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Responsiveness of Male Swamp Sparrows to Temporal Organization of Song

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In this paper, we investigate the ability of male Swamp Sparrows (*Melospiza georgiana*) to discriminate between their own species' songs and those of the congeneric Song Sparrow (*Melospiza melodia*) using the temporal pattern of syllable delivery as a cue. Male Swamp and Song sparrows often hold adjacent or overlapping territories in eastern North America, and thus it must be important to male Swamp Sparrows to distinguish between Song and Swamp sparrow songs in order to avoid wasting time and energy by responding to singing Song Sparrows. Although there are striking differences between the temporal organizations of the songs of these two species, Peters et al. (1980, Anim. Behav. 28: 393) were unable to show preferential responsiveness of male Swamp Sparrows toward their own species-typical temporal organization compared to two different Song Sparrow-like patterns.

The temporal pattern of natural Swamp Sparrow song is exceedingly simple: a single, multi-note syllable is repeated in a constant rate trill. Natural Song Sparrow temporal patterns are much more complex. Typically, there are two to seven phrases in a Song Sparrow song, each composed of different notes or syllables. Trills of repeated syllables usually alternate with groups of unrepeated notes, called note complexes. Trills are delivered at either constant or accelerated rates.

Peters et al. (1980) demonstrated that territorial male Swamp Sparrows respond to single-speaker playback of conspecific song by approaching the speaker. In a choice experiment, male Swamp Sparrows were presented with Swamp Sparrow song from one speaker and Song Sparrow song from a second speaker; subjects responded by approaching significantly closer to the speaker playing Swamp Sparrow song. Peters et al. (1980) went on to investigate the nature of the cues used by Swamp Sparrows to distinguish between Song Sparrow and Swamp Sparrow song. In one experiment, male Swamp Sparrows were given a choice between (1) a synthetic copy of natural Swamp Sparrow song (Swamp Synthetic), composed of a single Swamp Sparrow syllable repeated in a constant rate trill, and (2) a song composed of Swamp Sparrow syllables assembled in a two-part, Song Sparrow-like temporal pattern. The latter song was composed of one Swamp Sparrow syllable in an accelerated trill followed by a second syllable in a constant rate trill. Contrary to expectation, male Swamp Sparrows responded by approaching significantly closer to the song with the two-part, Song Sparrow-like pattern. In a second experiment, male Swamp Sparrows were given a choice between (1) Swamp Synthetic and (2) a song composed of a single Swamp Sparrow syllable in an accelerated trill. The subjects were equally responsive to both these songs.

Although some of the test songs used by Peters et al. (1980) had temporal features typical of Song Sparrow songs and lacking in Swamp Sparrow songs, none of the songs approached the complexity of natural Song Sparrow song. We hypothesized that Swamp Sparrow males would show preferential response toward Swamp Sparrow temporal patterns over Song Sparrow temporal patterns of natural complexity.

To test this hypothesis, we gave male Swamp Sparrows a choice between Swamp Synthetic song and a newly synthesized song, the Complex song (Fig. 1). The latter song was synthesized by entering natural Swamp Sparrow syllables into a computer and manipulating them into the desired temporal pattern (see

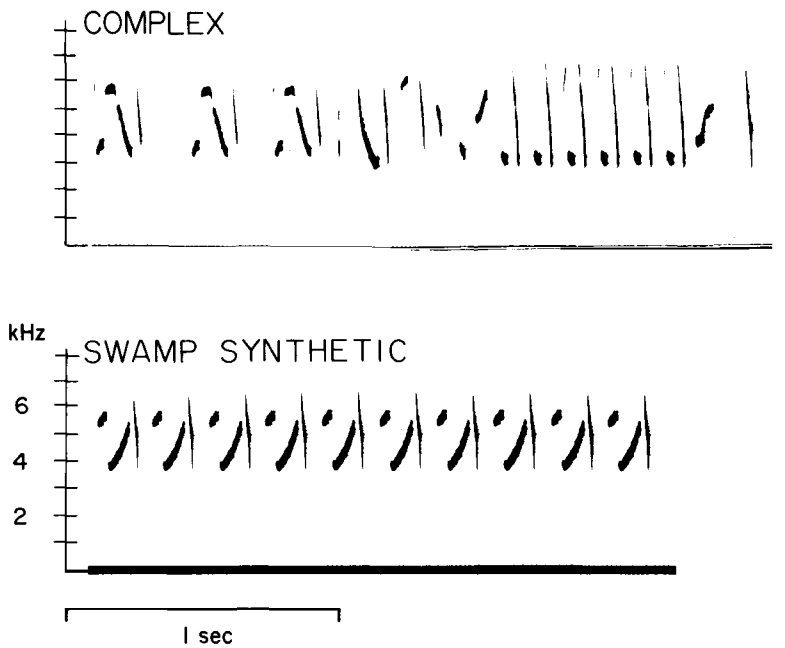

Fig. 1. Sonograms of test songs.

Peters et al. 1980; Zoloth et al. in press, Z. Tierpsychol.). The Complex song contains four phrases, assembled in the following order: (1) an accelerated introductory trill, (2) an unrepeated phrase composed of three different Swamp Sparrow syllables with intersyllable intervals matched to those of a Song Sparrow note complex, (3) a constant rate trill, and (4) a final, unrepeated syllable resembling a terminal Song Sparrow note complex. The Complex song imitates Song Sparrow song closely in being of many parts, in containing note complexes as well as trills, and in having an alternation of trills and note complexes.

