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Neighbour-stranger Recognition Based on Song in the Japanese Bush Warbler (*Cettia diphone*)

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Abstract A field experiment to demonstrate the ability of male territorial Japanese Bush Warblers to 'recognize' their neighbours and strangers was performed. Both the neighbour song and the stranger song were played back to the territory owner from inside the neighour's territory, from which the neighbour bird was removed beforehand. When the neighbour song was played, the owner approached the speaker as close as the territory boundary and sang the type-H dominant, ordinary songs that he usually sings when patrolling in the territory. When the stranger song was played, however, the owner went beyond the boundary, approached close to the speaker and sang aggressive songs mainly composed of type-L songs. The results show that the owner can recognize neighbours by songs alone, and that if the neighbour is replaced by a stranger the owner ignores the previously established territory boundary and attacks that new male. The latter result suggests the possible advantage for the territory owner to sing individually distinct songs: if he sang unclear songs he would be attacked by his neighbours. It was pointed out that the occurrence of clear song-based neighbour recognition in the Japanese Bush Warbler is deeply related to its habitat; dense bush where birds cannot recognize individuals by visual keys, and therefore must rely on vocal communication for that purpose.

Key words Vocalization, Auditory communication, Species recognition, Aves, Passeriformes, Sylviidae

Introduction

Individual 'recognition' based on individually distinct differences in the signal structure is widespread among birds and is observed in many aspects of the life of birds such as interaction between mates (Brooke 1978), between parents and chicks (Beer 1969), and between territory owners who share the common boundary (Brooks & Falls 1975). The last one, commonly called neighbour-stranger recognition, gives an interesting problem of how the recognition or discrimination is achieved and maintained since most of the signals, namely the songs, are learned, and a wide variety in organization and complexity of signals is found among species.

Japanese Bush Warbler, *Cettia diphone*, is a common breeder of the secondary for-

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ests all over Japan and the nearby area. Males occupy large territories in the forest with dense undergrowth. The males sing loud, low, simple and stereotyped songs. Examining the song structure in a population of Bush Warblers, Momose (1988, 1999) revealed the following characteristics of the species' song system: [1] stable, short and loud song with small repertoire size (average 2.8, range 2-5), [2] neighbours tend to share some of the song patterns in their repertoires, [3] clear individual difference in the combination of the repertoire, which was mostly unique to each individual.

Maintaining large territories in the bush, birds must be able to recognize each other by vocal cues rather than by visual ones. Here I report the results of neighbour-stranger recognition experiments in this species as an example of clear neighbour-stranger recognition found in bird species with repertoire song system.

Materials and Methods

Neighbour-stranger recognition experiment was performed at Togakushi (Nagano Prefecture, 35°45′ N, 138°05′ E, Alt. 1220m) in Japan from May 30 to Jun 3, 1985. Five pairs of neighbouring males were used for the experiment. Although the exact breeding stages were not examined, most of them were probably in incubation or nestling period judging from the behaviour of females encountered during the experiment and other observations. All the birds were caught with mist net and colour-banded before the experiment. At least 90 minutes' early morning census was done beforehand for each male to determine his territory boundary. The songs of each male were tape-recorded during this period for use in the later playback experiment. The one of each two neighbouring males was used as the neighbour model and the other was used as the experimental bird (the territory owner). Songs of a stranger bird was recorded at about 4km away from the experimental area. Tapes of neighbour songs and the stranger songs were edited so that all had the same sequence, interval and loudness. Time intervals, sequence and the loudness of the songs were set to be roughly equal to that of the natural vocalization.

The experiments were done from 10 AM to 4 PM. During this period, the activity of Bush Warblers was low but constant. Time schedule of one experiment was as follows: 15 min silent period / 15 min playback of the neighbour songs / 15 min playback of the stranger songs / 15 min silent period. The speaker was placed inside the neighbour's territory 25m away from the territory boundary. To avoid disturbance from the real neighbour, the neighbour male was removed from the territory just before the experiment using the mist net, kept in a cotton bag during the experiment and released after the experiment. During the experiment, the observer recorded all the vocalizations of the territory owner and commented simultaneously the position of the bird each time the bird moved its position into the tape recorder.

Equipments for playback were : Sony WM-DD cassette tape recorder, a hand made amplifier and speaker system using a 15cm full range speaker unit. Equipments for recording were : Sony WM-DD cassette tape recorder, and Victor MU-510 shotgun microphone.

