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Evolutionary Significance of Geographic Variation: Some Examples From Birds

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INTRODUCTION

The study of geographic variation has probably taken up a well-known place in ornithology. For decades, most of researchers interested in evolutionary trends in birds focused on the study of geographic variation (e.g. Morrison 1983, Zink 1986, Atwood 1988, Johnson and Marten 1992, Johnston 1994, Roselaar 1995, Engelmoer and Roselaar 1998, Johnson 2002).

Study of the geographic variation in birds usually focused on morphologic variation, and the insights from the morphologic variation were used to solve the taxonomic problems (Johnson and Marten 1992, Escalente-Piliego and Peterson 1992, Johnson 2002). In addition to taxonomic problems, some other researchers of geographic variation in birds have also interested in the geography of intrapopulation variability to test ecological importance of morphological variation (James 1970, Aldrich 1984, Grant and Grant 1986, 1989, 2008, Kaboli 2007).

Thus, it is plausible to say that geographic variation is one of the most famous study topics in evolutionary biology. In this mini review, I concentrate on two main topics – taxonomy, and adaptation and speciation – and their relationships with geographic variation.

1. Solving taxonomic problems: Subspecies limits.

In general, each individual of animal or bird species can be recognized by us with using the specific characters (e.g. morphologic, voice and behaviour). Certainly, many species show geographical variation because of geographic barriers, which cause differentiation. Thus, one population of the species may differ slightly from another population of same species. Differences between both populations become increasing with time. It is possible to say that, therefore, it is essential to show patterns of character variation to understand the evolutionary process that cause geographic differentiation.

Biological Species Concept, which is usually accepted in ornithology (Zink and McKitrick 1995), was suggested under this perspective and is based on species being reproductively isolated from each other (Mayr 1942). Regarding to birds, differentiation between populations to evidence for speciation is widely accepted for resident bird species than migratory bird species. Gene flow in relation to

reproductive isolation is more restricted in different populations of resident species. As a result of the geographic differentiation, therefore, distinctive geographic forms are described as subspecies.

The problems about taxonomic inferences:

In ornithology, description of geographic variation based on geographic differentiation within and among populations was addressed taxonomic problems, especially subspecies limits (Brumfield and Remsen 1996, Massey 1998). However, geographic variation studies based on morphological variation clearly indicate that some taxonomic inferences are weak and probably not real. Regarding the problem, I reviewed number of examples:

Example 1.

Pied kingfisher (*Ceryle rudis*) subspecies from Turkey

A good example s is a subspecies of pied kingfisher (*Ceryle rudis*), described from Turkey. Roselaar (1995) described a new subspecies, *syriaca*, from Turkey (İzmir and Antalya). Populations from Cyprus, the Levant, Iraq and Iran have smaller measurements than Turkey locations. This suggestion was strongly refused by Kasparek (1996), because Bergmann's rule proposed increasing body size and/or its elements in northern latitudes. This minor variation is unwarranted at nomenclatural level.

Example 2

Greenfinch (*Carduelis chloris*) subspecies from Turkey

Roselaar (1995) listed 4 subspecies from Turkey for greenfinch (Figure 1). The description of the subspecies based on external morphologic characters without any statistical inferences. Albayrak (2007) revisited subspecies pattern of greenfinch and refused this suggestion, because any significance morphologic diagnosabilty between populations in Turkey was not found. Greenfinch populations in Turkey have little morphological variation. As stated above, the variation is not diagnosable and not important at nomenclatural level.

Example 3

House sparrow (*Passer domesticus*) subspecies from Turkey

Roselaar (1995) listed 5 subspecies from Turkey for house sparrow (Figure 2). Description of subspecies was stated as difficult to summarize, because most birds from Turkey were closely similar according to general color. Only birds from north-west and nort-east are clearly darker in general color of plumage. However, according to surveys, which I made recently, in north-west and north-east Turkey indicated that there is no difference according to color pattern than southern Turkey (unpublished data). According to Roselaar (1995), moreover, morphologic measurements did not give any significant pattern for subspecies differentiation. Thus, the variation is not diagnosable and not important at nomenclatural level.

