

would be a rather novel proceeding. The difference would be fully as great and as important as the differences on which many subspecies are named today, but they would be less tangible to the collector, who in most cases would have to depend on the locality to label his subspecies. I am rather of the opinion that the Rocky Mountain birds differ slightly from the eastern ones in plumage as well as in song. The naming of a new subspecies, however, if grounds for such, based on plumage or measurements, exist, I would prefer to leave to someone who has greater opportunities to study series of skins and to work out such problems.

---

## THE EVOLUTION OF BIRD-SONG.<sup>1</sup>

BY FRANCIS H. ALLEN.

THE evidence and arguments brought forward by Mr. Chauncey J. Hawkins in his paper on 'Sexual Selection and Bird Song' in 'The Auk' for October, 1918, make it seem very probable that bird-song had its origin — its first cause — in the "maleness" of the males. Mr. Hawkins fails to show, however, how the multiplicity of songs of the various species of birds, the extremely elaborate songs of some, could have acquired their present forms except by some continuous selective process.

Mr. Hawkins concludes his paper by saying (following Brooks) that "any variations in voice which might arise would be preserved in the male germ which assures the variation in the species, while the germ of the female guarantees the constancy of the species." I suppose this to mean that *all* variations that have arisen in the course of the evolution of a species are present potentially in the male germ, but that some of them are inhibited by the conservative action of the female germ. This seems to be going a little beyond the evidence, and it can, I think, only be regarded as a

---

<sup>1</sup> Read, in somewhat different form, before the Nuttall Ornithological Club, May 5, 1919.



theory. As a theory it seems to be open to the fatal objection that it fails to explain the relative uniformity of bird-song within the species. If every variation has a chance of being perpetuated, what is it, precisely, that decides for or against it and reaches the same or a similar decision in all individuals of the species? Can conservatism alone do this and thus permit progress in a definite direction?

It seems to me that something more positive in the way of an evolutionary process is needed to account for the multifarious distinctive songs of birds than the unregulated inhibition of variations. Granted that the song-impulse is rooted in the superabundant vitality of the male, there must still be some process that selects the variations to be preserved — whether it be sexual selection, natural selection, or some other agency, or a combination of two or more such agencies.

As Mr. Aretas A. Saunders has pointed out ('Auk,' January, 1919, p. 149), Mr. Hawkins has failed to make careful distinction between call-notes and song. Song probably originated in the rapid repetition or special adaptation of call-notes, as Mr. Charles A. Witchell has shown in his interesting book on 'The Evolution of Bird-Song' (London, 1896), but it has assumed an entirely different function in the bird's life, and, as Mr. Witchell and others have shown, it is as a rule transmitted from generation to generation in an entirely different way. Dr. Chapman, in his comprehensive discussion of 'The Voice of Birds' in the Introduction to his 'Handbook of Birds of Eastern North America,' indorses "the theory of the mimetic origin of bird-song," and says, "Birds inherit at least the calls they utter when in the nest, just as a child cries instinctively, but they apparently do not inherit their songs any more than the child inherits the language of its parents."

Call-notes are means of identification between individuals of a species and, being necessary in order to bring the sexes together and to prevent the separation of families, they have been evolved, whether through natural selection or otherwise, to meet the needs of the several species. No one thinks of attributing them to a surplus of sexuality. The songs are similarly differentiated for purposes of identification. Doubtless some, and perhaps many, songs were evolved either through the ordinary processes of evolu-



tion, whatever they may be, or through the special process of sexual selection. The evidence, however, seems to favor the belief that most songs are transmitted from generation to generation by imitation, each individual imitating, consciously or unconsciously, the songs of other individuals, whether the songs of his parents heard while he was in the nest or those of other birds. The songs would naturally be modified and improved by enterprising and gifted singers, but would, of course, always be subject to the conservative action of the herd instinct, which would repress and suppress any too great departure from the normal. (This last observation I offer as a substitute for Mr. Hawkins's theory of the opposing influences of the male and female germs.) In this way the characteristic songs of the species are preserved, just as primitive human language passes from individual to individual within the tribe, and as the folk-songs of the various races of men have been handed down from generation to generation.

