

USE OF TWO SINGING MODES BY HOODED WARBLERS AS ADAPTATIONS FOR SIGNALLING

by

R. HAVEN WILEY, RENÉE GODARD¹⁾ and ANDREW D. THOMPSON, JR.^{2,3)}

(Department of Biology, University of North Carolina, Chapel Hill, NC 27599-3280, U.S.A.)

(With 14 Figures)

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Summary

Hooded warblers *Wilsonia citrina* use two modes of singing, repeat mode (one pattern sung repeatedly) and mixed mode (2-4 other patterns sung in irregular sequence). Intensive focal-individual sampling of 14 males documented the use of these modes of singing throughout the nesting cycle. Males of different ages (first breeding season or later) did not differ in use of the two modes. Time spent singing in repeat mode decreased markedly after acquiring a mate, but time spent singing mixed mode did not change significantly across stages of the nesting cycle. Males sang more when their neighbors sang at a distance of 25 m or more. Repeat mode increased in this situation before a male acquired a mate, while mixed mode increased afterwards. Near a neighbor (within 25 m), males avoided use of repeat mode. Nearby females before the onset of incubation evoked increased use of repeat mode. More distant, calling females elicited little response before incubation, but thereafter calling females tended to suppress all singing. Males used mixed mode proportionately more in locations nearer neighbors. There were no indications that variation in singing influenced the dates on which males acquired mates. Unmated males late in the breeding season sang persistently in repeat mode, even more than eventually mated males had early in the season before they acquired mates. These results provide support, with some reservations, for three hypotheses for the evolution of distinct modes of singing: (1) specializations for male and female listeners; (2) specializations for indicating conditional behavioral tendencies; and (3) specializations for communication in low- and high-noise situations. These hypotheses are not mutually exclusive, and all three in combination might offer the strongest explanation for the evolution of distinct singing modes in this species and other paruline warblers.

Introduction

A striking feature of song in many birds is the use of multiple stereotyped acoustic patterns. There are few parallels in other forms of animal com-

¹⁾ Present address: Department of Biology, Hollins College, Roanoke, VA 24020.

²⁾ Present address: Department of Biology, Santa Clara University, Santa Clara, CA 95053.

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munication for this feature of birdsong. Also striking is the variation among species in the sizes of individuals' repertoires, from a single pattern, or song type, to repertoires of scores of patterns.

The evolution of large repertoires has several possible explanations (KREBS & KROODSMA, 1980). Some of these explanations focus on the variety of an individual's songs, a collective property of singing. For instance, large repertoires could result from sexual selection created by females' preferences for complex song (CATCHPOLE, 1982; SEARCY & ANDERSON, 1986; BAKER, 1988; SEARCY, 1988; but see KROODSMA, 1989), from selection for deception about the density of territorial birds (KREBS, 1977; YASUKAWA, 1981), or from selection for interference with territorial neighbors by preventing accurate ranging of songs (MORTON, 1982, 1986).

Other explanations for the evolution of large repertoires focus on the choice or order of an individual's songs, the component properties of singing. In this case, diverse repertoires would serve a purpose more like vocabulary in human language. Different patterns might indicate different behavioral states (SMITH *et al.*, 1978; GADDIS, 1983; SCHROEDER & WILEY, 1983; CAPP & SEARCY, 1991a, b), so a diversity of song patterns would allow negotiation between neighbors at territorial boundaries (SIMPSON, 1985). Such use of diverse repertoires to convey information during negotiations with rivals might reduce the chance of more energetic or risky interactions. None of these explanations, however, whether based on the component or collective properties of repertoires, completely explains the pronounced variation among species in sizes of repertoires.

The paruline warblers raise these issues particularly clearly. Especially in the genera *Vermivora*, *Parula*, *Dendroica*, *Setophaga* and *Mniotilta*, individuals have two nearly distinct modes of singing (or 'song systems', SPECTOR, 1992). In most species, these two modes differ in the number of song patterns employed. Often individuals sing either one pattern repeatedly (First Category Songs, SPECTOR, 1992) or a diversity of patterns in irregular sequence with little repetition (Second Category Songs, SPECTOR, 1992). In these species, the issues concerning the use of repertoires in communication apply to each individual.

The first reports of these two modes of singing in a paruline suggested that they indicated different aggressive tendencies (FICKEN & FICKEN, 1962, 1965, 1970). According to another early suggestion, the two modes

served for communication with females and males (MORSE, 1966, 1970). Subsequent support for sex-specific addressing of song include seasonal and diurnal patterns of use, degree of geographic variation, and social contingencies in use of the two modes (NOLAN, 1978; LEIN, 1978; KROODSMA, 1981; KROODSMA *et al.*, 1989; LEMON *et al.*, 1987; MACNALLY & LEMON, 1985; HIGHSMITH, 1989; STAICER, 1989; SPECTOR, 1991). On the other hand, evidence that the two modes indicate different tendencies in territorial defense includes differences in the spatial distribution of the two modes within individuals' territories and sequential use of song types before and after agonistic interactions (LEIN, 1978; HIGHSMITH, 1989; KROODSMA *et al.*, 1989).

The hooded warbler *Wilsonia citrina* provides another example of a paruline with two modes of singing. In *repeat mode*, a male sings one pattern repeatedly; in *mixed mode*, it sings a mixture of 2-4 patterns, different from those sung in repeat mode. In order to compare this species with other parulines and to examine hypotheses for the use of these two modes of singing in communication, we studied the normative use of repeat and mixed singing by intensive focal-individual sampling. We designed this study to collect systematic information on seasonal and diurnal variation in use of the two modes, as well as on their use in relation to females' and neighboring males' proximity and behavior and in relation to location within the singer's territory.

Methods

Subjects and study area.

Our study, conducted in 1987, included 14 territorial males: all nine territorial male hooded warblers in forested areas of the Mason Farm Biological Reserve, Chapel Hill, NC, and five males with territories in immediately adjacent areas. These forests, dominated by several species of oaks and hickories (*Quercus*, *Carya*) 22-28 m tall (WILEY, 1977; HALL & WILEY, 1978), supported a dense understory of the shrub *Viburnum rafinesquianum*, 1-1.5 m high. The hooded warblers usually built their nests in these shrubs and frequently foraged there. All forested areas of the Reserve had a permanent grid of stakes at 25 m intervals, which allowed us to determine birds' positions continuously. We could not obtain such accurate information on the locations of birds on territories outside the Reserve.

Our field work began on 14 April, before any males were detected on their territories. Systematic observation of each male's behavior began the day it was first detected. Subsequently, subjects and their territories were observed 5-6 days each week through May and less frequently until 12 June, by which time pairs in 7 territories had fledglings, 5 had lost their first nests (and 4 had begun second attempts), and 2 males remained unmated. Our detailed observations thus included the first nesting cycle of those males that mated.

All males were captured in mist nets and uniquely marked with colored bands between 18 May and 3 June. Because individual males were easily recognized by their distinctive songs, marking was postponed until after females had begun incubation, in order not to risk any interference with the process of mate acquisition, nest building and egg laying.

We located all nests on the territories under observation. Most were inspected during egg laying or hatching, so we could estimate the beginning of laying and incubation with an accuracy of 0-2 days. For the beginning of nestbuilding, we took the date on which a female in a territory was first observed carrying nest material. For the acquisition of a mate, we took the first date that a female remained on a males' territory throughout observations on two successive days. Females frequently uttered distinctive 'tsik' calls early in the season, which facilitated our detecting their presence.

Samples of each territorial male's songs were tape-recorded. In addition, territorial males in most of the same area had been tape-recorded in 1986. Comparison of spectrograms of songs from these recordings allowed us to identify males that had been present in this area in both years. Recordings of marked males have shown that individually distinctive song variants remain recognizable from year to year (GODARD, 1991, 1993). Furthermore, returning males nearly always re-occupy their previous territories; one exception moved 500 m. Consequently, we have assumed that all newly recorded males in 1987 were in their first breeding season. Our study included 8 such males and 5 older males, whose songs indicated that they had occupied approximately the same territories the year before. The remaining subject, the one located farthest from the Reserve's boundaries, could not be classified in this way, as no recordings had been made in this area in 1986. Extensive recordings of 10-18 territorial males in our study area each year since 1984 provided information about the repertoire sizes of individual males, information only summarized here. For recordings, we used Sony TCD5M cassette recorders and Sennheiser K3U/ME88 microphones. Spectrograms were prepared with a Uniscan II real-time spectrum analyzer (temporal resolution 6.25 ms, frequency resolution 125 Hz).

Behavioral observations.

Observations of these 14 territorial males rotated among the three observers and among hours of the morning, so that each individual was observed almost daily at roughly permuted times. Each period of observation began as soon as the observer reached the target territory, between 0630 and 1230 EDT, and continued for 50 min. These samples did not include the initial period of singing that began just before sunrise, between 0615 and 0530 EDT, and lasted 10-50 min. Low visibility in the forest at this time frequently precluded observations of social interactions or locations of the subjects.

