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Ritualized Distinctiveness of Song in Closely Related Sympatric Species

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Ritualized distinctiveness of song in closely related sympatric species

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There are so-called sibling species in all groups of animals. Sibling species are species, which are very similar in appearance, they inhabit the same area, but they do not pair.

Let us take, for example, our two Tree Creepers, the Short-toed Tree Creeper and the Tree Creeper. Only specialists are able to distinguish these two species in the field without hearing them singing or calling. But the songs of the two species differ in quite a striking manner (figure 1).

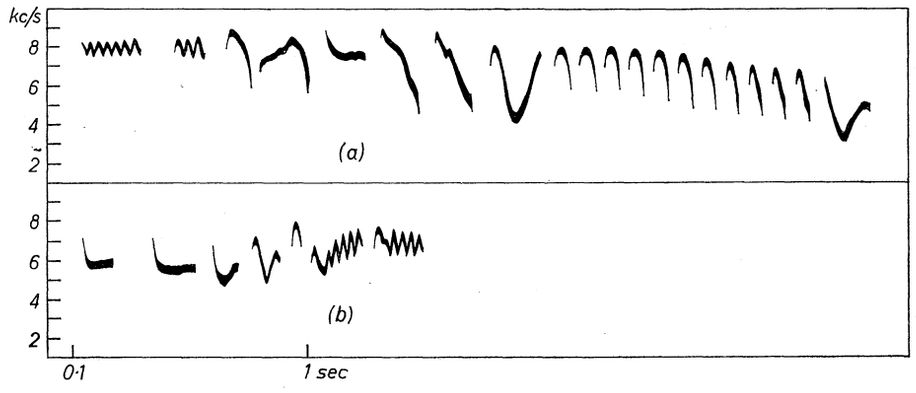

Figure 1. Song of (*a*) the Tree-Creeper and (*b*) Short-toed Tree Creeper.

The area of the Tree Creeper reaches from Japan to Middle Europe and England, while the Short-toed Tree Creeper lives in the north of Africa and in the south of Europe. In middle Europe both the species are to be found. The theory of Stresemann (1919) says that the area of the same ancestors of both species was divided into a western refuge and an eastern one by climate, for instance by the Glacial Period.

The two Tree Creeper species arose from this period of isolation. After a warmer period the new species came together without pairing.

But there is another explanation we have to discuss: the differences between the two forms after the secondary contact were not great enough to prevent pairing, but the vitality of the hybrids was reduced and so the isolating mechanisms increased during the secondary contact.

The second explanation is not probable with Tree Creepers, because there is no or little difference in singing between populations living in the area with both species present and in the other one without the sibling species, for instance in Spain, where only the Short-toed Tree Creeper lives (Thielcke 1965).

We find similar conditions about warblers. The Chiffchaff and the Willow Warbler are very similar in their outward appearance, but they sing quite differently (figure 2).

At all locations illustrated by dots, all Chiffchaffs sing in a similar way. But the Chiffchaffs

in Spain, Portugal, North Africa and in the Canary Islands sing in a quite different manner from our Chiffchaffs and Willow Warblers (figure 3). Willow Warblers are absent in Spain, and so the hypothesis arose that Spanish Chiffchaffs are able to sing like Willow

