Ritualization in Ontogeny. II. Ritualization in the Individual Development of Bird Song

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Ritualization in ontogeny. II. Ritualization in the individual development of bird song

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In my previous contribution, part I (pp. 311–319) I discussed some of the general principles involved in considering ritualization in ontogeny and referred specifically to the case of 'play' in animals. I now propose to discuss what is perhaps the second most remarkable example of ritualization—namely, that which is displayed by the development of song in a few groups of birds.

The main function of the full-song of many birds is to serve as a signal which is sufficiently stereotyped to function as a recognition mark *characteristic of the species*, and yet (within this overall fixity of pattern) capable of sufficient *individual* variation to differentiate one individual bird from another.

Chaffinches (*Fringilla coelebs*) reared in isolation produce an abnormally simple song. Experience thus plays a part in the development of the species' pattern. This experience particularly influences the selection of songs which will be imitated. It is as if in early spring the bird tailors its own song to match the patterns which it has heard. In the course of this imitative matching, one occasionally finds examples of a tendency, after a song has been developed from the subsong, for it to be further refined and stereotyped in the course of a few days or weeks of singing to make it 'tidier' and more precise. This often appears to be equivalent to the behavioural homeostasis—perhaps an example of the 'law of least effort' (Wheeler 1929; Tolman 1932) outlined in my previous contribution. But in these examples there is always the suspicion that this apparent homeostasis is nothing more than a gradual approximation to a pattern of song characteristic of the species and, therefore, probably genetically coded to a large extent. However, one sometimes sees this in the further development which takes place after an alien song has been learnt. As an example, if a hand-reared Chaffinch kept in auditory isolation is then taught, by tape playback, the song of a Tree Pipit—the notes of which are of similar tonal structure of those of the chaffinch—it will probably produce a fairly good copy of this although it will almost certainly reduce the overall length of song from 3 s or more to the 2·5 s which is the maximum normally found among chaffinch songs. However, even if a fairly good copy of a Tree Pipit (*Anthus t. trivialis*) song is achieved it may undergo further reduction and 'stream-lining', which consists in the elimination of unwanted frequencies, giving the song improved tonal purity (figure 1) (Thorpe 1958, 1961). But, even here one feels a little doubtful whether this 'stream-lining' is not in fact simply part of a process of approximation to a song pattern for which the bird has an innate proclivity.

Be this as it may, undoubtedly the best examples of ritualization in song behaviour are to be found in a few groups of birds in the tropics where an elaborate form of mutual vocal display occurs (Thorpe & North 1965). In this type of song the notes of the male and female are different, the sexes alternating so as to sing antiphonally, often with extraordinary precision. This is most in evidence in groups which live in dense scrub jungle or undergrowth. Presumably in such situations the visual display between members of a pair, so characteristic of birds of the temperate zones, is less effective; and so such display has been supplemented by mutual vocal display which may even come to exceed it in importance. Here, we do find what seems to be genuine ritualization, as the male and female work out their duets together.

