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AGGRESSION AND SONG DEVELOPMENT IN WHITE-CROWNED SPARROWS¹

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Key words: White-Crowned Sparrow; *Zonotrichia leucophrys*; social tutoring; song learning; song dialects; aggression.

The importance of social tutoring for proper song development in White-crowned Sparrows (*Zonotrichia leucophrys*) has been documented in both laboratory and field experiments (Cunningham and Baker 1983, Baker and Cunningham 1985, Petrinovich 1985, Baptista and Petrinovich 1986, Petrinovich and Baptista 1987, DeWolfe et al. 1989). Experiments in social tutoring that have been carried out in the laboratory generally involve one or more singing adult males in visual and/or auditory contact with one or several juveniles. Results from these experiments suggest that

the social stimulus of a live adult is a more potent stimulus during song development than is the presentation of songs through loudspeakers alone.

We explored the social tutoring paradigm by permitting direct physical contact between adult males and juveniles during the early phases of song development. When the experiment was conducted, we were uncertain how adults and juveniles would react to one another, and what effect, if any, such direct contact would have on song development. Although the main goal of the experiment was to assess the effect of physical interaction on development of dialects, we discovered instead that extremely aggressive behavior of adults towards juveniles affects song development adversely. Aggression exhibited by adult tutors may have caused arrested song development in juveniles, i.e., they either sang songs that resembled simplified versions of adult songs or sang highly aberrant songs. The relationship between aggression and song development has not been treated systematically in the past, although territorial interactions between adults and juveniles have been commented upon in many reports

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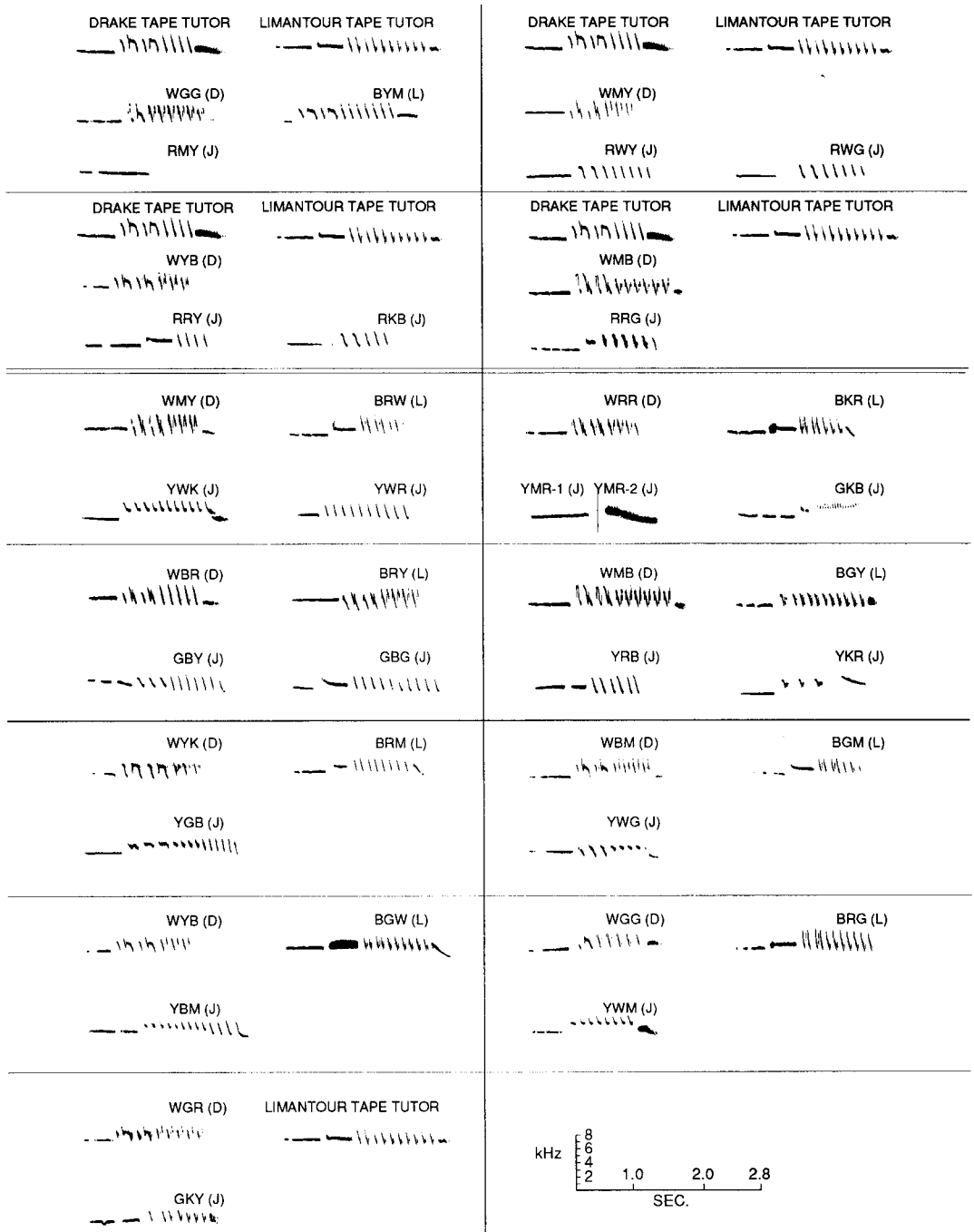


