

Dawn song repertoires of tree swallows (*Tachycineta bicolor*)

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Abstract: I describe the dawn songs of 38 male tree swallows (*Tachycineta bicolor*) recorded at five sites near Wolfville, Nova Scotia. Males deliver dawn song each morning during the hour before dawn, while flying elliptical paths above their nest sites. These dawn songs consist of syllables approximately 0.15 s long, delivered every 1.5 s. Each male has a recorded repertoire of one to seven discrete syllable types (average 2.6) and may repeat each syllable type an apparently random number of times before switching to the next. Most syllables could be classified on the basis of their structure into seven types, with much variation among renditions by different males of any given syllable type. Three of these syllable types were very similar to call notes that have specific uses at other times of day. Syllable types were randomly distributed among males and sites. In this species neither syllable type, the number of times each type is repeated (string length), nor the number of types a male sings (repertoire size) appears to carry particular messages or advertise male quality. Instead, syllable types may provide individual distinctiveness and variety in song sequences.

Résumé : On trouvera ici la description des chants émis à l'aube par 38 mâles de l'Hirondelle bicolor (*Tachycineta bicolor*), à cinq sites voisins de Wolfville, Nouvelle-Écosse. Les mâles émettent leur chant chaque matin au cours de l'heure qui précède le lever du soleil, tout en faisant des vols elliptiques au-dessus de leur nid. Ces chants se composent de syllabes d'une durée d'environ 0,15 s, émises à intervalles de 1,5 s. Chaque mâle possède un répertoire d'un à sept types différents de syllabes (2,6 en moyenne) et peut répéter chaque type de syllabe un nombre apparemment aléatoire de fois avant de passer au suivant. La plupart des syllabes peuvent être classifiées en sept types d'après leur structure et chaque type donné de syllabe est émis de façon particulière par les différents mâles. Trois de ces types sont très semblables aux cris d'appels qui ont des fonctions spécifiques à d'autres moments de la journée. Les types de syllabes sont répartis de façon aléatoire entre les différents mâles et entre les différents sites. Chez cette espèce, ni les types de syllabes, ni le nombre d'émissions de chaque type (longueur de la séquence), ni le nombre de types chantés par un mâle (répertoire) ne semblent transmettre de message particulier ou faire foi de la qualité d'un mâle. Les types de syllabes semblent plutôt refléter des distinctions individuelles et ajouter de la variété dans les séquences de chants.

[Traduit par la Rédaction]

Introduction

The many different sounds that make up the songs of birds can usually be classified into a few discrete (i.e., qualitatively distinct) song categories, known (depending on their length) as song, phrase, or syllable "types." Many hypotheses have been proposed to explain the function of these song categories, and all have received support in certain cases (Krebs and Kroodsma 1980; Searcy and Anderson 1986; Kroodsma and Byers 1991). These hypotheses differ mainly according to whether they treat song categories themselves or combinations of those categories as the most important signals in communication. Song categories themselves may be the most important signals because each category has a different meaning, or because by singing the same song category as a rival ("song matching"), a territory holder signals its readiness to defend the territory (Horn 1992). Combinations of song categories may also carry messages. For example, in some species, the faster new song categories are presented, the more likely the singer will interact inter- or intra-sexually; in others, the more song categories a male

can sing (i.e., the larger his "repertoire size"), the better his chances of attracting a mate (Krebs and Kroodsma 1980).

Although observations and experiments are the most direct ways to test these hypotheses, descriptions of the structure of song categories are critical. Relevant questions include: how different are song categories (within as well as between individuals)? how many song categories does each male sing? and how are song categories sequenced? The answers to these descriptive questions make certain hypotheses more or less likely. For example, if songs are not widely shared, they cannot be used to carry messages that will be understood by a wide audience; if they are not shared with at least some other individuals, they cannot be used in song matching.