During each 50-min period, the observer noted each song by the subject. Changes from one song pattern to another were readily detected by ear. When a subject sang mixed song patterns, different codes were used for each pattern. At the beginning of each minute, the observer recorded the subject's location and noted if a neighboring male was singing (if so, whether it was singing in repeat or mixed mode), if another male was within 25 m of the subject, if a female was within 25 m of the subject, or if a female was uttering "tsik" calls repeatedly within the subject's territory. For those territories within the Reserve, locations referred to the permanent grid. If more than one neighbor sang at any one time, only the singing mode of the closest was recorded. Each 50-min observation thus included information on the subject's singing and the behavior of neighbors and females. Altogether, we obtained 214 such samples.

From these observations, we used a subject's behavior at the beginning of each minute to determine the proportion of time it spent singing in each mode during each 50-min period. For instance, if a subject was recorded singing in mixed mode at the beginning of 10 different minutes during the sample, we estimated that it sang in this mode for 20% (10/50) of this sample.

To examine the possibility of systematic differences between observers, we used a general linear model (see below), in which we incorporated stage of nesting cycle, hour of the morning, identity of subject, and identity of observer as independent variables. The observer had no significant influence on time spent singing either mode ($p > 0.1$ in both cases). Consequently, we omitted identity of observer from other analyses.

Individual and seasonal differences in singing.

We examined associations between the time subjects spent singing in repeat or mixed mode and the following independent variables: age; individual identity nested within age; stage of nesting cycle; date; and time to the nearest hour of the morning. For these analyses, we recognized seven stages of nesting: (1) prior to obtaining a mate, as determined by the first appearance of a female regularly associated with a male's territory; (2) from then until the beginning of nest-building by the female; (3) nest-building; (4) egg-laying; (5) incubation; (6) feeding of nestlings; and (7) feeding of fledglings. There were insufficient data to analyze behavior during renestings following failures. For these analyses we used general linear models, as implemented in SYSTAT (WILKINSON, 1989). Because the independent variables included both categorical (the first three) and interval (the last two) measurements, these procedures are equivalent to analyses of covariance. We used each 50-min sample as an independent observation of the proportion of time a particular male spent singing in each mode.

Singing in relation to the timing of the nesting cycle.

To determine the possible influences of the males' singing behavior on their nesting cycles, we examined the following three associations between singing and the timing of events: (1) the date a female first appeared within a male's territory in relation to his rate of singing prior to obtaining a mate; (2) the date of the first egg in relation to a male's rate of singing during the period between acquiring a mate and the start of egg laying; and (3) the duration of the period between acquiring a mate and the initiation of egg laying in relation to singing during this period. In each of these analyses, we took the relevant date or duration as the dependent variable. As each male had only one value for each of these variables, we averaged his singing rates over all relevant 50-min samples to obtain single values for singing. Thus each individual represented a single independent observation in these analyses. As three males never obtained mates and thus were excluded from these analyses, we had a sample of 11 males for these analyses. In addition to measures of singing, the independent variables in these analyses included the male's age and, for analyses (2) and (3) above, the date of acquiring a mate.

Interactions with neighboring males.

Our observations allowed us to consider how a male's behavior might change when neighbors were singing or during relatively close-range (<25 m) encounters. For this purpose the data recorded at the start of each min during each 50-min period were cast into a $2 \times 4 \times 4$ matrix: neighboring male's proximity (<or >25 m) \times neighboring male's vocalizations (inaudible, singing in repeat mode, singing in mixed mode, and uttering "tsik" calls) \times subject's vocalizations (silent, repeat mode, mixed mode, calling). Neighbors' calling was recorded only during close-range interactions, which occupied parts of only 9 samples.

To study the influence of singing by neighbors on the subjects' behavior, we considered only periods when neighbors were more than 25 m away in order to exclude close-range encounters. For each sample, we obtained the proportion of time the subject spent singing in repeat or mixed mode when at least one neighbor was singing and when none was singing. These proportions for each 50-min sample were then averaged within stages of the

nesting cycle for each subject. To increase sample sizes for this analysis, we combined stages (2), (3), and (4) and stages (6) and (7) above, because of similarities in males' behavior in these stages, and thus recognized four stages: (A) before acquiring a mate; (B) from acquiring a mate to the beginning of incubation by the female; (C) incubation; and (D) feeding young, either nestlings or fledglings. For each stage, we used Wilcoxon signed-rank matched-pair tests to compare differences in the proportions of time singing in each mode when neighbors were singing or not. Thus each individual contributed a single comparison for each test. Matched-pairs tests that used each male as his own control also emphasized consistency in responses across males.

Our observations allowed us to evaluate the association between each male's singing and its neighbors'. We compared the observed proportion of time that each subject and its neighbors sang concurrently with the expected proportion under the null hypothesis that the subject and its neighbors sang independently. Separate analyses examined each mode of singing, as well as all singing without regard to mode, for each of the four stages above (A-D). For each analysis, the expected proportion of time singing concurrently with a neighbor equaled the product of the proportion of time the subject spent singing in a particular mode (across all 50-min samples in a particular stage) and the proportion of time the nearest singing neighbor spent singing in that mode (again across all relevant samples). We used Wilcoxon signed-rank matched-pair tests to compare differences between actual and expected proportions of time singing in each mode and without regard to mode. Each individual contributed a single comparison for each test.

Concurrent singing does not necessarily indicate that individuals respond to each other. It can occur by chance even when two birds sing independently. Even when there is a real association between two birds' singing, there is still the possibility that they respond simultaneously to some third stimulus, rather than to each other.

To establish that concurrently singing males respond to each other, rather than to some third stimulus, requires experiments. Nevertheless, the distances separating concurrently singing male hooded warblers in these analyses (25 to over 100 m) would require a third stimulus detectable over a comparable distance. During our observations we did not notice any such possibilities, such as responses to females or environmental changes.

To analyze interactions between males at close range (<25 m), we combined data for this situation across all stages. Only nine samples, involving six subjects in four stages (A-D), included periods of close-range interaction.

Interactions with females.

Our observations also allowed us to consider how a male's behavior was influenced by close proximity (<25 m) of a female or calling by a female at greater distances. For this purpose the data recorded at the start of each min during each 50-min sample were cast into a $2 \times 2 \times 4$ matrix: female's proximity (<or >25 m) \times female's vocalizations (inaudible or uttering 'tsik' calls) \times subject's vocalizations (silent, repeat mode, mixed mode, calling). We considered only the proximity and vocalizations of females within the subject's territory.

To compare subjects' vocalizations (1) when alone, (2) when near a female (<25 m) or (3) when a more distant female was calling, we calculated the proportion of time the subject spent in each mode under each of these three conditions. The observations for each subject were combined across all samples within each of three stages (B-D above; males rarely interacted with females during stage A). Once again Wilcoxon matched-pairs tests allowed comparisons of the proportions of time that subjects spent in each mode when alone and when near or within hearing of females.

Locations of singing.

For the seven males whose territories lay within the gridded forests, we plotted the distributions of each subject's locations while singing in repeat and mixed mode. Six of

these males' territories adjoined neighbors on approximately 30-50% of their perimeters; the seventh adjoined neighbors on approximately 75% of its perimeter. By calculating the vector mean (center of gravity) of the subject's locations while singing in each mode, we could evaluate the hypothesis that one mode tended to occur closer to boundaries with neighbors than did the other. We combined locations from all samples for each subject, so each subject contributed a single comparison in binomial tests. Our sample of six subjects was too small to evaluate possible changes in singing locations during the nesting cycle.

Results

General observations on singing.

Each hooded warbler in this population had 4-9 song patterns (Fig. 1), which remained stable in structure throughout the breeding season and from year to year. Of the song patterns in his repertoire, a male used one in repeat mode, in which the same song pattern was sung repeatedly at a rate of 5-6/min. The remaining 3-8 song patterns were sung in mixed mode, in which an irregular sequence of song patterns was sung at a rate of 10-12/min. Males normally used one mode for an entire bout of song (continuous singing with no gaps greater than 30 s). If a male switched from one mode to another, it continued in the new mode for minutes at a time. Consequently, it was not difficult to determine the mode of singing used by a subject at the start of each minute in a sample (our criterion was the consistent use of a particular mode for a 30-s period that included the start of the minute).

In our population song patterns used in repeat mode fell into two categories, those ending with two high notes followed by a lower chevron-shaped note (D songs) and those ending in a single high note followed by a lower chevron (S songs, Fig. 2). Each male sang only one of these two patterns. Song patterns used in mixed mode also fell into several categories based on general features of the structure of the final notes (Fig. 3). The song patterns of each male represented individually distinctive variants of these categories.

Infrequent exceptions occurred to all of the above patterns. An occasional male (approximately one in 20) consistently used for its repeat-mode singing a song pattern more typical of mixed mode in other males. One of the males intensively observed in this study was such an exception. In addition, most males sang briefly in anomalous ways. For instance, a male might rarely insert a D or S song into mixed singing; or a male singing in

mixed mode might repeat the same song pattern for a minute or more. In addition, males occasionally sang patterns that were very rarely used. Despite these exceptional occasions and individuals, most males in our population sang in two distinct modes, using a D or an S song in repeat mode and several other song patterns in mixed mode.

