The examination and description of variation in the songs of passerines have been the objects of numerous studies in recent years (Thielcke 1969, Nottebohm 1975, Krebs and Kroodsma 1980). These studies have dealt almost entirely with variation in the songs of males, which is understandable since singing by females is not as widespread. There are a few species, however, in which females do sing on a regular basis. For example, singing by females has been reported in the Northern Cardinal (Cardinalis cardinalis) (Laskey 1944, Lemon 1965), Rose-breasted Grosbeak (Pheucticus ludovicianus) (Ivor 1944, Dunham 1964), Northern Oriole (Icterus galbula) (Beletsky 1982), Red-winged Blackbird (Agelaius phoeniceus) (Beletsky 1983), and several other species (Armstrong 1963, Van Tyne and Berger 1976). Despite these reports of singing by female songbirds, there have been few, if any, studies that have provided a detailed examination of female song in a species. In the present study I examined intra- and interindividual variation in the songs of a population of female Black-headed Grosbeaks (Pheucticus melanocephalus).

STUDY AREA AND METHODS

I recorded female Black-headed Grosbeaks at Malibu-Guinavah Forest Camp (Cache National Forest), 10 km east of Logan, Cache Co., Utah. Individual females were captured in mist nets and provided with a unique color band combination to aid in individual recognition.

Songs were recorded during the breeding seasons of 1977 and 1978 using a Nagra IIIB tape recorder with an Altec 633A microphone mounted on a 62-cm parabolic reflector. Sonagrams of the songs were produced using a Kay Elemetrics 6061B Sona-Graph with the wide-band filter setting. These sonagrams were then examined to determine several quantitative parameters of individual songs, i.e., syllables per song, syllables/kind (the number of syllables in a song divided by the number of kinds of syllables in that song), and duration. I also determined the number of syllable types present in each female's repertoire and the patterns of similarity in the songs of females within the population. I define syllable as either a continuous tracing on the sonagram or a grouping of such tracings that always occurred together. Classifying syllables was difficult at times because of the variation in their form in successive songs. Fig. 1 illustrates the variation in two syllables used by one female grosbeak.

Recordings were made of the songs of 12 females. However, when the total number of syllables was graphed cumulatively against the total number of songs sampled, the curves were asymptotic for only five birds. Thus, only these five birds were used when determining the average syllable repertoire.

It was possible to compare the syllables of any female according to their similarity with
FIG. 1. Variation in the form of two syllables in the songs of a female Black-headed Grosbeak.

those of other females or males, thereby obtaining an indication of the overlap of syllable repertoires. The amount of syllable sharing between two grosbeaks was assessed by a formula derived by Harris and Lemon (1972):

$$\frac{2 \times \text{no. of syllables common to both repertoires} \times 100}{\text{Total syllables of bird 1} + \text{total of bird 2}}$$

RESULTS

The songs of female Black-headed Grosbeaks consisted of syllables of varied frequency lying between 1.5 and 5.0 kHz (Fig. 2). The mean number of syllables per song was 4.5 ± 1.8 and the mean song duration was 1.47 ± 0.41 sec (Table 1). An analysis of the songs of 24 male grosbeaks (N = 545) revealed an average of 10.3 ± 3.5 syllables per song while the mean song duration was 3.5 ± 1.3 sec. These differences between the songs of males and females were found to be significant (P < 0.01, t-test). Individual syllables utilized by females had a mean duration of 0.15 ± 0.03 sec (N = 126) while the mean intersyllable interval was 0.12 ± 0.02 sec (N = 200). A catalog of tracings from 264 audiospectrograms was used to distinguish a total of 126 different syllables (Figs. 3 and 4). The number of different syllables in the repertoires of the females studied ranged from 5 to 28 (Table 1).

Female grosbeaks showed a pronounced tendency to use a few of the
Table 1
SYLLABLE AND DURATION CHARACTERISTICS OF SONGS OF FEMALE GROSBEAKS

