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A Prairie Warbler with a Conspecific and Heterospecific Song Repertoire

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Song in most oscine passerines is suspected to develop through imitative learning (Kroodsma 1982, Spector 1992). In the genus *Dendroica*, it has been shown that both song and the context of its use are learned from adult tutors (Kroodsma et al. 1983, Spector 1992). The learning of heterospecific song may be constrained by many factors, including species-specific (genetic) auditory templates for learning (Marler

1975), limitations of the vocal apparatus (Thorpe 1961), and behavioral and ecological aspects that may isolate birds during critical learning periods (e.g. Lanyon 1957). Despite these constraints, learning of heterospecific song has been observed in both the field and the laboratory, particularly in the subfamily Parulinae (see Spector 1992).

In many reported cases of interspecific song learning, the learned songs differ structurally from those of the mimicked species, or are simply incorporated as components of conspecific song (e.g. Baptista 1972, Kroodsma 1972, Kroodsma et al. 1983, Payne et al. 1984). Aspects of singing behavior associated with heterospecific song are not often described in the wild.

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Here we report a male Prairie Warbler (*Dendroica discolor*) that was found singing a repertoire of both Prairie Warbler and Black-throated Green Warbler (*Dendroica virens*) songs, and we describe its response to playback of Black-throated Green Warbler song.

A wild, after-second-year plumaged male Prairie Warbler was discovered by P.R.M. and C. James near Lake Opinicon, Ontario, Canada (44°30'N, 76°23'W), on 15 May 1994, singing songs that were indistinguishable by ear from Black-throated Green Warbler accented songs (see Morse 1993). The bird sang these songs repeatedly over a period of an hour in late afternoon, from a rocky outcrop dominated by stunted red oaks (*Quercus rubra*), red junipers (*Juniperus virginiana*), and sapling sugar maples (*Acer saccharum*). On four other occasions from 16 to 29 May, the same bird (identified by singing location) was found singing both Black-throated Green Warbler accented songs (three occasions) and Prairie Warbler group A songs (one occasion; see Nolan 1978). It did not appear to be paired, and we did not observe or hear it on subsequent visits to the area in late June and early July.

On 27 and 29 May 1994, we broadcast Black-throated Green Warbler unaccented songs (see Morse 1993) to attract the bird into mist nets set up within its apparent territory. We used a Sony Professional WM-D3 cassette recorder and a Sony SRS-77G speaker to broadcast song, and a Sony Professional WM-D6C cassette recorder with a Sennheiser MKH816 unidirectional microphone (29 May) or Sony ECM-144 lapel microphone (27 May) to record songs sung by the male Prairie Warbler during playback.

On both 27 and 29 May, Black-throated Green Warbler song drew the focal bird in to within 2 m of the speaker. When close to the speaker (<8 m), it frequently sang quiet songs. Upon capture in a mist net (29 May), the bird was photographed, banded and released. It displayed plumage characteristics typical of a male Prairie Warbler greater than one year old (i.e. heavy black markings on face and flanks, prominent reddish-chestnut streaks on back; see Nolan 1978, Pyle et al. 1987) and showed no abnormalities of plumage (photos available from authors).

On 27 May, the Prairie Warbler sang Black-throated Green Warbler accented songs (Fig. 1a) and Prairie Warbler group A songs (Fig. 1c) prior to our playback presentation of Black-throated Green Warbler unaccented songs. Immediately after playback, the bird began singing Black-throated Green Warbler unaccented songs (Fig. 1b), effectively matching the song type broadcast from the playback speaker. The bird sang 11 unaccented Black-throated Green Warbler songs in the 3 min during which songs were recorded.

Prior to playback on 29 May, the bird was found singing Prairie Warbler group A songs exclusively. In response to Black-throated Green unaccented song (the same songs broadcast on 27 May), the focal male sang an assortment of songs consisting of Black-throated Green Warbler accented (two songs) and un-

accented songs (four songs), Prairie Warbler group A (14) and group B songs (9; Fig. 1d), and five songs that differed from any described for either species (see Fig. 2; cf. Bent 1953, Nolan 1978, Morse 1993). All 34 songs were recorded during an 11-min period in which Black-throated Green Warbler unaccented songs were broadcast.