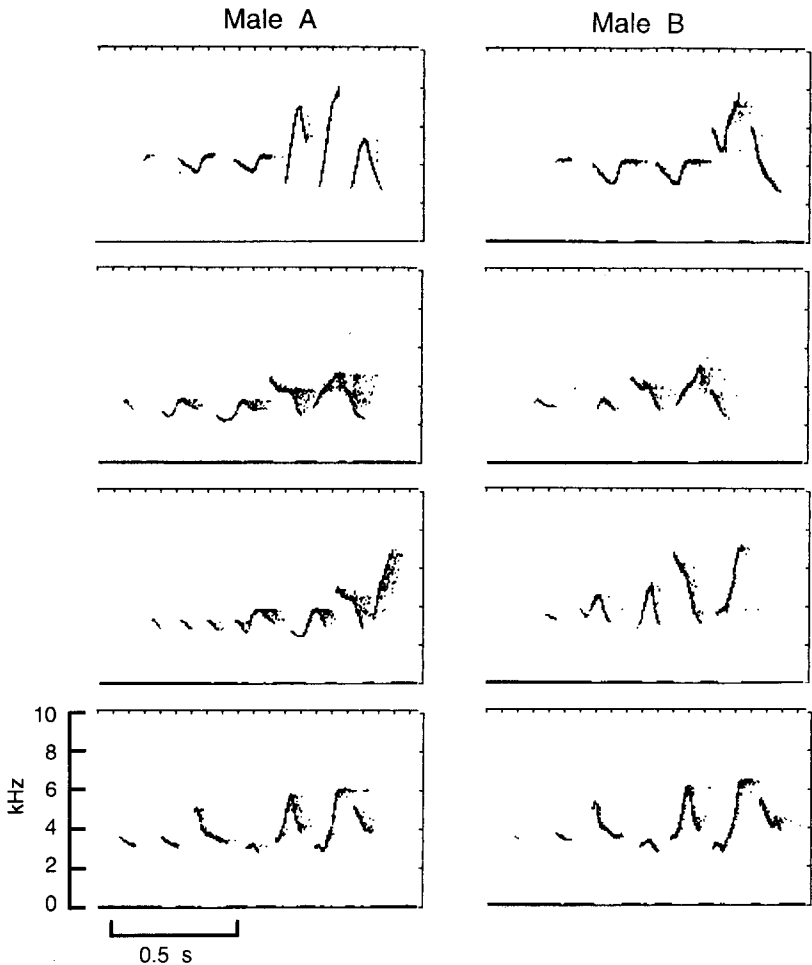


Fig. 1. Partial repertoires of song patterns of two males in the Mason Farm Biological Reserve population. Left column, four song patterns from one male; right column, four song patterns from another male. Top of each column, song pattern used predominantly in repeat mode; other song patterns were used predominantly in mixed mode.

Individual and seasonal differences in singing.

Previous experience had suggested that males might change their singing after acquiring a mate by reducing the amount of repeat mode in relation to mixed mode. In addition, singing appeared to decrease overall once males began to feed young. A preliminary analysis with general linear models, however, failed to reveal any significant associations of the pro-

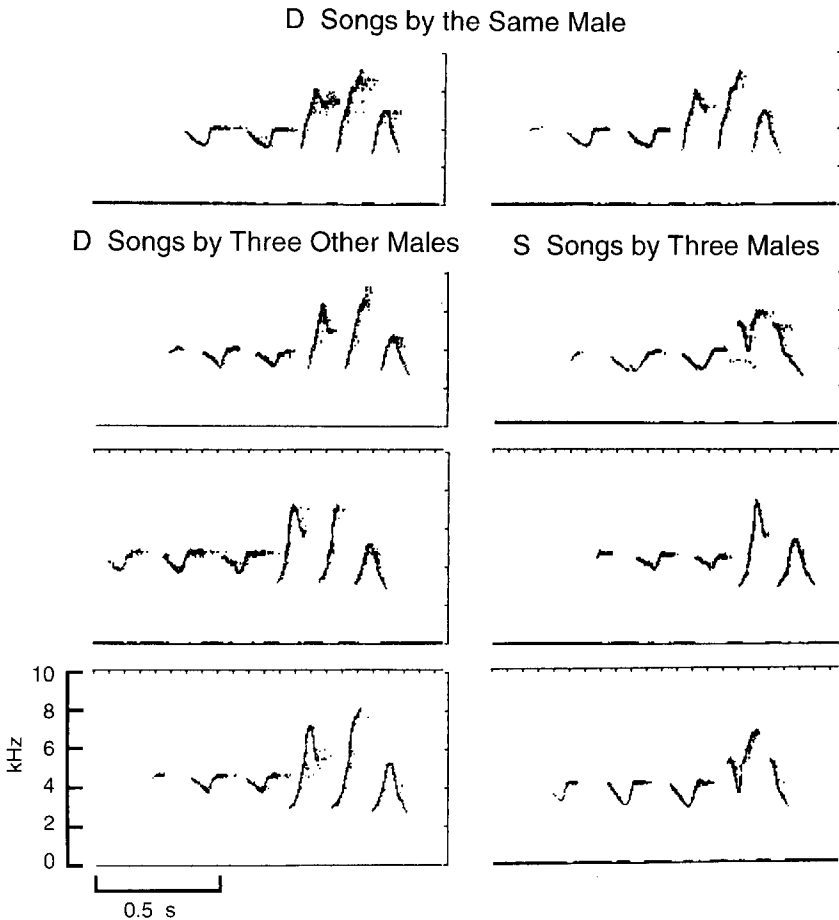


Fig. 2. Spectrograms of song patterns used in repeat mode by seven hooded warblers. Top two songs, same male recorded four weeks apart. Songs used in repeat mode usually end with a high-pitched inverted chevron or upward slur followed by a lower inverted chevron or downward slur. Some include two relatively high inverted chevrons before the final note (D songs); others include only one (S songs).

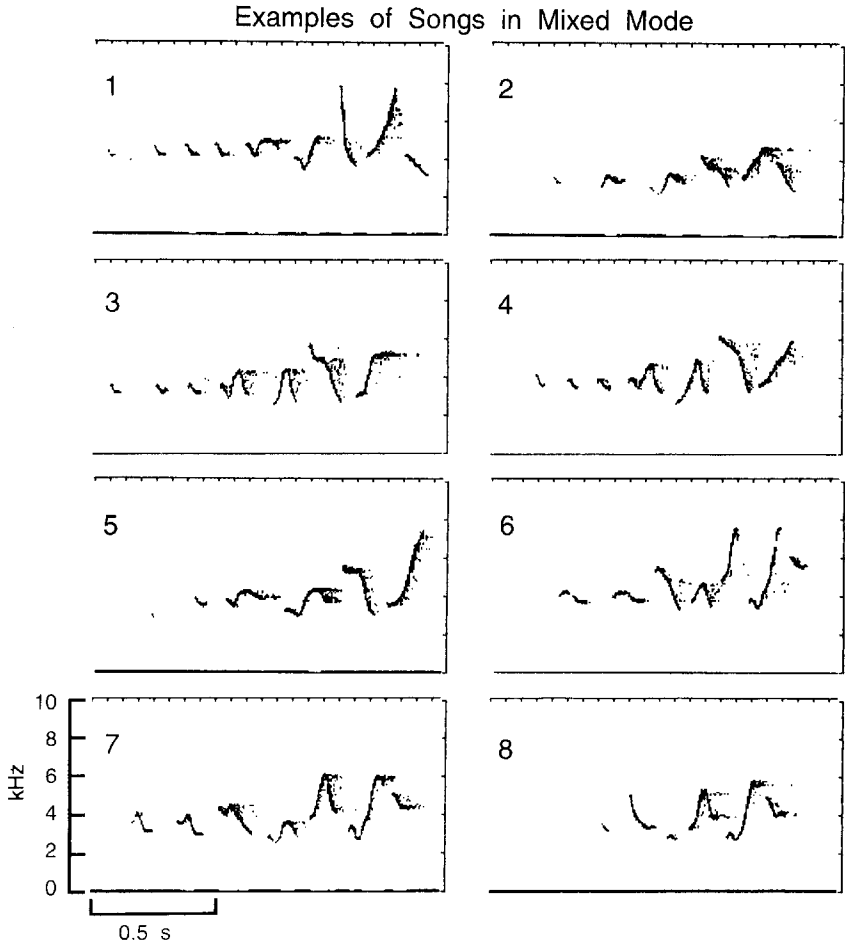


Fig. 3. Spectrograms of song patterns used in mixed mode. 1-2, two song patterns that end in downward slurs; 3-5, three song patterns that end in upward slurs; 6-8, song patterns ending with high-pitched final notes. Songs 2 and 5 were sung by the same male; all other songs came from different males. These differences are reliably distinguished by ear in the field.

portion of time spent singing either repeat or mixed mode and stage of the nesting cycle, date, hour, or individual male.