This growth and development by invention and imitation must, it seems to me, account in great measure for the *forms and general characters* of bird-songs as we know them, but surely some other process was necessary to produce the *beauties* of tone and melody and rhythm that characterize so large a percentage of the songs. Superabundant vitality produces noise in human beings and doubtless also in birds, but it cannot account for beauty, any more than it can account for the more or less intricate patterns of the vocal utterances that we call songs. Weismann remarks that "it is not easy to see why a more active metabolism should be necessary for the production of strikingly bright colours than for that of a dark or protective colour,"<sup>1</sup> and it would be fully as difficult, I think, to show how it could produce music out of noise. Equally impotent in this direction must be such an agency as natural selection, for obviously birds can pick up a living, escape their enemies, and propagate their kind without the help of music; many species do so. Imitation could not of itself *produce* musical qualities, and in the absence of any standards of taste it would be as likely to perpetuate harsh and unpleasing notes as beautiful ones.

All these agencies failing, unless we postulate some supernatural

---

<sup>1</sup> The Evolution Theory, English translation by J. Arthur Thomson and Margaret R. Thomson 1904, (original published in 1902), vol. i, p. 212.



force at work in the universe to produce beauty,—and that, of course, would be getting outside the realm of science,—how can we escape imputing the origin and development of this beauty in bird-song to an æsthetic sense in the birds themselves? And how can we imagine an upward evolution in the beauty of the song and the proficiency of the singer without postulating some form of selection as the active principle? Finally, is any theory more reasonable than that of sexual selection to account for the beauty of bird-song? Is there, indeed, any other workable theory left to us?

Mr. Hawkins has pretty thoroughly recapitulated the evidence in favor of the hormone theory of the origin of bird-song,<sup>1</sup> and I fail to find in his paper any argument that would apply against this view of the action of sexual selection in producing and developing beauty in song, except the evidence he cites that display and ardent singing serve the purpose of overcoming the coyness of the female, and that in many cases there is no indisputable evidence that the female exercises any choice between suitors (or possible suitors). This is a strong argument but not an insuperable one. For one thing, even though but one male may be seen with the female at a given time, she may nevertheless have had opportunities to choose,—just as in the human species it frequently happens that but one suitor is heard at a time! More observation is needed on this point. But many evolutionary questions must be decided by a nice balancing of evidence and arguments, and the difficulties of accounting for bird-song without admitting sexual selection as an important factor seem to be far greater than those of reconciling the latter with the theory of superabundant sexuality.

If we agree that sexual selection has thus played its part, we have, then, in addition to natural selection or whatever other evolutionary process may be the chief agency in the origin of species, these three coördinate factors in the production of bird-song: the hormones generated by the male sex glands originating the song-impulse; invention and imitation producing the variety and fixing

---

<sup>1</sup> He fails to mention a comparatively recent opinion on the other side of the question in the case of Weismann, who says in his 'The Evolution Theory,' "From [the] simple love-call the modern song of many species must have developed by means of sexual selection."



the form and character of the song; and sexual selection evolving, through both structural and psychological changes, beauty of tone and proficiency in execution.

The letter of Mr. Saunders in the January 'Auk' has suggested a further examination into the mode of development of the songs of birds. Mr. Saunders raises an interesting question in regard to the relation between the ordinary songs of certain species and the ecstatic flight-songs. He makes a radical distinction between the "ordinary song" and the "mating-song," and states that "the ordinary song is evidently not sung from sexual impulses, but is simply an outburst of vocal sounds expressing great vigor and joy of living," while "the mating-song, on the other hand, seems to be caused directly by sexual impulses," and he goes on to say, "If we would know the primary cause of bird-song in general, then the question to be solved is which of these forms of song is the more ancient." He decides this question in favor of the "mating-song," and cites as his only evidence a certain flight-song of the Eastern Meadowlark, which he says is almost identical with that of the Western species, while the ordinary songs of the two species are very different, indicating the ancestral character of this flight-song.

He describes this song as "a long-continued jumble of short, quick notes," and says that it "quite closely resembles the flight-song of the Bobolink (*Dolichonyx oryzivorus*)."

This song is also mentioned by Dr. Chapman in his "Handbook of Birds of Eastern North America" (Revised Edition, p. 64). I have never been fortunate enough to hear this song, which Dr. Chapman intimates is not very frequently uttered by our Eastern bird, and which I think, from my own experience and from inquiries I have made of other ornithologists, must be very uncommon in Massachusetts, where the "ordinary" song is certainly a mating-song, if not *the* mating-song. I should like, however, to cite a few other examples which seem to point to an opposite conclusion to that reached by Mr. Saunders as to the priority of mating-songs in general.

