

Long-term memory of individual neighbours in a migratory songbird

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CAPABILITIES for long-term memory and recall of information have evolved in non-human animals primarily for special requirements such as for learning species-typical vocalizations and caching food¹⁻⁶. Long-term memory of individual social partners has, however, not been demonstrated previously for non-human animals. The ability to recognize individuals has important consequences for the evolution of intricate social interactions⁷⁻¹¹ and provides a basis for more sophisticated forms of cognition in animal societies^{12,13}. Recognition of social partners has been documented for territorial songbirds, which discriminate between songs of different neighbours¹⁴⁻¹⁶ as well as between the songs of strangers and neighbours¹⁷. Here I show that male hooded warblers (*Wilsonia citrina*, Parulidae) not only recognize their neighbours individually by song during the breeding season, but also retain the memory of neighbours' songs after an 8-month period during which they cease singing and migrate to Central America before they return to former breeding territories.

I studied 25 mated pairs of hooded warblers at Mason Farm Biological Reserve, Chapel Hill, North Carolina, from 1987 to 1989. Males in this population returned from migration in April and established territorial boundaries with neighbouring males. During territorial establishment, I tape-recorded each male on at least two separate occasions. I mapped all boundaries by noting locations of singing and encounters between neighbouring males.

In 1988, playbacks of the tape-recordings demonstrated that males recognized each other individually by song. Hooded warblers in this population, like related species¹⁸, had repertoires of 2-9 song patterns used in two modes of singing. In the first mode, which predominated early in the breeding season, each male sang a single, individually distinctive pattern repeatedly (Fig. 1). For each male, I prepared a 3-min tape simulating the repeat mode of singing with six songs per minute. During May, I played tapes of two neighbouring males' songs to each of 12 male subjects from locations 15-20 m inside the subject's territory (Fig. 2). Each neighbour's song was presented near both correct and opposite boundaries of the subject's territory (N and XN playbacks, respectively).

To standardize the subject's behaviour and to ensure that he was within hearing distance, playbacks began only after the

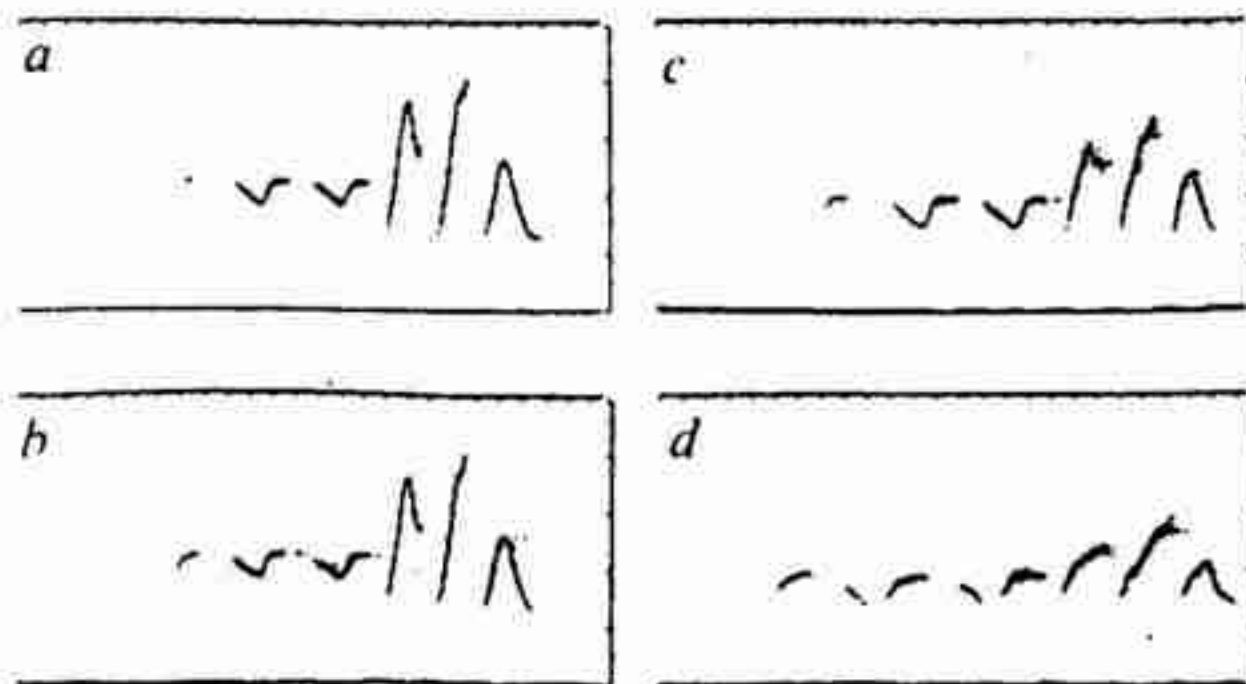


FIG. 1 Spectrograms (vertical divisions, 2 kHz; horizontal divisions, 61.5 ms) of song patterns used by three hooded warblers. *a, b*, Songs used in the repeat mode by the same male recorded on different days. *c, d*, Songs used in the repeat mode by two neighbouring males.