Closer analysis revealed that males sang repeat mode less after mating and later in the morning (Figs. 4 and 5). This analysis focused on the contrast between the stage before acquiring a mate (stage 1) and all stages afterward (stages 2 through 5) for the 11 males observed in both conditions. In this case, an analysis of covariance with date and hour treated as

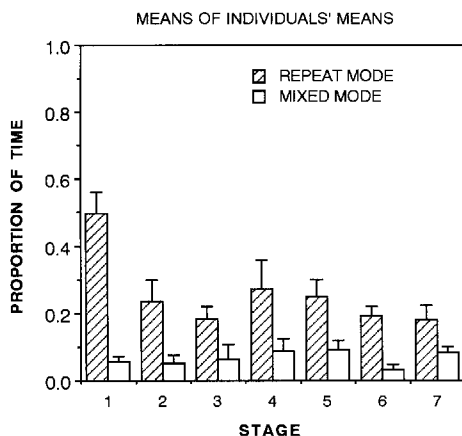


Fig. 4. Proportion of time spent singing in repeat and mixed modes during seven stages of the nesting cycle: (1) before acquiring a mate; (2) mated but before nest-building; (3) during nest-building; (4) during egg-laying; (5) during incubation; (6) during feeding of nestlings; and (7) during feeding of fledglings. See Tables 1 and 2 for statistical analysis. Numbers of males sampled in each stage = 13, 8, 8, 8, 9, 6 and 11 respectively. Bars indicate means of individual males' means; error bars show SE.

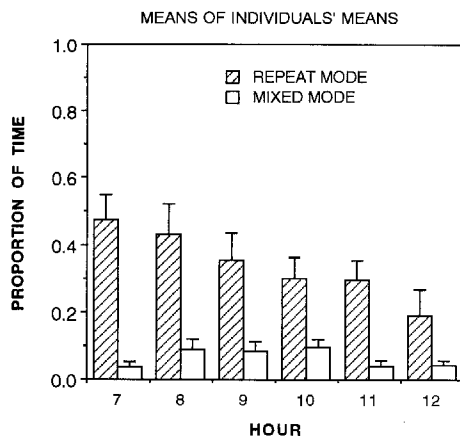


Fig. 5. Proportion of time spent singing in repeat and mixed mode at different hours of the morning, not including the period of dawn song between 0520-0630. See Tables 1 and 2 for statistical analysis. Numbers of males sampled in each stage = 13, 12, 10, 13, 11 and 10 respectively. Bars indicate means of individual males' means; error bars show SE.

continuous covariates, revealed a significant association of the proportion of time spent singing in repeat mode with stage and hour (Table 1). Stage of the nesting cycle rather than date influenced repeat singing. Individual males differed marginally in the amount of time they spent in repeat mode, but all altered their singing similarly following mating (as indicated by the absence of a significant interaction between individual males and stage of the nesting cycle).

A similar analysis of covariance for the proportion of time spent singing mixed mode revealed no changes following acquisition of a mate and no differences among individuals or hours of the morning (Table 2). Thus an increase in the relative amount of mixed mode resulted from a decrease in repeat mode rather than an increase in mixed mode (Fig. 4).

A male's age, as indicated by its presence the preceding year or not, had no relationship with the time it spent singing repeat mode before acquiring a mate (Table 3).

TABLE 1. Analysis of covariance of the time spent singing repeat mode by 11 male hooded warblers

| Variable | df | Mean square | F | p |
|--------------------|----|-------------|------|-------|
| Stage* | 1 | 867.0 | 4.22 | 0.04 |
| Individual | 10 | 385.1 | 1.87 | 0.053 |
| Hour of morning | 1 | 1019.5 | 4.96 | 0.03 |
| Date | 1 | 307.0 | 1.49 | 0.22 |
| Interaction | | | | |
| Stage × individual | 10 | 294.8 | 1.44 | 0.17 |

* Before acquiring a mate (stage 1) *versus* afterwards (stages 2-6).

TABLE 2. Analysis of covariance of the time spent singing mixed mode by 11 male hooded warblers

| Variable | df | Mean square | F | p |
|--------------------|----|-------------|------|------|
| Stage* | 1 | 0.5 | 0.01 | 0.91 |
| Individual | 10 | 56.1 | 1.40 | 0.18 |
| Hour of morning | 1 | 54.8 | 1.37 | 0.24 |
| Interaction | | | | |
| Stage × individual | 10 | 35.9 | 0.90 | 0.54 |

* Before acquiring a mate (stage 1) *versus* afterwards (stages 2-6).

TABLE 3. Analysis of variance of the influence of age on time spent singing repeat mode before acquiring a mate (stage 1) by 13 male hooded warblers

| Variable | df | Mean square | F | p |
|----------------------------------|----|-------------|-------|------|
| Age | 1 | 1.0 | 0.003 | 0.96 |
| Individual nested within age >1 | 4 | 468.8 | 1.43 | 0.23 |
| Individual nested within age = 1 | 7 | 545.0 | 1.66 | 0.13 |

Interactions with neighbors.

Males sang more often when a neighbor was singing farther than 25 m away than when no neighbor was singing. Although this difference appeared consistently in all stages of the nesting cycle, it reached statistical significance only before acquiring a mate (stage A, $T = 1$, $N = 12$, $p < 0.01$, Fig. 6). Because we noticed no possibilities for males to respond jointly to females or environmental cues, males appeared to sing in response to each other.

Before acquiring a mate, males specifically sang more repeat mode when a neighbor sang (repeat mode, $T = 1$, $N = 12$, $p < 0.01$; mixed mode, $T = 24$, $N = 10$, NS). In contrast, during the period between acquiring a mate and the beginning of incubation, a male specifically sang more mixed mode (mixed mode, $T = 5$, $N = 11$, $p < 0.02$; repeat mode, $T = 29$, $N = 11$, NS). After the onset of incubation, a trend for males to sing more when their neighbors sang was not significant (Fig. 6). Thus increased singing when a neighbor sang included both repeat and mixed modes, in different stages of the nesting cycle.

The proportion of time that subjects spent singing decreased across the stages of the nesting cycle, both when neighbors were singing and when they were not. For both repeat and mixed mode, changes across the nesting cycle tended to follow the same pattern regardless of singing by neighbors (Fig. 6). Notice, however, that the striking decrease in singing repeat mode after a male acquired a mate (stage B *versus* stage A, see preceding section) occurred most clearly during singing with a neighbor (Fig. 6).

Concurrent singing by a male and its neighbors followed similar patterns (Fig. 7). Before males acquired mates, concurrent singing with

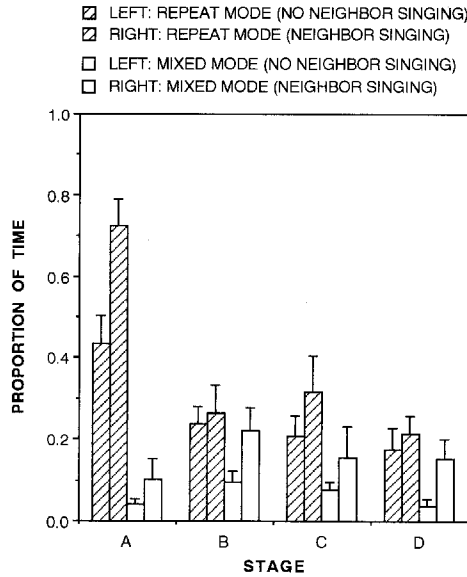


Fig. 6. Proportion of time spent singing in repeat and mixed mode when at least one neighbor was singing and when none was singing during four stages of the nesting cycle: (A) before acquiring a mate; (B) mated but before incubation; (C) during incubation; (D) during feeding of nestlings or fledglings. Numbers of males sampled in each stage = 13, 11, 11 and 9 respectively. Error bars indicate SE.

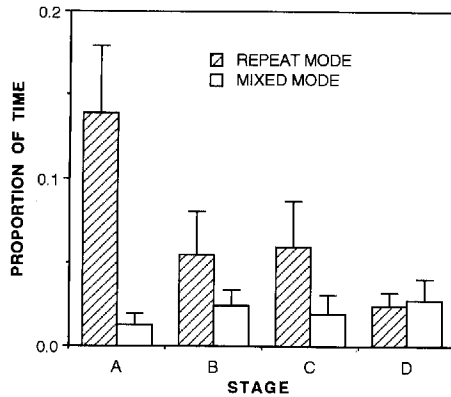


Fig. 7. Proportion of time spent countersinging in repeat mode and mixed mode with a neighbor more than 25 m away during four stages of the nesting cycle: (A) before acquiring a mate; (B) before incubation; (C) during incubation; (D) during feeding of nestlings or fledglings. Numbers of males sampled in each stage = 13, 11, 11 and 9 respectively. Error bars indicate SE.

neighbors in repeat mode significantly exceeded the time expected under the null hypothesis of independent singing ($T = 0$, $N = 12$, $p < 0.01$, Fig. 8). Males in this stage thus had a strong tendency to sing concurrently with their neighbors in repeat mode. In contrast, in stage B, after acquiring a mate but before incubation began, males tended to sing concurrently with neighbors in mixed mode ($T = 3$, $N = 9$, $p = 0.02$), although the mean proportions of time singing concurrently in mixed mode did not change much with stage of the nesting cycle (Fig. 8). Overall, the tendency to sing concurrently with neighbors, regardless of mode, was strongest in stage A ($T = 0$, $N = 12$, $p < 0.01$). In stage C, when females were incubating, patterns of concurrent singing showed some resemblance to those in stage A, although the proportions of time singing with neighbors did not (Fig. 7).