One of the most conspicuous examples of ecstatic flight-songs among our Eastern birds is that of the Ovenbird (*Seiurus aurocapillus*), and this song always (in my experience) contains a fragment of the ordinary song of the species interpolated among its rich, melodious warbles. Does it not appear more likely that this flight-



song has been evolved from the ordinary song, from which it has never quite succeeded in freeing itself, than that the warbling song should first have developed the *teacher teacher teacher* strain, and that then this new and comparatively uninteresting strain should have been selected to be lengthened and strengthened into the ordinary song of the species?

Another common Warbler, the Black and White (*Mniotilta varia*), possesses a song which is confined, I think, to the nesting-season, and this is so like the ordinary song of the species that the two must certainly have had a common origin. The song we first hear from newly arrived birds in the spring is a plain *wee-see wee-see wee-see wee-see*; then later we hear what is obviously the same song elaborated by lengthening the performance and lowering the pitch of two of the dissyllabic notes near the end, thus: *wee-see wee-see wee-see wee-see woo-see woo-see wee-see wee-see*. This latter song is uttered from a perch and is not an ecstatic performance like the Ovenbird's, but it is clearly a mating-song as distinguished from the ordinary song, and it is equally clearly an elaboration of that song. Of course, it may be argued that the more elaborate song is the regular one, and the other, which is heard first, is only a shortened, abortive form of it, used before the song-impulse has gained its full force; as, in the autumn, when the song-impulse is waning, we hear often only the introductory notes of the White-throated Sparrow's song; but is it not probable that in both these cases the shortened form is merely a reversion to an ancestral song, the song as it was before it was evolved into its present complete form? The ordinary course of evolution is, of course, from the simple to the complex rather than from the complex to the simple.

Again, the long-continued, richly intricate song that we hear from the Rose-breasted Grosbeak (*Zamelodia ludoviciana*) in the height of courtship excitement is obviously only an elaboration of its ordinary song.

Is it not reasonable to assume that courtship excitement should lead to a more and more elaborate form of song-expression as the development of the species goes on, and that the song of the more excited moments should always be somewhat in advance of the ordinary song in point of fervor and elaboration? This view of



the development of bird-song might be stated as follows: Let *S* represent the song first developed out of the call-notes of a certain species. *S* becomes elaborated as *SS* under stress of unusual emotion, and *SS* becoming fixed in the psychology of the species, the bird has two songs, *S* and *SS*, the latter a special mating-song uttered only at times of great sexual excitement; then *SS* tends to become the ordinary song, and a further elaboration, *SSS*, is evolved to express the unusual emotion for which *SS* is no longer adequate.

This process may go on indefinitely but so slowly that only in rare instances can we see any evidence of it. Do we not get a glimpse of it, however, in the case of the Baltimore Oriole (*Icterus galbula*)? Besides the harsh, chattering call which is suggestive of family relationships, this bird utters clear, pleasing whistles which are evidently in the nature of song-notes without amounting to actual songs. Out of these separate song-notes (*S*) has developed apparently the characteristic "ordinary song" of the Oriole (*SS*);<sup>1</sup> and out of this in turn has come the longer and more beautiful mating-song (*SSS*) which is so often uttered on the wing. (This is, of course, only an outline sketch of the possible development of these songs, and I do not mean to imply that there were no intermediate stages.) Here we seem to have three stages in song-development still in existence. It is conceivable that a fourth may be added in future ages and that the first or the second may eventually be dropped from the Oriole's repertoire.

