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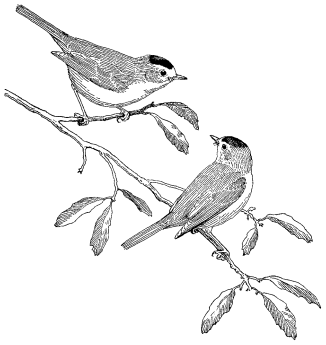
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SINGING BEHAVIOR VARIES WITH BREEDING STATUS OF AMERICAN REDSTARTS (*SETOPHAGA RUTICILLA*)

CYNTHIA A. STAICER,[1] VICTORIA INGALLS,[2,4] AND THOMAS W. SHERRY[3]

ABSTRACT.—We examined the relationship between singing behavior and breeding status in the American Redstart (*Setophaga ruticilla*) by analyzing song rates, singing mode (Repeat or Serial), and variability of song delivery in relation to the age and breeding status of 129 males in the Hubbard Brook Experimental Forest, New Hampshire. Unpaired males spent most of their time (>90%) after dawn singing in Repeat mode, whereas paired males sang sporadically, in Serial as well as Repeat mode (51% of their singing time). Males who lost their mates sang in Repeat mode at rates indistinguishable from males who had not yet obtained a mate. Overall, unpaired males sang in Repeat mode at significantly higher and less variable rates than did paired males. Although a larger proportion of second-year males were unpaired than after-second-year males, we found no evidence that age affected singing behavior.

We also assessed the effect of pairing status on male detectability in song-based monitoring surveys (e.g., point counts), and we suggest a field protocol for identifying unpaired males. Simulations of 5-min field samples, obtained from continuous samples >3 hr in duration, suggest that human listeners would be twice as likely to detect unpaired males as paired males. This result suggests that surveys based on aural detections may be biased in favor of unpaired males. In our population, >90% of males who sang >40 Repeat songs in 5 min were unpaired. Unpaired males were >3 times as likely as paired males to sing only Repeat songs in a given 5-min period. These results suggest that it may be possible to identify unpaired male American Redstarts by their high singing rates of exclusively Repeat songs. *Received 23 May 2005, accepted 30 March 2006.*

Recent interest in the song rates of male passerines has focused on the information contained in a male's singing, especially that available to females for assessing prospective mates (e.g., Hoi-Leitner et al. 1995). Many studies have found that females prefer males with a higher song rate (Gottlander 1987, Alatalo et al. 1990, Westcott 1992, Gentner and Hulse 2000, Nolan and Hill 2004), perhaps because song rate is correlated with male health (Saino et al. 1997, Smith and Moore 2003), dominance in winter flocks (Otter et al. 1997), food abundance before female arrival (Nystrom 1997), time on territory since arrival (Arvidsson and Neergaard 1991), territory quality (Radesäter and Jakobsson 1989), egg size (Smith and Moore 2003), feeding rate of older chicks by the male (Hofstad et al. 2002), and subsequent nest success (Hoi-Leitner et al. 1995). Thus, song rate appears to be an honest signal of male quality in many species.

Song rate also may be an honest signal of

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pairing status, since unpaired males typically sing more than their paired, nesting neighbors (Hayes et al. 1986, Rätti and Siikamäki 1993, Staicer 1996b, Gil et al. 1999, Amrhein et al. 2004), and males who lose their mates increase their song output (Johnson 1983, Hanski and Laurila 1993). Field experiments have shown clear effects of pairing status on male song, with an increase in singing after female removal and a decrease to pre-removal levels after female return (Krebs et al. 1981, Cuthill and Hindmarsh 1985, Staicer 1996b). If females can use these differences in singing behavior and song rates to locate unpaired males in a population, then perhaps male singing behavior contains sufficient information for humans to distinguish paired and unpaired males when monitoring songbird populations.

Typically, songbird monitoring techniques involve counts of singing males to obtain an estimate of the number of breeding pairs at a site (e.g., Ralph et al. 1995), but, if some proportion of singing males remains unpaired, these estimates may be biased and confound comparisons among sites (Rappole 1995). Males that remain unmated throughout the breeding season are not uncommon in many socially monogamous species (Breitwisch 1989, Marra and Holmes 1997). For example, in populations of the American Redstart (*Setophaga ruticilla*)—a Neotropical migrant species (Parulidae)—over half the yearling males remain unmated due to polygyny (predominantly in older males) and, possibly, to disproportionate female mortality at various times of the year (Secunda and Sherry 1991, Sherry and Holmes 1997). Moreover, in other parulids habitat fragmentation has been associated with edge- and patch-size-related excesses of unmated males (Faaborg et al. 1995, Faaborg 2002), possibly in relation to altered habitat quality or dispersal behavior. The resulting variability in male mating opportunities could influence life-history evolution. These considerations illustrate why precise determination of mating status is important, and song behavior provides a diagnostic tool (e.g., Gibbs and Faaborg 1990). Song behavior, and its interpretation, is also crucial for monitoring populations of migratory species like the American Redstart even if populations of many such species are not as imminently threatened as once thought (Faaborg 2002).