FIGURE 1. Sonograms of adult social tutors, tape tutors, and juveniles. ((D) = Drake adult; (L) = Limantour adult; (J) = juvenile). Songs from 1984 are shown above the double-bars and from 1985 below the double-bars. Each block shows the songs of adults and the respective juveniles they tutored. Drake tutors are shown on the left side of each block, Limantour tutors on the right, and one or two juveniles along the bottom. Juveniles were exposed to Drake songs during the first 50 days of life and then to Limantour songs during the second 50 days. In 1984 juveniles were presented taped songs as Drake adults did not sing until given testosterone and Limantour adults did not sing at all. In 1985 all Drake adults sang but one Limantour adult did not. Juveniles had continuous

(Baptista 1985, Baptista and Morton 1988, DeWolfe et al. 1989).

METHODS

1984. Between 24 May and 3 June 1984, five adult males and 25 nestlings were captured from the Drake dialect and five adult males from the Limantour dialect of Point Reyes National Seashore, Point Reyes, California. Nestlings were hand-fed an *ad libitum* diet (Lanyon 1979) until they fledged. They were fed every 60–90 min between 06:00–19:00 for 15 days after capture and every 90–120 min for another 15 days. Six nestlings survived to adulthood and sang full songs.

Drake adults and nestlings were placed in five separate cages (60 × 37 × 51 cm) on a three-tier shelf with opaque dividers between adjacent cages. Cages were housed in an aviary (2.0 × 1.4 × 2.4 m) made of opaque black plastic and a two-bulb, 1.8 m., 34-watt, “cool-white” fluorescent light. Wire mesh divided each cage vertically (hole diameter = 1 cm) to within a few inches of the cage floor. This permitted physical, visual, and aural interaction between adults and juveniles and provided an “escape route” for juveniles from one side of the cage to another. Adults and juveniles were paired as shown in Figure 1. The ages (in days) of juveniles when first paired with adults were: RRY(6), RKB(6), RRG(6), RMY(9), RWY(13), RWG(13).

Adults were placed on a 16L:8D photoperiod (6 June–17 September). Because Drake adults were not singing during the first few weeks after capture, juveniles were tape-tutored with a Drake dialect song 9–19 June. A Uher reel-to-reel tape recorder was attached to a single 8" loudspeaker in the aviary 1.0 m from the cages. A 45-min stimulus tape of a Drake dialect song was played for 11 consecutive days, 10–11 hr/day, beginning 08:00–10:00 and ending 19:00–20:00, with a 15-min silent period between each 45-min stimulus presentation. To induce singing, adults were implanted with testosterone propionate (Sigma Co.) on 14 June. Testosterone crystals were packed in 10 mm long silastic tubing (Dow Chemical) and implanted subcutaneously near the pectoral muscle. The incision was covered sparingly with collodion (Baker Chemical). Adult males came into full song on the following days: WMB—18 June, WYB, WGR, and WMY—20 June, WGG—21 June.