Both accented and unaccented Black-throated Green Warbler songs sung by this male Prairie Warbler were indistinguishable (by ear and sonographically; Fig. 1a, b) from those sung by Black-throated Green Warblers themselves (cf. Borror and Gunn 1985, Morse 1993). Prairie Warbler group A and B songs also were typical of other conspecifics (Fig. 1 c, d; cf. Nolan 1978). Thus, this individual sang a repertoire of songs of both species, as well as other songs undescribed for either species (Fig. 2).

The Prairie Warbler's use of its repertoire of Black-throated Green Warbler songs was consistent with the behavioral context and function described for the two song types (cf. Morse 1967, 1970, 1989, 1993). Both Black-throated Green Warblers and Prairie Warblers possess repertoires of two song modes that are used in different contexts and appear to have different functions; Prairie Warbler group A songs and Black-throated Green Warbler accented songs are sung predominantly by unmated males and appear to function in pair formation and maintenance, while Prairie Warbler group B songs and Black-throated Green Warbler unaccented songs are sung predominantly by males during territorial (male-male agonistic) interactions (Morse 1967, 1970, 1989, 1993, Nolan 1978). This apparently unpaired male Prairie Warbler sang Black-throated Green Warbler accented songs and Prairie Warbler group A songs from 15 to 29 May, when most males attempt to attract mates. Black-throated Green Warbler unaccented songs and Prairie Warbler group B songs were sung only in response to broadcast of Black-throated Green unaccented song (simulation of a male Black-throated Green Warbler within its territory).

We speculate that both male Prairie Warblers and Black-throated Green Warblers once acted as social tutors for this particular male Prairie Warbler. Such a situation could result from various circumstances, such as close proximity of Prairie Warbler and Black-throated Green Warbler nests, or both male Prairie Warblers and Black-throated Green Warblers feeding young in a Prairie Warbler nest (e.g. Skutch 1976:352-360). Although these two species occupy markedly different habitats in the Lake Opinicon area (P. R. Martin unpubl. data), the mosaic nature of the landscape produces abrupt changes in habitat that result in the two species nesting in close proximity, potentially even on overlapping territories.

By singing both conspecific and heterospecific songs, this male Prairie Warbler is likely at a selective disadvantage. While conspecific song serves to repel neighboring conspecific males (see Kroodsma and

