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Bird Song as a Possible Cultural Mechanism for Speciation

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Abstract

Dialects of song exist in song birds. It can be hypothesized that these dialects have no genetic basis: there are no genes to predict which notes should be sung and in what sequence; or how often they should be repeated; or how long they should be, etc. As such, bird songs can be considered purely cultural, behavioural phenomena with no determining roots in genetics. Combined with - equally culturally determined - differential preferences of females for male bird songs, one can hypothesize about cultural mechanisms which may increase genetic polymorphism in a population.

In other words, it can be hypothesized that nongenetically encoded phenotypic behaviour may cause actual isolation of subpopulations, leading to increased genetic polymorphism in the population and eventually to speciation in some taxa of sexually reproducing organisms.

In summary, purely cultural phenomena may act as an evolutionary drive, in nonhuman as well as human organisms, by causing important gene frequency alterations in a population and may eventually lead to speciation (cultural speciation).

Keywords: speciation, culture, bird song, genetic polymorphism, nongenetically encoded behaviour.

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1 Classical speciation theories usually require genetic changes to occur prior to overall genetic divergence between populations

Speciation, the formation of species, is still an ill understood phenomenon in biological evolution. The following quote summarizes how speciation is supposed to happen for species of sexually reproducing organisms:

> "*In the abstract, the following series of events must happen in the origin of a new species. We start with a single species, made up of a set of interbreeding organisms. A genetic variant (or several variants) must spread through part of the species, and the bearers of this genetic variant must mate only (or preferentially) with other bearers of the same genetic variant. If the reproductive isolation starts as a mating preference, it must eventually tighten up to exclusively breeding with its own type. Once it has done so, the species will have split into two: from one initial population, two separate interbreeding populations will have evolved. At some stage along the way, further phenetic, ecologic, and behavioural differences associated with reproductive isolation may also evolve. The big question about speciation is why, and in what circumstances, the genetic variant causing reproductive isolation should evolve.*" [11].

This is repeated elsewhere in the same handbook: "*The genetics of speciation have been studied, to see what kinds of genetic changes give rise to reproductive isolation.*" [11].

Important here is that current thinking about the onset of speciation events presupposes the occurrence of foregoing genetic mutations or genetic variants.

Different mechanisms for speciation have been proposed and in one mechanism, allopatric speciation, one need not presuppose the prior occurrence of some genetic variant(s). Allopatric speciation occurs when two initially interbreeding populations of the same species are spatially/geographically separated long enough such that there is no gene flow between these populations (allopatric isolation). As a consequence the populations may diverge genetically and epigenetically gradually (for instance by continuously increasing mutation load) to the extent that the individuals can no longer interbreed when both populations meet again. In all other cases however, current evolutionary theory invokes some foregoing genetic events which have to occur such that phenotypic changes (for example, altered mating preferences) prevent interbreeding. Once such genetic events have occurred, the two populations no longer interbreed, e.g. because the individuals of the different populations no longer recognize each other as potential sex partners. At that moment the situation is comparable to that of allopatric separation and the two populations start to diverge because of lack of gene flow. Again, finally eventual mating between representatives of these populations no longer produces viable (or fertile) offspring.

Paterson [9] has previously suggested that the crucial event for the origin of a new species is the evolution of a new mate recognition system. This is already a less orthodox point of view than that of Dobzhansky [2, 3] which holds "that isolating mechanisms will evolve under natural selection in order to prevent interbreeding among incipient species" [11]. In other words, Dobzhansky sees mate recognition limitations as a means to prevent further selectively disadvantageous interbreeding between two populations which, for other reasons, have already started to diverge[1]. On the other hand, Paterson [9] considers genetically induced changes in mate recognition as the possible cause for speciation initiation. Nevertheless, Paterson [9] insists that genetic variants are necessary to change the specific mate recognition systems.

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2 Nongenetically based changes of mate recognition systems can lead to genetic polymorphism and eventually to speciation

I will try to argue below how in some cases no genetic changes are needed for changing mate recognition. These behavioural changes in signalling and in preferring certain signals could be simply the consequences of cultural events, and need not to be genetically encoded. (Culture is defined here in a broad sense, whereby any information transmission between brains of animals is considered as being a cultural phenomenon.)

One of the problems - as I see it - with the need for genetic variants which alter mating preferences is that such mutations should occur in both sexes simultaneously and at very different loci. For instance, the male should have a mutation in his singing behaviour gene(s) which alters his song in a recognizable manner, and the female should have a mutation affecting a very different kind of behaviour in a very specific manner: she should have a mutation in her song preference gene(s) which should cause her to prefer this very specific mutant song. The probability of such events occurring simultaneously seems very small. (Notice that the same problem is encountered when trying to explain the origin of human language.)