subject had been singing for 3 min, 25 to 50 m from the speaker. Because the playback simulated a neighbour's singing, both the neighbour, whose song was used for playback, and the opposite neighbour, whose boundary was to be used for the XN test, had to be silent before playback could begin. For 3 min during the playback and for 9 min afterwards, I noted the subject's songs, flights, total time in the vicinity of, and closest approach to, the speaker.

Males approached more rapidly and spent more time near the speaker both during and after XN than N playbacks (Fig. 3). Males responding to XN playbacks often flew back and forth, as if looking for the intruder, and perched frequently on or near the speaker. Because these responses are probably not independent, I used principal component analysis to compute a composite score. One-way analysis of variance on these scores confirmed that males responded more strongly to XN playbacks (trial 1: $F_{1,22} = 18.028$, $P < 0.001$; trial 2: $F_{1,22} = 19.85$, $P < 0.001$). I conclude that males learned to associate each neighbour's song with its usual location, a form of individual recognition.

As in other migratory species¹⁹⁻²¹, returning male hooded warblers that had held adjacent territories in previous years engaged in fewer and less intense interactions than did males with new opponents. This reduction in interactions could result from mutual recognition of former territorial boundaries or of former neighbours. Recognition of neighbours' songs, however, would require memory of their characteristics for at least 8 months, as there is no evidence that neighbouring males either migrate together or sing in Central America²². Playback experiments in 1989 demonstrated that returning male hooded warblers