Few researchers have quantified the differences in male song rates with respect to mating status or breeding stage (e.g., Searcy et al. 1991, Nemeth 1996), nor have most researchers considered how song rate may bias population estimates (Best 1981, Hayes et al. 1986, Gibbs and Wenny 1993, McShea and Rappole 1997). If unpaired males could be distinguished from paired males by their singing behavior, then more accurate estimates of population density and habitat quality could be obtained. Although the American Redstart—a species in which many males often fail to obtain a mate—has been the subject of many studies (reviewed in Sherry and Holmes 1997), the species' song rate has not been examined.

Most of the closely related *Dendroica*, *Vermivora*, *Mniotilta*, *Parula*, and *Setophaga* species have two categories of song and they use these in different social contexts, suggesting a functional dichotomy (e.g., Ficken and Ficken 1965; Morse 1970; Kroodsma 1981; Lemon et al. 1985; Spector 1992; Staicer 1989; Weary et al. 1994; Staicer 1996a,b; Staicer et al. 1996). In Repeat mode, which is more common early in the season before pairing, males sing one song type in repetitive fashion; in Serial mode, which is more common later in the season, they alternate among two or more other song types (Lemon et al. 1985, 1987). Thus, any study involving song use in this species must consider song modes.

The delayed plumage maturation of American Redstarts has received much interest (e.g., Sherry and Holmes 1989, Lozano et al. 1996, Perreault et al. 1997). Yearling adult male American Redstarts, in their second calendar year of life (SY), are distinguishable by plumage from older males (after-second-year, ASY), making it easy to assess the effect of age on singing behavior. Most males that remain unpaired are SY (Lemon et al. 1987), but whether this can be explained by song is unclear (e.g., Morris and Lemon 1988).

The primary goal of our study was to examine differences in the singing behavior of paired and unpaired male American Redstarts with respect to song rates, regularity of song delivery, and use of song mode. In addition, we wanted to see whether (1) the breeding stage of females would influence the singing behavior of their mates and (2) whether SY

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versus ASY males differ with respect to singing behavior. Such information should be useful to those interested in monitoring breeding populations of American Redstarts and for stimulating similar investigations of related species.

METHODS

Study area and subjects.—Our main study area was a 140-ha stand of old, second-growth, northern hardwood forest dominated by yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*) in the Hubbard Brook Experimental Forest, White Mountains, New Hampshire (Holmes and Sturges 1975). Subjects were male American Redstarts, for which breeding data were being collected as part of a long-term population study that was independent of our vocal behavior study. Males defended contiguous territories across the study area, except where eastern hemlock (*Tsuga canadensis*) and other conifers dominated. Additional observations were made in adjacent experimental, regenerating clear-cuts dominated by dense stands of paper birch (*B. papyrifera*).

Classification of breeding stages.—For paired individuals, we classified breeding stages as early association (the first hours during which a female was on territory, or briefly visiting and then moving on to another territory, up to the first day the male had pair bonded with a female), nest prospecting (female associating with the male and visiting various tree crotches), nest building, egg laying, incubation, dependence (when adults were feeding nestlings or fledglings), or lost mate (some nesting females disappeared from the territories of seven males, usually coinciding with nest predation). Information on the presence, behavior, and pairing and breeding status of males was updated every few days by another team of observers who banded birds, mapped territories, and monitored nests.

Extensive song sampling.—To document what songs birds were singing and at what rates, we recorded singing males for short periods throughout the breeding season. We attempted to record each singing male in a given area for at least 5 min. Samples were well distributed across the study area, breeding season, and hours of the morning. It took 7 days to cover the entire study area; thus, we visited different sections on consecutive observation days, repeating the cycle every 7–10 days. These extensive samples composed our main data set for examining the relationship between singing behavior and breeding stage; they did not reveal, however, whether birds were singing at a given time of day, because we only recorded males that were already singing.

A total of 129 different males were recorded over parts of three breeding seasons (23 May–19 June 1991, 13 May–26 June 1992, and 8–23 June 1993). We recorded 10 males in 2 consecutive years and one male in all 3 years. Any males that were not uniquely color-banded were identified by individual plumage; chest markings vary among males, and drawings were made for those without bands. We used sonograms to confirm the identities of males. Individuals have fairly unique repertoires and the songs of each male have unique features, making sonograms the equivalent of fingerprints. We determined the age of males (SY versus ASY) by plumage coloration (e.g., Sherry and Holmes 1997).

We made recordings between 03:33 and 15:45 EST, mostly between sunrise (~04:15) and 11:00, when songbird population surveys are typically conducted. We recorded songs on Type IV metal tape using a Marantz PMD-222 monaural cassette recorder and a Dan Gibson parabolic microphone. Using Sound-Edit software on a Macintosh computer, we made a sonogram of each song type in each recording and compared sonograms to document repertoires and verify subject identity. Once the sonograms from all recordings had been examined, Repeat- and Serial-mode songs were identified for each subject. Typical songs recorded from the study population are presented in Sherry and Holmes (1997).

Intensive song sampling.—To assess how singing behavior changed throughout the morning hours, and to provide data for modeling detectability, we studied a subset of nine (five paired, four unpaired) focal males more intensively. Males were selected for ease of study (territories accessible at dawn) and to encompass a range of breeding stages. On mornings in early- to mid-breeding season, starting with a focal male's first song at dawn, we followed each male for 210 min continu-

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ously. To facilitate maintaining contact with the focal male, we mapped his territory boundaries and studied both his song repertoire and that of his neighbors prior to the sampling date. We made sonograms of the Serial and Repeat songs of the focal male and his neighbors, and learned to recognize them by ear. For each song the focal male sang, we noted the singing mode and time the song began (measured to the nearest second with a stopwatch). The first 30 min of song was recorded on magnetic tape, and for the remaining 180 min, time of song and singing mode were tallied on data sheets.