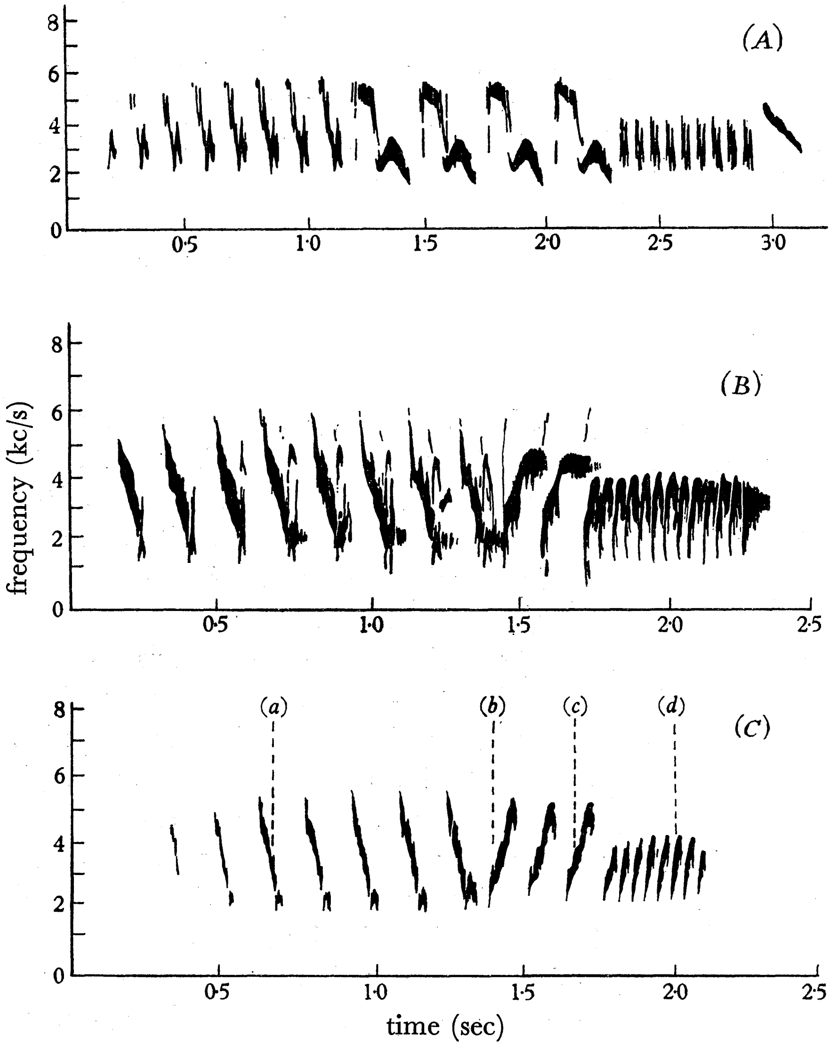

FIGURE 1. Learning, by Chaffinch (*Fringilla coelebs*), of song of Tree Pipit (*Anthus t. trivialis*) with subsequent simplification and better approximation to the model resulting from 'practice' after exposure to the model had ceased (Thorpe 1958). (*A*) Sound-spectrogram of tree pipit song used as a model for tuition by 'song tutor'. (*B*) Sound-spectrogram of hand-reared auditor isolate chaffinch imitating tree pipit's song after tutoring for three periods with song shown in (*A*) above. (*C*) Sound spectrogram of 'improved' tree pipit song produced by same chaffinch after a further period of practice without further hearing of the model.

Laniarius aethiopicus, the Tropical Bou-bou Shrike of Eastern Central Africa, provides one of the most interesting examples for our purposes. So far only a preliminary account of this work has been published (Thorpe & North 1965), but although a great deal remains to be done, a number of essential points already seem clear both in this species and in others of similar mode of life. In what follows I shall restrict myself to the one species. In this species *L. aethiopicus*, the duet is worked out during a long practice period (probably of many months) between a mated male and female in their territory. These duets are composed of notes, the quality of which is determined, no doubt, by hereditary constitution; but the pitch, timing and phrasing of which can, to a large extent be controlled very exactly, and can be varied by the singers as a result of this practice. It appears that, as also with some of the other species studied, (*a*) either sex can start and the other finish, (*b*) either bird can sing the whole pattern alone if the partner is absent, and (*c*) when the partner returns the two birds can either (i) duplicate in perfect time or (more usually) (ii) sing antiphonally again. Thus, it appears that in the course of duetting each individual bird has in fact learned the contribution of the other member and its relation to the whole. In the wild each pair of birds may have a considerable number of alternative duet patterns. Consequently, while some of the simpler patterns may be very widespread in a given population, some are likely to be peculiar to an individual pair. If this is correct, then the mate is that bird which can answer with the right pattern of notes in the right time. These

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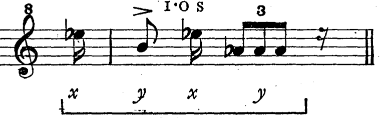

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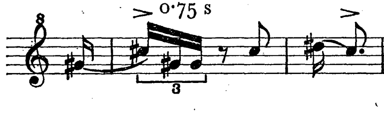

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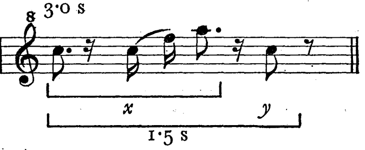

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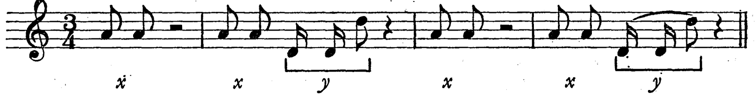

FIGURE 2. *Laniarius aethiopicus sublacteus*, Vipingo, Kilifi, Kenya, Dec. 1954. N.B. All the illustrations are given at approximately scientific pitch (middle 'C' = 256 c/s). Unless otherwise stated, as here, all the figures refer to race *major* (Thorpe & North 1965). N.B. The figure '8' above the treble clef symbol indicates that all that follows should be read as one octave higher than would otherwise be the case, *e.g.* middle 'C' becomes 512 c/s.