The purpose of this study was to describe the dawn song repertoire of tree swallows (*Tachycineta bicolor*). This species' song repertoire is interesting for at least three reasons. First, its song is simpler than those of most other species that have been described, consisting of short (0.1–0.2 s) syllables given every 2–3 s, delivered on the wing from just before dawn to just after sunrise during the egg-laying and incubation period (Robertson et al. 1992). Song categories in this species would consist of syllable types rather than song or phrase types. Tree swallows might therefore provide counterexamples to accepted notions about repertoires and singing behavior, which have been developed mainly from

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studies on birds with longer, often more complex songs (Krebs and Kroodsma 1980). Second, tree swallows sing a completely different song at dawn than during the day (Robertson et al. 1992). The reasons for such specialization in song structure might shed light on the functions of dawn singing in birds generally, which are still poorly understood (Staicer et al. 1996). Third, the tree swallow is one of the best studied species in North America (Robertson et al. 1992), yet the structure of its dawn song has not been described.

I examined three song features that would help clarify the functions of dawn singing and of song categories (in this case, syllable categories) in this species. First, do tree swallows have syllable categories, and if so, what is their repertoire size? Large repertoires are thought by some to result primarily from female preference for showier songs, while small repertoires are used mainly in territory defense (Catchpole 1982; but see, for example, Read and Weary 1992). Second, are syllable categories repeated a variable number of times, to form a "bout" or "string," as in species that use the number of times each song category is repeated (string length) as a signal of readiness to interact (Horn 1992)? Third, do males tend to share syllable categories, as they should if these categories have widely recognized messages or are used in song matching?

Methods

The five study sites (a field beside a river and four orchards) were within 15 km of Wolfville, Nova Scotia. Each site contained 23–32 nest boxes, occupied by 12–17 color-marked breeding pairs. Between 15 May and 14 June I recorded 6–10 males at each site (a total of 38) using a Dan Gibson parabolic microphone and a Marantz 450 cassette recorder with TDK chromium bias tape, at a distance of 30–40 m. Thirteen birds were recorded before incubation; 19 birds were recorded during incubation.

Beginning about 1 h before sunrise, males sing nearly continuously, on the wing, high over their nest site (every singer seen in good enough light was a male, females were never sighted before the end of the chorus, and no more than one singer was seen for each active nest, so females probably do not participate in the chorus). I arrived at a site at twilight before the chorus began, then walked around the study site in a circular path until the dawn chorus ended, recording each bird I encountered for at least 5 min, i.e., approximately 400 syllables (see below for terminology). During recording I noted the flight path of the bird and any interactions with conspecifics. Although birds were painted and color-banded, I usually could not identify individuals because they flew high and the light was dim. Therefore, to ensure that males were not repeatedly represented in the sample, I only included birds that (i) maintained flight paths that were at least 200 m apart or (ii) were seen to have non-overlapping flight paths at the time they were recorded.

I analyzed 30 s (41 ± 3.1 songs) of each male's singing to determine repertoire size, string length, and song rate. I used SoundEdit software (Farallon Computing, Berkeley, Calif.) both to listen to songs at reduced speed and to view sonograms of the songs at various settings. The setting used in the figures is 512 points, with high frequency emphasis.

Terminology is as follows: an "element" is a continuous sound separated from other sounds by a silence; a "syllable" is a set of elements separated from other such sets by a silence that is greater than the length of the set; a "note" is either a syllable or an element; a "syllable category" (or "syllable type") is a set of syllables that appears to be qualitatively distinct from other such sets; and a "rendition" or "token" of a syllable category is any particular example of that syllable category.

Sample sizes vary according to the availability of appropriate samples for the analysis concerned. For example, analyses of syllable sequences required long uninterrupted recordings with high signal to noise ratios. Means are presented \pm SE.

Results

Males usually began singing about 1 h before sunrise and stopped by or shortly after sunrise. During the dawn chorus, males flew 5–15 m high, usually following roughly elliptical paths that included at least one nest box (Fig. 1). When males alighted near or on the nest box, in every case in which they could be identified (13 males), they were the male of the pair nesting at that box. Seven out of 38 males perched within 20 m of their home box during part of their dawn singing.

Dawn song consisted of long strings of syllables approximately 0.15 s long, centered around 4–6 kHz, and given at a rate of 1.5/s. Each syllable consisted of very short whistles that were sharply modulated up or down by about 2 kHz. This rapid modulation gave the notes a chirpy or rough quality.

