

Overestimation of vocal characters in Suboscine taxonomy (Aves: Passeriformes: Tyranni): causes and implications

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Abstract

The difference in treatment of vocal features in Oscines and Suboscines passerine birds characterizes a large portion of the current studies on their taxonomy. In the former taxon, vocalization is supposed to be molded by learning, and consequently is not regarded as taxonomically informative. In the latter, a strong emphasis is given to vocalization because it supposedly reflects the genetic structure of populations. This paper reviews the various assumptions related to this difference in treatment, including the overestimation of the vocal characters in suboscine alpha taxonomy due to the alleged importance of vocalization under the framework of the species mate recognition system. The innate origin of suboscine vocalizations remains to be rigorously demonstrated and the use of vocalization as “super-characters” is prejudicial to bird taxonomy. Despite the possibility of being learned, vocalization should also be used in the taxonomic studies of oscine passerines.

Keywords: Vocalization, Oscines, Suboscines, Birds, Passeriformes

Introduction

Vocalization has been widely used in taxonomic studies of suboscine passerines and recent proposals (Isler et al. 1998, 1999) have contributed to the development of methods to analyze the structure of vocal characters. Despite the importance of the development of this practice, the foundations and the consequences of using vocalization to establish species limits in birds are seldom discussed.

This paper intends to review the utilization of vocalization in suboscine taxonomy and to establish a critical view of its conceptual parameters. It reviews the two main assumptions of current methods used to establish species limits in Suboscines: the innate origin of vocalization in this taxon; and the greatest efficiency of vocal characters to the taxonomy of these Passeriformes. The paper also proposes an alternative methodological approach to the taxonomic use of vocal characters.

BACKGROUND

Innate vocalizations

Many oscine passerines have the capacity of developing microgeographic variations of song called dialects (Kroodsma, 1994) and many experimental studies have shown that there is a strong correlation between these variations and the presence of learning ability within the group (Thorpe, 1958; Marler & Isaac, 1960; Baptista, 1975; Lemon, 1975; Gill & Murray, 1972; Nottebohm, 1972; Kroodsma, 1977, 1981; Lein, 1978; Lanyon, 1979; Falls, 1982; Weary et al., 1990). As a result, the

dialects within Oscines are thought to be a cultural phenomenon.

As regards Suboscines, studies on species of the genera *Empidonax* (Johnson, 1980; Payne & Budde, 1979) and *Myiarchus* (Lanyon, 1978) have shown that these species do not exhibit well marked geographical variation in vocalizations. Experimental studies (Kroodsma, 1982; Kroodsma & Konishi, 1991) also showed that *Empidonax alnorum*, *E. traillii* and *Sayornis phoebe* are incapable of song learning. In these studies, the authors analyzed the repertoire development in captive individuals. Furthermore, some studies of suboscine cerebral structure indicate that members of this group seem to lack the brain control centers which are responsible for controlling feedback learning mechanisms in Oscines (Brenowitz & Kroodsma, 1996). These conclusions have been extrapolated to all suboscine passerine families which are considered to be unable to develop dialects due to their inability to learn, an ability considered important to generate the kind of geographical vocal variation present in the Oscines (Kroodsma, 1982, 1984).

This way of thinking can be found, for example, in the affirmations of Krabbe & Schulenberg (1997: 50-51) “[...] vocal characters are entirely inherited in *Scytalopus*. Although the latter assumption has not been demonstrated specifically for tapaculos, it may be true of all sub-oscines (Kroodsma, 1982, 1984)” and “... as is typical of most Suboscine Passerines, vocalizations generally show lack of plasticity over geographic distance”.

Thus, a clear polarization has been established in the interpretation of vocalizations in the order Passeriformes and, consequently, in the taxonomic treatment of song features in Oscines and Suboscines. In the former, with some exceptions (e. g. Payne, 1986), vocalizations are supposed to be molded by learning, and consequently are not regarded as taxonomically informative. In the latter suborder, a strong emphasis is given to

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the vocalizations because they supposedly reflect the genetic structure of populations.

From these generalizations it has been inferred that the homogeneity in syrinx structure in Oscines, when compared to the extensive syringeal variation in Suboscines, is related to greater sexual selection pressure on the syrinxes of the latter. In Oscines this pressure would be dissipated by cultural evolution (learning) in different species (Prum 1992). Later on, this inference has been used to corroborate suboscine incapacity for learning (Isler et al., 1988).

