics and epigenetics have shown, however, that this approach is untenable, because neither the gene, nor its expression are as simple as believed by the proponents of neo-Darwinism (see, e.g., Zemek 1983, Zemek et al. 1985). As a consequence of these findings, the

concept of multilevel heredity was recently elaborated (Zemek et al. 1985), in which the term heredity is understood broader than in neo-Darwinism and includes also hereditary transmission of information through the behavioral channel (see Zemek et al. 1985, Mlíkovský and Zemek 1986, and Zemek and Mlíkovský 1986 for details and further references).

The present paper will focus on only one of the problems relevant to the evolutionary diversity of animal behavior, namely on intraspecific geographical distribution of behavioral characters and patterns. Two basic sub-problems may be distinguished here: (1) distribution of individual learned characters, or *memes* in Dawkins' (1976) terminology, and (2) distribution of whole pools-of-knowledge. In the frame of both these sub-problems, either stationary distributional patterns, or their dynamics (including processes leading to it) may be studied. Combining these two classification criteria, we obtain four basic problem fields relevant to the distribution of behavioral characters, which are discussed below.

PATTERNS OF MEME DISTRIBUTION

Initially, patterns of the meme distribution have been recognized by European bird keepers in the song of several bird species, particularly in the Chaffinch *Fringilla coelebs*. They were later studied on a scientific basis and termed *dialects* (Promptov 1930, Sick 1939, and many others -- see Thielcke 1969, Krebs and Kroodsma 1980, and Mundinger 1982 for current reviews). This term, borrowed from human linguistics, where it was already then in common use (see, e.g., Bloomfield 1933, Pop 1950, Hall 1964), has been since then used for geographic variants in all vocal signals in both non-human animals and man. More recently, some authors attempted to give it a more general meaning, extending it on all acoustical signals (Payne 1973), or on all displays used in communication (Wilson 1975: 582). In a previous study (Mlíkovský 1979), I suggested to define dialects as geographical variants of any learned trait. I believe that such an extension of the term dialect is more readily acceptable than an equivalent term *pegmatype* proposed by Kalmus and Smith (1966).

The methods and scope of the study of meme distribution need not be analyzed here in more detail, because they are obviously quite analogous to methods and scopes of the so-called gene geography (Serebrovskij 1929, Timofeev-Ressovskij et al. 1977, pp. 168-173), and phene geography (Jablo-

kov 1980). Note, that just like as in the case of genes and phenes, memes need not be geographically exclusive (cf. also Peitzmeier 1942). Good examples are the preference for breeding habitat in the Ring Dove *Columba palumbus* in Europe (Tomiałojć 1976), or song dialects in the Great Tit *Parus major* in Fennoscandia (Bergman 1980).

DYNAMICS OF THE MEME DISTRIBUTION

Analyzing the dynamics of meme distribution, we have to note that the origin of a meme (i.e. its discovery) seems always be the work of a single individual (organism) and, therefore, that any meme has initially a point distribution. Via imprinting and/or learning this particular meme may become still more and more distributed in the population to which the respective discoverer belongs. The tempo and mode of the spread of memes is determined by the so-called social selection (West-Eberhard 1983), by the ability and efforts of individuals to take them over (see e.g., Kawamura 1959, Myiadi 1959), and by what human linguisticians call frequency or density of communication (Bloomfield 1933, Hall 1964). The spread of memes has been well exemplified in various birds and mammals. The examples are the knowledge of a specific food type in the Japanese Macaque *Macaca fuscata* (Kawamura 1959), or in the Greenfinch *Carduelis chloris* (Pettersson 1956, 1961), the knowledge of a specific type of feeding behavior in the Blue Tit *Parus caeruleus* (Fisher and Hinde 1949, Hawkins 1950, Hinde and Fisher 1951), or the preference for breeding habitat in the Ring Dove *Columba palumbus* (Tomiałojć 1976).

PATTERNS OF THE POOLS-OF-KNOWLEDGE DISTRIBUTION

Using appropriate statistical analysis, we may find that distributional patterns of individual memes often correlate with one another. It follows from this observation that certain inter-correlated sets (or pools) of memes exist in nature. Mathematically, they may be best understood and described as fuzzy sets (sensu Zadeh 1965) of memes. These groups are since ever known in man, where the pool-of-knowledge common to a certain subpopulation is usually called *culture*, and the group characterized by a common culture generally known as *ethnos* (see Bromlej 1983), or *nation* (autorum). In non-human vertebrates, equivalent groups were initially discovered in several bird species during 1930s in Great Britain (Huxley 1938, 1939),

and in Germany, where there were denoted with German terms *Stammesgenossenschaft* (Schiermann 1939), and *Sippe* (Stresemann 1943). Other terms referring more or less to such groups are *biological species* (Cholodkovskij 1910; not autorum), *natio* (Semenov-Tjan-Šanskij 1910), *ecological subspecies* (Alpatov 1924), *biotypic form* (Svårdson 1949), *microsubspecies* (Blaxter 1958), *ecological race* (e.g., Morel 1969), *ecological form* or *ecoform* (see Nikol'skij 1980), and *biological race* (see Severcov et al. 1983). Most of them, however, with the notable exception of the *Stammesgenossenschaft* (Schiermann 1939; see also Peitzmeier 1939, 1942, 1949), were introduced in belief that characters considered in respective studies were all genetically determined, what often turned out to be not the case. Unfortunately, none of these terms is now -- for most various reasons -- suitable for international use. Moreover, researchers in the so-called social sciences would certainly not agree if I would apply the terms culture and ethnos to non-human beings. I will, therefore, suggest the terms *bio-culture* and *bio-ethnos* for the use in them.

If culture, or bio-culture, change not more or less abruptly, but gradually, we may speak of *ethoclines* (Johnsgard 1972). This term was coined by analogy to the Maslin's (1952) term morphocline, and is a special case of phenoclines proposed by Brand et al. (1973).

DYNAMICS OF THE POOLS-OF-KNOWLEDGE DISTRIBUTION

The distribution of any pool-of-knowledge (culture does not differ from bio-culture in this respect) changes in time. These changes are quite analogous to changes in the distribution of taxa which have been thoroughly analyzed by biogeographers. This is not surprising, because gene exchange seems obviously to be statistically highly correlated with meme exchange (cf., e.g., Ruyle 1973). Respecting the terminology of biogeography, we may call the range of distribution of a culture or bio-culture an area, and the changes in the area's extension spread, regression, and oscillation, respectively. These terms are understandable by common sense. Examples for these changes may be best taken from ethnology. A spread of a culture is well exemplified by the westward spread of the Mongolian culture during the 12th-15th centuries (Tot and Firštejn 1970, Saunders 1971), or the spread of Christianity in Kazakhstan (Tursunbaev 1950). On the other hand, a regression of a culture can be, perhaps, best exemplified by the regression of the Aztec culture (Vaillant 1965, Davies 1980).

CONCLUDING REMARKS

The methods and scopes of the geographical analysis of the distribution of behavioral characters are analogous to those of the classical biogeography which deals with the distribution of taxonomic and ecological groups. This paper aimed to clarify these analogies and to define some relevant terms.

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