Syllable types and repertoire size

Successive syllables in a male's singing were easily assigned to types, i.e., sets of syllables that were categorically distinct from one another. A typical example of one male's singing is shown in Fig. 2. By looking at a sonogram of a song sequence (or listening to it at low speed), repetitions ("strings") of one syllable type and switches to another were easily distinguished. The whole set of syllables that a male produced could also be sorted into types. Syllable types differed in the number of component sounds and (or) the direction of frequency modulation of component sounds (up, down, or both; Fig. 3). Within syllable types, some component sounds sometimes differed slightly in frequency or in their pattern of frequency modulation, but (by definition) syllable types did not intergrade.

Recorded repertoire size was the total number of discrete categories of syllables (syllable types) that a male sang. Plots of the number of new syllable types encountered against the number of syllables recorded leveled off for half the birds by 4 syllables and for all birds by 14 syllables; the mean of these plots leveled off after 13 syllables (Fig. 4a). That is, at most 14 syllables had to be analyzed to determine repertoire size; I analyzed 41 ± 2.7 syllables for each bird (minimum 14). Recorded repertoire size ranged from 1 to 7, with a mean of 2.6 (Fig. 4b).

Sequencing of syllables

The number of times each syllable type was repeated before a switch to the next (i.e., string length) varied from 1 to 20 in birds with at least two syllables in their repertoire. I tested whether string length was random by comparing the observed number of strings with that expected by chance. By restricting the analysis to birds with two syllable types, I could use the expected value given for the Runs test (Taylor 1990). Strings were no longer or shorter than expected by chance (observed number of strings 22 ± 4.1 , expected 21 ± 3.5 , paired $t = 0.64$, $df = 8$, $p = 0.54$).

Neither maximum string length nor recorded repertoire size was correlated with song rate ($r_s = 0.23$, $n = 15$, $p = 0.39$ and $r_s = -0.08$, $n = 15$, $p = 0.66$), and none of these

Fig. 1. Flight paths of eight males at the riverside site. Circles represent nest boxes, numbers identify boxes where each male nested, and "P" indicates that the male sang from a single perch (males 6 and 8 sang only from perches).