I want to hypothesize that in some cases the initial events leading to speciation need not be genetically encoded. Such events can be solely caused by phenotypic behaviour, not encoded by genes, in other words by cultural behaviour. The families or orders where such an explanation may be valid are limited, but at least the mechanism could work for song birds (*Passeriformes*)[2].

2.1 Male song behaviour

Song birds do sing. They can, because there are genes which encode for the processes for syrinx development, genes which encode for hormones and for hormonal receptors on cells leading to singing behaviour, etc. However, it can be stated that the songs themselves are (except for some stereotypic sounds which may have a genetic basis) the consequence of behavioural phenomena which cannot be traced back directly to genetics. The reason is that genes also encode for the possibility to mimic, a straightforward form of learning. The mimicking behaviour enables young song birds to preferentially sing the songs sung by older males[3]. Since this process is not rigid stereotypic genetically encoded behaviour, but a difficult exercise, errors can be made in mimicking and this leads to new variations of songs. In addition, the possibility to recombine phrases leads to variation. Because of their capacity to mimic, other birds - singing nearby - can take over this variation, and this may be the explanation for regional dialects. Indeed, cultural transmission of songs, that is change in behaviour, which has no direct genetic basis, is well recognized in song birds [4, 6, 7, 14].

Probably dialects of human language originate and can be maintained in pretty much the same manner. As such, the existence of bird song dialect could be considered as an emergent characteristic, having no direct roots in genetics. In other words, cultural differences in song birds emerge from their ability to sing combined with the ability to mimic songs.

2.2 Female song preference

Bird song variation by the male is only part of the story. To understand the differential preferences for songs we have to look at female behaviour. It is feasible that females, who hear the songs of their father more frequently than the songs of other males, tend to prefer these songs. Again, this can be considered a purely cultural phenomenon, since all that should be encoded is some behaviour which makes females prefer songs with which they are familiar. Which song that is, depends on which culture the female is raised in, so again there is no direct link with genetics. Similar processes have been observed for humans. For instance, it has been shown that we tend to feel more sympathetic to people whose faces we see more frequently [8] and that we unconsciously prefer sequences of notes which we have heard before [13].

In summary, preference for the familiar may be due to genetically encoded behaviour. The behaviour of "preferring what you are familiar with" may itself have been naturally selected, for instance because it might be a useful fist rule that familiar things are less dangerous than unusual things. However, with what you will be familiar, is itself the outcome of purely environmental cues and is not encoded in genes.

Therefore, female birds may preferentially mate with males from their own region, own dialect and own culture. This may prevent gene flow from the rest of the population (from the other cultures) to a large extent and as a consequence gene frequency changes in parts of the population compared to the rest of the population should be observable. In extreme cases, for instance, after a short period of total isolation of a part of the population[4], the dialect of a population might have diverged from those of its neighbours to the extent that females may strongly "dislike" the dialects of the strange males. We get a de facto split between two populations, which may start to diverge genetically until the moment when even sexual intercourse does not give rise to viable (or fertile) offspring (postmating isolation).

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3 Factual evidence

The above ideas were developed largely on the basis of theoretical reasoning with limited knowledge of current literature on the topic and, therefore, were presented as what I believed to be a rather original hypothesis. During the review process, a reviewer drew my attention to a recent publication by Grant & Grant [4], experts in the field who developed a completely coinciding theory based on real data and a better specific knowledge of the literature. I have chosen to maintain the original structure of this manuscript to illustrate that it is possible to develop probable hypotheses, once the genetic paradigm can be put aside partially - in other words, once one learns to give to genes what genes should get and to memes what memes should get.

However, it is incumbent on me to present some of the arguments of Grant & Grant [4] as literal quotes:

> "*... hybrid females bred with males that sang the same species song as their fathers. All G. fortis x G. scandens F1 hybrid females whose fathers sang a G. fortis song paired with G. fortis males, whereas all those whose fathers sang a G. scandens song paired with G. scandens males.*" (page 7769).

> "*Rather, young birds imprint on parental phenotype [1, 5], and visual and auditory stimuli*

they receive in early life influence their choice of mates much later in life." (page 7770).

"*To summarize, the particular song a male sings, and the behavioural responses of females to song and morphological signals, are not genetically inherited in a fixed manner but are determined by learning early in life.*" (page 7770).

"*Experiments with playback of tape-recorded song demonstrate that resident males are capable of discriminating between songs produced by members of their own population and members of a related population on a near island. Residents' songs elicit stronger responses than do those of the potential immigrants [10].*" (page 7771).

"*In tests of several species the discrimination was often weak, implying that song difference, by itself would not be sufficient to prevent interbreeding.*" (page 7771).