When the youngest juveniles were 50 days old, Drake adults were replaced by Limantour adults (23 July). Drake adult songs were recorded on 13 August. Because Limantour adults initially were not singing, juveniles were tape-tutored with a Limantour dialect song 23 July–2 August using the same protocol as in Drake sessions. To induce singing, Limantour adults were given a subcutaneous implant of testosterone propionate on 28 July using the same procedures as above.

When the youngest juveniles were 100 days old (10 September), Limantour adults were removed from the cages. On 13 September, the only singing Limantour

adult (BYM) was recorded. Adults and juveniles were cycled through a “short-day” photoperiod as follows: 12L:12D (17 September), 8L:16D (1 October), 10L:14D (2 January), 12L:12D (9 January), 14L:10D (20 January), and 16L:8D (1 February). Songs of juvenile males (now yearlings) were recorded 2 March–2 May. Thus, juveniles were allowed 30 days to move from a short-day to long-day photoperiod and an additional 30 days to acquire full song before being recorded. Juveniles came into full song about one week after returning to the long-day photoperiod (i.e., 220–230 days of age).

1985. Between 20–26 May 1985, five adult males and 32 nestlings were captured from the Drake dialect and 10 adult males from the Limantour dialect of Point Reyes. Juveniles were raised using the same procedures as in 1984. Thirteen survived to adulthood and sang full songs. Five Drake adults from 1984 were used as tutors in 1985; all Limantour adults were new birds.

Because of high levels of aggression between adults and juveniles observed during the 1984 experiments, a different cage arrangement was used in 1985. Triplets of cages (each 46 × 23 × 26 cm) were placed on a five-tier shelf. An adult male occupied the center cage and nestlings occupied each adjoining cage. Within a triplet, visual and aural contact were possible between adults and juveniles, but not unassisted direct physical contact. Adults and juveniles were paired as shown in Figure 1. The ages (in days) of these juveniles when first paired with adults were: GBY(8), GBG(8), GKB(9), GKY(9), YWK(11), YWM(11), YWR(11), YWG(11), YKR(12), YBM(13), YMR(14), YRB(14), YGB(14).

All birds were placed on a 16L:8D photoperiod (1 February–1 September). Beginning 12 June physical interaction between Drake adults and juveniles was begun by placing juveniles individually in the cages of their respective adult tutors for 30 min in the morning (between 08:00–12:00) and 30 min in the afternoon (between 12:00–16:00). Intense aggression was observed between adult-juvenile pairs during these sessions. To avoid mortality, on 19 June the duration of contact was reduced to 10 min in the morning and 10 min in the afternoon. Even this short period of interaction appeared traumatic for juveniles.

By 14 June, all Drake adults were singing. Because of difficulty in getting Limantour adults to sing in the laboratory in 1984, they were given testosterone implants on 9 March and 25 June, 1985.

When the youngest juveniles were 50 days old, Drake adults were replaced by Limantour adults (13 July) and recordings were made of Drake adult songs. By 19 July, all Limantour adults were singing except BGK. To ensure that its pupil GKY received adequate auditory stimuli, tape tutoring with a Limantour dialect song was begun. An 8" loudspeaker was placed 1 m directly behind BGK. The Limantour tutor song was played at a rate of four songs/min, 6 hr/day (10:00–16:00), and continued until 1 September. From 1 August–1 September, physical interaction between Limantour adults

← visual/aural/physical contact with live adults in 1984; they had continuous visual/aural contact but restricted physical contact in 1985.

and juveniles was permitted using the same procedures as in Drake sessions.

When the youngest juveniles were 100 days old (1 September), Limantour adults were removed from the cages. On 2 September, all Limantour adult songs were recorded.

Juveniles were cycled through a "short-day" photoperiod as follows: 15L:9D (1 September), 14L:10D (3 September), 12L:12D (6 September), 8L:16D (13 September) and 16L:8D (1 January 1986). Songs of juvenile males (now yearlings) were recorded 1 March–1 May. As in the previous year, juveniles were allowed 30 days to move from a short-day to long-day photoperiod and an additional 30 days to acquire full song before being recorded. Again, juveniles came into full song about one week after going on the long-day photoperiod (i.e., 220–230 days of age).