Detectability.—We used the intensive samples to obtain an estimate of detectability for paired and unpaired males. Samples were divided into 5-min intervals; we considered a male ''detected'' if he sang at least one song (in either Repeat or Serial mode) during a given 5-min interval. We compared the proportion of intervals in which the 5 paired and 4 unpaired males sang. Median values were used as estimates of the detectability of paired and unpaired males.

Calculations for song rate and song cadence.—For each extensive sample, we calculated song rate (number of songs/min) and cadence (the time between the beginnings of successive songs; Reynard 1963). The time from the start of one song to the beginning of the next consecutive song was measured with a stopwatch; the median value per sample was used for all analyses. Cadence is essentially a measure of the male's singing ''rhythm.'' To quantify the variability of this rhythm, we used the coefficient of variation (CV) of the cadence (corrected for small samples; Sokal and Rohlf 1995) expressed as a percentage, and hereafter referred to as cadence CV; a higher cadence CV indicates a more irregular delivery of songs. Whereas song rate and cadence should be negatively correlated (i.e., as song rate increases, time between songs necessarily decreases), song rate and cadence CV need not be. Additional information associated with each sample included sample duration, date and time of day, and the male's identity, age, pairing status (paired or unpaired), breeding stage (if paired), and singing mode (Repeat or Serial).

Statistical analyses.—We used nonparametric tests to determine whether pairing status, breeding stage, or time of day affected song rate or cadence CV. Data were not normally distributed and sample sizes for some groups were small, so we report medians instead of means as a measure of central tendency. Multiple samples of the same male were averaged so that each male contributed a single datum to a given group. We used Mann-Whitney *U*-tests to compare two groups of males, and all tests were two-tailed unless otherwise noted. To determine the significance of Mann-Whitney *U*-tests involving multiple comparisons, we used a sequential Bonferroni test (k comparisons by the Dunn-Sidak method) and an experiment-wise $\alpha = 0.05$ (Sokal and Rohlf 1995). We report the significance level of each test; if the Bonferroni revealed significance, we also report the Bonferroni-adjusted critical value (P_{adj}). We also calculated Spearman's rank correlations to examine the relationship between song rate and cadence CV.

RESULTS

Song modes.—The total singing time captured in our 514 samples of 129 males was 27.5 hr (median sample duration = 3.2 min). In few samples (<2%), males switched singing modes; for these, we separated the Serial song bouts from the Repeat bouts before analysis.

The dawn chorus was a period of intense singing of Serial-mode songs. Males sang in Serial mode at greater rates at dawn (14.4 songs/min, $n = 17$ males) than they did later in the day (10.3 songs/min; $n = 76$ males; Mann-Whitney *U*-test: $P < 0.001$). For a subset of eight paired males, we recorded Serial mode sequences during their dawn singing bouts as well as during later morning bouts on the same day. These males sang in Serial mode at higher rates at dawn (15.3 songs/min) than they did later in the morning (9.7 songs/min; one-tailed Wilcoxon Matched Pairs test: $P = 0.006$). Because of the robust difference between dawn and daytime song rates, subsequent analyses include only recordings obtained after sunrise (i.e., daytime songs).

Post-sunrise use of song modes varied with pairing status and nesting stage. When multiple samples from the same male in the same breeding stage were averaged, Repeat mode comprised 68% of the 225 resulting samples. Unpaired males sang in Repeat mode in 91%

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of 69 samples and males who lost their mate sang in Repeat in 100% of 7 samples. In the early association stage, males sang in Repeat mode in 93% of 15 samples and in 100% of 7 samples during the nest prospecting stage. Once males were nesting, their use of Repeat mode declined. Paired males sang in Repeat mode in 51% of 71 samples during the nest-building period, 54% of 13 samples during the egg-laying period, 36% of 31 samples during the incubation period, and 67% of 12 samples during the dependence period. Overall, use of song mode after sunrise was dependent on pairing status: paired males sang in Repeat mode in only 51% of 134 samples compared to unpaired males or males who had lost their mates; these males sang in repeat mode in 92% of 76 samples (Chi-square test of independence: $\chi^2 = 26.95$, df = 1, $P < 0.001$).

After dawn song rates and cadence CV.—Unpaired males sang in Repeat mode at significantly higher rates (8.0 songs/min, $n = 68$ males) than did paired males (6.3 songs/min, $n = 82$ males; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.001$, $P_{adj} = 0.013$; Fig. 1A). Unpaired males also sang in Repeat mode with a significantly less variable cadence (cadence CV = 25.3%) than did paired males (37.8%; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.001$, $P_{adj} = 0.013$; Fig. 1B).