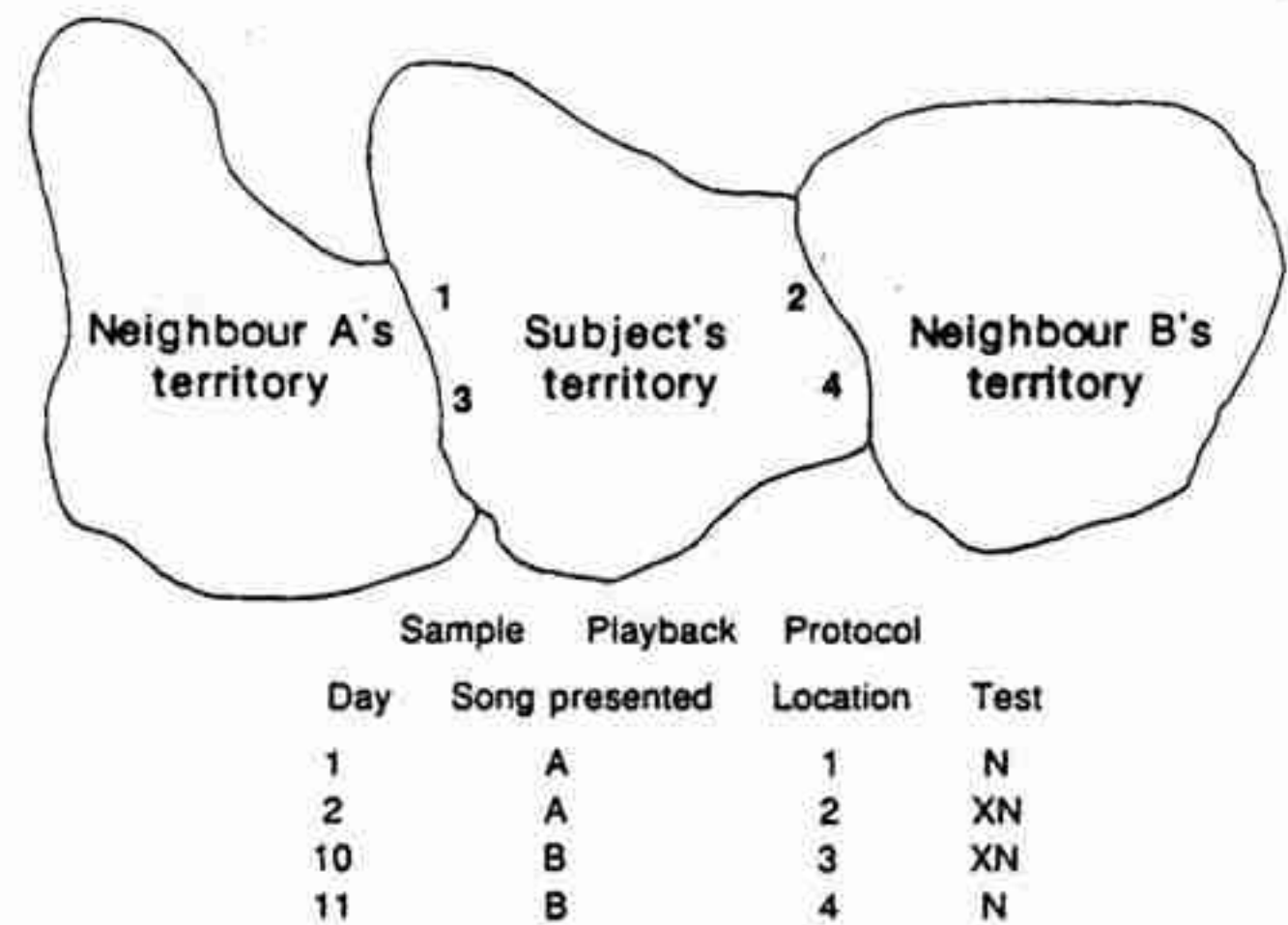


FIG. 2 Schematic representation of the experimental protocol. The enclosed areas are territories of a subject and two neighbours, A and B. Each neighbour's song was presented twice, once near the boundary that the subject shared with that neighbour (neighbour test; N) and once near the boundary on the opposite side of the subject's territory (cross-neighbour; XN). For the first playback, location 1 was selected 15 to 20 m inside the subject's territory, the speaker was placed 2-2.5 m above the ground and connected with a 20-m lead to the monitor output of a Sony TC-D5M recorder. All playbacks were standardized at 90 dB 1 m away, a level typical for singing birds. A coin toss then determined which neighbour's song would be played, with the constraint that equal numbers of subjects received XN and N playbacks first. On the next day at the same time, the same tape was played back on the opposite side of the subject's territory at location 2. Twice playbacks attracted a neighbouring male who interacted with the subject. These playbacks were terminated and repeated 5 days later. For these tests, 12 different playback tapes were used for the 12 subjects. Seven to ten days later, similar tests with each subject used the songs of the other neighbour at locations 3 and 4, 5-10 m away from the previous locations in order to reduce the possibility of subjects' becoming sensitized to specific locations. The complete experiment included 16 different playback tapes: the total is less than 24 (12 subjects \times 2 neighbours each) because some subjects shared neighbours.