A Uher tape recorder and microphone were used to record songs of singing males. Audiospectrograms were generated on a Kay Elemetrics Sonagraph. All recordings were made in anechoic chambers (Casey 1988).

Five judges classified juvenile songs (Baptista and Petrinovich 1986). Judges had no experience with sonagrams and were unaware of the experimental design and goals. Just prior to the testing period, judges were briefed on the syllabic structure and song elements of White-crowned Sparrow songs and were shown examples of typical adult songs from several different dialects. The sonagram of each juvenile was placed with the sonagrams of its respective social tutor(s) (and tape tutor(s) where appropriate). Sonagrams were coded so as to be unidentifiable by judges. Judges classified juvenile songs in the following ways: (1) If the juvenile song was a reasonably accurate copy of one of its tutors, it was classified as a copy of that tutor; (2) If juvenile song could not be classified with one of its tutors, was missing specific song elements, lacked the complexity and detail of normal adult White-crowned Sparrow song, but had an appropriate syllabic structure, it was classified as a simplified adult song; and (3) If juvenile song was missing specific song elements and lacked appropriate syllabic structure, it was classified as an aberrant song. (Note that Baptista and Petrinovich (1986) subdivided aberrant songs into "simple isolate song" and "complex isolate song"; this distinction was not made here).

RESULTS

During these experiments, we observed intense aggression between adults and juveniles. When direct physical contact was permitted, there was considerable fighting between tutor pairs, including chases, tumbling, pulling of feathers, and pecking. Adults dominated juveniles and there was little or no retaliation by juveniles. (Similar dominance relationships have been observed in wild Gambel's White-crowned Sparrow, *Z. l. gambelii* (Parsons and Baptista 1980). To avoid juvenile mortality, we restricted the duration of encounters. In the 1984 experiments, the wire divider in the middle of the cage allowed juveniles to escape from the adults temporarily. However, juveniles were clearly still under duress and, apparently, high levels of stress. In 1985, separation of tutor pairs into adjacent cages improved the situation. Although brief periods of di-

rect physical contact appeared highly stressful for the juveniles, they recovered and functioned normally when separated from adults. Nevertheless, adults still attempted to attack juveniles through cage bars. Even when separated, juveniles often adopted subordinate postures and behavior.

The results of the panel of judges were as follows. Four of five judges classified the song of GKY as an accurate copy of the Limantour tape tutor; the remaining judge classified it as a simplified adult song. All judges agreed that juveniles RWY, RWG, RRY, RKB, RRG, YWR, GBY, GBG, YRB, YGB, and YBM sang simplified adult songs. All judges agreed that juveniles RMY, YMR, GKB, and YKR sang aberrant songs. (Note that YMR sang two distinct songs both of which were considered aberrant by all of the judges). Two of five judges thought that YWG sang an aberrant song, whereas three remaining judges classified it as simplified adult song. One of five judges concluded that YWK and YWM sang aberrant songs, whereas the remaining four judges classified them as simplified adult songs. Thus, the panel concluded that none or one of the juveniles (0%–5%) copied their tutor's song, eleven to fifteen juveniles (58%–79%) sang simplified adult songs, and four to seven juveniles (21%–37%) sang aberrant songs. (Judges did not agree on four juvenile songs, thus accounting for the variance in percentages).

It is noteworthy that judges classified only one juvenile song as an accurate copy of its tutor and the rest as either simplified adult songs or aberrant songs. The judges often commented that although many of the juvenile songs followed the basic White-crown "model" (i.e., introductory whistle, simple syllables, partially correct syllabic structure) they also stated that juvenile songs often lacked the detail and complexity of normal adult songs, or were missing specific song elements (i.e., complex syllables, terminal notes).