Having elaborated this theory at some length, I have to confess that it remains only a theory, and I ought, perhaps, to apologize for presenting it in its present "half-baked" condition. If my presentation of it, however, leads to the presentation of further evidence or argument in favor of Mr. Saunders's view, or if some one can show that "ordinary" songs and "mating" songs originated quite independently of each other, I shall be satisfied. One objection that may be raised to the theory of progressive improvement from *S* to *SS*, etc., is, of course, the marked differences

---

<sup>1</sup> I think I am justified in speaking of the Baltimore Oriole's "ordinary song," for though the song is subject to so much individual variation that hardly any two birds sing the same tune, yet its quality is highly characteristic; it is never to be mistaken for the song of any other species with which the Oriole is commonly found, and in that sense it is a very definite entity.



between the ordinary and the mating songs, the absence of connecting links. The Baltimore Oriole's ordinary song is not merely a slight advance over the single song-notes; it is a much more elaborate performance. If the former originated in the latter, there must have been intermediate stages. What has become of these? Why have they been lost in the process of song-evolution while the single song-notes persist? Perhaps because they would represent simply an inferior form of song and would have no place in the Oriole's life, while the separate notes can be uttered easily while the bird is feeding and can be used in a sort of conversational way when he is not moved to utter a set song. There may be similar reasons for the persistence in other cases of songs which retain a place in a bird's repertoire, while other, more advanced songs have given place to still others, still more advanced.

There is another consideration. Some of the special "mating-songs" are not merely more elaborate performances than the "ordinary songs" and thus clearly an advance upon them; they are ecstatic and confused, less orderly than the every-day songs, and are interspersed with call-notes and chattering. This is the case, sometimes at least, with the Baltimore Oriole. Such a song in its present condition could hardly be expected ever to become the regular song of the species. It would need to be modified and regulated — standardized, so to speak. I see no reason why this should not happen, but neither have I any proof that it does happen. This whole question of the relation of these two types of song to each other is a complicated one, and while I do not believe that Mr. Saunders has settled it, neither do I claim to have settled it myself. It may, indeed, prove that in this, as in some other matters, no one formula will apply universally, but that the nature and origins of the mating-songs are radically different in some species from what they are in others.

I have quoted Mr. Saunders as saying that "the ordinary song [of birds possessing also a special mating-song] is evidently not sung from sexual impulses, but is simply an outburst of vocal sounds expressing great vigor and joy of living." It would be more exact to say that the ordinary song is not sung from *conscious* sexual impulses — using the word "conscious" in no strict sense, of course. Those who believe with Mr. Saunders that "sexual selection is the



primary cause of the evolution of bird-song" must agree with Mr. Hawkins that the bird's "joy of living" itself arises out of the sexual impulse, and those of us who consider the evolution of song more complex must still trace its origins back to sexuality. Even without accepting the Freudian theories in their entirety, we must recognize the power of the primary instincts, and there can be little doubt that it is the reproductive instinct that accounts for bird-song, however various were the processes through which it was evolved.

---

## REVISION OF THE GENUS BUTHRAUPIS CABANIS.

BY THOMAS E. PENARD.

THE generic name *Buthraupis* was proposed, without designation of type, by Cabanis (Mus. Hein., i, 1850, p. 29) for *Tanagra montana* d'Orbigny and *Tanagra eximia* Boissonneau, with *Tanagra cucullata* Jardine listed as synonym of *B. eximia*. Subsequent writers have used either *T. montana* or *T. cucullata* as type of the genus. The first mention of a type, however, seems to have been by G. R. Gray (Cat. Gen. and Subgen. Birds, 1855, p. 73), who selected "*Tanagra montana* Lafr." [= *Tanagra montana* d'Orbigny, = *Aglaia montana* d'Orbigny and Lafresnaye], the first species listed by Cabanis under the new genus.

As at present understood, *Buthraupis* is a composite group. Ridgway (U. S. N. M., Bull. 50, pt. ii, 1902, p. 32) has called attention to the widely differing structural characters in its members, stating, however, that on the basis of the shape of the bill alone the genus could not be subdivided without making four groups, the first to include *B. cucullata* and *B. montana*, the second *B. arcæi* and *B. cæruleigularis*, the third *B. chloronota*, and the fourth *B. eximia*. He also called attention to the very much shorter tails in the group containing *B. arcæi* and *B. cæruleigularis*, but preferred to leave the genus with the usually assigned limits.





Allen, Francis H. 1919. "The Evolution of Bird-Song." *The Auk* 36, 528–536.  
<https://doi.org/10.2307/4073347>.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/54107>

**DOI:** <https://doi.org/10.2307/4073347>

**Permalink:** <https://www.biodiversitylibrary.org/partpdf/85974>

**Holding Institution**

Smithsonian Libraries and Archives

**Sponsored by**

Smithsonian

**Copyright & Reuse**

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.