

FEMALE SONG IN THE HOODED WARBLER

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ABSTRACT - One female Hooded Warbler (*Wilsonia citrina*) was discovered singing in July 1993, and another in May 1996 among a color-banded breeding population under investigation. The first female's song structurally resembled the typical male Hooded Warbler mixed-mode song in duration, frequency range, and number of syllables, although it had an atypical raspy quality. Males responded similarly to playbacks of the female song and a male song from the same population. We suggest that age and high breeding density may be explanatory factors for this rare behavior.

INTRODUCTION

Female song occurs regularly among only a small proportion of temperate-zone breeding passerine species (e.g., Baptista et al. 1993; Beletsky 1982; Ritchison 1983, 1986) whereas the incidence of female song is much greater in tropical resident species, where females of several species sing "duets" with their mates (Morton 1996). This pattern is exhibited clearly among the wood-warblers (Parulinae) (Spector 1992). Currently, there are nine species of temperate zone wood-warblers representing six genera (*Vermivora*, *Dendroica*, *Setophaga*, *Seiurus*, *Geothlypis*, and *Wilsonia*) where females have been documented to sing rarely to uncommonly (reviewed in Spector 1992, see also Gilbert and Carroll 1999). Several hypotheses have been suggested to explain the finding, albeit rare, of female song among temperate-zone warblers. Female song may be the result of male-like behavior in older females (Nolan 1978), female-female conflict in very dense populations (Hobson and Sealy 1990) or may function in intra-pair contact (Gilbert and Carroll 1999).

Here we describe the first reported occurrences of female song in the Hooded Warbler (*Wilsonia citrina*, Boddaert), and summarize the results of a preliminary playback experiment to test whether males re-

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spond differently to a female song compared to a male song from the same population. We discuss potential explanations for this rarely observed phenomenon.

METHODS

The research was conducted in July 1993 and May 1996 as part of an ongoing study of Hooded Warblers in Crawford County, PA (41° N, 79° W) (see Stutchbury 1998 for details). Hooded Warblers are sexually dichromatic, however older females may appear male-like compared with first-year females (Lynch et al. 1985). Birds were individually color-banded, and sexed (by presence of a brood patch or cloacal protuberance) during first capture enabling individual identification of all males and females. One singing female was located by LJEO on 1 July 1993, and observations were made on several subsequent dates (3, 5, 9, 11 July 1993). The song of this female was recorded with a Panasonic Digital Audio Tape Recorder and a Sony shotgun microphone. The female song recording is archived in the Texas Bird Sound Library, Sam Houston State University, Huntsville, TX (TBSL #236).

To test how males responded to the female song, we performed 10-min playbacks in the territories of 10 different males. We conducted all playbacks between 06:30 and 12:00 EDT from 8 to 14 July 1993. A playback of a single male "mixed mode" song (Goddard 1993) was used on the same territories on alternate days. Playback order was assigned randomly by a coin toss. Six of the males received the female playback first and four of the males received the male playback first. Songs were played back at a rate of 10 songs per min, a typical rate for Hooded Warblers (Wiley et al 1994). The male song used in the playback was recorded on the study site in the 1993-breeding season. Behavior of territorial males was observed during the 10-min playback as well as five min before and five min after the playback. Behaviors recorded were: latency of response to the playback, closest approach to the playback speaker, and song rate before and after the playback. A response was defined as an individual approaching within 20 m of the playback speaker. Because male responses to playback may vary among individuals, our experiment compared each male's responses to the playback of male versus female song in a paired design. Wilcoxon signed-ranks tests were used to compare male responses to the two different songs.

RESULTS

Song observations

The song of the female Hooded Warbler observed singing on 1 July 1993 (Fig. 1a) was similar to a typical male mixed mode song in duration,

frequency range and number of syllables (Fig. 1b), but sounded atypically raspy. This banded female was at least four years old and had male-like plumage, scoring six out of a possible 10 on the plumage score developed by Stutchbury et al. (1994). At the time of detection of song, this female was feeding three fledglings of her first and only successful brood of the season. Her mate did not appear to be assisting with the feeding of fledglings, but, following the female's initiation of a second brood, the

