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Individual recognition of song repertoires in two wood warblers

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Abstract We examined recognition of individual neighbors in hooded warblers (*Wilsonia citrina*) and Kentucky warblers (*Oporornis formosus*) by comparing responses to playbacks of neighbors' songs from appropriate and inappropriate boundaries of the subjects' territories. Kentucky warblers, which sing one song type each, responded more strongly to the songs of neighbors broadcast from incorrect than from correct boundaries. Hooded warblers use their repertoires of three to nine song types in two distinct modes of singing: repeat mode involves repeated presentation of one song type; mixed mode involves presentation of two or more song types in irregular sequence. Playbacks of neighbors' mixed-mode songs from appropriate and inappropriate boundaries indicated capabilities of individual recognition similar to those reported previously for repeat-mode songs (Godard 1991) and to those of Kentucky warblers. Repertoires of moderate size, therefore, have no pronounced influence on eventual recognition of individual neighbors in hooded warblers.

Key words Song recognition · Kentucky warblers · Hooded warblers · Repertoires

Introduction

Many studies have documented the ability of territorial male songbirds to discriminate between the songs of neighbors and strangers (for reviews see Falls 1982; Ydenberg et al. 1988). The subjects in these studies responded more vigorously to playbacks of recorded songs of strange birds than to those of neighbors near

appropriate boundaries. An adaptive explanation for differing responses could be that strange birds, unaware of existing boundaries, pose an immediate threat to subjects' territories and require prompt investigation by the territorial owners. On the other hand, familiar birds singing near established boundaries might pose less of an immediate threat.

As individuals' repertoires of song types increase, discrimination between neighbors and strangers presumably becomes more difficult. In some studies, species with large repertoires showed fewer differences in responses to playbacks of neighbors' and strangers' songs than did those with smaller repertoires (Kroodsma 1976; Falls and d'Agincourt 1981; Searcy et al. 1981). Other studies, however, indicated that repertoire size did not influence the ability to discriminate between neighbors' and strangers' songs (Stoddard et al. 1990; Weary et al. 1992). Weary et al. (1992) examined the effects of repertoire size on neighbor/stranger discrimination both within and between closely related species, American redstarts *Setophaga ruticilla* and yellow warblers *Dendroica petechia*. Like many warblers (Lein 1978; Lemon et al. 1987; Kroodsma 1988; Kroodsma et al. 1989; Spector 1992), these species sing both a mixture of different songs (serial or mixed mode) and a single repeated song (repeat mode). Both species were equally able to discriminate between neighbors' and strangers' songs presented in either mode. Moreover, the species with the larger repertoire, the yellow warbler, showed discrimination as strong as the species with the smaller repertoire.

Playbacks of neighbors' and strangers' songs provide evidence for a binary differentiation between two classes of opponents, familiar and unfamiliar. These experiments do not demonstrate recognition of individual neighbors, a more complex task and a prerequisite for more complex social behavior (Axelrod and Hamilton 1981; Archawaranon et al. 1991).

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Tests for individual recognition of territorial neighbors have compared responses to playbacks of neighbors' songs broadcast from appropriate (shared) and inappropriate (opposite) boundaries. In six of the eight such studies, subjects responded more to the songs of neighbors when they were broadcast from inappropriate boundaries than from appropriate ones (positive results: Falls and Brooks 1975; Wiley and Wiley 1977; McGregor and Avery 1986; Brindley 1991; Stoddard et al. 1991; Godard 1991; negative results: Schroeder and Wiley 1983; Godard 1993a). These studies thus indicate that subjects associate each neighbor's songs with their usual locations, a form of individual recognition.