Males within 25 m of a neighbor appeared primarily to avoid singing with repeat mode (Figs. 9 and 10). Although concurrent singing, especially in mixed mode, occurred frequently in these situations, the observed minus expected proportions of time do not clearly indicate an association in males' singing. Statistical analysis was not possible for the few observations of close-range interactions.

Interactions with females.

We obtained sufficient data to analyze the responses of 10 males to females less than 25 m away during the period before the onset of incubation (stage B). In this analysis, we compared the proportion of time spent singing when near a female and when no female was in evidence (neither nearby nor calling at a distance). When near a female during this stage, a male increased his time singing repeat mode but not mixed mode (Fig. 11; repeat mode, $T = 6$, $N = 10$, $p < 0.05$; mixed mode, $T = 19$, $N = 10$, NS). For stage D (feeding young), there were sufficient data to examine the responses of only five males to nearby females. Although this number is not enough for statistical analysis, there were no indications that males responded markedly to nearby females at this stage (Fig. 11).

Responses to calling females at distances greater than 25 m showed the opposite pattern. During stage B (preceding incubation), males gave little indication of responding to distant calling females in their territories (Fig. 12). However, during stages C (incubation) and D (feeding young), males

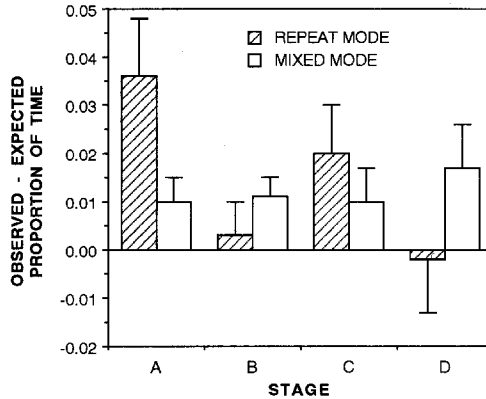


Fig. 8. Tendencies to countersinging in repeat or mixed mode when males were more than 25 m apart (observed simultaneous singing minus expected under the assumption of independent singing) in four stages of the nesting cycle: (A) before acquiring a mate; (B) before incubation; (C) during incubation; (D) during feeding of nestlings or fledglings. Numbers of males sampled in each stage = 13, 11, 11 and 9 respectively. Error bars indicate SE.

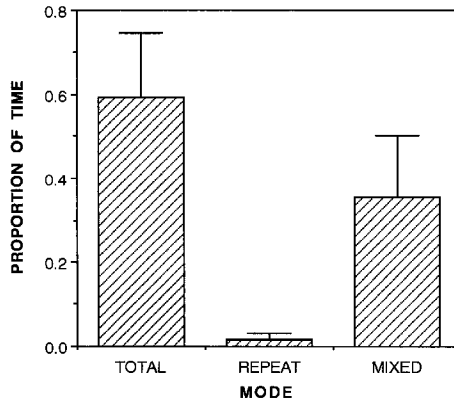


Fig. 9. Proportion of time spent countersinging in repeat mode and mixed mode with a neighbor less than 25 m away. $N = 9$ males. Error bars indicate SE.

characteristically responded to calling females by reducing their time singing, particularly in repeat mode (Fig. 12). During incubation, a male typically ceased singing as soon as his mate began uttering 'tsik' calls while she foraged after leaving the nest; the male then resumed singing soon after she returned to the nest.

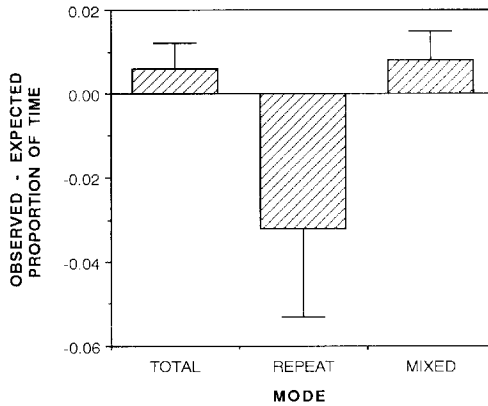


Fig. 10. Tendencies to countersing in repeat or mixed mode when males were less than 25 m apart (observed simultaneous singing minus expected under the assumption of independent singing). N = 9 males. Error bars indicate SE.

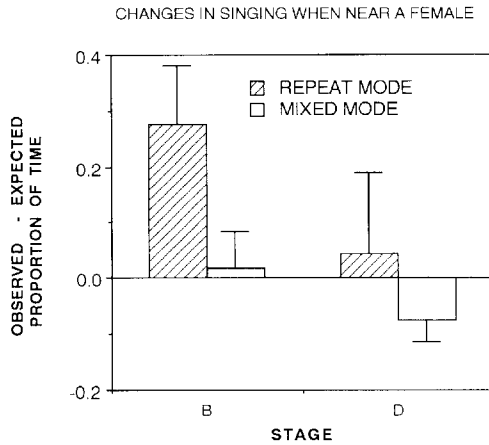


Fig. 11. Changes in singing repeat and mixed mode when less than 25 m from a female during stages B (before incubation) and D (during feeding of nestlings or fledglings). Number of males sampled in each stage = 10 and 5 respectively. Error bars indicate SE.

CHANGES IN SINGING WHEN A DISTANT FEMALE IS CALLING

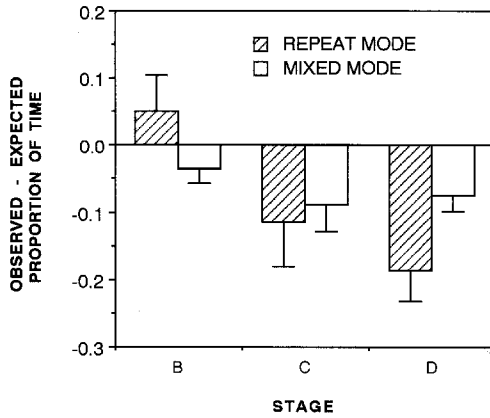
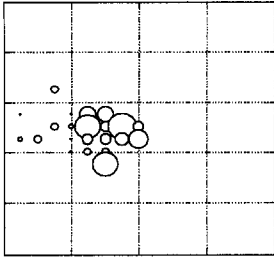


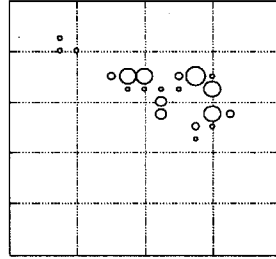
Fig. 12. Changes in singing repeat and mixed mode when a female called at a distance of more than 25 m during stages B (before incubation), C (during incubation), and D (during feeding of nestlings or fledglings). Number of males sampled in each stage = 11, 8 and 8 respectively. Error bars indicate SE.

Locations of singing.

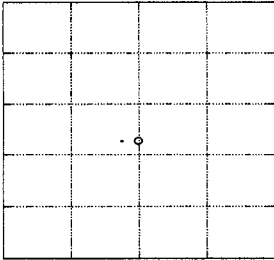
We plotted all locations of repeat and mixed singing for each of seven males with territories in the gridded portions of the forest. In each case, the vector mean of locations for mixed singing was closer to boundaries with neighbors than that of locations for repeat singing (binomial probability, $N = 7$, $p = 0.016$, two-tailed) (Fig. 13). In five of these territories the female built her nest on the far side of the male's territory away from boundaries with neighbors and also tended to feed near her nest or farther from boundaries with neighbors; in each of these cases locations used by the male for repeat mode were closer to the nest and to the female's usual feeding areas than those for mixed mode. In one case, the female built her nest within 25 m of a boundary with a neighbor, although when she left the nest she normally flew at least 150 m away from the boundary. In this case, the male sang repeat mode close to the places she foraged but not close to the nest. Because nesting females seemed to avoid locations near boundaries with neighbors, it is not clear whether males tended to sing mixed mode near boundaries with neighbors or repeat mode near areas used by females or both.