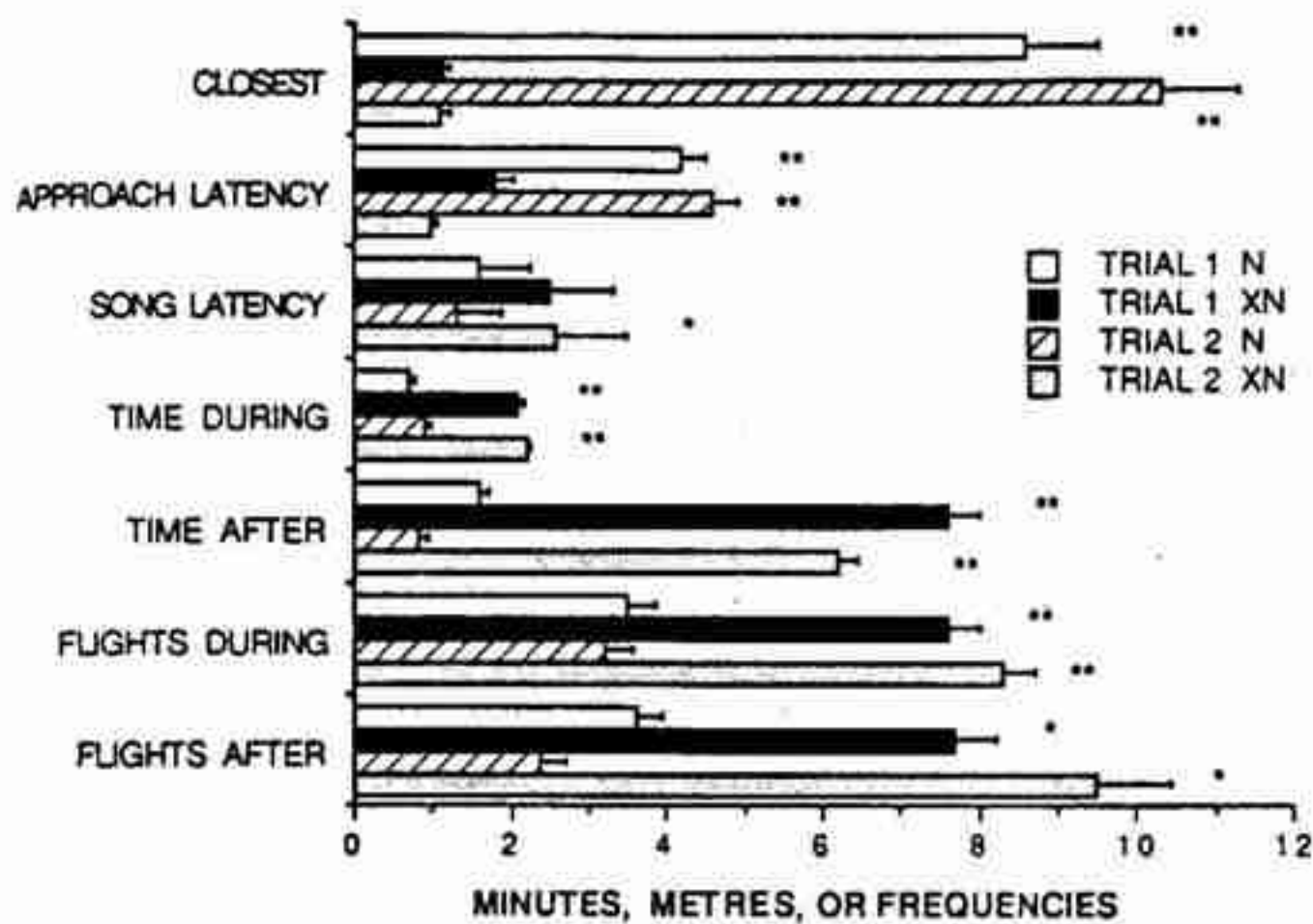


FIG. 3 Average responses and standard errors for male hooded warblers responding to playbacks of neighbours' songs on the correct (N) and opposite (XN) boundaries of the subjects' territories. Responses to current year's neighbours ($N=12$), with the first series of N and XN tests (trial 1) separated from the second series (trial 2, 7–10 days later). Responses are the closest approach to the speaker (m/2), latency (min) to approach the speaker within 10 m, latency (min) to the first song (responding males usually approached the speaker quietly and only began singing after the playback ended, whereas males that did not respond usually continued singing in the same manner as before the playback), time (min) spent within 10 m of the speaker during and for 9 min after the playback, and the number of flights during and after the playback. A strong response is indicated by small values for closest approach and latency to approach and large values for the other five measures. **, $P < 0.01$, Wilcoxon matched-pairs test (1-tailed); *, $P < 0.05$, Wilcoxon matched-pairs test (1-tailed).

remembered their individual neighbours' songs from year to year.

Of 17 males with mapped territories in 1988, seven returned on different days in 1989. Of these, five had had territories with at least two contiguous neighbours. On the day of his return, as detected by daily surveys of the study area, I presented each male with a 3-min tape of a neighbour's songs from the previous year at each of two locations, 15–20 m inside a correct and an opposite boundary from the previous year. Playbacks at the two locations took place one hour apart, with the order of presentation alternated (three subjects heard XN first, two heard N first); otherwise procedures followed those described above. Only one male had a neighbour in an adjacent territory at the time of playback.

If males remembered only former boundaries, I expected no difference between responses to N and XN presentations. But if males remembered both former neighbours' songs and their proper locations, I expected a greater response to XN playbacks,