Only 6 (8.7%) of the unpaired males we recorded sang in Serial mode after dawn, and they did so only on 1 day of observation for a brief period (median duration of recording = 1.0 min) in the first few days after arrival. Their Serial song rates were not significantly different (11.6 songs/min) than those of paired males (10.1 songs/min, $n = 69$ males; Mann-Whitney *U*-test: $P = 0.82$; Fig. 1A). Furthermore, when unpaired males sang in serial mode after sunrise, their cadence CV was similar to that of paired males (Mann-Whitney *U*-test: $P = 0.61$; Fig. 1B).

Overall, males sang in Serial mode at significantly higher rates than they sang in Repeat mode, regardless of pairing status (Mann-Whitney *U*-test and Bonferroni adjustment for paired males: $P = 0.010$, $P_{adj} = 0.017$; for unpaired males: $P = 0.017$, $P_{adj} = 0.025$). Paired males sang in Serial mode with a lower cadence CV (29.0%; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.012$, $P_{adj} =$

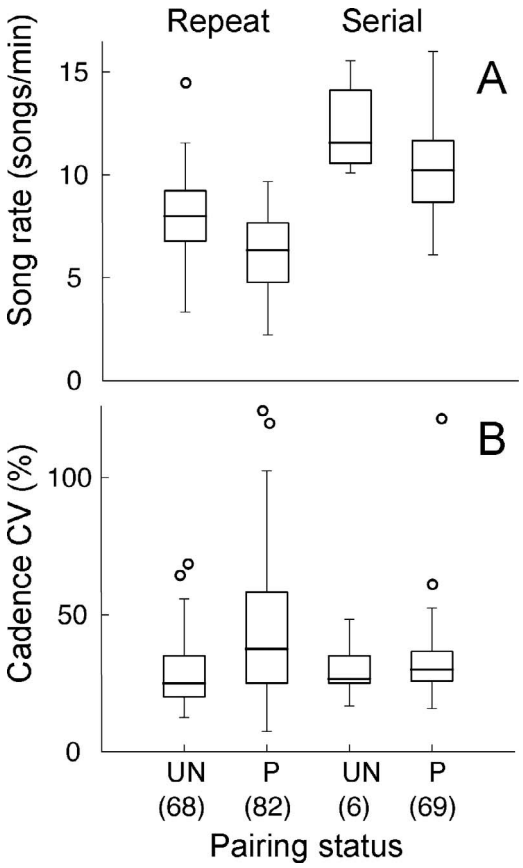


FIG. 1. Effects of pairing status on (A) song rate and (B) variability of song delivery (cadence CV) for male American Redstarts at Hubbard Brook Experimental Forest, New Hampshire, 1991–1993. Repeat and Serial mode sequences of paired (P) and unpaired (UN) males were recorded after 04:15 EST. Higher cadence CV values indicate more variation in timing between songs. Sample sizes in parentheses indicate number of males; for a given status, multiple samples per male were averaged, so that each male contributed a single datum. Samples from males in the early association stage (early stages of pairing or unpaired males who were visited briefly by unpaired females) could not be classified unambiguously and were excluded from this analysis. Box plots show the medians (horizontal center lines), interquartile ranges (between the upper and lower edges of the box, within which 50% of the data lie), values within ±1.5 times the interquartile range (bars extending from box edges), and outliers (open circles). Unpaired males sang in Repeat mode significantly faster and with a more regular cadence than paired males (Mann-Whitney *U*-test; Bonferroni adjustment for both comparisons: $P_{adj} = 0.013$). See text for additional results and statistical tests.

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0.017) than they sang in Repeat mode (Fig. 1B). Unpaired males sang in Repeat mode with a similar cadence CV as did paired males singing in Serial mode (CV = 27.0%; Mann-Whitney *U*-test: $P = 0.36$).

Cadence CV was negatively correlated with song rate for combined Repeat- and Serial-mode samples (Spearman's rank correlation: $r = -0.41$, $n = 219$, $P < 0.001$). Results were similar for Serial mode when samples were analyzed separately ($r = -0.46$, $n = 75$, $P < 0.001$). For Repeat-mode samples, the negative correlation between cadence CV and song rate was strong for paired males ($r = -0.61$, $n = 76$, $P < 0.001$) and weak for unpaired males ($r = -0.24$, $n = 68$, $P = 0.050$); thus, unpaired males sang in Repeat mode with a more regular rhythm than paired males, regardless of song rate.

Rates of Repeat mode song also changed with breeding stage (Fig. 2A). Males who lost their mate sang at rates similar to those who had not yet paired (8.3 versus 8.0 songs/min; Mann-Whitney *U*-test: $P = 0.90$). Males sang at greater rates before pairing than did males whose mates were nest prospecting (5.0 songs/min; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.006$, $P_{adj} = 0.010$), nest building (6.6 songs/min; $P = 0.001$, $P_{adj} = 0.007$), incubating (6.1 songs/min; $P = 0.009$, $P_{adj} = 0.013$), or feeding dependent young (4.2 songs/min; $P = 0.002$, $P_{adj} = 0.009$). Repeat-song rates of unpaired males did not differ significantly from those of males in early stages of pairing (early association stage, 6.5 songs/min, $P = 0.16$), or in the egg-laying stage (6.9 songs/min; $P = 0.11$; Mann-Whitney *U*-tests).