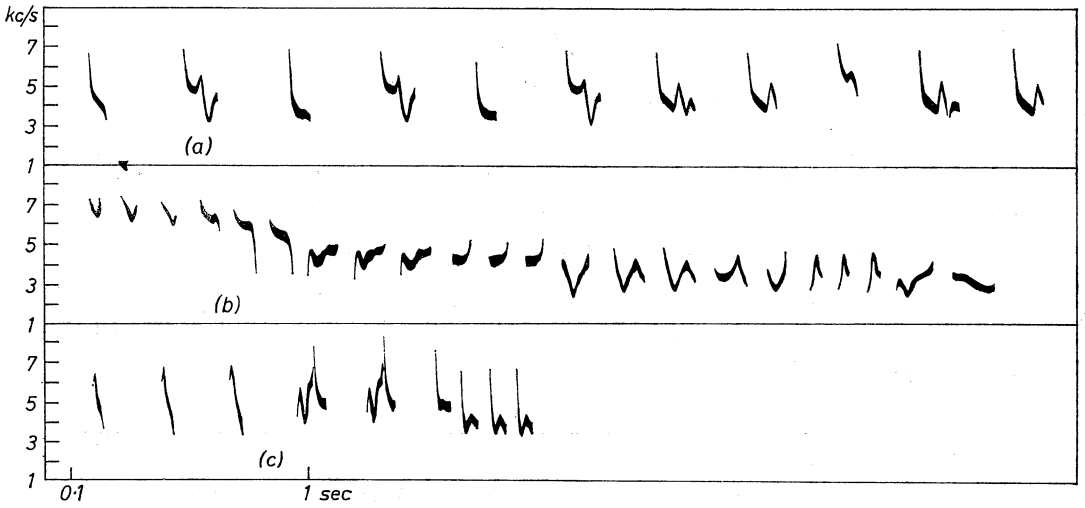

FIGURE 2. Song of (*a*) the Chiffchaff, (*b*) Willow Warbler and (*c*) Spanish Chiffchaff.

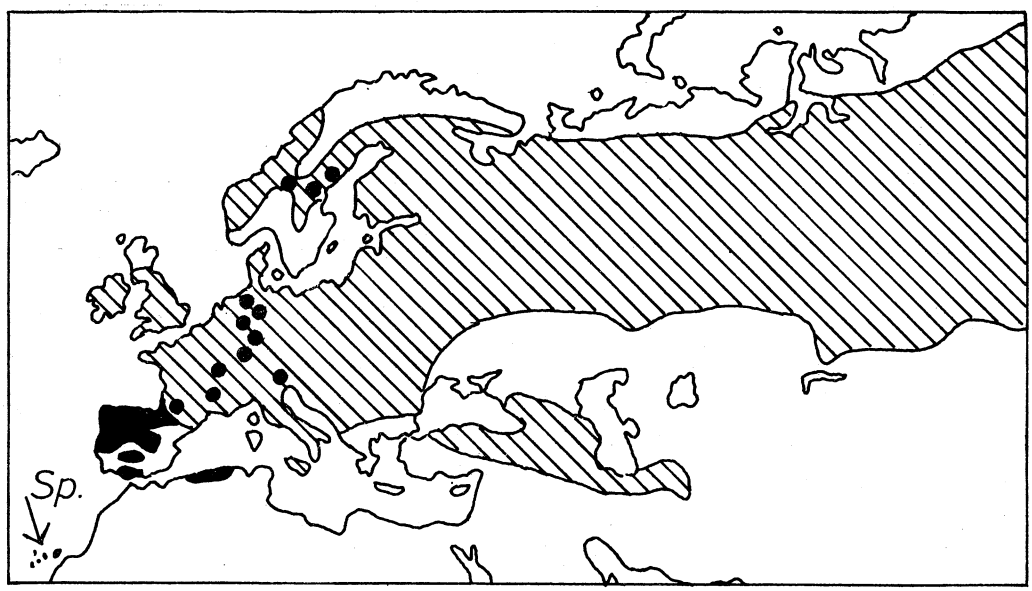

FIGURE 3. Distribution of the Chiffchaff. *Black*: 'Spanish' singing Chiffchaffs. *Hatched*: Distribution of the Chiffchaff outside of the Spanish–North African area (after Voous 1962). *Black dots:* Places where 'normal' singing Chiffchaffs were tape recorded.

Warblers because these are not to be found there. But this is not true, because Spanish Chiffchaffs do not sing like Willow Warblers. And there are other arguments against the hypothesis of arising isolation-mechanisms in the two species of warblers (Thielcke & Linsenmair 1963).

First, the south limit of the area of the Willow Warbler and the contact zone between Chiffchaff and 'Spanish' singing Chiffchaffs are not identical.

Secondly, the contact zone between the song forms of the Chiffchaff is very small. It is similar to contact zones of other species.

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In the same way the secondary contact zones between the Carrion Crow and the Hooded Crow are also very small and constant. According to Thönen (1962) the distribution of the two song forms of Willow Tits shows the same picture in Middle Europe. The one form is limited to the Alps and the other to the lowlands.

I believe that all these pictures of distribution have developed by secondary contact of the different forms.

But what has all this to do with ritualization? We know something about the 'raw material' of the song only of one species, and it seems that the song of the Short-toed Tree Creeper has arisen by ritualization.