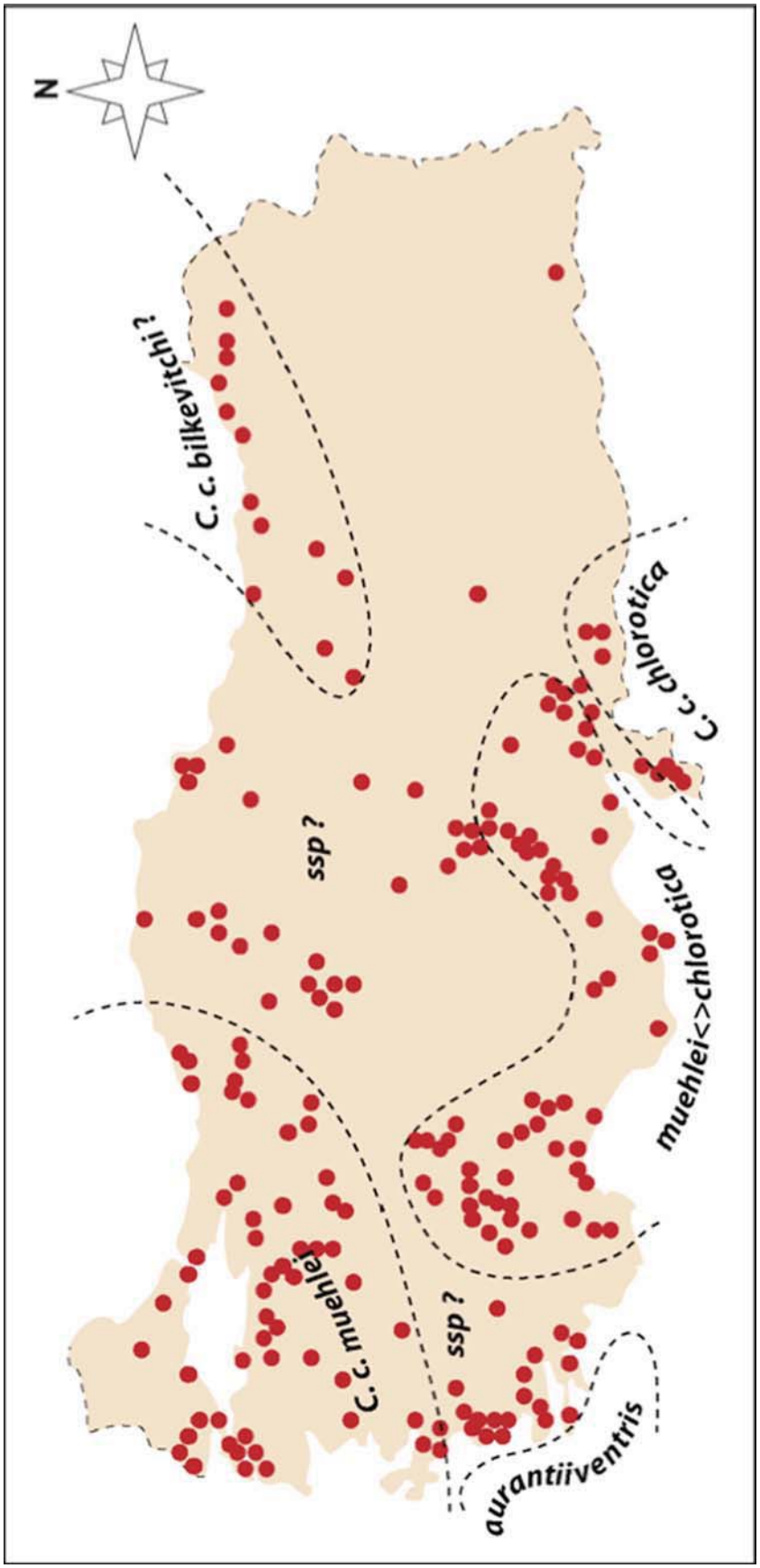

Figure 1. Possible subspecies of greenfinch (*Carduelis chloris*) suggested by Roselaar (1995). Red dots indicate breeding localities and lines indicate possible subspecies border.