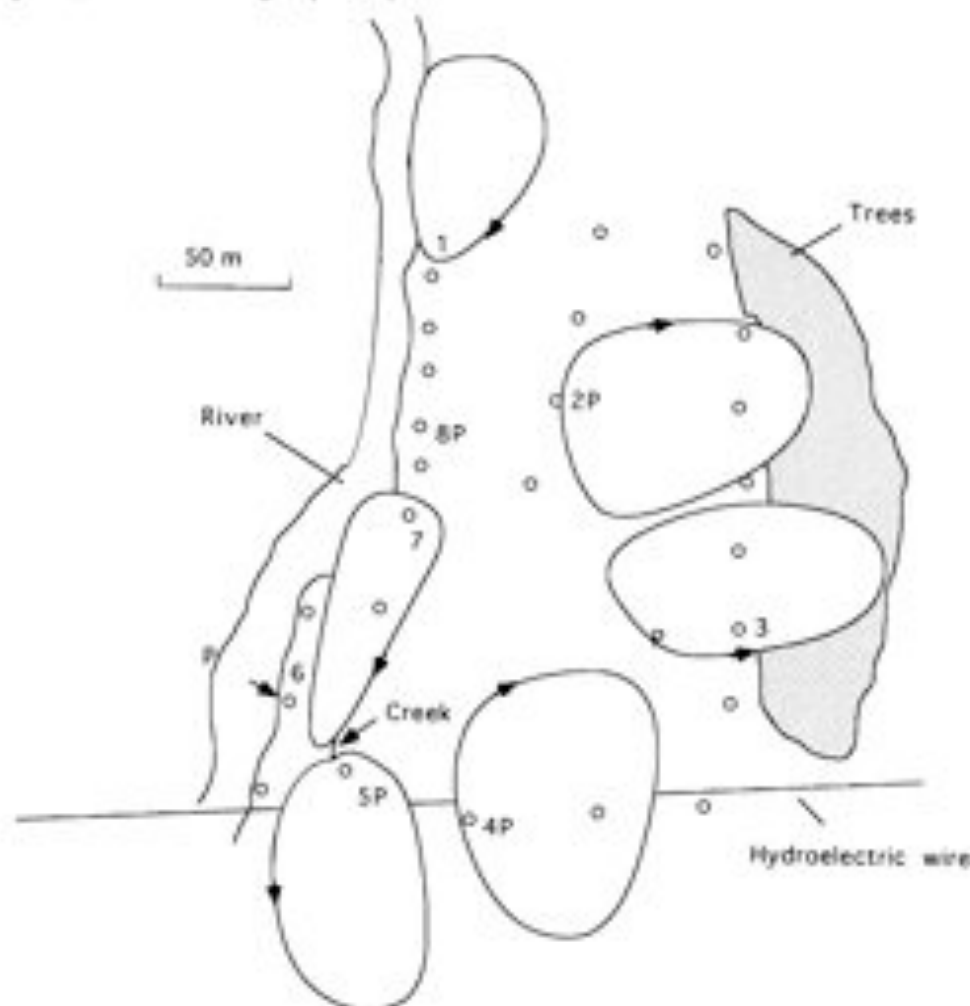
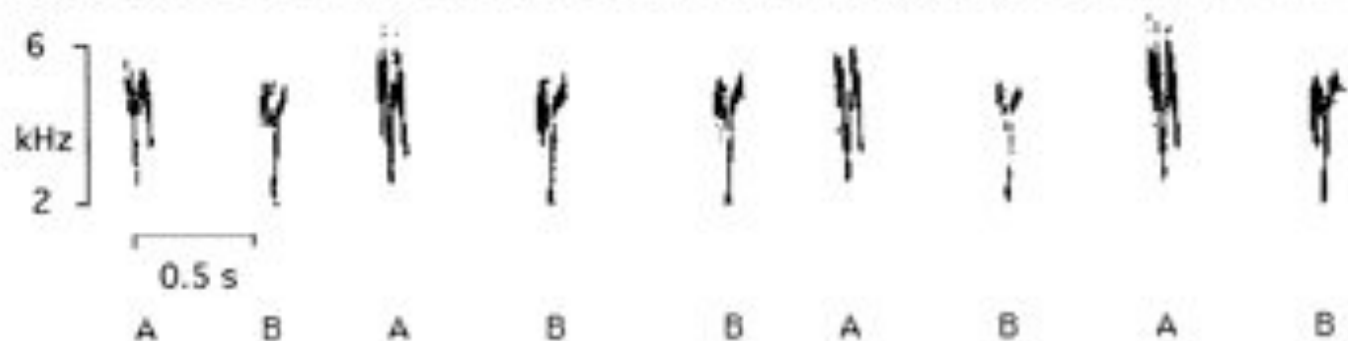


Fig. 2. Sonograms of nine successive syllables from one male's dawn singing. His two syllable categories are labeled "A" and "B."



three variables differed between birds recorded before versus during incubation (*t* tests, $df \geq 17$, $p \geq 0.21$).

Comparison of syllables among males

Comparison of the repertoires of different males showed that the renditions given by different males varied widely. Nonetheless I was able to sort them into seven categories (Fig. 5) according to whether they possessed certain characteristics, which are listed below. Some categories appear to be derived

from other call notes in the tree swallow's vocal repertoire:

1. Chip notes: characterized by one or two series of at least three abrupt, downward, linear frequency sweeps given in rapid succession. Similar in structure to tree swallow "contact" notes (Robertson et al. 1992).

2. Chevron notes: characterized by at least one chevron-shaped sound, i.e., a note that rises, then abruptly changes direction to fall in frequency.

3. Sweep notes: characterized by at least one sound that

Fig. 3. Syllable responses of nine males.