Cadence CV of Repeat songs also changed with breeding stage (Fig. 2B). Again, the cadence CV of males who lost their mates (22.5%) was similar to that of males who had not yet paired (25.1%; Mann-Whitney *U*-test: $P = 0.79$). Before pairing, males sang with a significantly more regular rhythm than did males who were beginning to associate with a female (37.0%; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.008$, $P_{adj} = 0.013$) or paired males whose mates were nest prospecting (46.3%; Mann-Whitney *U*-test and Bonferroni adjustment: $P = 0.001$, $P_{adj} = 0.007$), nest building (38.7%; $P = 0.001$, $P_{adj} = 0.009$), or feeding dependent young (68.5%; $P = 0.002$; $P_{adj} = 0.010$). Cadence CV of unpaired males did not differ from that of males whose mates were in the egg-laying stage (CV = 22.4%; Mann-Whitney *U*-test: $P = 0.88$) or incubating (35.9%; $P = 0.09$). Thus, although song rates of unpaired males and males in the early association stage did not differ, the latter sang with a less regular rhythm. Conversely, although song rates of unpaired males were significantly greater than those of paired males whose mates were incubating, both groups sang with a similarly regular rhythm.

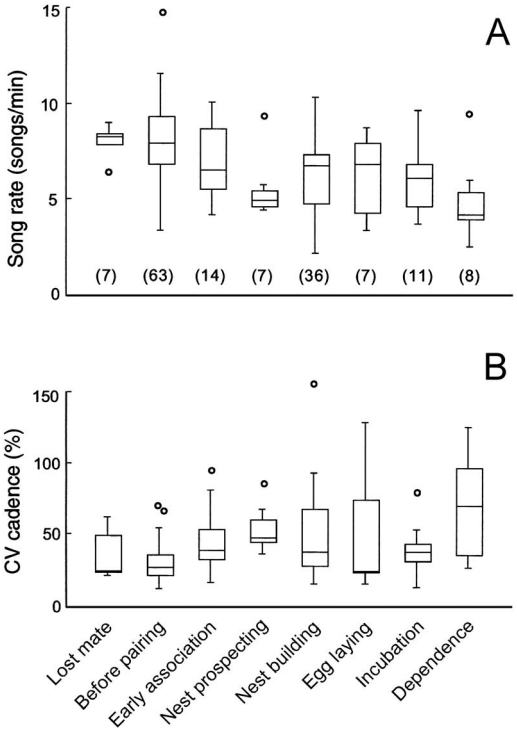


FIG. 2. Effects of breeding stage on (A) song rate and (B) variability of song delivery (cadence CV) for Repeat-mode sequences for male American Redstarts at Hubbard Brook Experimental Forest, New Hampshire, 1991–1993. Breeding stage: lost mate, before pairing, early association, nest prospecting, nest building, egg laying, incubation, and dependence (feeding nestlings or fledglings). Sample sizes in parentheses indicate number of males; often a given male contributed data to more than one stage, but within each stage, all data were independent (i.e., multiple samples per male were averaged to obtain a single datum). See text for explanations of statistical tests and the Figure 1 caption for an explanation of the box plots.

Age and song rate.—We found no signifi-

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cant age effects on song rate (SY versus ASY males). Unpaired SY and ASY males sang in Repeat mode at similar rates (8.6 versus 8.0 songs/min, $n = 32$ versus $n = 28$, respectively; Mann-Whitney *U*-test: $P = 0.24$). Paired SY and ASY males also sang in Repeat mode at similar rates (4.9 versus 5.7 songs/min, $n = 17$ versus 49, respectively; Mann-Whitney *U*-test: $P = 0.10$). Only 3 of the 36 unpaired SY males that we observed sang in Serial mode after the dawn bout. For paired SY and ASY males singing in Serial mode, song rates were similar (10.6 and 10.2 songs/min, $n = 11$ and 43, respectively; Mann-Whitney *U*-test: $P = 0.76$). Thus, song rate was not affected by male age, regardless of pairing status. The similarity in singing behaviors of SY and ASY males can be seen in the 3.5-hr samples of the nine focal males (Fig. 3).

Temporal patterns in song activity and pairing status.—Obvious differences between paired and unpaired males with regard to their singing behaviors are illustrated by 3.5-hr song counts for the nine intensively sampled males (Fig. 3). Typical of breeding males, the five paired males (Fig. 3A) sang a large number of Serial mode songs at rapid rates during their dawn bouts. Around sunrise, however, paired males usually stopped singing and for the rest of the morning sang sporadic, but typically distinct (not mixed), bouts of Repeat- or Serial-mode songs. During the incubation stage, some males (e.g., 10 June; Fig. 3A) sang little on their territory after their dawn bouts, whereas others (e.g., 16 June; Fig. 3A) sang during most of the 5-min periods after sunrise. Temporal patterns in Serial- and Repeat-mode song activity were similar for the five paired males (two SY and three ASY males).