These studies provide conflicting evidence concerning effects of repertoire size on individual recognition of territorial neighbors. White-throated sparrows, *Zonotrichia albicollis*, each with one distinctive song, can recognize the songs of their individual neighbors (Falls and Brooks 1975). Using the same methodology, Stoddard et al. (1991) demonstrated individual recognition of neighbors by song sparrows *Melospiza melodia*, a closely related species with a repertoire of eight songs per male on average. Apparently repertoire size does not prevent individual recognition in song sparrows (but see Searcy et al. 1981). However, studies of tufted titmice *Parus bicolor* (Schroeder and Wiley 1983; repertoire size 8–12 songs per male) and great tits *Parus major* (McGregor and Avery 1986; repertoire size 1–5 songs per male) suggest that repertoire size might affect individual recognition, as great tits recognize their individual neighbors while tufted titmice do not.

Two other studies demonstrate individual recognition of neighbors in species with repertoires: striped-back wrens *Campylorhynchus nuchalis* (Wiley and Wiley 1977, repertoire size 5+ duet patterns per pair) and European robins *Erithacus rubecula* (Brindley 1991, repertoire size 100–250 phrases per individual). Both species, however, remain in or near their breeding territories year-round. The duration of neighbors' associations could affect the learning of opponents' songs. Red-eyed vireos *Vireo olivaceus*, a migratory species with large repertoires, do not recognize individual neighbors' songs (Godard 1993a).

Comparison of results from studies of different species with more or less different procedures raises many problems (Krebs and Kroodsma 1980; Kroodsma 1982; Weary et al. 1992). As Weary et al. (1992) indicate, species that sometimes sing a mixture of different songs and at other times sing only one song repeatedly make ideal subjects for a test of the effects of repertoire size on recognition.

Hooded warblers *Wilsonia citrina*, like other Parulinae, have two modes of singing (Wiley et al. 1994). A previous report showed that territorial males can recognize individual neighbors singing in repeat mode (Godard 1991). We now report similar experi-

ments on individual recognition of neighbors singing in mixed mode. In addition, we use the same procedures to investigate individual recognition of neighbors in Kentucky warblers *Oporornis formosus*, each of which sings only one song (Tsipoura and Morton 1988).

Materials and methods

Study area

The study area in the Mason Farm Biological Reserve in Chapel Hill, North Carolina, is a bottomland oak-hickory forest with a dense shrub understory. Stakes located every 25–50 m on a grid facilitated accurate mapping of the birds' territories. In 1988, we mapped territories of 19 hooded warblers and 12 Kentucky warblers by noting frequently used singing posts and locations of boundary encounters. We also recorded the repertoires of these birds with a Sony TC-D5M recorder and a Sennheiser K3 U/ME88 ultra-directional microphone.

Hooded warblers in this population had repertoires ranging from three to nine song types with an average of 4.5. Each male used one song-type almost exclusively for singing in repeat mode (Wiley et al. 1994). Repeat mode singing occurred throughout the breeding season, but it predominated early in the breeding season before the arrival of females. Mixed mode, on the other hand, involved singing an irregular sequence of two or more song types (Wiley et al. 1994). In almost all cases these song types differed from those used in repeat mode singing. Males sang in mixed mode throughout the breeding season. Each male Kentucky warbler had only one individually distinctive song.

General experimental protocol

To test for individual recognition by territorial males, we broadcast the songs of a neighbor from the boundary shared with the subject (neighbor playback; N) and from a boundary on the opposite side of the subject's territory (cross-neighbor playback; XN). For convenience, these locations are also called the appropriate or correct boundary and the inappropriate or incorrect boundary. We set the playback speaker 10–15 m inside the subject's territory, 2–2.5 m above the ground, connected with a 20-m lead to a PermaPower S-702 amplifier and a Sony TC-D5M recorder. All playbacks were standardized at 90 db at 1 m in a virtually anechoic environment (in a large field with 1-m-deep vegetation). On the first playback to each subject, after the speaker had been placed in position, a coin toss determined which neighbor's song would be played, subject to the constraint that equal numbers of subjects received XN and N playbacks first.