Experiments were performed on 23, 24, and 25 June and 1 July 1980, on property of the Cary Arboretum of the New York Botanic Garden in Dutchess County, New York. The experimental design is described in detail in Peters et al. (1980). Briefly, two speakers were set out 16 m apart on a male's territory. Distance marking poles were set at the 4-, 8-, and 12-m points between them. The two test songs were recorded on separate channels of a stereo tape; on each channel, there were 8-s intervals between successive songs. We played one test song from the left hand speaker and the second from the right for 3 min. After a 3-min silent period, the speaker jacks were reversed, and the songs were played for another 3 min, with the song that had been heard from the left hand speaker now heard from the right, and vice versa. The distance of the subject to the speaker was recorded during both 3-min playback periods on flow sheets broken into 5-s blocks. Distance categories used were 0–2 m, 2–4 m, 4–8 m, 8–16 m, and greater than 16 m. In calculating average distances, we considered a bird in the 0–2-m range to be 1 m from the speaker, a bird in the 2–4-m range to be 3 m, in the 4–8-m range to be 6 m, in the 8–16-m range to be 12 m, and in the greater-than-16-m range 24 m. We attempted to place the speakers so that they were both well within a single territory's boundaries; several trials were aborted, however, when more than one male Swamp Sparrow approached the speakers.

Successful trials were completed for 22 males. For both playback periods combined, these 22 males averaged 14 m from the Swamp Synthetic song and 15 m from the Complex song. This difference is not significant according to a Wilcoxon Matched Pairs Signed Ranks Test ($T = 94$, $P > 0.10$). Thus, male Swamp Sparrows did not respond differentially toward Swamp Sparrow temporal patterns and Song Sparrow temporal patterns of natural complexity.

Only one Swamp Synthetic song and one Complex song were used in the experiments. Thus, there is a possibility that there were some unique characteristics of the particular songs used that influenced the outcome of the experiment; in other words, the syllables in the Complex song may have been particularly powerful or the syllable in the Swamp Synthetic song may have been particularly weak in evoking

response. Although this possibility has not been disproven, there is no evidence to date that one Swamp Sparrow syllable is more powerful than another.

It is always easier to fail to reject the null hypothesis of no discrimination than to support the alternative that discrimination occurs. Using the same experimental design and with smaller sample sizes, however, Peters et al. (1980) were able to show discrimination by male Swamp Sparrows on the basis of syllable type (i.e. Swamp Sparrow syllables versus Song Sparrow syllables). Furthermore, they were able to show discrimination by Song Sparrows on the basis of temporal pattern, again with smaller sample sizes than used here. Thus, we are probably safe in concluding that (a) male Swamp Sparrows are much less sensitive to temporal pattern than they are to syllable type, and (b) male Swamp Sparrows are less sensitive than are male Song Sparrows to temporal pattern.

Our results also contrast to those of Searcy et al. (in press, Anim. Behav.) on song discrimination in adult, female Swamp Sparrows. These authors examined the response of captive, female Swamp Sparrows to the same test songs used here. The number and intensity of copulation solicitation displays were used to measure response. Female Swamp Sparrows showed significantly weaker response to the Complex song than to the Swamp Synthetic song. We have shown here that male Swamp Sparrows do not respond differentially towards these two songs. Thus, we can also conclude that male Swamp Sparrows are less sensitive to temporal pattern than are female Swamp Sparrows.

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The Development of Effective Endothermy and Homeothermy by Nestling Piñon Jays

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Hatchling altricial birds begin life as obligate ectotherms but develop into endotherms within a few days. The literature characterizing the development of endothermy by individual chicks has grown considerably over the past two decades, yet the relevance of such characterizations to broods in nature has been questioned (Dunn 1975).

Individual endothermy is the ability of an isolated chick to maintain its metabolism within its thermoneutral zone (TNZ) and to raise its metabolism in response to ambient temperatures (Ta) outside its TNZ. This may not coincide with the development of effective endothermy, i.e. the ability of an individual within a brood and nest to maintain its metabolism within its TNZ and to raise its metabolism at Ta's beyond its TNZ. Furthermore, the degree to which chicks are able to maintain a constant body temperature (Tb), i.e. homeothermy, may differ between isolated individuals and broods. This study was designed to determine the degree of these discrepancies. The reasons such discrepancies exist and the potential ecological importance of effective endothermy and homeothermy will be addressed elsewhere (Clark in prep.).

The Piñon Jay (*Gymnorhinus cyanocephalus*) nests early in the year (as early as February in the Flagstaff, Arizona area), when Ta is characteristically low (Balda and Bateman 1972). Diurnal Ta during incubation and the nestling period is often at or below 0°C. Female jays incubate the eggs and brood the young continuously. During this time the female and the young are fed entirely by the male. When chicks are capable of thermoregulation, the females leave the nest to forage with the males, leaving the young jays unattended for a period of 60–70 min (Bateman and Balda 1973). Thus, young jays exist under conditions that can be considered harsh for a passerine bird.

Piñon Jays commonly raise broods of 4 and 5. The modal clutch size in 1976 and 1977 was four. Chicks were removed from their natural nests and taken to the lab for metabolic tests. In all cases one