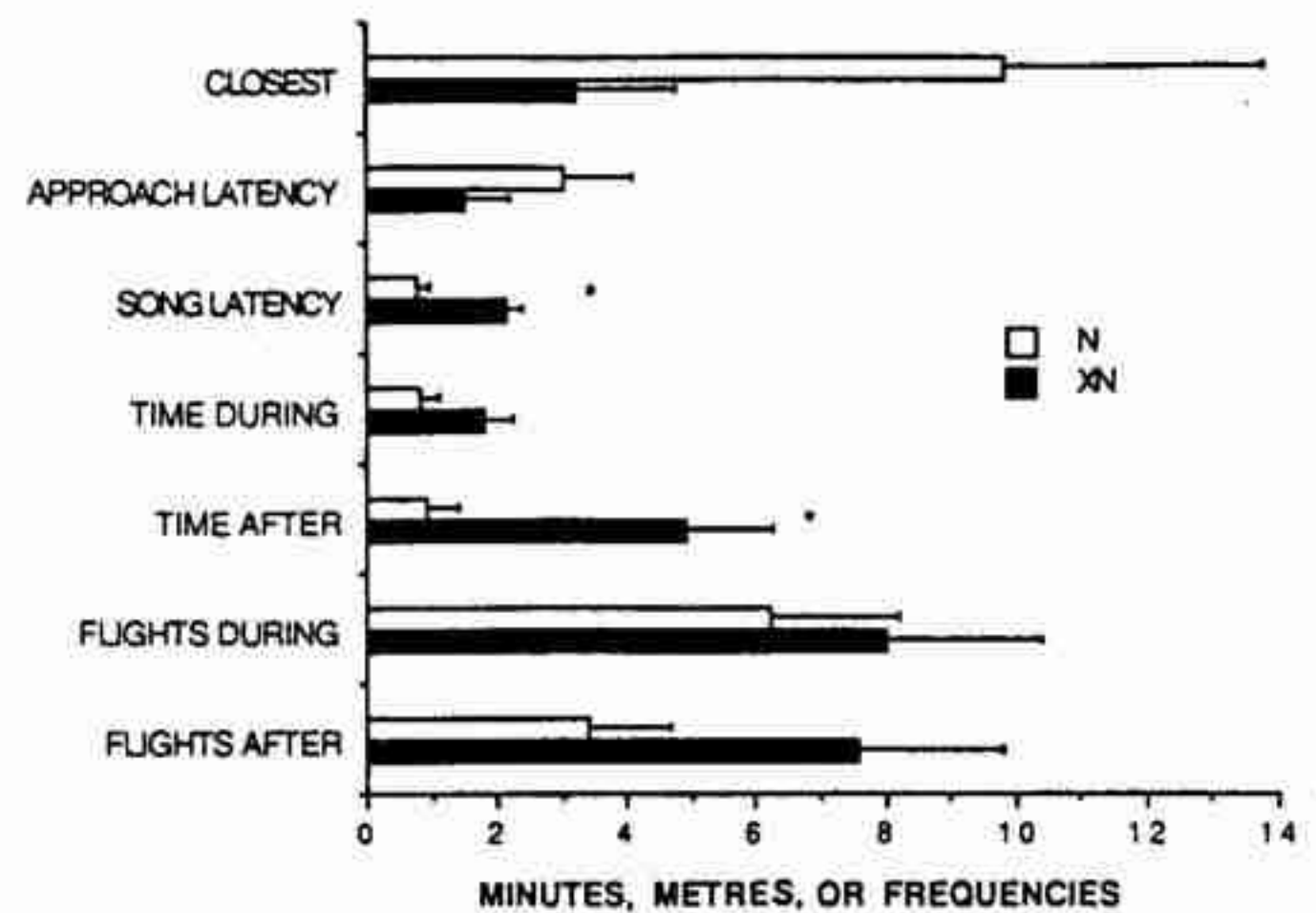


FIG. 4 Average responses and standard errors for male hooded warblers responding to N and XN playbacks of the previous year's neighbours ($N=5$). Responses measured are the same as those described in Fig. 3. * $P < 0.05$, Wilcoxon matched-pairs test (1-tailed).

as these might indicate a former neighbour attempting to expand his territory.

All differences in measured responses to N and XN playbacks resembled those in the 1988 experiment (Figs 3 and 4). A one-way analysis of variance on the composite scores derived from principal component analysis confirmed that males responded more to XN playbacks ($F_{1,8} = 8.017$, $P < 0.021$). I thus conclude that hooded warblers not only learned to associate different neighbours' songs with accustomed locations, but also remembered and recalled these associations after eight months without singing.

Recognition of neighbours, as demonstrated by a stronger response to XN playback, could be explained by habituation. But hooded warblers returning from migration had not heard neighbours' singing for 8 months, yet they responded more strongly to XN playbacks. This finding supports a previous report that recognition of neighbours involves associative learning, rather than habituation²³.

Long-term recognition of individual neighbours might provide immediate benefits in reproduction. Establishment and defence of territorial boundaries take time that males could spend attracting mates. If males with familiar neighbours can spend more time courting females, it would benefit them to return to their former territories and to remember neighbours²⁴. It thus seems plausible that long-term memory and recall of individual neighbours might represent an evolutionary adaptation in cognitive abilities in migratory species like the hooded warbler. □

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