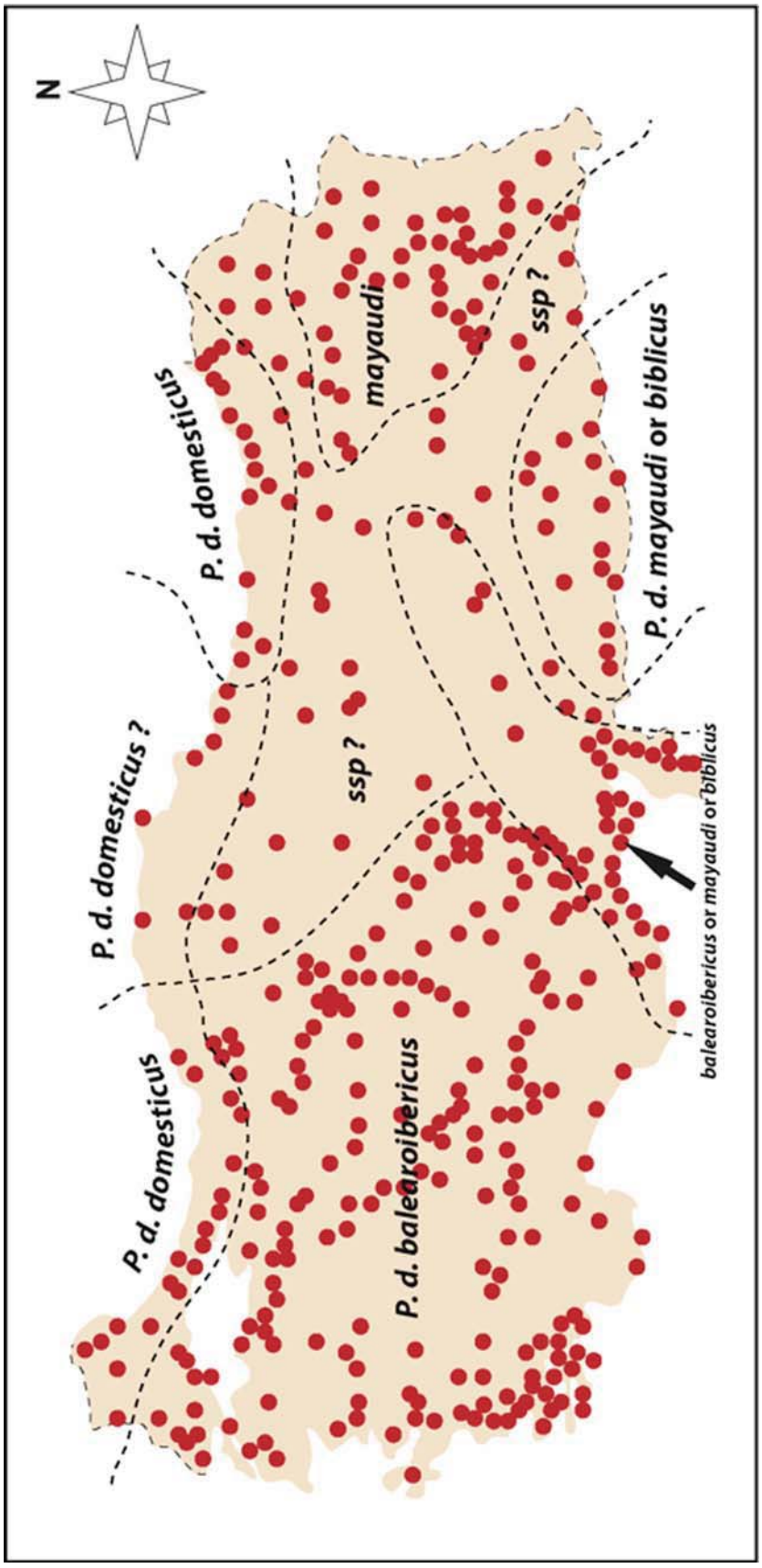

Figure 2. Possible subspecies of house sparrow (*Passer domesticus*) suggested by Roselaar (1995). Red dots indicate breeding localities and lines indicate possible subspecies border.

The validity and utility of subspecies is a continuous subject of argument in systematic ornithology. A set of important commentaries was published more than two decades ago in the Auk and authors discussed the validity of the subspecies (Barrowclough 1982, Gill 1982, Johnson 1982, Lanyon 1982, Mayr 1982, Storer 1982). Like the examples, subspecies frequently mislead the taxonomy. Certainly, its border and description are not recognizable. Beside morphological data, therefore, subspecies rank must be discussed in the light of molecular data to robust taxonomic inferences.

2. Natural selection, Adaptation and Speciation

Nothing in evolutionary biology makes sense except in the light of ecology (Grant and Grant 2008).

The importance of geographic variation studies is also based on adaptation as a result of natural selection. This issue characterized many ornithological works. Because character variation is assumed to be produced by adaptation. Therefore, natural selection is an important issue to understand the causes of geographic variation patterns. The good example on natural selection pattern in the geographic variaiton studies is on the morphology of Galapagos finches (Grant and Grant 1989). Peter Grant and his colleagues have discussed a major problem in evolutioanry biology, why populations show variation in morphological, ecological, behavioral traits. They documented natural selection and its effect on the morphology of Galapagos finches. They showed that the natural selection causes morphological variation. Therefore, one of the important causes of geographic differences is the natural selection. Darwin's Finches in Galapagos Islands gave some important insights to understand how species differentiated. In especially their last review on the Galapagos finches, they set out their studies to explain the adaptive radiation of finches from different perspectives (e.g. geographic, behavioral, genetical and