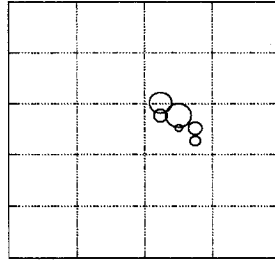
TERRITORY 2 -- REPEAT MODE



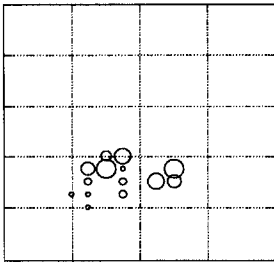
TERRITORY 1 -- REPEAT MODE



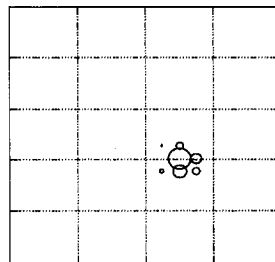
TERRITORY 2 -- MIXED MODE



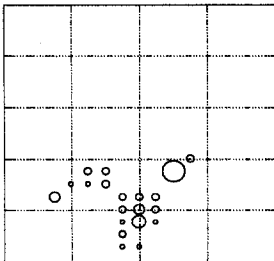
TERRITORY 1 -- MIXED MODE



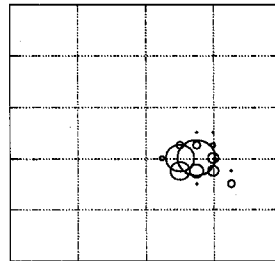
TERRITORY 4 -- MIXED MODE



TERRITORY 3 -- MIXED MODE



TERRITORY 4 -- REPEAT MODE



TERRITORY 3 -- REPEAT MODE

Fig. 13. Locations of singing in repeat mode and mixed mode for four males with contiguous territories. Each diagram shows the same 500×400 m portion of a forest with surveyed markers at 25 m intervals (diagrams show grid points only at 100 m intervals). Circles have areas proportional to the time a male spent singing in each mode closest to each point in the grid. Four central diagrams show locations used by four males when singing in mixed mode; diagrams at top and bottom show locations used when singing in repeat mode. These four males held contiguous territories in a 25 ha tract of forest, and none had other neighbors.

Singing in relation to timing of the nesting cycle.

Does singing preceding acquisition of a mate influence the date on which a male obtains a mate? Ten subjects studied both before and after mating obtained females between 25 April and 2 May. Among these males, there was no relationship between date of acquiring a mate and any measure of singing. We considered, for instance, proportion of time singing in either mode, as well as total singing; in addition, we considered singing when a neighbor also sang and when there was no neighbor in hearing, as well as singing without regard to neighbors' behavior. Furthermore, among these 10 males, there was no association between date of acquiring a mate and date of arrival or age (Table 4). Thus this study provided no evidence that variation in singing among eventually mated males influenced the dates on which they acquired mates.

Is a male's singing related to the duration of the period between a female's arrival on his territory and the first egg? The duration of this period was estimated for 11 males' territories. In all but two cases, this period lasted an estimated 8-15 days. In the two exceptional cases, only two days passed between our first detecting a female in the territory and the first egg. These very short durations suggest that we missed the arrival of the female on these territories, although it seems likely that the time between the female's arrival and egg-laying was still shorter than in other territories.

If all eleven territories are included in our analysis, the duration of the period between the female's arrival and the first egg showed strong relationships with a number of measures of singing. The two measures that explained the greatest variance in a multiple regression (Table 5) were the proportion of time singing when the female was calling >25 m away and the proportion of time singing when the female was neither calling nor near the male. The duration of the period before egg-laying decreased with the first of these measures and increased with the second. Apparently, either singing by a male when his mate was calling promoted her reproductive development or, conversely, a female intensively building a nest in preparation for egg-laying stimulated singing by the male in response to her calls.

In this analysis the time between the female's arrival and egg-laying was inversely related to the date of the female's arrival (Table 5). Females

TABLE 4. Analysis of variance of possible influences on the date of acquiring a mate for 10 males that obtained mates

| Variable | df | Mean square | F | p |
|------------------------------|----|-------------|------|------|
| Age | 1 | 0.60 | 0.10 | 0.77 |
| Arrival date | 1 | 0.00 | 0.00 | 0.99 |
| Time singing in repeat mode* | 1 | 1.74 | 0.29 | 0.61 |
| Time singing in mixed mode* | 1 | 8.93 | 1.48 | 0.28 |
| Error | 5 | 6.02 | | |

* Arcsine transformation of proportion of time singing when no neighbor was singing.

TABLE 5. Analysis by multiple regression of possible influences on the duration of the period between a female's arrival and the laying of her first egg ($R^2 = 0.779$)

| Variable | Coefficient | t | p |
|---|-------------|-------|------|
| Time singing while female calling >25 m away* | -5.57 | -3.16 | 0.02 |
| Time singing while female neither calling nor near* | 13.70 | 3.41 | 0.01 |
| Date of female's arrival | -0.73 | -2.45 | 0.04 |

* Arcsine transformations of proportions of time spent singing in each situation.

that arrived later took less time to lay their first egg. However, this effect, as well as all those of singing, disappeared if we excluded the two cases with very short periods between female arrival and egg-laying (all p values >0.2). Thus it seems likely that either (1) late-arriving females had already developed reproductively and their mates responded by singing more or (2) we did in fact miss the earlier arrival of these females. Consequently, we can provide no compelling evidence that a male's singing influenced his mate's reproductive development.

Singing by unmated males.

The three males that never attracted a mate sang persistently in repeat mode, behavior that made them conspicuous in the field after other males had paired. This characteristic singing even differed from that of eventually mated males before they obtained mates. The unmated males spent a greater proportion of their time singing, especially when neighbors were not singing ($U = 0$, $p = 0.01$, $N = 3$, 10), than did eventually paired males during the period before they had mates. The difference was particularly

marked in the proportion of time spent singing in repeat mode, both when neighbors were not singing ($U = 0$, $p = 0.01$) and when they were ($U = 1.5$, $p = 0.02$) (Fig. 14). Both classes of males sang mixed mode infrequently; the small differences between them were not significant (Fig. 14). Thus unmated males, after other males had obtained mates, spent unusually large proportions of their time singing in repeat mode.

The characteristic singing by unmated males late in the season was emphasized by the case of an unmated male, B, that replaced a mated neighbor, RW, between 22 and 28 May. Prior to this time, B sang persistently in repeat mode. On 28 May male RW had disappeared. Male B had taken over his territory and mate and sang much like other mated males.

None of the three unmated males was present in the area during the preceding year. Although one arrived within a week of many other males (16 April), the other two arrived late (on 5 and 29 May). It is interesting that the first male, like other males, sang in mixed mode on occasion until 6 May and only later began persistent singing in repeat mode. Although

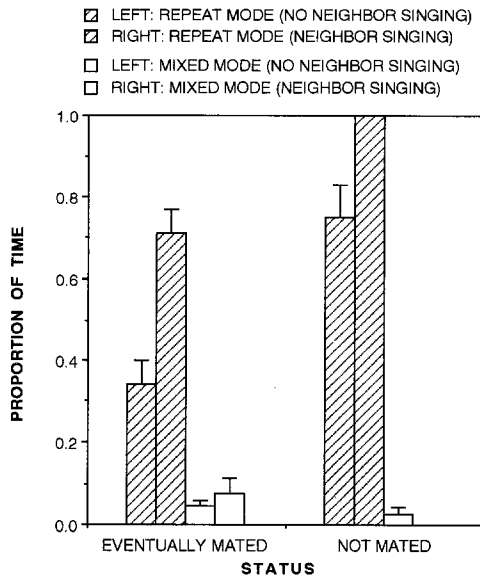


Fig. 14. Proportion of time singing in repeat and mixed mode by unmated males ($N = 3$) and by eventually mated males during the period before they acquired mates ($N = 10$), both when at least one neighbor was singing and when no neighbor was singing. Error bars indicate SE.

the very late arrival of the last male suggested that occasional males might move to new locations if they do not acquire mates, the persistence of the first male in his original location showed that not all do so.

Dawn song and additional observations.

The initial bout of singing at dawn, not included in our quantitative samples, differed from singing later in the morning. Hooded warblers normally sang in mixed mode for 30-50 minutes beginning 0-10 minutes before sunrise (0615-0530 EDT between 15 April and 15 June). At this time of day, light levels in the interior of forests permitted only dim vision. While singing their first few songs at dawn, males often flew 50-75 m to a location used frequently for mixed singing later in the day and 50-100 m from a singing neighbor. Males occasionally approached within 25 m of each other at dawn. They often used perches much higher than later, 16-20 m above ground, and, after the first few songs, normally remained stationary for long periods. When they did move, it was rarely more than 10-20 m. Singing rates were high even for mixed mode, often over 15 songs/min, compared to 10-12 songs/min for mixed mode later in the morning, or 5-6 songs/min for repeat mode. Early in the season, before males had acquired mates, this distinctive bout of singing at dawn sometimes included repeat mode. After pairing, a male ceased this characteristic singing at dawn within 1-2 mins of the first calls from a female in its territory. The male then tended to return toward the center of its territory and the female. Thus the dawn bout consisted of rapid singing at a distance of 50-100 m from a neighbor during a period when it was too dark to forage and females were not active.

Males had no specialized flight song. On a number of occasions, we watched males sing in flight between perches, but these occasions involved no peculiarities in singing nor any modifications of flight beyond the minimum necessary to accommodate vocalization. We never observed singing by a female hooded warbler.

Discussion

In having two distinct modes of singing, hooded warblers resemble many other parulines. In his review of paruline singing, SPECTOR (1992) distinguished two groups of species: those in which males use a single song

pattern for singing from perches and have specialized songs for flight displays and those in which males have at least two song patterns and two distinct modes of singing from perches and usually lack a specialized flight song. Hooded warblers clearly fall into the second category.

Descriptions of the singing of these species indicate many close similarities with singing by hooded warblers, but no previous study has obtained so much quantitative information on the use of two singing modes by a sample of males in known stages of their nesting cycles and in specified social contexts. A first step in assessing these singing modes is to compare our results with observations on other parulines with similar singing.