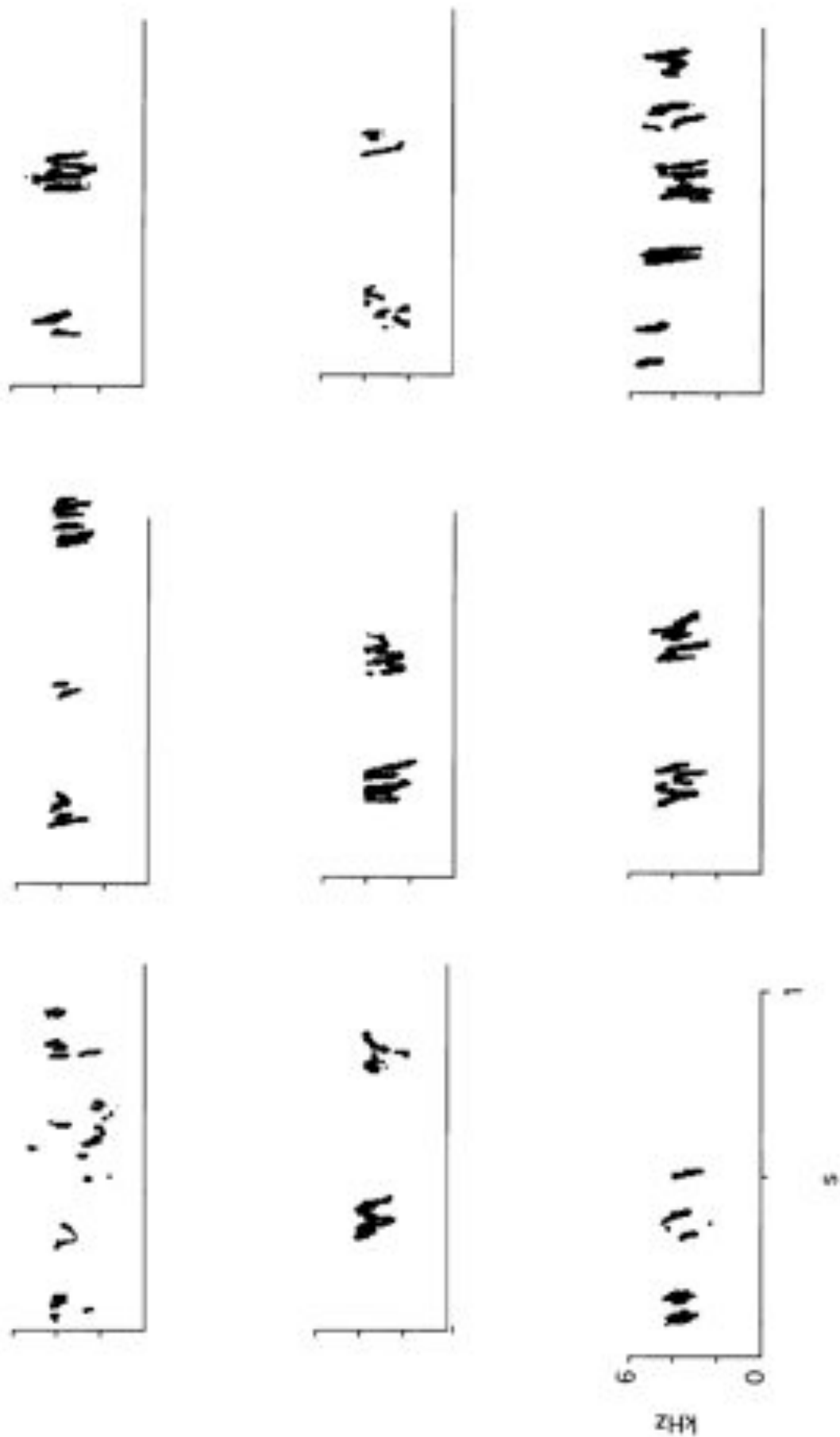
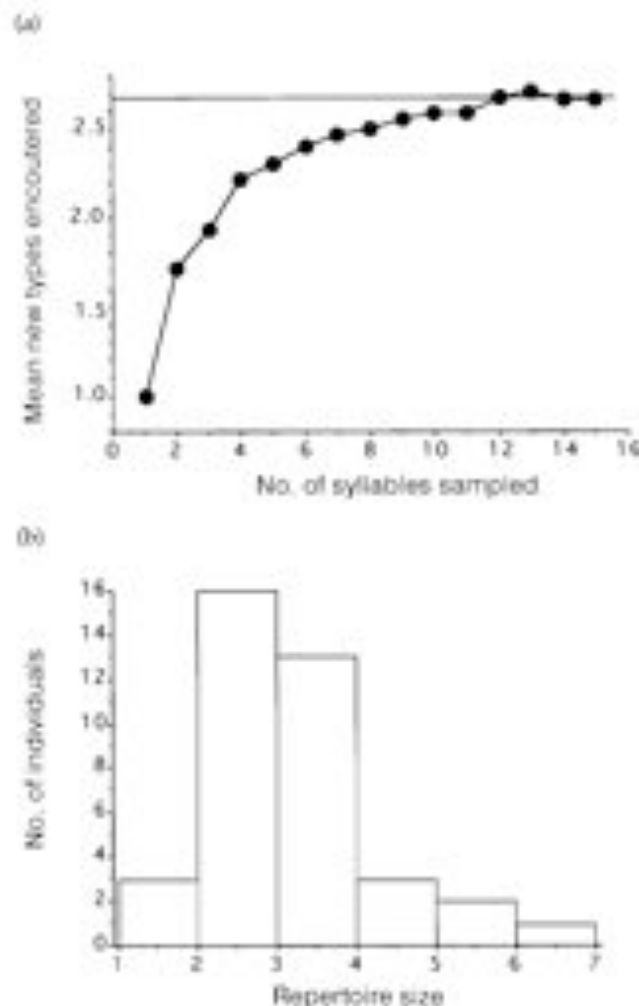