In contrast, the four males who lacked established pair bonds (Fig. 3B) sang only in Repeat mode after sunrise, and did so more frequently and at higher rates than paired males. A male's time on territory rather than date or pairing status seemed to influence whether he sang Serial mode in the dawn chorus. The two unpaired males that did not sing in serial mode during a dawn bout, but sang only in Repeat mode before 04:00, were late arrivals in the study area (28 May and 10 June; Fig. 3B). Although these SY and ASY males were observed at different times of season, both had been singing for only a few days on territories that were adjacent to contiguous clusters of established territories. The other two unpaired males (13 June and 15 June; Fig. 3B), which had defended territories within a contiguous cluster of ASY males for ≥10 days by the time they were recorded, sang dawn Serial bouts like those of their paired neighbors but then switched at sunrise to Repeat mode and steadily sang in that mode through the morning. The male who attracted a mate during the observation period (13 June; Fig. 3B) sang only in Repeat mode but at a rate that decreased through the morning. On the previous days, no female was present; after the sample date, he remained paired and commenced nesting. The male who lost his mate after her nest was depredated (15 June; Fig. 3A) sang only in Repeat mode after sunrise, but at a slightly lower rate and with less regularity than did the males who had not yet paired.

Confounding factors.—To test whether time of day or time of season influenced Repeat-song rates, we calculated Spearman's rank correlation coefficients. Song rates of unpaired males were negatively correlated with time of day ($n = 70$, $r = -0.350$, $P = 0.010$). For paired males, however, there was no significant relationship between song rate and time of day ($n = 54$, $r = -0.10$) or time of season ($n = 54$, $r = -0.05$), and, for unpaired males, there was no correlation between song rate and time of season ($n = 70$, $r = -0.12$; all $P > 0.10$).

Sampling duration was another potentially confounding factor. Although Repeat-song rates of paired and unpaired males differed significantly, data for the two groups did overlap to some extent (Fig. 1). Overlap between paired and unpaired males, however, decreased as sample duration increased (Fig. 4). In samples lasting ≥5 min, Repeat song rates of paired and unpaired males overlapped little. In samples of ≥5-min duration, 82% of 27 unpaired males, but only 7% of paired males, sang ≥8 Repeat songs/min. In samples of 10- to 15-min duration, the median for the first 5 min was similar to the median for the entire sample.

Detectability.—Data for the nine intensively sampled males (Fig. 3) were split into 5-min intervals and each was examined for occurrence of song. Only intervals after the dawn chorus were used (median = 37, range = 35–

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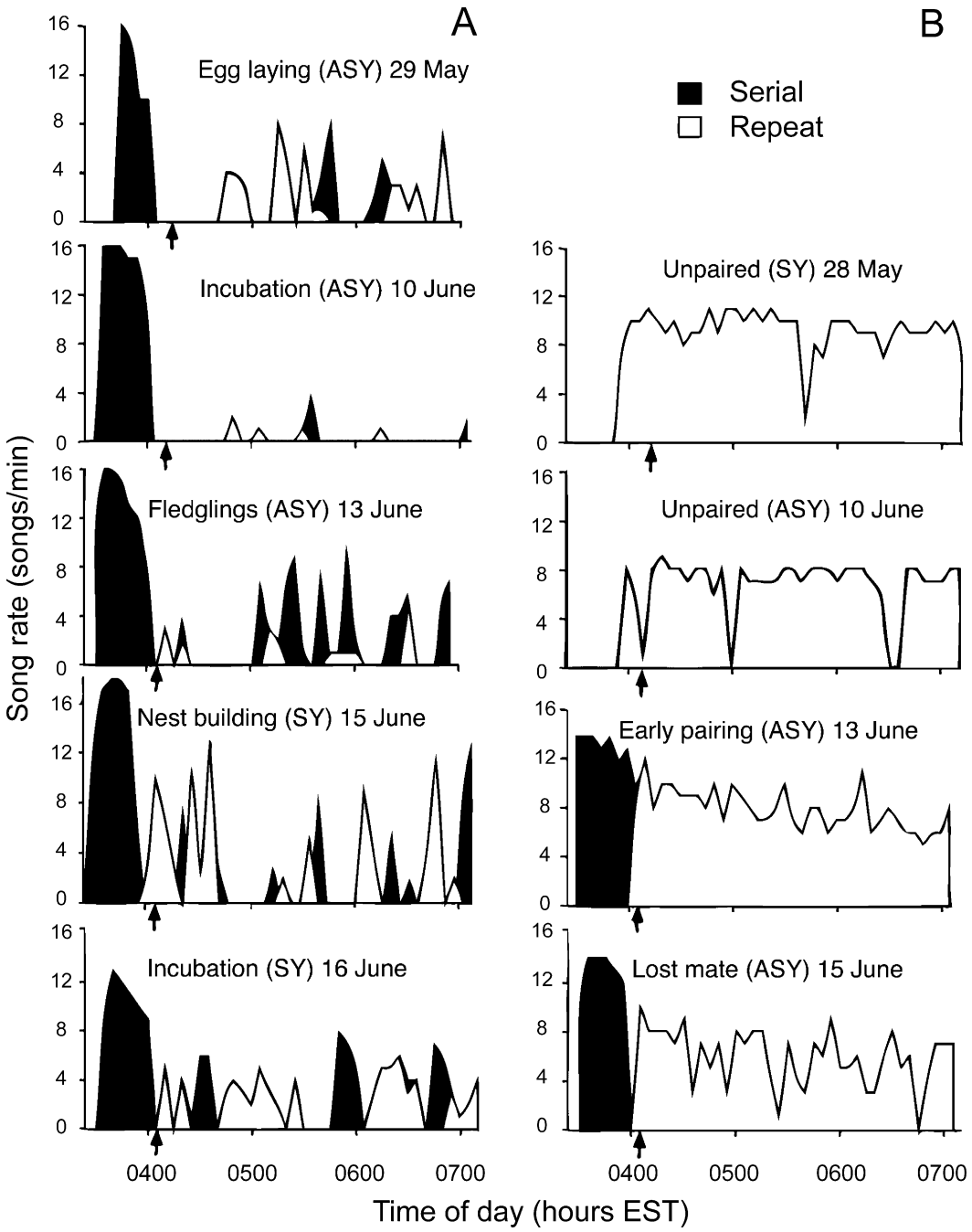