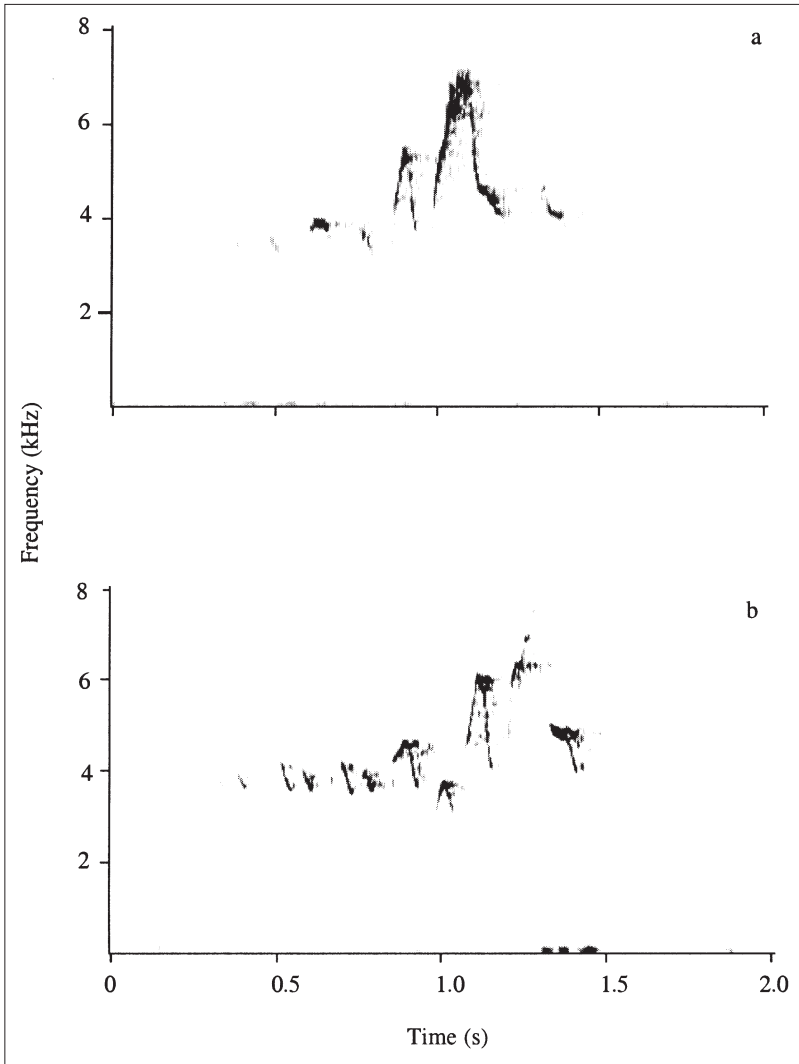


Figure 1. (a) Wide band sonogram of the female Hooded Warbler observed singing in July 1993; (b) Wide band sonogram of a male Hooded Warbler mixed mode song recorded in July 1993 and used in the playback experiment.

male assumed care of all first brood offspring. The female was not heard to sing again after the male took over care of all first brood fledglings.

During a one-hour observation on 7 July, this female averaged 5.8 ± 1.2 songs per min while making frequent feeding trips to her fledged offspring. Her mate appeared to counter-sing in response to the song of the female. On 5 July a five-min recording of the song was played back to the female, and she stopped singing immediately. Two min after the playback ended, the female resumed singing.

This female did not return the following season, and in light of the philopatry of this individual, who had bred in the same area (neighboring territories) for at least two years, it is likely that mortality was the cause of her failure to return. Between-year comparisons of the singing behavior of this individual were thus not possible.

A second female at the same study site was observed singing by TEP on 20 May 1996. She sang both repeat-mode and mixed-mode songs, typical of Hooded Warbler males. TEP observed the female from a distance of not more than 2 m and clearly saw the female's color bands, plumage and singing behavior. The female had been chip calling from a shrub, low to the ground (0.5 to 1.75 m), typical female behavior, just prior to initiating song. The female sang two, repeat-mode songs followed by four, mixed-mode songs. This female was at least four years old with male-like plumage, (scoring 8/10 for amount of black), and was known to be nest-building at the time singing was observed. The female produced two broods that season (one successful and one unsuccessful) and was observed incubating on at least one occasion. The female was captured and bled on 11 June and was observed to have a full brood patch at that time. This female was observed singing only once, and subsequent observations yielded no further records of singing (TEP), thus no recording was possible. The female was first caught on the study site in June 1994 on a neighboring territory and given a plumage score of 6/10, making her at least four years old at the time she was observed singing. The female successfully fledged one brood in 1994 and paternity analyses indicated an absence of extra-pair young. In 1995, she occupied the same territory with the same male as in 1994, and was given a plumage score of 8/10 and she also successfully fledged one brood. The female switched territories and mates in 1996. Her original territory was still occupied by her previous mate. The female was last seen in 1997 in the same area of her previous two territories. She successfully produced one brood but her mate was never identified.