Fig. 4. Determination of repertoire size. (a) Mean number of new syllable types encountered versus the number of syllables recorded ($n = 31$ males); the horizontal line shows mean repertoire size for these males. (b) Histogram of repertoire sizes of all 38 males in the study.



falls, then rises in frequency, usually with a less abrupt transition than category 2.

4. Gurgles: at least six very short unconnected sounds given rapidly and alternating between various high and low frequencies. Similar in structure to the gurgle in the "pleasure" call (Robertson et al. 1992).

5. Frequency drops: characterized by few (1–4) component sounds, at least one of which drops in frequency by at least 2 kHz.

6. Short notes: syllables whose component sounds appear to share characteristics with any of the above syllables, but which are too short to be placed unambiguously into one of those categories.

7. V-notes: syllables that fall then rise in frequency, in a more linear fashion than category 3; very obviously derived from the "anxiety" call (Robertson et al. 1992).

Syllables did not differ significantly in their distribution across sites (Table 1). The total number of males having each syllable type also did not significantly differ from random. Specifically, the number of males having each syllable type fit a log-normal distribution (Table 1), which means that no

Table 1. Number of males at each site that had each syllable type in their repertoire

Site ^a	Syllable type						
	1	2	3	4	5	6	7
One (8)	3	3	2	3	3	0	3
Two (9)	6	5	4	1	2	2	0
Three (8)	4	1	4	2	2	1	0
Four (9)	5	2	4	0	4	5	1
Five (4)	3	0	0	1	2	2	2
Total ^b	21	11	14	7	13	10	6

^aNotes: Numbers in parentheses show the number of males recorded at each site.

^bDistribution of syllables among sites: $\chi^2 = 25.82$, $df = 24$, $p = 0.36$.

^cThe abundance of syllables fit a log-normal distribution; regression of log rank abundance versus abundance (Horn and Falls 1988): $R^2 = 0.97$, $df = 15$, $p = 0.0001$.

syllables were either particularly common or particularly rare, at least according to this preliminary classification.