Results

Song type

Figure 1 shows an example of the songs used as the neighbour model and as one of the stranger models. In this case, the songs of the two birds were not very different from each other except the last note in H1 version of the song type-H. Figure 2 shows an example of the results of one experiment. The four graphs correspond to four 15-min experimental time blocks; (from the top) Silent, Neighbour song playback, Stranger song playback and silent period again. Each bar shows the number of three types of songs sang by the territory owner at different distances from the territory boundary and from the speaker, which was placed 25m away from the territory boundary. The dotted line in the centre indicates the boundary, owner's territory is on the left side of the figure and the neighbour's territory is on the right side. When the neighbour songs were played from inside the neighbour territory (the second graph from the top), the owner approached the speaker as close as the boundary, but did not cross it, and sang type-H dominant songs. When the stranger song was played back, however, the owner did cross the boundary, approached the speaker and sang type-L dominant songs.

Figure 3 shows the combined results of the five experiments. The measures of the response were as follows. Number of songs sang by the owner in 15 min, song type ratio, average distance from the speaker when the owner sang the songs and the total number of flights during 15 min. The song type ratio was calculated from the following equation.

Song Type Ratio Index = (H-L) / (H+L)
(H and L means the number of type-H and type-L songs)

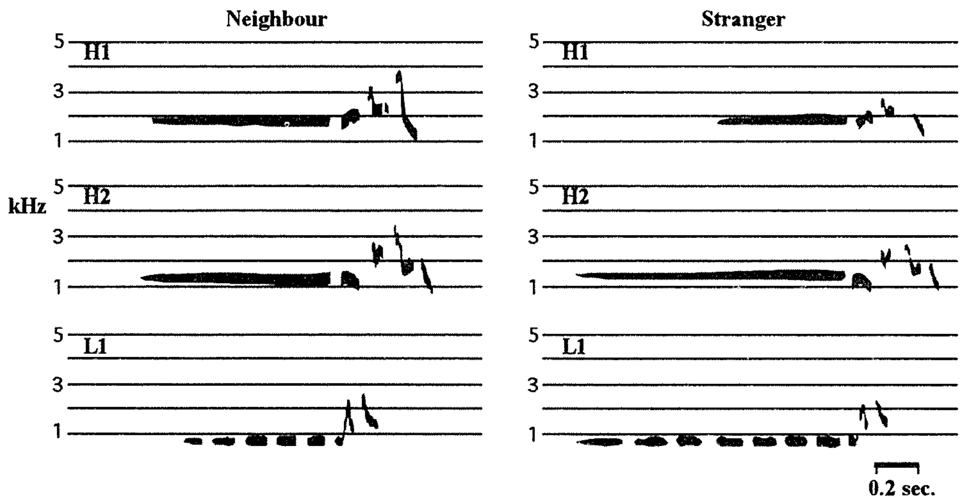

Fig. 1. Example of the songs used in the Neighbour-Stranger Recognition Experiment. The three sonograms shown in the left are the repertoire of a male used as 'Neighbour' bird. Songs in the right are the repertoire of a 'Stranger' male.