ecological). Among these perspectives, ecological perspective seems the most important one, because it shapes mostly the morphologic variation pattern. The good example on that is environmental changes in Galapagos Islands. Because of climatic conditions, some good opportunities may appear for new species in the islands. So, new species may colonize one of the islands (e.g. Ground Finch, *Geospiza magnirostris*), and species established a breeding population. Then, because of the major climatic event (e.g. El Nino), population may experience a genetic bottleneck due to founder effects and inbreeding. Therefore speciation may start with this event. In this example, effect on natural selection on morphologic variation and therefore speciation process can be understood.

Charles Darwin indicated that adaptation process is formed all through the natural selection. Patterns of geographic variation in morphology are usually described by adaptation, via natural selection. On the other hand, ecologic interactions may characterize the variation pattern on morphology (e.g. adaptive radiation). Therefore, the power of ecologic process in natural systems should be taken in to account to understand the evolutionary significance of geographic variation.

Win-Win Conclusion

Ecologic interactions are usually shape the geographic variation pattern on morphology in birds. Therefore, lost of subspecies based on morphologic variation have been suggested for birds. For example, Roselaar (1995) suggested 156 subspecies for non-passerine birds in Turkey according to morphology. This is huge numbers for a country. The most probably geographic variation pattern based on morphology is usually affected by biotic and abiotic factors, and therefore it may be a good evidence for natural selection. Otherwise, the geographic variation pattern on morphology may not be important at nomenclatural level as I state above. Therefore, taxonomic inferences based on geographic variation of morphology (e.g. describing subspecies, determining subspecies limits) must be made cautiously, and should be supported by molecular markers.

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