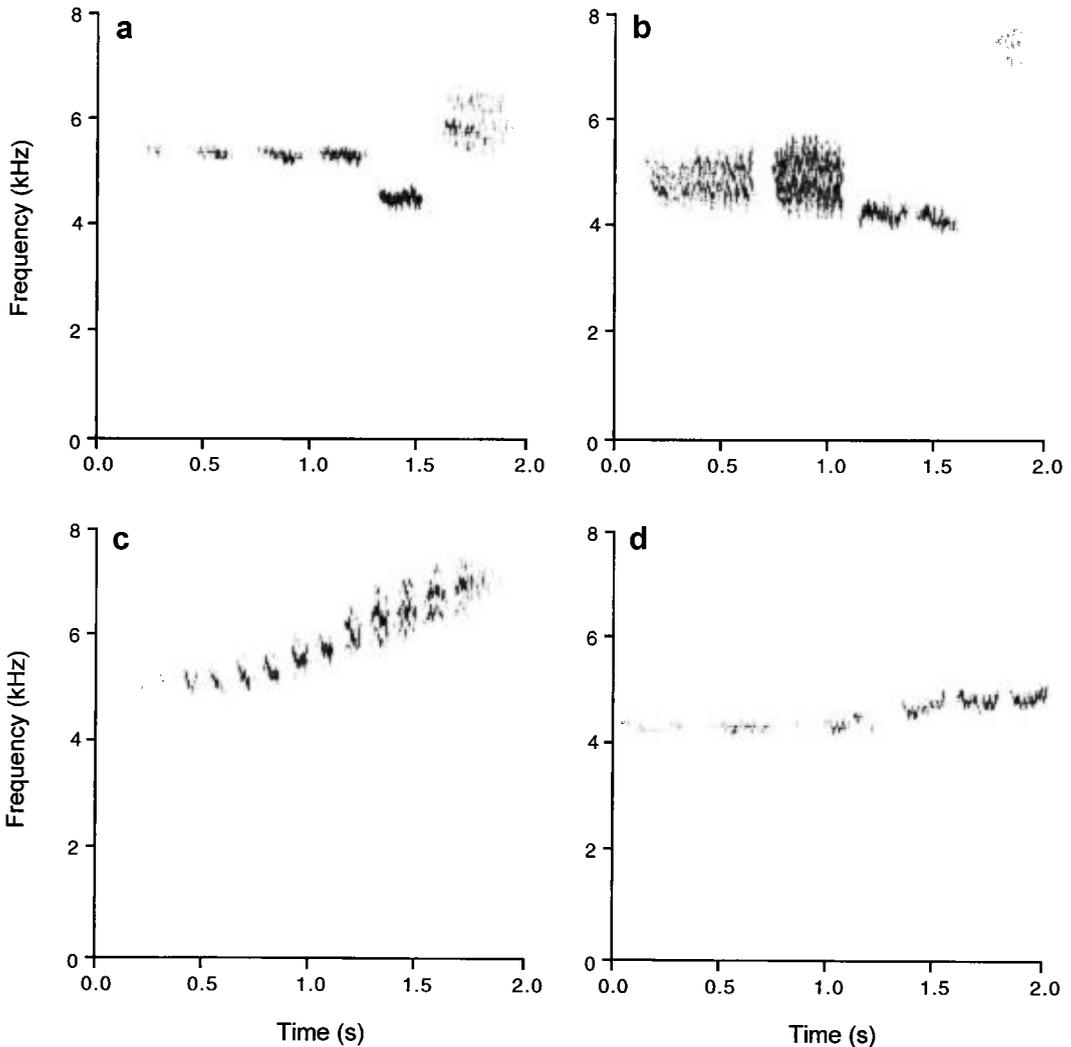


Fig. 1. Sonograms digitized from recordings of wild, after-second-year-plumaged male Prairie Warbler recorded on 27 and 29 May 1994 near Lake Opinicon, Ontario, Canada. The bird sang songs indistinguishable from Black-throated Green Warbler (a) accented and (b) unaccented songs, in addition to Prairie Warbler (c) group A and (d) group B songs (see Nolan 1978).

Byers 1991), singing of heterospecific song may increase the incidence of conspecific male territorial intrusions, resulting in cases of intense fighting with other male Prairie Warblers. Such a fight was observed on 18 May. By singing Black-throated Green Warbler songs, this Prairie Warbler may have repelled neighboring Black-throated Green Warbler males, although different ecologies of these two species suggests little benefit to interspecific territoriality (cf. Nolan 1978, Morse 1993). In addition, the ability of this male to attract a mate was probably hampered by its use of heterospecific song (see also Kroodsmma 1973), and no evidence of pairing was observed. The chance

of cross-species pairing and consequent hybridization may have also been increased by the singing of accented Black-throated Green Warbler song (e.g. Le-maire 1977).

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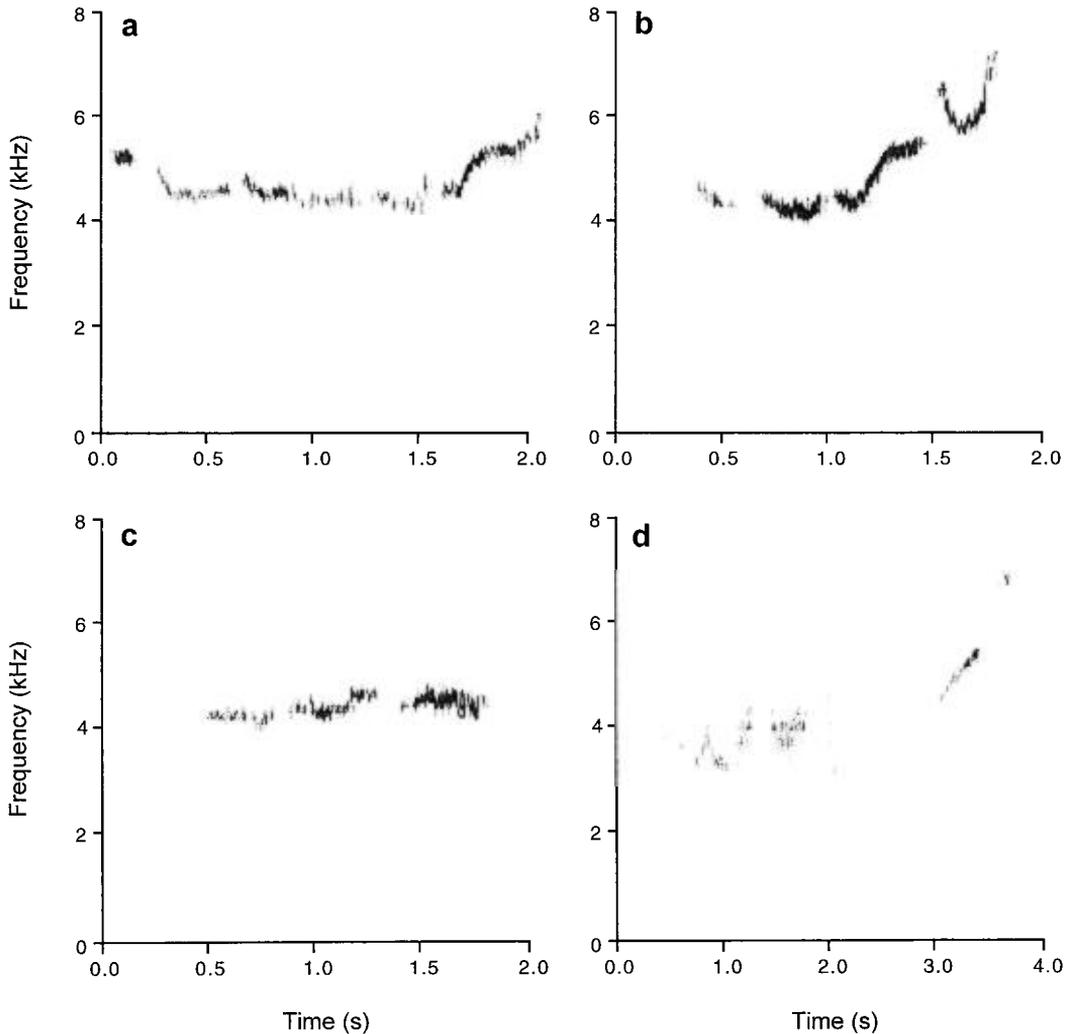