Playback experiment

Males responded similarly to the female song and male song playbacks (Tables 1, 2). Song rates of males did not differ significantly in

response to playback of female versus male song (female: Wilcoxon signed-rank test, $P = 0.78$; male: $P = 0.48$).

DISCUSSION

Results from our playback experiment suggested that male Hooded Warblers did not distinguish between the female song and male song that we presented. Most males exhibited behavior typically seen when an intruder male is heard on their territory; rapidly approaching the song source, and continuing to sing. Despite its slightly unusual form, male reaction to the playback of the female song, suggests the song was within the normal range of individual variation for male songs (Goddard 1993). Alternatively, males may have recognized the song as from a female, but reacted to it with a similar level

Table 1. Responses of male Hooded Warblers ($n = 10$) to playbacks of female (top row) and male (bottom row) song on their territories. Males that did not come within 20 m of the playback speaker during the 10-min playback were given a latency score of 600s.

Male	Date	Latency to respond(s)	Closest approach (m)	Song rate before (number/min)	Song rate after (number/min)
O10	7/8	136	1	0	0
	7/9	600	30	6	6
G6	7/8	73	5	0	0
	7/9	10	10	9.2	9.2
R18	7/11	0	20	3.8	5.4
	7/10	0	10	6	6.2
O16	7/10	0	2	5.2	4
	7/11	0	20	2.8	0
Y19	7/11	0	2	6.6	7.7
	7/10	240	10	5	9
O15	7/11	232	20	5.5	10
	7/13	90	20	5.6	0
T14	7/14	0	15	5.6	4.1
	7/13	0	10	4	4
T19	7/13	600	40	5.8	3
	7/14	600	50	6.2	4.7
W19	7/14	600	30	9	7.7
	7/13	17	5	6.8	7.5
Y22	7/13	163	15	4.6	3.6
	7/14	120	20	5.6	4.5

Table 2. Median responses of males to playbacks and results of Wilcoxon signed-rank tests comparing responses to playbacks of male and female songs.

Response	Female Song Playback	Male Song Playback	P
Latency (s)	104.5	53.5	0.75
Closest approach (m)	15	15	0.40
Song rate before (number/min)	5.4	5.8	0.68
Song rate after (number/min)	4.1	5.4	0.44

of interest. The mate of the singing female did not react aggressively to her song, which is suggestive of recognition.

Because we used only one female song and one male song in our playback experiment the results of this experiment must be considered preliminary. We cannot generalize to explain how male Hooded Warblers would react to any male or female song, but rather our results pertain to the specific songs we used (Fig. 1). We conclude that males showed a similar level of responsiveness to a female song as they did to a single, typical male song from the same population. However, further playback experiments using multiple male and female songs would be necessary to make generalizations about male recognition of female song.

As observed for Prairie Warblers (*Dendroica discolor*, Vieillot; Nolan 1978), the two Hooded Warbler females we reported singing were at least four years old. The advanced age of both female Hooded Warblers observed in our study suggests that changes in circulating levels of sex hormones due to age (e.g., Armstrong 1963, Tella et al. 1997) may have been responsible for eliciting singing behavior. Alternatively, high breeding density and numerous territorial interactions among females may also result in elevated testosterone levels and song (Arcese et al. 1988, Hobson and Sealy 1990). Female Hooded Warblers on our study site nest at high densities with 4–8 neighbors and nearest neighbor distances of 50–75m (Tarof et al. 1998). However, we did not observe female song being used in territorial encounters with other females. Furthermore, one of the two females was observed singing late in the breeding season when territorial aggression and hence song should be decreasing.

Given the rarity of female song in this species (only two observations in over 12 years of study by BJMS and associates) it is unlikely that it serves any ultimate function in Hooded Warblers. Rather, female song in this species may be a proximate artifact of elevated androgen levels resulting from advanced age, high breeding density, or some unknown factor. Future study should involve quantification of plasma androgen and estrogen levels in female songbirds of various ages and breeding densities as well as in those species where rare observations of female song are made.

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