<table>
<thead>
<tr>
<th></th>
<th>No. of songs analyzed</th>
<th>No. of syl. in repertoire</th>
<th>No. syl/song (X ± SD)</th>
<th>Song duration in sec (X ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red I</td>
<td>28</td>
<td>(14)</td>
<td>7.5 ± 2.6</td>
<td>2.26 ± 0.77</td>
</tr>
<tr>
<td>Bridge</td>
<td>26</td>
<td>(15)</td>
<td>5.5 ± 1.2</td>
<td>1.21 ± 0.28</td>
</tr>
<tr>
<td>Island</td>
<td>11</td>
<td>14</td>
<td>4.5 ± 2.4</td>
<td>1.13 ± 0.52</td>
</tr>
<tr>
<td>UB</td>
<td>47</td>
<td>(28)</td>
<td>5.7 ± 1.3</td>
<td>1.60 ± 0.22</td>
</tr>
<tr>
<td>Riverside</td>
<td>42</td>
<td>(5)</td>
<td>4.0 ± 1.3</td>
<td>1.32 ± 0.36</td>
</tr>
<tr>
<td>Guinavah</td>
<td>15</td>
<td>11</td>
<td>5.3 ± 1.7</td>
<td>1.29 ± 0.35</td>
</tr>
<tr>
<td>Ballfield</td>
<td>8</td>
<td>14</td>
<td>4.1 ± 1.1</td>
<td>1.34 ± 0.35</td>
</tr>
<tr>
<td>Black</td>
<td>3</td>
<td>7</td>
<td>3.3</td>
<td>0.85</td>
</tr>
<tr>
<td>1978</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cs 28</td>
<td>39</td>
<td>(26)</td>
<td>5.2 ± 1.6</td>
<td>1.21 ± 0.39</td>
</tr>
<tr>
<td>LM</td>
<td>11</td>
<td>15</td>
<td>5.4 ± 1.8</td>
<td>1.14 ± 0.38</td>
</tr>
<tr>
<td>Red I</td>
<td>25</td>
<td>(12)</td>
<td>6.5 ± 1.5</td>
<td>1.90 ± 0.48</td>
</tr>
<tr>
<td>East Ballfield</td>
<td>7</td>
<td>4</td>
<td>6.1 ± 1.1</td>
<td>1.32 ± 0.27</td>
</tr>
<tr>
<td>AL</td>
<td>2</td>
<td>4</td>
<td>4.0</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td>264</td>
<td>x = 16.7</td>
<td>4.5 ± 1.8</td>
<td>1.47 ± 0.41</td>
</tr>
</tbody>
</table>

* Same female recorded in different years.

* Only those numbers in parentheses were used to determine average.

syllables from their total repertoires much more than other syllables. For example, one female uttered a total of 211 syllables in 28 songs. Although this female had a repertoire of 14 syllables, three syllables made up 82.0% of the total. Another female uttered 196 syllables in 38 songs and two syllables (out of a total syllable repertoire of 26) made up 56.6% of this total. Four syllables made up 73% of the total. This tendency to repeat syllables was also apparent when songs were analyzed in terms of syllables/kind. Analysis of the songs of eight females (10 songs/female) revealed a mean value of 1.41 ± 0.22. Similar analysis of the songs of their mates gave a mean value of 1.02 ± 0.02, a significantly lower value (P < 0.001, t-test).

Sharing of syllables among females was uncommon. Ninety-nine of the 126 syllables (78.6%) were limited to one female's repertoire. Furthermore, 21 syllables (16.7%) were found in the repertoires of just two females, and five syllables (4.0%) were noted in the repertoires of three females. The remaining syllable was found in the repertoires of seven females. In contrast, syllable sharing among males appeared to be more common. For example, the songs of six of seven males present in the
Malibu-Guinavah study area in 1978 typically began with the same four syllables. Furthermore, the songs of five of these males typically began with the same six syllables (Ritchison 1980).

A catalog of the syllables in the repertoires of 22 male Black-headed Grosbeaks was also prepared (Ritchison 1980) and a comparison of the 156 syllables used by males with those used by females revealed that there was some sharing of syllables between the sexes. Approximately one-fourth of the syllables used by females resembled those found in the repertoires of the males. Much of this sharing between the sexes (60.5%) was the result of females using syllables similar to those of their mates.
Fig. 3. Catalog of syllable types of female Black-headed Grosbeaks (Syllables 1–66).
Fig. 4. Catalog of syllable types of female Black-headed Grosbeaks (Syllables 67–126).
DISCUSSION

The songs of female Black-headed Grosbeaks appear to differ in certain respects from the songs of many male songbirds. One such difference is that females do not accurately reproduce specific syllable types in successive songs. Several studies have illustrated the consistency with which many male songbirds reproduce specific syllable types (Kroodsma 1975, Lein 1978, Martindale 1980, Chew 1981). However, highly variable syllable types or song types have been reported in male songbirds during song development (i.e., plastic song) and in canaries (Serinus canarius) when males begin to sing again after a period of several months when they sing very little or not at all. Nottebohm (1981:1368) noted that at the end of this period the “male canaries start to sing once more . . . in the tentative, highly variable manner typical of early plastic song.” Nottebohm (1981) suggested that such variability may be related to low levels of testosterone in the blood and the effect of these low levels on the areas of the brain that control singing behavior. The variable nature of the syllables produced by female Black-headed Grosbeaks could similarly be due to low testosterone levels. Previous investigators have suggested that hormone levels may influence the singing behavior of females in other species. Falls (1969:210) noted differences in the songs of male and female White-throated Sparrows (Zonotrichia albicollis) and indicated that the songs of females are often “short, quavering and variable in speed . . . [and] lack the precise control of pitch and timing characteristic of males.” He further suggested that these qualities in the songs of females may be a function of the low levels of testosterone in females.