Discussion

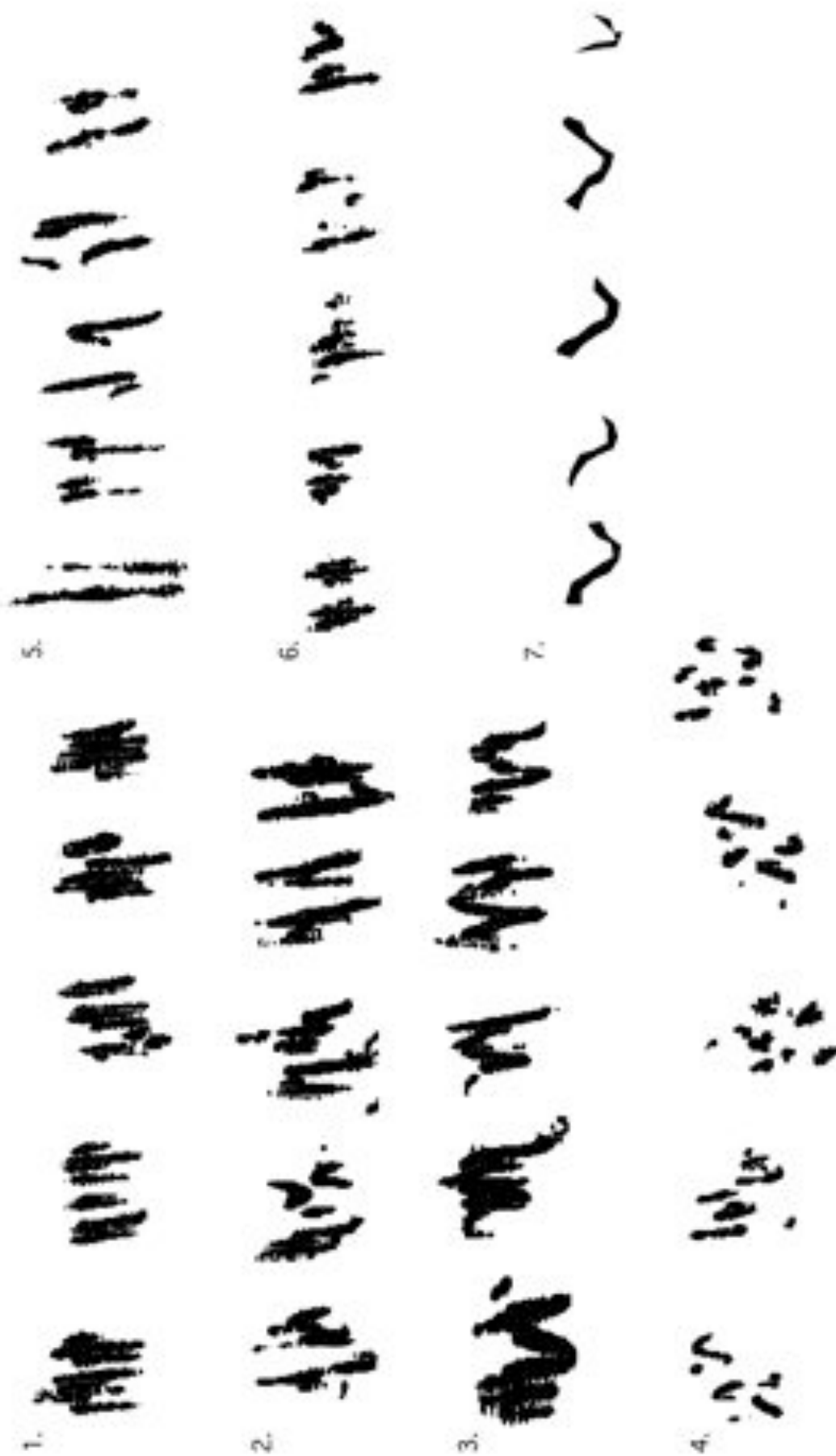
The results show different patterns of two levels of song variation in tree swallow dawn song. Within individuals, syllables could be easily classified into a repertoire that apparently consisted of two or three discrete syllable types. Between individuals, syllables could be classified into types, but there was high variation among renditions of syllable types sung by different individuals. Based on my preliminary classification of syllable types, males showed no tendency to include particular syllables in their repertoire or to have syllables that were similar to those of males in nearby territories. I will discuss the function of dawn singing in tree swallows in general before turning to the particular function of song types.

Why sing at dawn?

The functions of the dawn chorus are not known (Staicer et al. 1996), but several functions are unlikely in tree swallows. The dawn chorus is given throughout the incubation period, making any hypothesis involving mate guarding or mate attraction unlikely. Although females could have heard males when they passed by the nest site, males followed routes that wandered far from the nest box, so the male's mate is probably not the primary target audience. The dawn chorus does not begin until just before laying, after nest sites have been selected (Robertson et al. 1992; personal observation). Thus, dawn singing probably does not serve to establish territories.