Size and organization of repertoires.

Although sizes of repertoires are not easy to compare among species with present information, hooded warblers' repertoires of 4-9 song types clearly exceed those of several species that use only two distinct song types (golden-winged warbler *Vermivora chrysoptera*; HIGHSMITH, 1989; and black-throated green warbler *Dendroica virens*; MORSE, 1967). Our results for repertoires of hooded warblers seem comparable to those reported for American redstarts (*Setophaga ruticilla*) and Canada warblers (*Wilsonia canadensis*) (LEMON *et al.*, 1983). Somewhat larger repertoires (frequently 10-15 song types) are reported for yellow and chestnut-sided warblers (*Dendroica petechia* and *D. pensylvanica*) (LEMON *et al.*, 1983; SPECTOR, 1991). It remains possible that an extensive study of song variation in our population of hooded warblers would reveal that males use additional, infrequent patterns and thus have larger repertoires than we have measured so far.

Like American redstarts and yellow warblers, male hooded warblers have two modes of singing, a repeat mode and a mixed mode (called repeat and serial mode for American redstarts, LEMON *et al.*, 1985; and types I and II for yellow warblers, SPECTOR, 1991). In each of these species, each male normally uses a single song pattern in its repeat mode. As in yellow warblers, this pattern is usually an individually distinctive variant of one of two widespread patterns. Furthermore, the pattern used in repeat mode is not, with rare exceptions, used in mixed mode. Thus hooded warblers, like other parulines, employ largely distinct sets of song

patterns in their two singing modes. Like other parulines with two singing modes, mixed mode of hooded warblers involves more rapid delivery of songs and greater immediate variety than does repeat mode. These similarities in organization of repertoires and modes of singing suggest that we might also find parallels in the use of these two modes of singing.

Use of the two singing modes.

In our study of hooded warblers, singing in repeat mode became much less frequent after a male acquired a mate. Many studies of other parulines have also reported that one singing mode, analogous to the hooded warbler's repeat mode, decreased later in the nesting season or after the acquisition of a mate (MORSE, 1967; LEIN, 1978; KROODSMA *et al.*, 1989; LEMON *et al.*, 1985, 1987; STAICER, 1989; SPECTOR, 1991; review by SPECTOR, 1992). Our analyses of variance of singing by hooded warblers confirmed that the decrease in repeat mode after acquiring a mate was independent of other seasonal changes. Furthermore, repeat mode decreased in all contexts, including in response to singing neighbors. In contrast, singing in mixed mode was not significantly affected by acquisition of a mate.

In several parulines, experimental removal of mates or anecdotal observations following the disappearance of mates (NOLAN, 1978; HIGH-SMITH, 1989; KROODSMA *et al.*, 1989; SPECTOR, 1991) have also indicated that unmated males increase their use of singing modes like the hooded warbler's repeat mode. Nevertheless, singing in repeat mode by unmated male hooded warblers late in the season, after all females had arrived, differs from singing by unmated males earlier, when females are first arriving. Possibly these differences in singing affect males' chances for mating. Alternatively, the distinctive singing of unmated males late in the season might result in part from changes in the behavior of their mated neighbors, once boundaries are established and most males are mated.

As in other parulines, the hooded warbler's two modes of singing have different spatial distributions. Mixed mode, like the analogous mode of singing in chestnut-sided warblers and American redstarts, tends to occur closer to boundaries and in locations where countersinging and interactions with other males have occurred than does repeat mode (LEIN, 1978; LEMON *et al.*, 1987). It is difficult to separate the effects of location with

respect to boundaries, the center of the territory, the nest, or the mate. However, in our study, when a male had neighbors on only one side of his territory, he tended to sing mixed mode on that side only. Thus peripheral or central location in itself seemed unimportant in choice of singing mode.

Social situations are also known to influence the use of singing modes by parulines. Grace's warblers, for instance, are significantly more likely to use Type A songs (analogous to hooded warblers' repeat mode) when less than 15 m from a female prior to pairing. Type B songs (analogous to mixed mode) are significantly more likely when countersinging with neighbors after pairing (STAIGER, 1989). Yellow warblers use Type I and Type II songs more often in close interactions with females and males, respectively (SPECTOR, 1991), and chestnut-sided warblers show similar trends for AE and UE songs, although close proximity to a female tends to inhibit all singing (LEIN, 1978, KROODSMA *et al.*, 1989).

Our information on hooded warblers singing near females or rival males at different stages of the breeding cycle indicated that social situations have a more complex influence on singing than indicated in these previous studies. Before the start of incubation, males responded to females with increased singing in repeat mode, a response that occurred both when a female was nearby (<25 m away) and when a female was more distant but calling. On the other hand, no such change occurred once incubation began. In contrast, tendencies to sing mixed mode were not influenced by females. During incubation and feeding of nestlings, a calling female inhibited all singing. Thus only preceding incubation did interactions with females stimulate singing in repeat mode, and at no time did females specifically inhibit mixed mode.

Hooded warblers' sang more overall when neighbors sang. Although experiments are necessary to establish that males actually responded to each other, the lack of any indications of joint responses to other cues make it likely that neighbors did influence each other. The nature of this influence, however, depended on the stage of the breeding cycle. Before a male paired, repeat mode increased when a neighbor was singing, while after pairing mixed mode increased. Thus singing by neighboring rivals did not have a simple influence on choice of mode. More limited information showed that, in interactions at close range (<25 m), males sang mostly mixed mode. This trend, however, resulted from an inhibition of

repeat mode rather than any increase in the tendency to sing mixed mode.

Singing and reproductive success.

In some passerines, the proportion of time devoted to singing reflects the abundance of food in a male's territory (MORTON, 1982; YDENBERG, 1984; DAVIES & LUNDBERG, 1984; TAMM, 1985; RADESÄTER & JACOBSSON, 1988; STRAIN & MUMME, 1988; ALATALO *et al.*, 1990; ARVIDSSON & NEERGAARD, 1991). In some migratory species, males that arrive earlier sing more and pair earlier (GOTTLANDER, 1987; ARVIDSSON & NEERGAARD, 1991). Such results suggest that females might use singing as an indication of territory quality, which might in turn influence nesting success. In our study, however, singing prior to acquisition of a mate failed to correlate with the date of obtaining a mate among males that eventually mated. Arrival order and age also had no significant influence on singing. Our results, however, can eliminate only the possibility of a large effect. Our sample size was small; the arrival of some females might have been missed; and detecting the arrival of some females might require more extensive searching within a male's territory than our 50-minute samples permitted.

Hypotheses for the use of two singing modes.

Most discussions of singing modes in parulines have considered variants of two broad hypotheses: (1) the singing modes or specific song patterns address two different categories of receivers, females and rival males (MORSE, 1970; NOLAN, 1978; KROODSMA, 1981); and (2) the modes or song patterns serve to indicate different aggressive tendencies (LEIN, 1972, 1978). The literature also briefly mentions a third alternative: (3) the singing modes serve for long- and short-range communication (LEIN, 1978).

These hypotheses proposed for paruline singing are related to the hypotheses outlined in the Introduction for the evolution of repertoires in general. For instance, the general hypothesis that diverse repertoires evolve as a result of sexual selection produced by female preferences predicts that singing in mixed mode should address females. In contrast, the hypothesis based on deception of rivals predicts that mixed mode

should address males. This same prediction follows from the hypothesis that diverse repertoires prevent ranging of songs by neighbors and thus interrupt their activities. Thus each of the general hypotheses based on collective properties of repertoires makes clear predictions about which sex is the intended receiver of song.

The general hypothesis that diverse repertoires convey information in negotiation with rivals also predicts that mixed song should address other males; the use of repertoires to indicate aggressive tendencies is just a variant of this proposal. Specialization of singing modes for long- and short-range communication also requires that diverse repertoires convey information, at least at close range, but this hypothesis does not necessarily make a prediction about which sex is addressed by each mode of singing.

Thus the three hypotheses for paruline singing do not map clearly onto general hypotheses for the evolution of complex repertoires. Furthermore, they are not mutually exclusive and could conceivably all apply simultaneously. They do, however, prompt explicit questions about the use of the two singing modes.

Sex-specific addressing.

Is repeat mode used principally during interactions with females, while mixed mode is used in interactions with males? The principal evidence for the use of repeat mode specifically for communication with females comes from its predominant use by unpaired males, both early and late in the season, a nearly universal finding in studies of paruline singing. Unmated males are presumably trying to attract mates and thus address their songs to any females within hearing. More definite evidence for this hypothesis comes from our finding that repeat mode increased during interactions with females, during the period before egg-laying, regardless of the female's distance.

On the other hand, repeat mode also increased in response to singing neighbors during the period before pairing. This response might, however, represent an attempt to compete with the neighbor for any unpaired females in the area and thus might be addressed primarily to females, rather than to the neighbor. Other studies have noted that interacting males sometimes use song analogous to the hooded warbler's repeat mode

when a female is nearby (NOLAN, 1978; KROODSMA *et al.*, 1989). Male hooded warblers, before pair formation, use repeat mode during interactions with rival males regardless of the immediate presence of a female.