Vocalizations as a “super-character”

Vocalizations are regarded as one important set of characters in bird taxonomy (Lanyon, 1963a, 1969, 1978; Sick, 1979; Payne, 1986). In many groups, mainly in Suboscines, songs are thought to be less conservative than morphological features at the species level, and thus, more informative in detecting recently divergent species. This point of view became stronger with the establishment of the assumption that suboscine songs and calls are genetically based, which is well illustrated by the following statement of Whitney (1994: 588) “[...] because plumage appears to be more conservative (and certainly more confusing) than voice, and because vocal differences appear to be correlated closely with genetic differences [...]”. Subsequently, all the above-mentioned statements have become associated with the biological species concept and its corollaries, such as the species mate recognition system (Paterson, 1985) and the concept of subspecies, as well as with the assumption that vocal signals are the major recognition factors amongst birds (Lanyon, 1963a, 1963b, 1969, Krabbe & Schulenberg, 1997).

Consequences of these associations to the study of avian relationships are not difficult to predict. Given the condition that individuals of the same species should recognize each other in order to reproduce, when potentially interbreeding populations are in allopatry they should be considered subspecies of the same species. Based on this reasoning, allopatric populations that possess the same song might interbreed and consequently could not be treated as different species. On the other hand, populations with different songs might not be able to interbreed, because they would not be able to recognize each other. Moreover, different vocalizations would inevitably imply some degree of genetic divergence between populations, which could not, in theory, develop well marked geographic variation in song.

A good example of this kind of approach are the traditional playback experiments. According to Payne (1986: 87), “The similarity of songs among different populations provides a test of the species identity of isolated remote populations”. Therefore, allopatric populations that respond mutually to a playback test should be considered conspecific, even if they are morphologically distinguishable, and those that do not respond should be treated as different species. In sum, according to this philosophy, because songs are used in intraspecific territory and in mate advertising, playback experiments could be used to test biological species limits in allopatric forms (see also Lanyon, 1963a; Bierregaard et al., 1997).

One of the most representative examples of the excessive weight given to vocalization as a taxonomic character is the

dilemma faced by Isler et al. (1997: 367) when they came upon morphologically diagnosable allopatric forms of *Thamnophilus* antbirds with unknown vocalizations: “Without further knowledge of their vocalizations, we cannot recommend that *leucogaster* or *huallagae* be elevated to species rank, nor given the unique qualities of their plumages and geographic isolation, can we recognize them as subspecies of another form. We therefore consider *leucogaster* and *huallagae* to be taxa of uncertain rank.”

From the example above we may see how vocalization has been treated as a superior set of characters in alpha taxonomy.

The reasoning described above can also be exemplified by the statement of Ridgely & Tudor (1994: 189-90): “[*Dendrocolaptes concolor* is so dramatically different [from *D. certhia*] that it has often been regarded as a separate species [...]. However, recent recordings of its song, which seem very similar to those of *D. certhia* from elsewhere in Amazonia, appear to confirm the contention [...] that *concolor* is best considered only a subspecies of *D. certhia*”. However, as described above, the songs of cis- and trans-Andean populations of *D. certhia* differ so strikingly that, despite their close plumage similarity, two species are probably involved.”

It is evident, from the quotation, that the authors consider vocal characters to be phylogenetically more informative than morphology. According to their rationale, other characters can exhibit geographical variation, while vocalization can not.

In Suboscines, despite the fact that most authors use mainly vocalizations in analyses of “species groups”, few completely disregard morphological features. In general, vocalizations have been used as an inductive factor of the overall analysis as can be exemplified by the title of the study of Isler et al. (1998). In establishing species limits for allopatric antbirds, these authors establish three vocal characters as the minimum number to distinguish the syntopic pairs and propose that when populations differ strongly in non-vocal characters fewer vocal characters are required.

One of the few cases in which morphological characters were completely discarded can be found in Whitney et al. (1995). In spite of examining museum specimens (skins), including types, these authors elevated *Hylopezus nattereri* to species rank without describing the morphological features that would diagnose it. No measurements are given, no colors are described, nor is any attention given to intermediate specimens, or to the description of geographical variants. When examining vocalizations, these authors perceived some geographical variation in the one of the putative species (*Hylopezus nattereri*), and indicated the possible presence of a third species, a coherent conclusion under the conceptual parameters applied. The authors were not concerned with presenting the specimens of birds that were singing (the owners of the voices used in the analysis). Thus, a species was validated based on vocalizations from an unknown individual that was supposed to fit morphological diagnoses that were not presented.