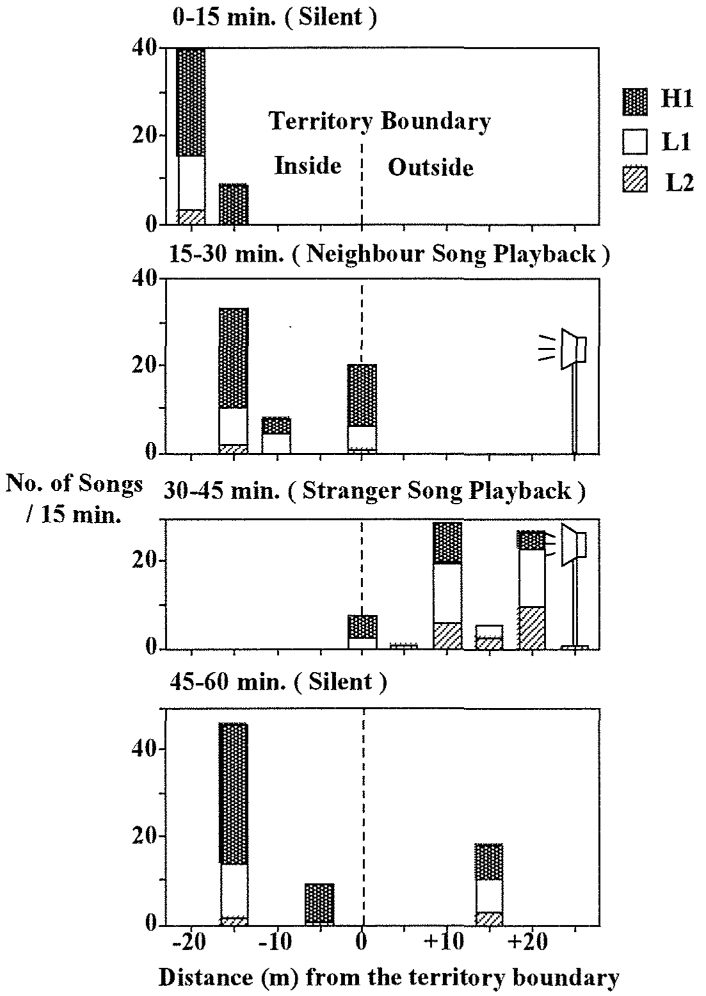

Fig. 2. An example of the Neighbour/Stranger Song Playback Experiment. The height of each column shows the number of songs sang by the experimental bird (territory owner) during each 15 min block using one of his three song types (H1, L1 and L2). The abscissa shows the distance from the territory boundary between the neighbour bird, which was removed from its territory during the experiment.

There were significant overall differences among the four 15 min blocks in all measures except number of songs (one way ANOVA $p<0.01$). Examining block to block differences revealed the stronger response to the stranger song playback than to the neighbour song playback and to the two silent periods in three measures other than number of songs ($p<0.01$ in song type ratio and distance from the speaker, $p<0.05$ in number of flights, T-test, two tailed). No significant difference was found between the initial silent period and the neighbour playback period.