Fig. 2. Sonograms digitized from recordings of wild, after-second-year-plumaged male Prairie Warbler recorded on 27 and 29 May 1994 near Lake Opinicon, Ontario, Canada. In addition to conspecific songs and those indistinguishable from Black-throated Green Warbler songs, this male sang these songs undescribed for either species (cf. Bent 1953, Nolan 1978, Morse 1993).

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Unusual Metabolic Shifts in Fasting Hummingbirds

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Nectar is the main source of energy for hummingbirds (Suarez et al. 1986). They also prey on small insects, which serve as a protein supplement to their diet, although they can survive long periods feeding only on nectar (Brice and Grau 1991). Hummingbirds are among the smallest living endothermic vertebrates and, as a consequence of their minute body mass, have extremely high mass-specific metabolic rates. At the same time, they have limited space for food and/or energy storage. In addition, hummingbirds are only able to forage during the light phase of the day. Fat as substrate would seem to be the best alternative to address both problems. Fat has the highest energy delivery per unit mass among the different foodstuffs, and it does not need water for storage. Therefore, it is reasonable to expect hummingbirds to transform most of their carbohydrate intake into fat to overcome the starving hours of the night (Blem 1976, Powers 1991). Fat would guarantee not only the night-period survival, but also could be used to support migratory flights in a number of hummingbird species that migrate (Suarez et al. 1990). Since fat is not the main constituent of hummingbirds food intake, it has to be biosynthesized from another

item of the diet. Carbohydrates become the main candidates for this biotransformation.

The respiratory-exchange ratio (RER) is the ratio between carbon dioxide production ($\dot{V} \text{CO}_2$) and oxygen consumption ($\dot{V} \text{O}_2$). Under steady-state conditions, RER is equal to the respiratory quotient (RQ), which has specific values for different kinds of substrates metabolized by the animal. A RQ of 1.0 indicates the utilization of carbohydrates, and 0.7 indicates the use of fats. Values between these two extremes are achieved when proteins are used, or when a combination of carbohydrate, fat and protein oxidation represents the animal's overall catabolism. Soon after feeding, hummingbirds have respiratory quotients above 1.0 (Powers 1991). Such RQ values are probably explained by biosynthesis of fat from sugars (Powers 1991, Schmidt-Nielsen 1991), as proposed above. After the last feeding, the RQ drops, reaching values close to 0.7 (Suarez et al. 1990, Powers 1991). The use of fat during fasting conditions is well established among animals (Allen 1976, Schmidt-Nielsen 1991) and is the result of a high specific-energy delivery of this substrate.

Hummingbirds may or may not go into torpor dur-