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4 Further remarks and considerations

Above I have tried to argue how cultural phenomena might influence population genetics in birds. This hypothesis reached by theoretical reasoning coincides with current song bird speciation theory as it has been developed independently in a more detailed manner by others [4]. Several general remarks and further considerations are possible with respect to the above proposed point of view with regard to the influence of culture on evolutionary events.

4.1 The role of females in cultural heredity

Firstly, I would like to comment on the last quote from [4]. It should be noted that it is usually male singing and male song response behaviour that is studied [4]. However, it is especially the female song response behaviour that is of importance with respect to the question of whether premating isolation can be caused by song preference. It is most probably the ability of the female to prefer one song above another which is the major cause of maintenance and increase in genetic and cultural diversity. Unfortunately, female behaviour has been poorly studied when compared with the work that has been done on male song.

Also, in most species parental care is largely a female responsibility. Therefore, females play a predominant role in transgenerational passing on of acquired habits and knowledge (for instance which organisms should be feared). Therefore, in many cases, which information is passed on from generation to generation and which behaviour will result from `education' can be hypothesized to follow a maternal lineage of behavioural inheritance.

Finally, and probably most importantly, although the example of song bird population genetics deals with the influence of cultural variability, it should be noticed that the existence of stable cultural heredity is quite often overlooked. Most students of evolution think about genes when considering heredity. However, heredity of habits may have higher copy fidelity than genetically encoded heredity. When considering social behaviours, which have to be learned through social contacts and thus are culturally inherited to a large extent, one can say that these are quite stably inherited over hundreds of generations. In the meantime the genetic make-up of these populations may have changed thoroughly, illustrating how memetic heredity might be even more stable than population genetic heredity.

4.2 The difference with sexual selection theory

Cultural inheritance of sexual traits differs from `sexual selection' as it is usually understood or studied (for instance as an explanation for the long peacock tail) in that in sexual selection, female preference is concerned with some genetically encoded male trait (for instance tail length). Also, female preference itself may be more easily genetically encoded when it concerns a simple trait like tail length than when it involves preference for a specific kind of song (out of many possible songs). Finally, where sexual selection occurs, preferences of all females of a species are oriented in the same direction (for instance towards a longer male tail), while the hypothesis presented here, predicts that cultural preferences of females with respect to male songs may differ strongly and diverge within a species.

4.3 The difference with use-inheritance

By the way, this hypothesis has nothing to do with use-inheritance[5], which claims that phenotypic changes during life can influence the genotype. Here we discuss how cultural variation (that is differences in phenotypic behaviour) in a population may alter gene frequencies (that is increase genetic polymorphism[6]) and eventually lead to speciation.

4.4 Cultural speciation as a possible explanation for species radiation

The possibility of cultural elements to influence population genetics, as presented above, could also provide a partial explanation for the extensive radiation in the order of the Passeriformes which is the most species rich order of birds. Also, cultural sympatric isolation might occur faster and more frequently than allopatric isolation - since the latter mostly relies on the existence of physical (that is geographical or climatological) barriers - and seems much faster and more feasible than mechanisms dependent on the development of genetically induced changes in mating preference.

4.5 Speculations about the possible influence of cultural inheritance on early hominid evolution

Below we will argue that this kind of approach might as well and a fortiori be used for better understanding of early hominid evolution. Indeed, one could speculate on the possible influence on human evolution of cultural isolation between early hominid tribes. Besides the spatial isolation of separately living tribes - necessary because of limitations in environmental carrying capacity - cultural isolation may have caused additional alienation between these small groups of hominids, such that sexual intercourse between members of these groups and gene flow between these groups was rare.

There are indirect indications that original tribes were strongly alienated. For example, there is the observation that kidnapping females still occurs in some presently living Amazon tribes. The practise of kidnapping females from other tribes may have been widespread and it has been suggested (reference unknown) that females may have been an important reason for early warfare. This may be reflected in the Roman legend of the kidnapping of the Sabine virgins and in the events leading to the Trojan war (kidnapping of Helena). In addition, the fact that cannibalism among humans may once have been widespread is an even stronger indicator for alienation between organisms belonging to the same species, alienation to a degree not seen in any other species[7]. Also, some extant tribes use the designation `human' only for members of their own tribe.

All of these observations are indicative that early hominid tribes had little or no contact with one another, and were even hostile towards each other[8].

This culturally reinforced alienation resulted in a virtual small population size, thereby increasing the probability of cementing or fixing new mutations. Indeed, even selectively advantageous mutations are difficult to maintain in high number populations, because of stochastic reasons [11].

In extreme cases this isolation may have led to speciation but in most cases it may simply have increased genetic polymorphism within the species. The latter is dependent on a minimal degree of gene flow to maintain species integrity, thereby "avoiding" both speciation and tribal extinction - the latter being a more likely outcome because of inbreeding due to a too small population size. (The danger of extinction of `demes' may be less likely among birds, because of much higher average population numbers.)