FIG. 3. Singing activity of nine American Redstart males in various breeding stages at Hubbard Brook Experimental Forest, New Hampshire, 1992–1993. SY = yearlings, ASY = older adults. Areas under curves show median number of Serial (black) and Repeat (white) songs that the subject sang per minute for each 5-min period, from his first songs at dawn until 3 hr after sunrise. Sunrise varied from 04:10 (28 May) to 04:05 EST (15 June), as indicated by arrows on the x-axis. Subjects were (A) five paired males and (B) two unpaired males within a few days of territory establishment, one male who first attracted a mate during the observation period, and one male whose mate had disappeared when her nest was depredated. Note the larger output of Repeat-mode songs from males who lacked an established pair bond (B).

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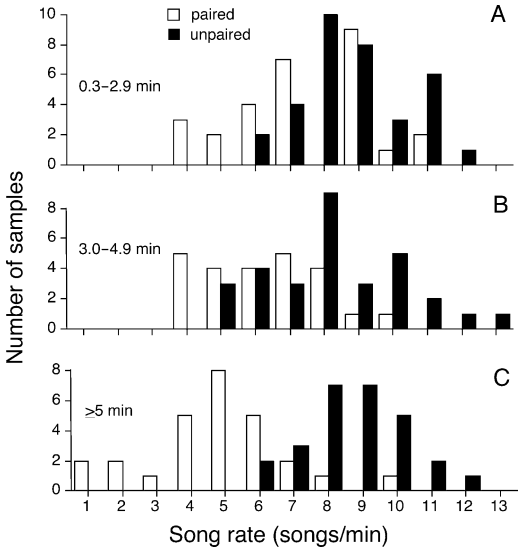


FIG. 4. Repeat-song rates of paired versus unpaired male American Redstarts using samples of three durations at Hubbard Brook Experimental Forest, New Hampshire, 1991–1993. For each duration, a given male was entered into the analysis only once. (A) Samples of short duration (0.3–2.9 min) for 37 paired and 34 unpaired males. (B) Samples of medium duration (3.0–4.9 min) for 24 paired and 31 unpaired males. (C) Samples of long duration (5–15 min) for 27 paired and 27 unpaired males. Note that as sample duration increased, the amount of overlap between the two samples decreased.

38 intervals per male). Unpaired males (n = 4) sang in 99% (median; range = 92–100%) of the 5-min intervals, whereas paired males (n = 5) sang in only 49% (median; range = 16–74%) of the 5-min intervals. Detectability was defined as the proportion of 5-min intervals in which a bird sang one or more songs. Detectability of unpaired males (0.99) was significantly greater than the detectability of paired males (0.49; Mann-Whitney U-test: P = 0.014).

DISCUSSION

Singing behavior and breeding status.—We identified three ways in which the singing behavior of unpaired male American Redstarts differed significantly from that of paired males: (1) after sunrise, unpaired males sang in Repeat mode almost exclusively, whereas paired males sang in both modes; (2) unpaired males sang Repeat songs at a significantly faster rate than did paired males; and (3) unpaired males sang with a more regular cadence than did paired males. We also documented variation in song rates and regularity of cadence in relation to breeding stage of paired males.

After the dawn bout ended, use of Serial mode varied with pairing status and breeding stage. In almost all cases in which we heard Serial mode after dawn, it was delivered by a paired male. Use of Serial mode after dawn may reflect the presence of nests or young (see also Ficken and Ficken 1965, Lemon et al. 1985), and males seem to have the greatest propensity to use Serial mode (or the equivalent song category in other species) when their mates are incubating (this study; Staicer 1989, 1996b; but see Lemon et al. 1987).

Breeding stage also affected Repeat-song rates and cadence. As males began to pair, they continued singing primarily in Repeat mode, but cadence became more irregular. Lowest rates of singing in Repeat mode were found in males whose mates were building nests and males who were feeding nestlings or fledglings. Slower song rates and more irregular cadences have been associated with the activities of foraging and associating with females (e.g., Nolan 1978, Gil et al. 1999). Although we had relatively few song samples from the egg-laying stage, these males sometimes sang for brief periods at rates that overlapped those of unpaired males. Our males, however, were silent while following their mates; thus, we found no evidence that song functions to guard females during their fertile period (see also Titus et al. 1997). Males sang in Repeat mode least often when their mates were incubating, a pattern shared with other parulid species (Staicer 1989, 1996b; but see Lemon et al. 1987).

Time of season did not appear to alter these singing patterns. Pairing and nesting were asynchronous in our population due to different arrival times of males and high rates of nest predation, after which females sometimes disappeared or, rarely, changed mates. Thus, at any given time, neighboring males often were in different breeding stages. Males who lost their mates sang at high rates, similar to males before they were paired. This change in behavior has been noted for other wood-warblers (Nolan 1978, Kroodsma et al. 1989, Spector 1991, Staicer 1996b) and other groups

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of passerines (e.g., Wasserman 1977, Krebs et al. 1981).