In order to insure that the subject heard the playback and to standardize its behavior, we began a playback only after we heard the subject singing or calling for 3 min 25–75 m from the speaker. As these playbacks simulated a slight intrusion by a neighbor into the subject's territory, we also required that both the neighbor whose song was used in the playback and the neighbor from whose boundary the song was being broadcast be quiet. After these conditions were met, we played the recorded songs for 3 min. During the playback and for 9 min afterwards, we recorded the subject's behavior every 5 s. Behavior noted included number of vocalizations (songs or calls), song type, distance from the speaker, and the number of flights > 2 m. All playbacks were conducted between 5:30 a.m. and 12:30 p.m. EST.

On the following day at approximately the same time, the same tape was played on the opposite side of the subject's territory, again only after the above preconditions were met. Thus each subject received one N and one XN test with the same neighbor's songs (trial 1).

Seven to twelve days later, we carried out similar tests with the same subjects, but we used the songs of the other neighbors, those whose boundaries were used in the earlier XN playbacks (trial 2). The speaker was placed 5–10 m from the previous playback sites in order to reduce the possibility of subjects' becoming sensitized to specific locations.

Specifics of experiments

Hooded warblers were tested for individual recognition with both repeat-mode and mixed-mode songs. The experiments with repeat-mode songs conducted during 5–19 May were described by Godard (1991).

Experiments with neighbors' mixed-mode songs were conducted from 6 to 20 June. For each male, we selected 1 min of cleanly recorded singing with two song types in mixed mode. This segment was used to produce a 3-min playback tape with 8–12 songs/min, the normal rate for mixed-mode singing (Wiley et al. 1995). Eight males were tested for recognition of neighbors' mixed-mode songs following the protocol for N/XN tests described above. On three occasions the subject interacted with the neighboring male during playback. These playbacks were terminated and repeated 4 days later. A total of ten tapes was used as some of these males shared neighbors.

Kentucky warblers arrived on the study area 1–2 weeks after hooded warblers. From 21 May to 2 June, we used seven Kentucky warblers as subjects in N/XN tests following the protocol described above. The number of Kentucky warblers was less than the study population of 12 because only 7 had at least two neighbors, a necessary qualification for this experiment. Most of the subjects had mates beginning incubation. We selected clean songs from recordings of these Kentucky warblers and used them to make a 3-min playback tape with 3–4 songs/min (the normal rate) for all neighboring males. A total of 10 tapes was used in the experiment as some males shared neighbors.

Results

As described previously (Godard 1991), hooded warblers responded more strongly to the repeat-mode

songs of their neighbors broadcast from an incorrect boundary than from the correct boundary. Hooded warblers also responded more strongly to their neighbors' mixed-mode songs when broadcast from an incorrect boundary than from the correct one (Fig. 1). In tests using neighbors' mixed-mode songs, males approached more rapidly and came closer to the speaker in response to the XN than the N playback. They also were more active (number of flights) in the vicinity of the playback speaker both during and after the XN playback. As these responses were not independent, we used principal component analysis of the measures of response to determine a composite score. Wilcoxon tests of the first principal component scores revealed a significant difference between responses to N and XN playbacks for both trials (trial 1, $T = 1$, $n = 8$, $P < 0.01$; trial 2, $T = 0$, $n = 8$, $P < 0.01$).

Kentucky warblers also showed stronger responses to neighbors' songs broadcast from incorrect, rather than correct, boundaries (Fig. 2). Wilcoxon tests on the first principal component scores revealed a significant difference between responses to N and XN playbacks for trial 1 ($T = 0$, $n = 6$, $P < 0.02$) and the difference nearly approached significance for trial 2 ($T = 4$, $n = 7$, $P = 0.055$).