Chestnut-sided warblers use accented song, analogous to the hooded warbler's repeat mode, immediately preceding copulation (KROODSMA *et al.*, 1989), another indication that this singing mode is addressed especially to females. We have twice observed loud, repeat-mode songs preceding copulation in hooded warblers, although copulations on other occasions have not been accompanied by song. Below, we speculate that song might precede extra-pair copulations in particular.

After incubation begins, we found no evidence that song plays any role in interactions with females. Thus our observations agree with the hypothesis that repeat mode serves for attracting a mate and interacting with females, but only until egg-laying begins. The use of repeat mode for interaction with a mate goes against evidence from other species that variety in singing stimulates females (CATCHPOLE, 1983; BAKER, 1986; SEARCY, 1986; SEARCY & YASUKAWA, 1990). In parulines, like the hooded warbler, the singing mode used to stimulate females involves a single song pattern repeated at a relatively slow rate, despite the males' use of a faster and varied mode in other circumstances.

In contrast to singing in repeat mode, interactions with females have little influence on mixed singing. There is no change in the frequency of mixed singing after pairing, and no change in mixed singing when females are nearby before egg-laying. Instead, mixed singing is associated with interactions between males. Mixed mode is more frequent near boundaries, although it occurs to some degree throughout most of a male's territory. Mixed mode also characterizes the bout of rapid singing at dawn, a time when males often move toward mutual boundaries and females are not yet in evidence. Mixed singing increases in response to singing neighbors, although before a male obtains a mate singing neighbors evoke increased repeat mode instead. Thus hooded warblers, like other parulines, tend to use mixed mode in circumstances associated with interaction with neighbors.

Nevertheless, mixed mode occurs frequently without any evidence of an ongoing interaction with another male. Some of this spontaneous mixed singing occurs near locations where interactions have occurred previously and might thus represent attempts to provoke or to continue

an interaction. Also contrary to the hypothesis that mixed mode serves specifically for intrasexual communication, males in close-range encounters do not increase their rates of singing mixed mode. Instead, the proportionate increase of mixed mode in this situation results from an inhibition of repeat mode.

In summary, our information on the contexts of hooded warblers' modes of singing agrees roughly with the hypothesis of sex-specific addressing. Mixed mode in particular seems addressed primarily to other males. Repeat mode, on the other hand, is less clearly addressed to one sex. These results are not compatible with the general hypothesis that diverse repertoires evolve by sexual selection. They are roughly compatible with predictions derived from either deception of rival males or interference with neighbors. Nevertheless, the use of mixed singing in close-range interactions with neighbors or at locations where such interactions tend to occur conflicts with these hypotheses. This tendency to use mixed singing at close range suggests that we should also consider the component, in addition to the collective, properties of diverse repertoires.

Indication of behavioral tendencies.

Does use of different song patterns indicate tendencies to attack or withdraw from encounters? This evidence is difficult to obtain, and only a few studies have documented use of song patterns in situations suggesting different aggressive tendencies (LEIN, 1978; HIGHSMITH, 1989; KROODSMA *et al.*, 1989; SPECTOR, 1991). It was our impression that mixed singing by hooded warblers might indicate an escalation of a singer's response to a neighbor. Infrequent song patterns tended to occur during particularly heated parts of a bout of countersinging; the initial and final stages of such encounters usually involved mixed singing with just two common patterns. We still lack full documentation of this possibility, however. LEIN (1978) also argued that the song patterns of chestnut-sided warblers used predominantly near boundaries indicated less confidence in territorial defense than those used predominantly near the centers of territories. Our results confirm similar differences in the spatial distributions of the two singing modes of hooded warblers, but it is not clear that mixed mode in itself indicates lower aggressive tendencies.

There is difference of opinion about the evolution of communication in contests. Initially, it seemed that contestants should not reveal their

tendencies (CARYL, 1979). Nevertheless, evidence suggests that they often do (SMITH *et al.*, 1978, SCHROEDER & WILEY, 1983; NELSON, 1984; CAPP & SEARCY, 1991a, b). It certainly seems unlikely that unconditional indications of an individual's tendencies to attack or retreat would have advantages in contests. On the other hand, during escalating conflicts or bargaining for divisible resources such as space, incremental revelations of tendencies or indications of conditional tendencies might prove advantageous (see ENQUIST, 1985).

LEMON *et al.* (1987) drew a similar distinction between 'honest advertisement' of a male's commitment to defend a location, as proposed by LEIN (1978), and 'assessment' of male quality by American redstarts. Honest advertisement and assessment correspond to unconditional and conditional signalling of a singer's tendencies. They suggested that, at high densities with small territories, honest advertisement would lead to increased use of signals indicating maximum commitment; assessment, on the other hand, would predict increased use of a graded series of signals in this situation. Thus, if the two singing modes were unconditional indications of aggressive tendencies, the hooded warbler's repeat mode (or its analog in other species) should increase at high densities. On the other hand, if singing modes served for graded assessment in contests, mixed mode should increase. Although we have no such data for hooded warblers, a study of other parulines found the latter result (MORSE, 1970). Although this evidence argues against unconditional signalling of tendencies in contests, it is still not strong support for assessment by conditional signalling. We could also explain an increase in mixed singing at higher densities as a result of increased intrasexual or short-range signalling.

Long- and short-range or high- and low-noise communication.

The two modes of singing in many parulines might represent specializations for long- and short-range communication. Long-range communication is inherently noisy, in the sense that receivers are likely to make errors in detecting or recognizing a signal (WILEY & RICHARDS, 1982; WILEY, 1983, 1994). This situation favors stereotyped signals at the expense of varied and potentially more informative signals. Short-range communication, with less noise, permits the use of complex repertoires to convey information, in the sense that listeners can make choices based on the patterns heard. Stereotyped, repetitive signals characterize long-

range acoustic communication in a variety of animals, while diverse or intergrading signals characterize short-range communication (MARLER, 1973; WILEY & RICHARDS, 1982; WILEY, 1983). The hypothesis that singing modes are specialized for short- and long-range communication thus predicts that hooded warblers and other parulines should use mixed mode at short range and repeat mode at long range.

Our results conform in several ways to these predictions. Away from territorial boundaries hooded warblers make more use of the repeat mode of singing. Near boundaries and especially during close-range (<25 m) interactions with neighbors, repeat mode decreases. In addition, attraction of mates is likely to involve long-range signalling, and repeat mode predominates during singing before pairing.

In other ways our results conform less closely to expectations for short- and long-range signalling. Repeat mode increases in response to countersinging with distant (>25 m) neighbors before pairing, but mixed mode increases in this situation after pairing. Also contrary to expectations for short- and long-range signalling, repeat mode increases during interactions with nearby females before egg-laying. Occasionally, loud songs in repeat mode immediately precede copulation.

Although contrary to simple expectations for short- and long-range signalling, these results are not necessarily contrary to expectations for low- and high-noise communication. From the signaler's point of view, interactions even at short range with unfamiliar opponents and with choosy females have the characteristic property of noisy communication: low probability of a correct response from the signaler's point of view (see WILEY, 1983, 1994). Thus interactions with territorial rivals early in the breeding cycle and with females early in the nesting cycle might well constitute 'noisy' communication from the singer's point of view. These considerations lead to predictions that unfamiliar opponents later in the season would evoke more singing in repeat mode and that unfamiliar females would also.

Conclusion.

Many of the hypotheses for the use of different singing modes by hooded warblers and other parulines are complementary. Repeat mode could serve for attraction and stimulation of females, both situations likely to be

noisy from the signaler's point of view and thus to favor stereotyped signals. Mixed mode might serve primarily for interactions with established neighbors at relatively short range or in locations where short-range interaction might develop, situations in which greater variability of signals would allow assessment and negotiation. In this combined view, the receiver primarily addressed by a singer, whether potential mates or rival males, would determine the optimal form of signalling, either more stereotyped and recognizable or more variable and informative. To obtain responses from females, the former might serve best; to interact with established neighbors, the latter might serve best.

In natural circumstances, attraction and stimulation of unfamiliar females is often likely to require long-range or, from the signaler's point of view, noisy communication but little communication of behavioral tendencies; stereotyped signals, like the hooded warblers's repeat mode, would then offer advantages. In many parulids, song patterns used in repeat mode have wide distributions across populations (KROODSMA, 1981), a feature that would also have advantages for communication with unfamiliar individuals in noisy circumstances. Negotiation and reaffirmation of relationships with familiar territorial neighbors is often likely to have just the opposite requirements; variable signals, like singing in mixed mode, would then have advantages.

In the interests of fostering further investigation of adaptations for signalling in high- and low-noise situations, we close with some specific predictions. The complexity of natural situations will often frustrate simple tests, but these predictions should at least serve to clarify the issues. (1) Males distant from neighbors should use less variable singing than males close to neighbors. (2) Unfamiliar rivals should evoke less variable singing than familiar neighbors. (3) When females choose mates quickly after their arrival, they should use less variable signals; when they have more time to assess potential mates, they should use more variable signals. (4) Males should use less variable singing in interactions with unfamiliar females, for instance when seeking mates or extra-pair copulations, than in interactions with familiar ones.

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