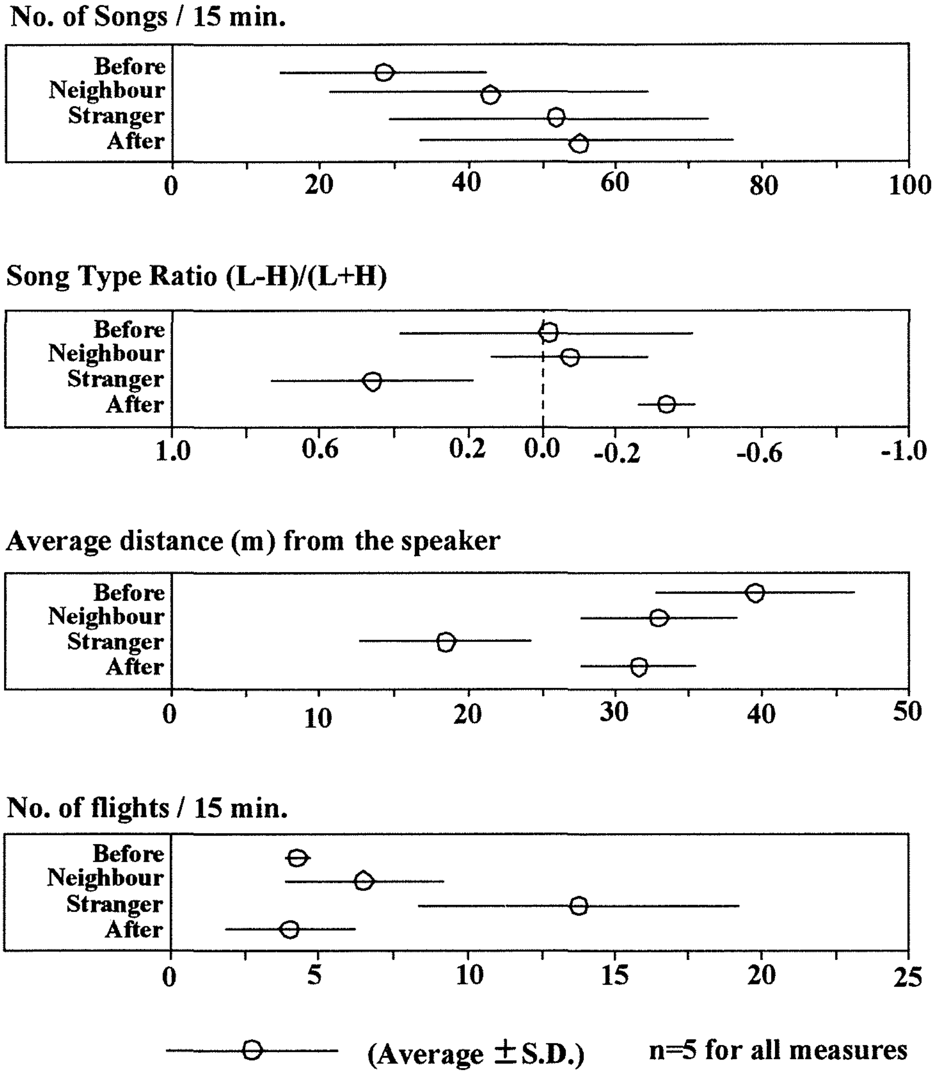

Fig. 3. Results of the Neighbour/Stranger Song Playback Experiment. The absissa shows the intensity of the response by the experimental birds (territory owners) measured by four different ways (No. of songs, Song type ratio, Average distance from the speaker, No. of flights). The four bars in each category corresponds to the four 15 min experimental blocks. 'Before' and 'After' correspond to the silent periods at the beginning and at the end of the experiment. 'Neighbour' and 'Stranger' correspond to the 15 min playback periods when the songs of the neighbour birds and a stranger bird were broadcasted from the loud speaker placed 25m inside the neighbour's territory.

Discussion

In this experiment, the order of model presentation was always neighbour-stranger, and the reverse was not tested. Although there were clear differences in the response of territory owners to neighbours and to strangers, stronger response to the stranger songs might be interpreted as a result of initial sensitization caused during the neighbour song playback period. This is not likely to be so. Another experiment in which only the stranger songs were played back from the neighbours' territory, the response occurred within five minutes in all cases (Momose in prep. a).

In all measures except number of songs, the response of the territory owner to the stranger was always stronger than to the neighbour. The owner responded to the stranger's song by changing the ratio of the two song types rather than by increasing the number of songs. In this species, changing the song type ratio seems to send a strong message than increasing overall song rate. In usual territory patrolling, the owner sings type-H dominant songs, but to an intruder, he sings mainly by type-L songs (Momose in prep. b). The song rate rather tends to be reduced during the song playback because the recipient bird (the territory owner) is busy flying around and searching for the intruder.

Falls (1982), reviewing the results of neighbour-stranger recognition experiments obtained from many species with different levels of song organization and complexity, argued that clear neighbour-stranger recognition is usually found in species with a single song type, discrimination is rather unclear in species with large song repertoire (repertoire size of 10 or more) and species with small repertoire size show somewhat intermediate results between the former two. This tendency is understandable when we consider the matching effort necessary to identify an individual, which must be parallel to the repertoire size.

In this respect, it is interesting that such a clear 'recognition' was found in the Japanese Bush Warbler, which is a 'repertoire' species. The result seems to suggest the existence of an individual recognition mechanism even in repertoire species. In the case of the Japanese Bush Warbler, individual difference lies in the combination of song patterns as a repertoire, for neighbours tend to share some of their song patterns. It is fairly easy for a human observer to identify an individual in the field by listening to the songs because the bird does not repeat the same pattern but tends to switch to other patterns (Momose 1999), and the entire repertoire can be monitored within a few minutes. If the repertoire size was larger, identification would become more difficult as found in other large repertoire species (Kroodsma 1976a).

Neighbour recognition seems to be one social factor that reduces repertoire size in forest-living passerine birds. Other aspects of social interaction favour large repertoire size such as attraction of mates (Kroodsma 1976b) or repulsion of intruding males (Krebs 1976, 1977). The Japanese Bush Warbler's case may be an example of a compromise between the repertoire singing and the necessity for accurate identification of an individual, and the small repertoire size (2-5) might be the optimal solution for this.

While the advantage of neighbour recognition is easily understood from the listeners point of view: territory owner can discriminate neighbours from strangers against whom he must fight intensively, that of the signal sender is less easily understood. Why must the owner sing individually distinct songs? The results of this experiment showed not only that males could recognize neighbours by songs alone but also showed that, when the neighbour is replaced by a stranger, the territory owner ignores the previously established territory boundary and attacks it. The latter result seems to suggest a possible advantage for a singer to sing individually distinct songs. If he sang unclear songs, he would be mistaken as a stranger and attacked by his neighbours. It also demonstrates another source of asymmetry between the territory owner and the intruder. Even if an intruder succeeds in taking over a territory, he still has to fight neighbours to determine new territory boundaries between them. So setting up a new territory becomes an even more difficult task for the intruder.

Maintaining a territory in a dense forest gives several difficult problems to the territory owner. The most vital of them seems to be the individual recognition. Living in the habitat of dense bush, the Japanese Bush Warblers tend to rely on vocal rather than visual signals even at close distances, and visual cues are virtually not usable in long range communication such as territory advertisement. The clear song based recognition of the neighbours found in the Japanese Bush Warblers might have evolved as an adaptation to the species' special habitat structure.

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