Indeed, isolation (enhanced by cultural differences) between tribes may have been so substantial that extreme measures were required to maintain a minimal degree of gene flow in order to avoid excessive inbreeding. This may explain the above mentioned phenomenon of kidnapping females[9].

The alternation between temporary genetic isolation and occasional gene exchange may be a powerful mechanism to explain rapid evolution (and eventual speciation[10]) because the possibility of the fixation of mutations is increased. Again, the isolation which is needed for this to occur may be strongly enhanced and most easily explained by nongenetic cultural isolation mechanisms. Paleoanthropology does not contradict this point of view since it indicates that frequent branching of hominid species (speciation) occurred and that there was important heterogeneity within the species (genetic polymorphism).

4.6 The role of females in genetic and cultural exchange

As a consequence of exchange of females (for instance, by the above mentioned phenomenon of kidnapping), not only genetic exchange will occur (see Section 4.5). Also, females may be the major carriers of cultural exchange, introducing cultural novelty in other populations and counteracting too extreme cultural alienation between populations.

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5 Conclusion

Above I have tried to argue how culture might influence population genetics, in birds and even more strongly in humans. This hypothesis reached by theoretical reasoning coincides with current song bird speciation theory as it has been developed in a more detailed manner by others [4]. It is suggested that ethologists should focus on female song preference behaviour in birds and on female cultural behaviour in general.

More in general, it should be realized that besides genetic heredity, cultural heredity is a real phenomenon, as is illustrated by the fact that, for instance, culturally transmitted behaviours may be stable over hundreds of generations.

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Notes

Note 1

This is the reinforcement hypothesis which is strongly contradicted by factual evidence in song birds [4].

Note 2

Possibly this mechanism might work for other animal families like crickets (*Orthoptera*, *Gryllidae*) and toads/frogs (*Amphibia*, *Anura*), although the sounds produced by these animals show less intraspecific variability and thus appear to be more rigidly encoded by genes. Of course we should not forget some mammals, e.g. cetaceans.

Note 3

As a matter of fact, young males will in many cases mimic their fathers' songs and are determined to do so very early in life, a phenomenon called `behavioural imprinting' [4]. Many behavioural cues in avians are determined by imprinting early in life. For example, it is the explanation of why chickens of some species accept as their mother any creature or moving object they observe immediately after hatching.

Note 4

This is in contrast with allopatric isolation where long periods of geographic separation are needed to enable sufficient cultural divergence leading to postmating isolation and speciation. Moreover, in the case of cultural isolation, geographic separation is not really necessary, but could accelerate the process of genetic divergence.

Note 5

I held use-inheritance (e.g. because the hammersmith develops strong muscles because of the heavy work he does, his children are supposed to inherit stronger muscles as well) as the hallmark of Lamarckism, but recently learned that Darwin as well accepted use-inheritance as an explanation [12].

Note 6

Similar suggestions have been made previously by others, as becomes obvious from the following quote from [14]: "*Song dialects in the white-crowned sparrow Zonothrichia leucophrys may have promoted genetic differentiation between neighbouring demes (Marler & Tamura 1962, Baker & Mewaldt 1978, Baker et al. 1982a, 1982b). This view remains highly controversial, as above studies were seriously criticized (Zink & Barrowclough 1984, Hafner & Petersen, 1985).*" (cited references not available.) Others have used the concept of `memes' for better understanding of the evolution of bird song culture [7].

Note 7

For instance, chimpanzees may show already quite hostile behaviour towards members of other groups.

Note 8

Recent events indicate that indeed even in modern societies different cultures may live next to each other with no or little social and cultural exchange, which eventually serves as an important factor leading to civil war and genocide.

Note 9

I realize that this is highly speculative. People have not only a tendency to consider other cultural habits as repellent, ridiculous or as at least funny, but there is also the opposite tendency of finding people of other cultures (`races') physically attractive (attractiveness of the exotic). Of course, these observations might also reinforce the hypothesis that on the one hand cultural differences increased isolation between populations, while on the other hand physical attractiveness of strangers could have a more direct genetic background, which could explain why one would endorse risky adventures like kidnapping, inadvertently avoiding both inbreeding and ascertaining gene flow, whereby the latter ensures the different tribes remain one species and that mutations fixed in one population can flow to other populations of the same species.

Note 10

Speciation might be considered as a side effect of evolution caused by prolonged separation of initially interbreeding subpopulations. Speciation may eventually accelerate evolution. However, speciation itself does not necessarily need to be an evolutionary important phenomenon with respect to increasing complexity of life, since much evolution can occur within species. After all, it is among members of the same species that competition and natural selection is strongest, because organisms of the same species occupy the same niche. Our obsession with species and speciation is of course quite understandable.

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