Discussion

The results show that territorial males of both species can recognize individual neighbors' songs. All of the measured responses were more intense to a neighbor singing from an inappropriate boundary (XN) than from an appropriate boundary (N). In fact, more of the behavioral responses were significantly different

Fig. 1 Mean responses (+ SE) of hooded warblers to playbacks of their neighbors' mixed-mode songs from the correct (neighbor: N) and incorrect (cross-neighbor: XN) boundaries. Responses are the closest approach to the speaker, latency to approach the speaker, time within 10 m of the speaker during and after playback, and the number of flights > 1 m during and after playback. A strong response is indicated by a small value for the first two measurements and large values for the other four

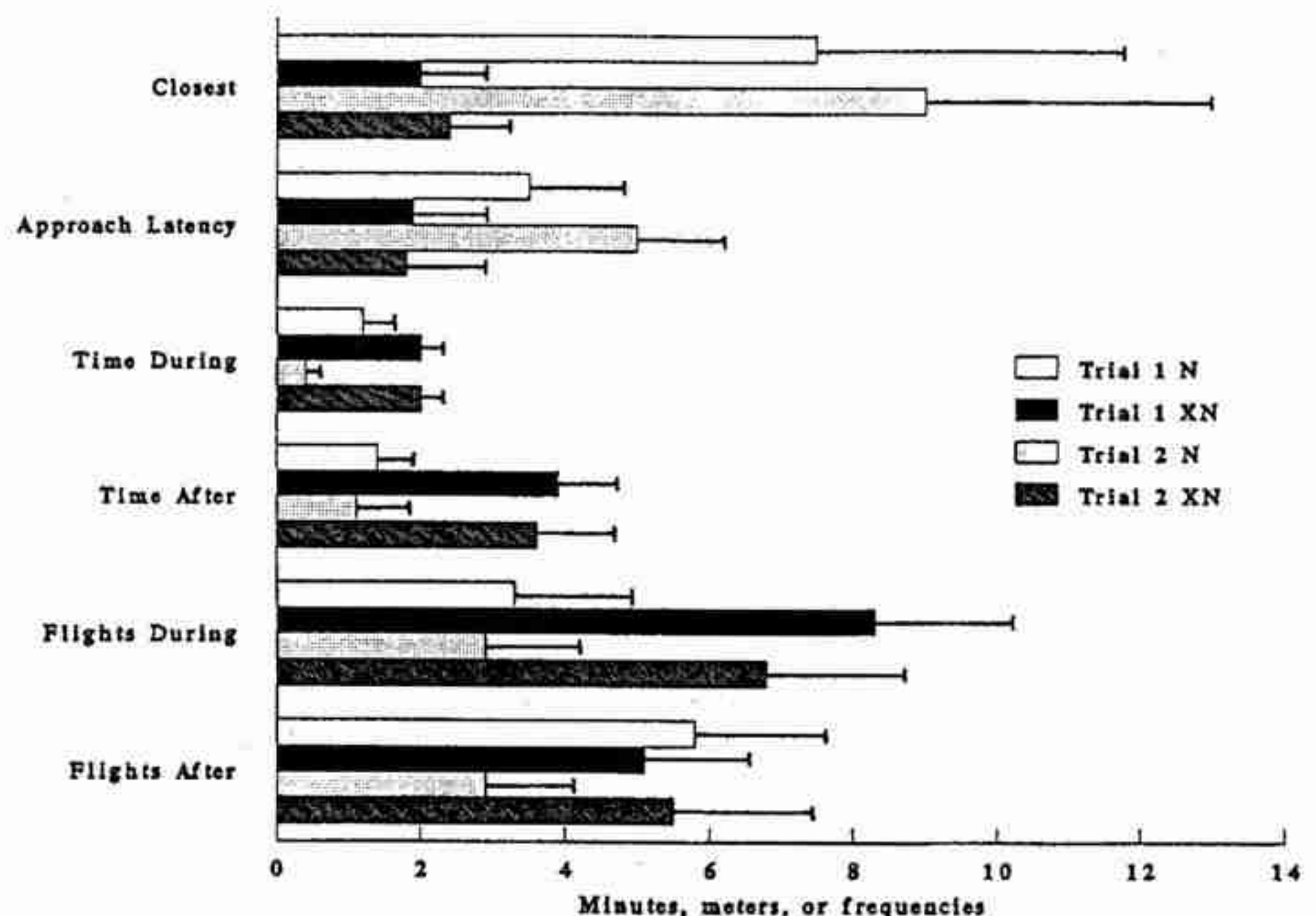
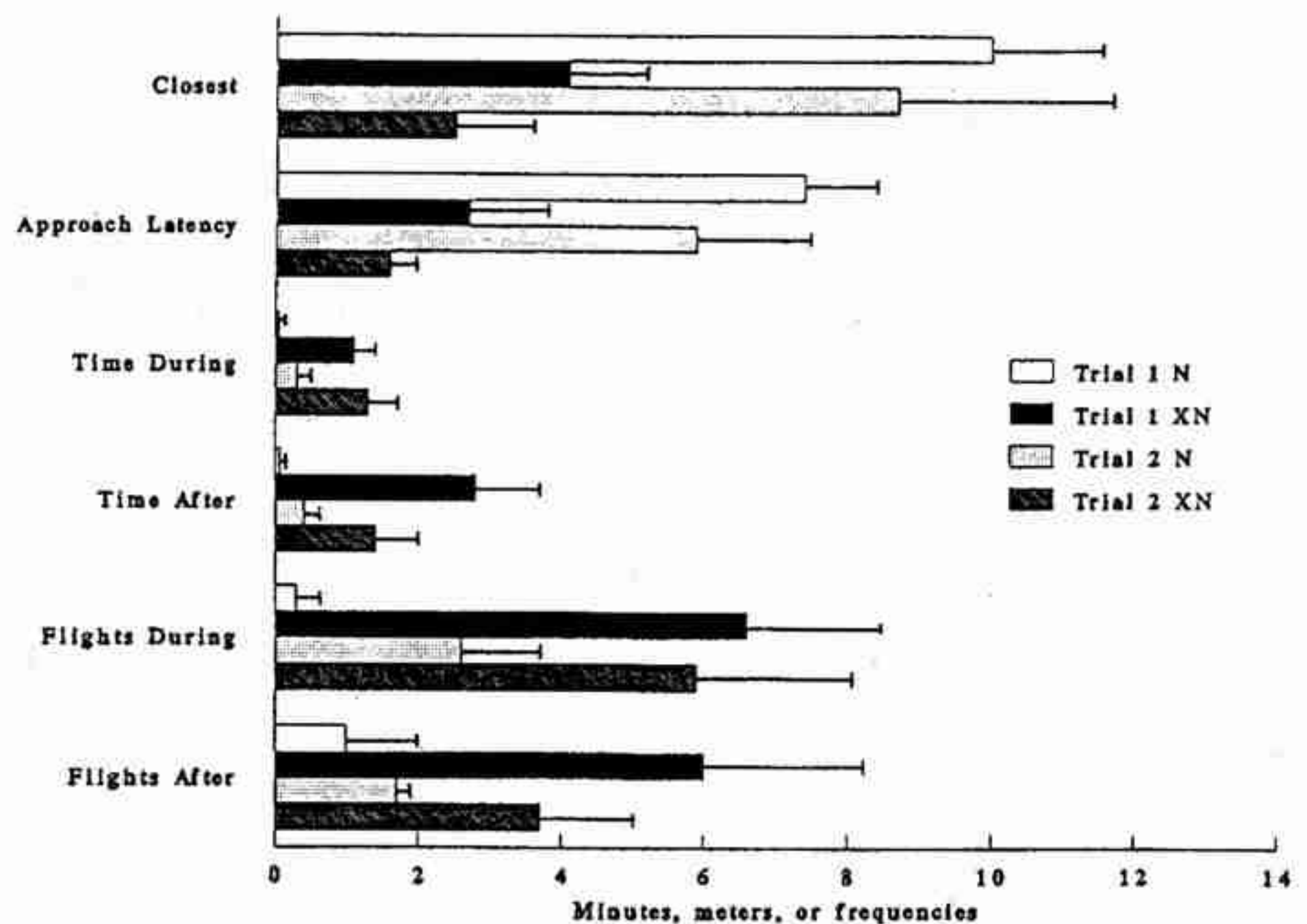


Fig. 2 Mean responses (+ SE) of Kentucky warblers to playbacks of their neighbors' songs from the correct (N) and incorrect (XN) boundaries. Responses are the same as those indicated in Fig. 1.



between N and XN playbacks for hooded warblers singing mixed mode than for Kentucky warblers each singing a single song type.