Discussion

The premises

An accurate analysis of the premises involved, for instance, the belief that the vocalizations are innate in Suboscines and that these birds cannot have song dialects, reveals a series of

errors and misunderstandings of the existing literature. The belief that vocalization or any other feature can be used as a “super-character” also needs to be re-evaluated.

As mentioned above, statements like the one of Nowicki et al. (1998: 179-180) “All songbirds [Oscines] appear to learn their species-typical songs [...] .Other birds, including “suboscine” passerines, do not learn to sing by imitation (Kroodsma & Konishi, 1991; Kroodsma, 1996).” or the one of Isler et al. (1998: 578) “[...] we assume that vocalizations in thamnophilid antbirds are innate [...]”, are very common in the recent ornithological literature. Paradoxically, all of them are based on the study of only three closely related (see Traylor Jr., 1977; Lanyon, 1986) species of tyrannids that appear to be unable to learn: *Empidonax alnorum*; *E. traillii* (both in Kroodsma, 1984); and *Sayornis phoebe* (Kroodsma & Konishi, 1991). These species represent less than 1 % of the species of Tyrannidae and this is only one of 12 families of Suboscines or suborder Tyranni (Cracraft, 1981). From this, to assume that Suboscines have innate vocalizations is to grossly overinterpret the available evidence.

It is pertinent to mention that the study of Snow (1970) on the behavior of *Procnias averano* should be enough to demonstrate how misleading are the studies that postulate that vocalization is innate in all Suboscines, but this has been surprisingly overlooked by subsequent authors that have examined this subject. In his paper, Snow affirmed that young males of *Procnias averano* learn their vocalization from adult males.

Knowledge of suboscine neurophysiology is still incipient. The available data suggest that these birds lack a vocal control pathway similar to that of oscine passerines, however the lack of this neurophysiological element in suboscines does not necessarily preclude them from the ability to learn songs, at least, to some degree (Kroodsma, 1984). As stated by Nottebohm (1972), several pathways could lead to vocal learning. Not a single species of Suboscines has had its neuroethology studied, and only few species of Oscines are, in fact, well known in this respect (see the detailed review by Brenowitz & Kroodsma, 1996).

Moreover, classification of characters in learned and innate has been regarded as conceptually wrong and may induce a taxonomist not to apply useful vocal characters in oscine studies. Wenzel (1992) warned to the deficiency of this perspective based on three principal reasons: 1 – “learned” and “innate” have largely evaded definition; 2 – how something is learned rather than what is learned may be phylogenetically informative; 3 – criteria of homology (which is the foundation of taxonomic analysis) rely more on simple persistence of character across taxa than on details of genetic architecture and heritability that produce it.

Futuyma (1986: 53) pointed out other drawbacks of the uses of such dichotomies in evolutionary biology: He states that because each aspect of the phenotype is a product not of the genes or of the environment alone, but of the interaction between the two, it is fallacious to say that a characteristic is “genetic” or “environmental”. In other words, it would be incorrect to assume that, given the appropriate stimulation, a sparrow (Oscine) will sing like a bellbird (Suboscine) or that a song of a tapaculo (Suboscine) is the unique and inevitable expression of its genotype.

There are no available data that could lead to the conclusion that Suboscines vocalizations are more innate than those of Oscines. Vocalization in these two taxa, probably, are a result of both innate and environmental factors. One possible conclusion is that the learned component is usually larger in Oscines, but it would also be incorrect to confront reaction norms of different taxa (Futuyma, 1986: 53-4). It is hard to objectively compare learning capacities between groups, because the comparison has to be founded on the amount of variation that each taxon maintains in response to environmental forces. At the same time, for example, it would be quite difficult to give values in a comparison between an apparently slight variation in a *Scytalopus* song and an apparently highly variable *Zonotrichia* song, due to the different nature of the vocalizations (different syringes) and the absence of non arbitrary parameters to do this.

Something similar has occurred with the claimed correlation between syrinx complexity and inability of learning. The generalization that suboscine syringes are more variable than those of Oscines remains poorly substantiated. Like the comparison between songs of different groups, it is very difficult to confront levels of complexity in two taxa. At the same time, the degree of syrinx complexity also varies extensively within each suboscine and oscine group. In Suboscines, for example, the Pipridae apparently show much more variation in syrinx morphology than the Dendrocolaptidae (Ames, 1971; Prum, 1992). Following such assumptions, one could propose that woodcreepers (Dendrocolaptidae) have more homogenous syringes because they have an increased ability to learn when compared to manakins (Pipridae).