FIGURE 3. *L. aethiopicus*, Dundori, Nakuru, Kenya, 17 Mar. 1964 (Thorpe & North 1965).

FIGURE 4. *L. aethiopticus*, Kabale, Uganda, 15 Feb. 1962 (Thorpe & North 1965).

FIGURE 5. *L. aethiopicus*, Meadow Point, Lake Nakuru, Kenya, 17 Mar. 1964 (Thorpe & North 1965).

FIGURE 6. *L. aethiopicus*, Hippo Pool, Lake Nakuru, Kenya, 17 Mar. 1964. Note that this is a rather more elaborate duet than the previous ones. The contribution of the two birds is not indicated in this case since it seemed to vary a good deal (Thorpe & North 1965).

FIGURE 7. *L. aethiopicus mossambicus*, San Martino, Mozambique Coast (C. Haagner). The timing in this example is very precise but the bar length might vary between 0·75 and 1·5 s (Thorpe & North 1965).

FIGURE 8. *L. aethiopicus mossambicus*, San Martino, Mozambique Coast (C. Haagner). This is a duet with a more complex time pattern. Bar length 1·5 s (Thorpe & North 1965).

vocalizations have, of course, been recorded and analysed by means of the sound spectrograph, but with this particular species the notes are of such a pure flute-like quality that they can be rendered perfectly satisfactorily in ordinary musical notation, and consequently this method is adopted here instead of presenting the sound spectrograms. The illustrations very largely speak for themselves. Since it is usually impossible in the field to distinguish the sexes apart, the contribution of the two members of the pair are simply indicated as 'x' and 'y' rather than by the male and female signs. Rather more than 135 different duet patterns of race *major* of this species have been recorded and analysed. In addition, some recordings of other races have been obtained for comparison. The characteristic selection of these duet patterns almost entirely from sub-species *major* are shown here in illustration. Figures 2 to 8 show a characteristic selection, proceeding from the rather simple to the more complex. Note the way in which the total time taken by a duet can be varied considerably, even by a single pair of birds more or less irrespective of the number of notes which it contains. Note also, how the second bird may add or interpolate a single note within an already well-established pattern. Sometimes this note almost exactly duplicates one of the existing notes; in which case it can usually be distinguished only when the record is analysed by a sound spectrograph. At other times it can be distinctly heard as in figure 9k. With several of those species which sing antiphonally, trio-singing is sometimes observed. The meaning of this is at present quite obscure, though it in some ways recalls the well known 'visiting' of the Fulmar Petrel (*Fulmarus glacialis*) and the 'piping parties' of the Oyster-catcher (*Haematopus ostralegus*). In more than one instance of trio singing in *L. aethiopicus* besides the three birds partaking, a fourth bird was observed standing silently by; possibly the mate of no. 3. Figure 10 and 11 show examples of such triple performances. Trio singing is also very frequent in *Cossypha heuglini*, Heuglin's Robin Chat, and it may be more widespread amongst tropical birds than is at present suspected. At least we can say, that in *L. aethiopicus* both duetting and trio-singing reveal a highly sophisticated ritualization of song pattern, the details of which are almost entirely unrelated to any innate factors which may be concerned with song productions.