Recent evidence indicates that differences in the central nervous systems of males and females may contribute to differences in behavior. For example, Nottebohm and Arnold (1976) noted sexual dimorphism in the song control areas of the brain of canaries which appears to be related to differences in the singing behavior of males and females. Adult male canaries have a complex song repertoire while females normally do not sing. Even when testosterone is administered, females sing a less complex song than do males. Such dimorphism may contribute to some of the differences in the songs of male and female Black-headed Grosbeaks. That is, the songs of males were more “complex” in terms of the number of syllables per song, kinds of syllables per song, and duration.

The results of the present study indicate that individual female Black-headed Grosbeaks possess syllable repertoires that are largely unique. Furthermore, female grosbeaks apparently possess rather limited “functional” repertoires, with only a limited number of syllables out of the total repertoire normally being used. Such small and largely unique rep-
ertoirines suggest that individual recognition may be of importance to female grosbeaks (Harris and Lemon 1972, Falls 1982). This appears to be the case since the songs of females apparently are important in family-group maintenance (Ritchison 1980, 1983a).

As noted above, analysis revealed several differences between the songs of male and female Black-headed Grosbeaks. Furthermore, playback experiments have shown that both sexes apparently use such differences to differentiate between the songs of males and females (Ritchison 1983b). The possible significance of such differentiation has been discussed by various authors. For example, singing by female White-crowned Sparrows (Z. leucophrys) reportedly is confined to the early part of the breeding season (Blanchard 1941, Kern and King 1972, Baptista 1975). Baptista (1975) suggested that such singing behavior is probably adaptive because the songs of these females are similar to those of males and such songs evoke aggressive behavior from territory-holding males. Early in the breeding season white-crown males are less aggressive and respond weakly, if at all, to playback of recorded songs. The lack of response by territorial males to the songs of female grosbeaks appears to be equally adaptive. That is, after the young fledge, family groups begin to wander and female grosbeaks use their songs to maintain contact. If the songs of females were similar to those of males and evoked aggressive behavior from territorial males, then females would risk being chased or attacked each time they sang. Under such conditions, maintaining contact with young grosbeaks would be difficult or impossible.

SUMMARY

Although numerous investigators have examined variation in the songs of male passerines, there are few descriptions of such variation in the songs of females. In the present study I examined intra- and interindividual variation in the songs of female Black-headed Grosbeaks (Pheucticus melanocephalus). The songs of individual females consisted of a series of syllables of varied frequency lying between 1.5 and 5.0 kHz. The mean number of syllables per song was 4.5 and the mean song duration was 1.47 sec. The number of syllables in the repertoires of female grosbeaks ranged from 5–28.

The songs of female grosbeaks differed from the songs of males in that females appeared unable to reproduce consistently specific syllable types as accurately as males and the songs of females were less complex than the songs of males. Such differences may be due to differences in the levels of testosterone found in males and females. Previous investigation suggests that this hormone affects the development and maintenance of areas in the brain that control singing behavior.

Sharing of syllables among females was uncommon with 78.6% of all syllables limited to the repertoire of one female. Such distinctiveness generally indicates that individual recognition may be important. Young grosbeaks appear to recognize parental songs and use this ability to maintain contact with their parents after fledging.
ACKNOWLEDGMENTS

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LITERATURE CITED


JOINT MEETING OF THE WILSON AND COOPER ORNITHOLOGICAL SOCIETIES

The Fourth Joint Meeting of the Cooper and Wilson Ornithological Societies will be held 5-9 June 1985 at the University of Colorado, Boulder. A 3-day scientific program is scheduled with contributed papers and several half-day mini-symposia. Morning field trips are planned to ponderosa pine stands in the foothills, water bird habitats and heronries on the prairie, and open meadows, coniferous and aspen forests in the mountains. All day trips on 9 June will tour Rocky Mountain National Park or Pawnee National Grassland. Tours of interest are scheduled for non-ornithological spouses/guests. The banquet will be at the Denver Museum of Natural History. The meeting announcement will be mailed in January; abstracts are due by 6 March. Questions can be directed to CYNTHIA CAREY (Local Committee on Arrangements) or CARL BOCK (Scientific Program) at Department of EPO Biology, Univ. of Colorado, Boulder, Colorado 80309.