The results also show that hooded warblers can recognize their neighbors' songs regardless of the singing mode. A comparison of individual recognition between the two modes of singing in hooded warblers allows an assessment of the effects of repertoire size on recognition without the confounding effects of other possible differences between species. Despite the increased complexity of mixed-mode singing, hooded warblers appear equally capable of recognizing their neighbors singing in mixed mode or repeat mode. At least in this species, recognition of individuals' songs does not appear to be affected by the number of songs an individual sings or the way the songs are presented.

It is reasonable to predict that discrimination between repertoires of song types would be more difficult than discrimination between single song types, because larger repertoires in general place a larger demand on memory and require finer discriminations among song types. This general prediction would not apply if each individual had some distinctive feature in all of its songs, a "voice quality" (Weary and Krebs 1992). In addition, because discrimination presumably depends in part on duration of exposure, differences in the temporal properties of singing might affect discrimination of individuals' songs regardless of repertoire size. Our experiments with repeat and mixed mode were timed to allow male hooded warblers opportunities to become familiar with their neighbors' songs. Hooded warblers use repeat mode especially before acquiring a mate (Wiley et al. 1994). The experiments with this mode were conducted shortly after the peak use of this mode at the beginning of the nesting season, by which time

males presumably had had opportunities to become familiar with neighbors' repeat-mode songs. Mixed mode has no comparable peak in use. Even though males sing mixed mode less than repeat-mode in all stages of the nesting cycle (Wiley et al. 1994), they sing mixed mode at approximately twice the rate of repeat mode. Consequently, by the time the experiments with this mode were conducted after the first nesting cycle, males had presumably become familiar with neighbors' mixed-mode songs. Our experiments thus demonstrate that males recognize neighbors on the basis of either repeat- or mixed-mode songs, once they have had a chance to become thoroughly familiar with the songs involved.

If recognition of neighbors reduces the amount of time a bird interacts with an established neighbor, then those males that are easier to recognize might interact less with neighbors. A male that sings more frequently or at a faster rate can increase his neighbors' exposure to his songs. As a result, his neighbors could learn his songs sooner and subsequently initiate fewer interactions.

This reasoning provides an alternative explanation for why birds with large repertoires often sing at higher rates than birds with one or a few songs. Birds with repertoires could sing more in order to allow neighbors ample opportunity to learn their songs. This hypothesis assumes advantages to the neighbors of mutual restraint or reciprocity (Axelrod and Hamilton 1981; Getty 1987; Godard 1993b) and requires some additional explanation for the evolution of repertoires in the first place. Hartshorne's "monotony threshold hypothesis" (Hartshorne 1956, 1972; Kroodsma 1982, 1990; Weary and Lemon 1988, 1990) makes the opposite prediction. Rather than repertoires leading to faster

or more prolonged singing, more singing leads to more variety in repertoires.

Although this study has found no evidence that repertoires affect individual recognition of songs, hooded warblers have relatively small repertoires. Further comparative studies should focus on species with larger repertoires or more sharing of song types by neighbors. Some reports of reduced capabilities of discrimination between neighbors' and strangers' songs or of individual recognition have involved species with much larger repertoires than those in this study (Falls and d'Agincourt 1981; Godard 1994) or more extensive sharing of song types (Schroeder and Wiley 1983).

In addition, all experiments conducted so far on individual recognition of neighbors have used subjects with at least several weeks' experience with their neighbors. Any increased difficulty of discriminating neighbors with repertoires might appear only during the initial phase of learning a new neighbor's features. Strong responses to neighbors early in the season might result from unresolved boundaries as well as from failure to recognize individuals. Nevertheless, it would be instructive to investigate individual recognition earlier in the breeding season, when males were just beginning to learn new neighbors' songs.

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