Although the hypothesis is interesting, the supposed differences in complexity between Oscines and Suboscines could be related to a worse ability of Suboscines to learn songs rather than to an absolute absence of that capability.

It is interesting to note that a great part of the studies that reviewed this subject considered learning ability as a derived character (Jarvis et al., 2000). But taking into account the fact that this capacity was also demonstrated to occur in five bird clades, i. e. Oscines, Suboscines (Snow *op. cit.*), hummingbirds (Jarvis et al., 2000), parrots (Snow, 1968; Nottebohm, 1972), and toucanets (Wagner, 1944), it is clear that such conclusion should be reconsidered. It might be more appropriate to refer to the presence of the learning process not as independent origins of this complex ability but as the independent increase in sophistication of a characteristic that may be present in all or many avian taxa to a various degree of conspicuousness.

Even if one considers the dichotomy of learned *versus* innate vocalization useful to the study of bird systematics, there would not be much sense in considering suboscine vocalization as not exhibiting well marked geographical variation. All “genetic” characters vary in many different ways, as mosaics, smooth clines, step clines, residual clines, “leapfrog” patterns etc.

In fact, genetic variation is one of the most important corollaries of the evolutionary theory (Gould & Johnston, 1972). Without genetic variation at the population level, it would be very hard even to conceive evolution. To deny geographical variation of song is to deny the possibility of the evolution of this character.

One of the strongest arguments in favor of the absence of geographical variation in suboscine vocalizations is that there are no documented cases in the literature (Kroodsma, 1984; Brenowitz & Kroodsma, 1996). However, the assumption that Suboscines have innate songs will inevitably lead to the interpretation of geographic differences as variation among species. In contrast, in Oscines all well marked geographical variations tend to be immediately interpreted as dialects. Recent papers demonstrated that non-migratory Furnariidae have some degree of geographical variation in their vocalizations (Kratter & Parker, 1997; Lindell, 1998).

On the other hand, most of Suboscines that have had their repertoires studied over geographical gradients are migrant flycatchers, in which the lack of geographical variation can be explained by the genetic or cultural flow between populations (Payne & Budde, 1979).

In the case of playback experiments, it has not been taken into account that a simple case of clinal geographic variation (*sensu* Endler 1977) may result in different songs and consequently, different recognition abilities. Two populations of the “same species” might not recognize each other’s vocalizations, if they are effectively separated by distance. This phenomenon is known to occur in the Oscines (Lanyon, 1982; Robbins et al., 1986).

The prior discussion leads to another weak point in assumptions of oscines/suboscines vocalization. Natural diagnosable groups that have already vicariated are not necessarily supposed to have evolved different songs. Some data suggest, for example, that in one species of *Hylophylax* (Formicariidae) while vocal characters may be used to divide populations into two groups, molecular and morphological features allow the recognition of at least seven groups (John Bates, pers. com.). This phenomenon is easily understood if one assumes allopatric speciation resulting from an imposition of a geographic barrier. In this case, two allopatric species might recognize songs of each other. It would be unreasonable to expect that, after speciation, these forms must have unique songs to be considered as different species. This might well be regarded as an oversimplification of the Biological Species Concept.

The arbitrary minimum number of three vocal characters to determine species limits is also inadequate. Operationalism has never worked very well (Wiley & Mayden, in press), mainly, when one searches for the natural unities (taxa in general) that are the foundation of the entire comparative biology (Nelson, 1989; Cracraft, 1992). This procedure, if allowed to persist, will negatively influence suboscine taxonomy at two levels. First, it will obscure even further the already confusing knowledge of species distributional patterns. Second, it will have an indirect negative effect on the attempt to understand phylogeny and evolution of higher avian taxa due to the inconsistency of terminals (species) used in phylogenetic analysis.

In the search for explanations about the natural system, well-founded premises and concepts are very important. In this context, the persistence of the application of the Biological Species Concept and of the trinomial nomenclature have been very prejudicial to ornithology. In fact, both practices are philosophically related to the “super-valorization” of song in suboscine taxonomy. It is worth mentioning that some of the

proposed methodologies combine the two practices. For example, Isler et al. (1997, 1998, 1999), proposed that all allopatric, vocally diagnosable forms that are not morphologically distinguishable should be regarded as subspecies. Unfortunately, this method combines an ill-based assumption (the absence of dialects in Suboscines) with an ill-defined concept (the subspecies concept) (Ehrlich, 1961; Sokal & Crovello, 1970; Nelson & Platnick, 1981; Cracraft, 1989; Parkes, 1982; Zusi, 1982; Donoghue, 1985; McKittrick & Zink 1988; Nixon & Wheeler, 1990).