To determine whether females select males with higher song rates, additional data, such as pairing order, male condition or quality, and territory quality must be obtained (e.g., Hoi-Leitner et al. 1995, Nystrom 1997). If vocal behavior is important in mate choice, however, we might expect to find differences between SY and ASY male American Redstarts. We found no evidence that age affects song rate or singing mode when pairing status was taken into account. Although age influences competitive ability (Sherry and Holmes 1989), pairing success (Morris and Lemon 1988), and extra-pair fertilizations (Perreault et al. 1997), these effects appear to be caused by the later arrival of yearlings rather than age effects on song behavior (Lozano et al. 1996; TWS unpubl. data).

Implications for population monitoring.—Few researchers have examined the possibility of distinguishing unpaired from paired males based on their song behaviors, despite the potential utility of such information in population monitoring. Our results suggest that a considerable amount of potentially useful information is available in the singing behavior of male American Redstarts. Unpaired males sang at steadier and higher rates, took fewer and shorter breaks from singing (usually $\leq$5 min), and typically sang only in Repeat mode after sunrise. After the dawn chorus, Serial mode was heard from paired males almost exclusively; typically, if a male sang in Serial mode, he was paired. A trained ear can easily distinguish Repeat from Serial mode. In Repeat mode, the same song type is repeated, whereas in Serial mode, males rapidly alternate between 2–5 noticeably different songs (e.g., Lemon et al. 1985).

In 5-min samples from a large number of males, the Repeat-song rates of unpaired and paired males overlapped little. We further assessed the information available in a 5-min sample by combining estimates of detectability (whether a male sang any songs in the 5-min period) with the likelihood that a male already detected was singing in Repeat mode. The probability that a singing male sang in Repeat instead of Serial mode differed for paired (0.51) versus unpaired (0.92) males. Detectability also differed for paired (0.49) and unpaired (0.99) males. The chances that a paired male would sing any Repeat songs within a 5-min interval was only 0.25 (0.51 $\times$ 0.49). In contrast, the chances that an unpaired male would sing in Repeat mode within a 5-min period was 0.91 (0.92 $\times$ 0.99). Thus, unpaired males were 3.6 times (0.91/0.25) more likely to sing in Repeat mode in a given interval than were paired males.

Our results suggest that unpaired males should be distinguishable from paired males in field surveys. When conducting point counts, an observer could listen to a singing male for a prescribed period of time, note whether he is repeating the same song (Repeat mode) or alternating songs (Serial mode), and tally the number of Repeat songs he sings per minute or the number of seconds that lapse between successive songs. In our study population, a critical song rate of 8.0 Repeat songs per min for 5 min (>40 songs total) would identify the male as ''unpaired'' with reasonable certainty. If a male sang in Serial mode during the same 5-min period, we could be reasonably certain that he was ''paired.''

The presence of unpaired males can confound estimates of the numbers of breeding birds. Unpaired males are common in American Redstart populations, with yearlings forming the bulk of males that are unsuccessful in obtaining mates (Sherry and Holmes 1997). Our data show that unpaired males are about twice as likely as paired males to be detected during brief listening intervals (e.g., 5 min). Similar results have been reported for several other species (Best 1981, Mayfield 1981, Gibbs and Wenny 1993).

The utility of such a protocol for detection of trends over time (or space) is demonstrated in the following hypothetical case. Assume that 100 males are within earshot, 5-min counts are conducted, and the listener always detects and correctly identifies a given song. If, in year 1 (or habitat A), all males are paired, only 49 males would be reported (using our calculated detection probability = 0.49). If only half of the 100 total males are paired in year 2 (or habitat B), then only ~25 (50 $\times$ 0.49) of the paired males would be detected while nearly all of the unpaired males (50) would be detected (using our calculated detection probability = 0.99), for a total of ~75 males reported. Based on the data, we

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would erroneously conclude that the population increased from year 1 to year 2 (or that the population in habitat B was larger than that in habitat A).

Correcting the data by removing unpaired males from the total detected and taking into account the lower detectability of paired males provides a very different picture of population status. Assume we use the protocol whereby, for a given male, detecting ≥40 songs per 5-min sample indicates that he is unpaired, and 10% of males are misclassified (based on the type of overlap illustrated in Fig. 4C). In year 1 (or in habitat A), we would correctly classify 44 (and misclassify 5) of the 49 paired males that were detected, and then double this number for a total estimate of 88 breeding pairs. In year 2 (or in habitat B), 22 of the 25 paired males detected would be correctly classified as paired and 5 of the detected unpaired males would be misclassified as paired, for a total of 27 paired males (22 + 5) detected. Correcting for the 0.49 detection rate of paired males yields a total estimate of ~54 pairs in year 2 (or in habitat B). Both corrected estimates fall within 10% of the actual number of breeding pairs. The large population decline from year 1 to year 2 becomes visible (or the lower population density in habitat B becomes obvious). Thus, the information about the relationship between pairing status and song rates in this species, and perhaps others, can potentially be used to obtain more accurate population estimates.

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