In a number of cases among song birds, particularly those in which songs of unusual richness and variety are known, we frequently encounter what appears to be musical 'invention'. This includes (*a*) re-arrangement of phrases, both innate and learnt, and (*b*) the invention of really 'new' material. It seems for instance that the individual Blackbird (*Turdus merula*) (Messmer & Messmer 1956), the Sprosser Nightingale (*Luscinia luscinia*) (Sotovalta 1956), the Indian Shama (*Copsychus malabaricus*) do produce new songs by the combination of phrases they have used before—some of which are probably inherited—others certainly learnt. Blackbirds are able to adopt patterns from their neighbours in a short time. In spring new compositions suddenly occur amongst the learnt patterns. In this way each male may obtain a repertoire of five to seven patterns, and the young birds sing a number of variations of their motifs. Hall-Craggs (1962) has followed in close detail the development of song in some wild blackbird individuals, and gives some striking examples of the development and elaboration of phrases to an extent which seems to suggest something similar to real musical invention. A characteristic example of her work is provided by figure 12. It seems then that while the duetting Shrikes provide perhaps the

FIGURE 9 (*a* to *q*). *L. aethiopicus*, Reed Inlet, Lake Nakuru, Kenya, 5 Sept. 1963. The separate figures *a* to *q* show the seventeen different duet patterns produced by a single pair of *L. ae. major* during the course of a single day. The last four patterns were transcribed in notation (see Myles North 1950). All the rest were recorded directly on tape. All were presumed to be duets but the distribution of the parts between '*x*' and '*y*' is only inserted where the evidence is clear. The expression 'chatter scold' denotes a characteristic harsh pulsed sound of wide frequency distribution. The term 'snarl' is expressive of a common note, not markedly pulsed, but with the energy though widely spread, showing a peak at the frequency indicated by the wavy line (Thorpe & North 1965).

clearest and perhaps most convincing cases of individual ritualization of song pattern—clear because it appears that the two birds are together working out motifs more elaborate and integrated than either bird can do singly—yet it may be that this form of ritualization is far more widely spread amongst the song birds than is yet realized.

10*a*

10*b*

11

FIGURE 10 (*a*, *b*). *L. aethiopicus*, Lake Bunyoni, Kabale, Uganda, 14 Feb. 1962. *a*, represents a duet pattern heard as a very long, precisely timed series. During one considerable stretch of this series a third bird '*z*' joined in. It was far away from the others but nevertheless inserted its single note remarkably accurately. *b*, it tended to intervene in every second duet of '*x*' and '*y*' (Thorpe & North 1965).

FIGURE 11. *L. aethiopicus*, Dundori, Nakuru, Kenya, 3 Apr. 1964. A remarkable trio. All three birds were in the same tree. Note that bird '*x*' gave a D sharp every 2 s and bird '*y*' a D sharp every other 2 s whilst bird '*z*' gave a G sharp and an A natural every other 2 s in alternation (Thorpe & North 1965).