An alternative

Behavioral features have been proven to be a good source of characters for taxonomy (e.g. Prum, 1990, 1994; Prum & Lanyon, 1994, de Queiroz & Wimberguer, 1993; de Pinna, 1991, 1997; McCracken & Sheldon, 1997; Zyskowski & Prum, 1999) and the vocalizations are certainly useful to future on bird taxonomy. Nevertheless, their utilization must follow the strict methods of phylogenetic systematics and the former ill-based paradigms should be abandoned.

When using vocal characters in suboscine taxonomy, taxonomists should be concerned with the possibility of the existence of geographical variation in vocalizations. Well marked and clinal variations should be expected to occur. Some of these variations would certainly fit the definition of dialect given by Kroodsma (1994) and by Loughheed & Handford (1992).

Vocalizations should be treated as any other character but perhaps with even greater attention because of the lack of knowledge about the functional anatomy of vocalizations in Suboscines and the absence of solid data about factors which have influenced the genotype of these birds. For instance, Lanyon (1978) demonstrated a correlation between body mass and the properties of vocalizations in species of the suboscine genus *Myiarchus*. Consequently, altitude and latitude might have some influence on avian songs because of their effect on body mass (Kendeigh, 1969; James, 1970; Zink & Remsen, 1986). The sound produced by birds is also closely related to the pressure in the syrinx and interclavicular airsac (Gaunt & Gaunt, 1985; King, 1989), and changes in atmospheric pressure is known to affect avian song (Nowicki, 1987; Catchpole & Slater, 1995). This phenomenon was quite well demonstrated in *Zonotrichia capensis* (Nottebohm, 1975). Recordings of this species song in Argentina indicate a gradual reduction of song length with increasing altitude. Vocalization in this species also shows some correlation with availability of food and with temperature. The influence of environmental factors in sound-producing mechanisms is also well established in poikilothermic animals (Gerhardt, 1978; Duellman & Trueb, 1994: 104) and should not be overlooked in avian studies.

Within taxa such as the Rhinocryptidae of the genus *Scytalopus*, which has a typical Andean distribution, different altitudes could affect the distributional patterns of songs of different populations. This factor, among others, should be taken into consideration when using vocalizations in a taxonomic revision of the group. Krabbe & Schulenberg (1997) used song and altitudinal range to define their supraspecific groups: “Allopatric taxa with the same body mass and elevational distribution and with relatively similar, but yet distinctive

songs are united into superspecies.” Although the authors appear to be working with three independent variables, they are probably working with three correlated factors, which might have led them to various misinterpretations of the data.

Recorded vocalizations, preferably well sampled, should also be associated with voucher specimens, since the type series are still, generally speaking, morphological. Although this step has usually been neglected in recent studies, it is quite useful in allowing the researchers to identify the species which was emitting the analyzed vocalization.

In view of the lack of objective differences between vocalizations in the Oscines and Suboscines and contrary to what has been common practice, vocalizations should also be used, with all the necessary care, in the taxonomy of oscine passerines. After all, as noted by Wenzel (1992: 378) “Analysis of relatively more learned behavior is more complicated than for relatively more innate behavior, but is still possible from a phylogenetic viewpoint.”

Although it is argued that in Suboscines vocal populations might exhibit a genetic identity, it is known that oscine dialects may also show close correlation with the genetic structure of populations (Lougheed & Handford, 1992). Moreover, some degree of genetic variation is expected in virtually all different populations (Wilson & Brown, 1953; Barrowclough, 1982).

Experimental research is highly recommended in this area. Such studies may provide valuable information on which elements in vocalizations are more sensitive to environmental forces. However, one should not expect to find in Suboscines the same kind of learning that is usually found in Oscines. Therefore, the simple transfer of knowledge from Oscines to the studies of suboscine song can be misleading.

In the case of utilization of vocal characters in bird taxonomy, the trap of treating them as “super-characters” used to unite populations or species into groups using *a priori* reasoning must be avoided because of the already discussed inconsistency of this practice. Such practice hinders the real purpose of taxonomic work because it aims to obtain an immediate classification that has no correlation with the reconstruction of natural phenomena.

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