The song of the Short-toed Tree Creeper contains elements which are very similar to

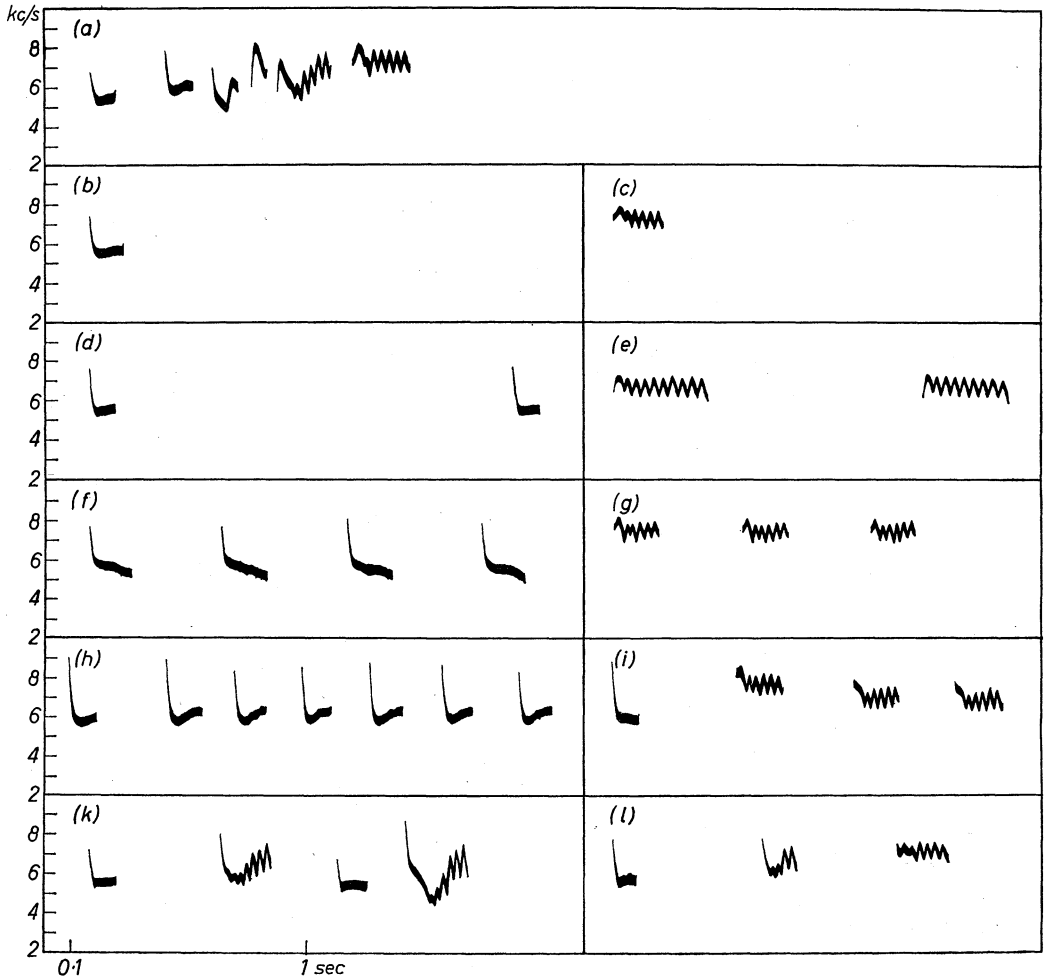

FIGURE 4. Song and sounds of the Short-toed Tree Creeper:
(*a*) 'Normal' song of the Short-toed Tree Creeper.
(*b*) Single tyt-sound, which is similar to the first three notes of the song.
(*c*) Single srih-sound, which is similar to the last note of the song.
(*d*) Slowly-lined tyt-sounds.
(*e*) Slowly-lined srih-sounds.
(*f*) Tyt-sounds quickly following each other.
(*g*) Srih-sounds quickly following each other.
(*h*) Tyt-sounds following each other at high speed.
(*i, k, l*) Examples for combinations of different sounds (after Thielcke 1964).

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sounds of the same species. Song and sounds have different social functions. The problem is, in which direction the influence is running during phylogeny: from the sounds to the songs, or from the songs to the sounds. It may be of help to answer this question by employing the characteristics of ritualization. According to Lorenz (1951), ritualized behaviour is characteristic for instance by fixation of variable series to a stereotypical one.