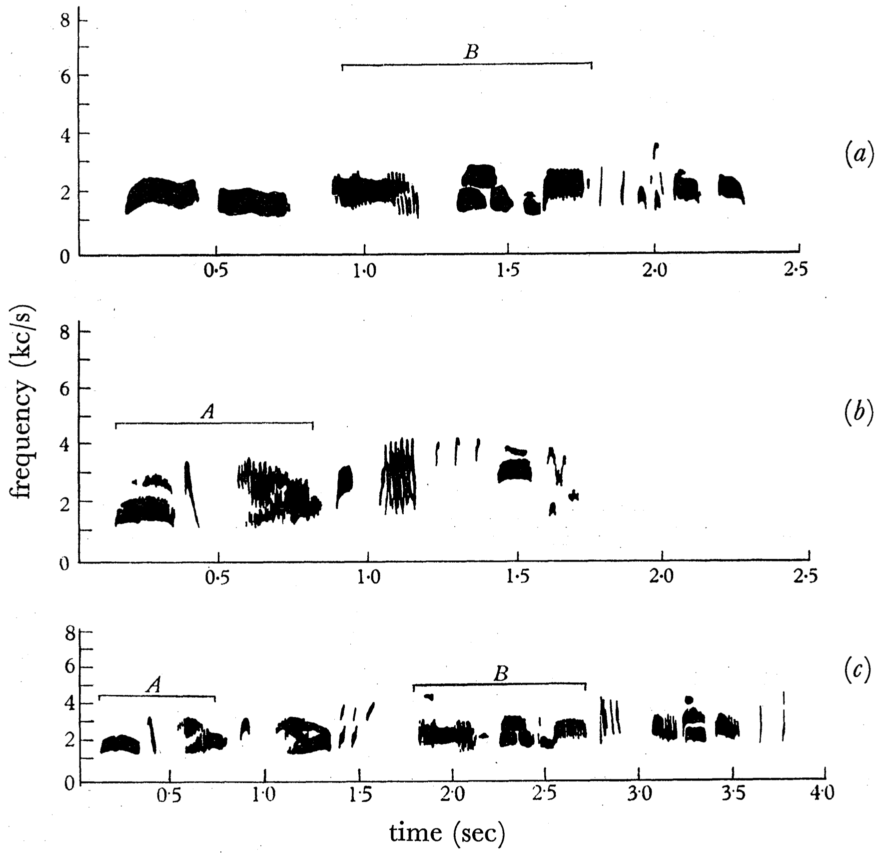

FIGURE 12. Records of song development in a single wild blackbird, showing the development and elaboration of an end phrase, suggesting musical invention. (*a*) Phrase 4; (*b*) phrase 17; (*c*) phrase 17/4, which includes parts of phrases 4 and 17 (Hall-Craggs 1962).

Such performances are ritualized in the true sense, in that the song becomes stereotyped and used as an 'agreed' social signal—as is shown by the way in which they are employed. Waite (1903) described how two tame Australian Magpies (*Gymnorhina tibican*) shared a 15-note tune, learned from a flute, so as to sing antiphonally; one bird always restricting itself to the first phrase and the other to the second. When bird no. 2 died no. 1 performed the whole tune which it had never been heard to do during the years the birds had been together. It was as if the survivor was calling its lost companion by name.

Much bird song in the tropics appears less aggressive then does that of the temperate regions. It often seems to have relatively little relation to territorial proclamation and defence. Since antiphonal song and also the development of the highest powers of vocal imitation (e.g. parrots and mynahs) are rather characteristic features of the tropics and sub-tropics, this would lend support to the view of Gwinner & Kneutgen (1962) that imitative ability may have a primary function in strengthening pair and social bonds. In *Laniarius* (Thorpe & North 1965) the ability of each bird to learn the normal contribution of its mate as well as its own enables it to use this appropriately for maintaining contact with the partner and probably for recalling him or her when absent. Recently a striking observation was made by one of us (W. H. T.). An older and well-established *L. aethiopicus* was provided, in a tropical aviary at Madingley, with a new associate, a female bird only just entering adulthood. After a few weeks antiphonal singing was in process of development. By the beginning of August 1965 it was still elementary, the contribution of the young female bing notably more squeaky and ill controlled than that of the older bird. On 11 August the female died suddenly. Immediately the survivor took to performing the whole duet pattern, including the perfectly imitated notes of the juvenile female, which it had never been heard to utter before (Thorpe & North 1966). Gwinner & Kneutgen (1962) came to a similar conclusion as a result of studies of three pairs of captive Shama (*Copsychus malabaricus*) and some captive Ravens (*Corvus corax*). Here the males and females each had sounds or song elements which were principally, if not exclusively, their own private utterances, and were not normally employed by their mates. When their partner was absent the remaining bird of the pair would produce the phrases normally reserved for his partner, as well as his own, with the result that the said partner would return as quickly as possible as if called by name. So at least in *Laniarius* these mutually ritualized performances appear to serve an important biological function.

Over and above this the 'musicality' of these songs of the Shrikes strikes all that hear them. This is partly because of the purity of tone and the low pitch compared with the song of most birds. Whether the musical tonal system employed and the manner of using it provides any justification for assuming the beginnings of a true artistic ability is still an open question. There are, in fact, good biological and physiological explanations of a great deal of bird song and sound production. It would, however, be dishonest to suggest that the biological theories at present available offer a complete explanation for *all* bird vocalizations. There are many instances of songs which seem to transcend biological requirements and to suggest that the bird is actively seeking a new auditory and vocal experience. Thus the twilight song of the Wood Pewee (*Myochanes virens*) (Craig 1943) appears to have no territorial function and is said to be independent of the breeding cycle. The daytime song of this species also continues long after the breeding season. A number of writers have stated that the song of late summer and autumn is, in many American song birds, 'superior' to that of the breeding season, and the song may at this period, not only lengthen and be further elaborated, but may sometimes show a complete change of pattern. These changes often seem, to our ears, to take the form of aesthetic improvement. Certainly in such cases there seems no obvious biological reason for the ritualization. Work on this matter is in progress, and the results are as yet far from clear, but it is certainly not yet possible to rule out the aesthetic argument.

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