However, dawn singing may help maintain territories once they are established. Males flew in roughly elliptical patterns that included their nest and one or more other nest boxes or cavities. The main benefit of defending additional nest boxes may be attracting a second mate (Quinney 1983) or providing sites for re-nesting in case the first nest is depredated (Rendell and Robertson 1989). These benefits are likely to be most important after the first female is settled and on eggs, which is when most dawn singing occurs.

Fig. 5. Five tokens of each of the seven syllable categories found in the population. Numbers correspond to descriptions in the text.



In combination with the distinctive syllables of each male, this flight pattern delineated areas occupied by different males more clearly than the more erratic, silent flight patterns seen during foraging later in the day. Birds range quite widely during the day, often leaving nesting areas altogether, so before dawn may be the best chance for males to mark their territories, before the environment becomes noisy and foraging competes for advertising time.

In tree swallows, dawn song employs different syllable types than day song (Robertson et al. 1992; unpublished data). This specialization in structure might stem from differences in the functions of dawn and day song. Day song appears to be used mainly in interactions between pair members near the nest site (personal observation), and therefore likely has an intersexual function, in contrast to the territorial, intrasexual function of dawn song. Thus, in tree swallows, as in many other species (Staicer et al. 1996), dawn singing appears to be specialized for a territorial function. Experimental tests of these apparent specializations (e.g., by playback of dawn versus day song) may be a promising way to isolate the function of the dawn chorus.

Function of song categories in tree swallows

The apparently small size of tree swallow repertoires, along with the low variation in repertoire size, suggest that they are unlikely to be the result of "runaway" sexual selection by female choice. Such selection would probably not stabilize repertoire sizes at only two or three syllable types, unless females preferred small or intermediate repertoire sizes. The best evidence of selection for elaborate singing performances through female choice, however, comes from birds with much larger repertoires than tree swallows (Searcy and Anderson 1986). For similar reasons, repertoire size probably does not advertise male quality. In several species with more elaborate songs and repertoires, low-quality males might not be able to afford the costs of learning or even producing more song types (Lambrechts 1992). Such costs probably do not apply in tree swallows, with their shorter, simpler songs and smaller repertoires.

Syllable types probably do not carry different messages. First, they are used in rapid sequence in the same circumstances, and so do not each carry distinct information about what the singer is doing. Second, they are not widely shared among individuals, and so could not conform to a shared code. Nor are they likely to be used in song matching, both because of the low sharing in general and because there was no tendency for males at the same site, i.e., males that might have more reason to be able to match one another, to share syllable types.

String length also is unlikely to carry messages. In many songbird species, shorter string lengths signal the singer's readiness to engage in territorial or sexual interactions (Horn 1992). I could not observe the behavior of males in sufficient detail to relate it to their song patterns. However, presuming that males would send similar messages over the 30-s segments of singing that I analyzed, I would expect string length to stay shorter or longer over short periods of time than expected by chance. Instead, string length was random over these time periods. String length also did not correlate with song rate, as one would expect if it advertised the singer's readiness to interact.

If syllables do not have different meanings, are not used in matched countersinging, do not advertise repertoire size, or signal varying string lengths, what is their function? One possibility that has not been considered is that syllable repertoires are an epiphenomenon of selection for individual distinctiveness. If dawn singing serves to delineate individual territories, as the pattern and timing of dawn flights suggest, each male's songs should be distinct from his neighbor's. Selection for individual distinctiveness would increase song variation between males and decrease song variation within males (i.e., make their songs more consistent in structure). Having a second or third syllable type might add redundancy to this individual distinctiveness or add variety to the song sequence overall.

Song categories may be defined in different ways depending on what characters are used to define categories and on the relative weight given to intra- and inter-individual variation in song structure. These various classifications may all be relevant to the birds because different functions might be served by different levels of variation (Horn 1992). The real test of any classification is to play songs back to the birds and see whether they recognize the same song categories we do.

The results of the present study suggest that dawn song in tree swallows serves mainly in territory defense, and I have suggested that song categories might serve to produce variety and individual distinctiveness in this signal. Playback experiments are underway to test whether the birds themselves recognize syllable types and whether they serve the hypothesized functions, and if so why the functions seem to require what appear to be categorically distinct, rather than graded, signals.

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