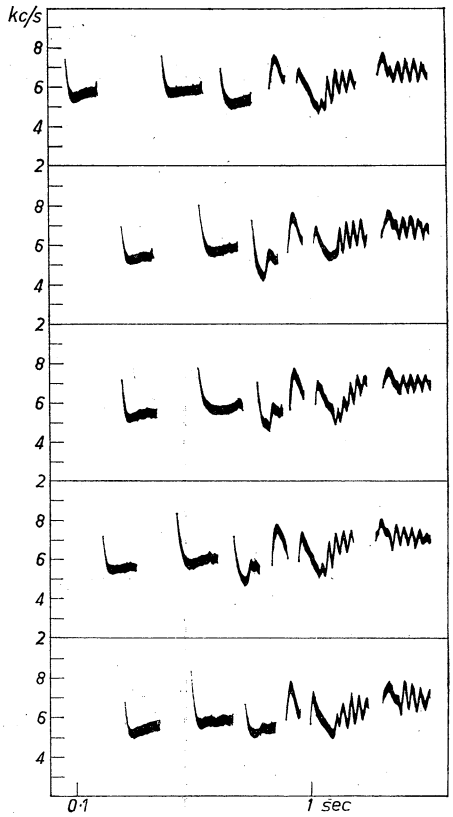

FIGURE 5. Song of five Short-toed Tree Creepers.

The call tyt of the Short-toed Tree Creeper (figure 4*b*) being similar to the first notes of its song may be uttered with great distances (figure 4*d*), with small distances (figure 4*f*) and with very small distances (figure 4*h*). You can see the same with the call srih (figure 4*c*, *e*, *g*), that is similar to another note of the song.

Furthermore, there are many combinations between different calls. Examples are to be seen here (figure 4*i*, *k*, *l*).

On the other hand, Short-toed Tree Creepers sing very similarly. Figure 5 illustrates the songs of five different individuals. So the influence seems to run from the calls to the songs, because the calls are variable, but the songs are stereotyped.

We get the same result comparing the last note of the Short-toed Tree Creeper's song with its homologous call (figure 6). The song elements are much more uniform than the call. And this is another character of ritualization (Morris 1957).

So I have found six characters which suggest an influence from the calls to the song and only one in the opposite direction. After this I believe that the song has its origin in the calls. This is the fact concerning the Short-toed Tree Creeper and perhaps other species too.

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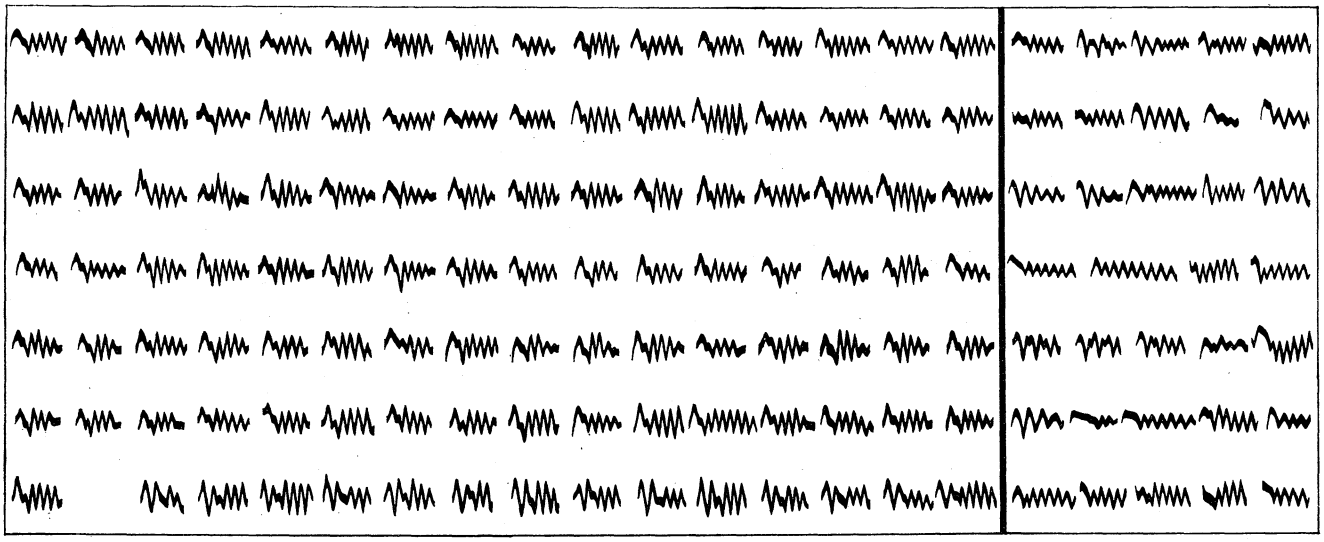

FIGURE 6. The last element of the song of the Short-toed Tree Creeper (left) and the homologous srih-sound of the Short-toed Tree Creeper (right).

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