Visual inspection of sonagrams yielded additional insights. Although experimental procedures changed between years, this did not alter the song development process. In 1984, Drake and Limantour adults did not sing during the first few weeks of interaction with juveniles; therefore, taped songs were used. After testosterone injections, Drake adults came into full song but only one Limantour adult sang. Thus, juveniles were exposed to both live and taped songs. One juvenile developed an aberrant song, while the remaining five juveniles developed simplified adult songs. The latter juveniles sang the introductory whistle and simple syllables typical of White-crown songs, but not the complex syllables or terminal notes. Furthermore, the four Drake social tutors had simple syllables that consisted of multi-note figures, whereas the simple syllables of juveniles consisted only of single, down-slurred notes.

In 1985, all nine Drake adults and eight of nine Limantour adults sang from the beginning of the experiment, hence, taped Limantour song was only presented to one juvenile, GKY. Some judges considered the song of GKY an accurate copy of the Limantour tape tutor, several juveniles sang aberrant songs, and the rest sang simplified adult songs. As in 1984, judges often commented that some juvenile songs appeared to be converging on an adult song motif, but that they either were missing song elements, song elements were

"distorted," or the pattern of repeated notes was unlike adult songs (i.e., the simple syllables of YGB and YBM increased in frequency range from beginning to end). Therefore, whether juveniles were exposed to songs of social tutors only or a mix of social tutor songs and taped songs did not seem to alter the fact that some juveniles developed aberrant songs and some developed simplified adult songs.

The aberrant songs of several juveniles resembled those of birds raised in acoustical isolation (Marler 1970) or deafened early in life (Konishi 1965). Aberrant songs developed despite exposure to extensive auditory stimulation.

DISCUSSION

Excessive, aggressive physical interaction between adult male White-crowned Sparrows and juvenile males whom they were tutoring disrupts or inhibits song development. In contrast to other experiments in which only visual and auditory contact were permitted, juveniles developed songs that were either simplified versions of adult songs or aberrant songs when adult male tutors were allowed direct physical contact with juveniles. Although the principal goal of the experiment was to determine the role of physical interaction in dialect development, we found arrested and aberrant song development in juveniles exposed to adult aggression.

Petrinovich and Baptista (1987) raised juvenile male White-crowned Sparrows in the presence of live tutors. They first housed a singing adult male from one dialect next to juveniles 10–50 days old and then switched to a second adult male singing a different dialect during the next 51–100 days of age. When juveniles reached adulthood, their songs were recorded. Although juveniles were permitted visual and auditory contact with adults, they were not allowed direct physical contact. Songs of these juveniles appeared very similar to those of normal, field-raised adults. Syllabic structure, song elements, and complexity of songs were similar to those of normal adult White-crowned Sparrows. This contrasts with the simplified and aberrant songs we observed. In the experiments of Petrinovich and Baptista and those reported here, juveniles were exposed first to songs of one dialect and then to songs of another dialect, delivered by live social tutors. However, extreme aggression between adults and juveniles when physical contact was allowed apparently inhibits full song development. This aggression apparently arrested song development at an intermediate stage in many juveniles, and resulted in aberrant song in others.

Despite extensive auditory stimulation, songs of several juveniles in this study resemble those of birds raised in acoustical isolation (Konishi 1965, Petrinovich 1985). Some songs had little syllabic structure, consisted mostly of whistles, buzzes, or pulsed whistles and notes, and contained no complex syllables or terminal notes. Juveniles raised in acoustical isolation develop aberrant songs unlike those of normal adults or those of juveniles raised with exposure to live or taped adult songs (see Marler 1970, Baptista and Petrinovich 1984, Petrinovich and Baptista 1987). During direct physical interactions between adults and juveniles, we noted that juveniles adopted a submissive

role, made little or no attempt to retaliate against adults, and generally tried to "hide and freeze" in the corners of the cages. It may be that because of this relationship song development was arrested at an early stage or disturbed to such a degree that normal development was prohibited.

In wintering foraging flocks of the related Gambel's White-crowned Sparrow (*Z. l. gambelii*), Parsons and Baptista (1980) observed complete dominance of adults over juveniles (all of 75 encounters at three sites). Gambel's White-crowns are sexually monomorphic. Although they could not reliably determine the sex of adults, they surmised that some were males. In this dichromatic subspecies, adults have white crowns and juveniles brown crowns. Parsons and Baptista postulated that crown color was associated with high social dominance, which accounted for adult dominance over juveniles. In a related laboratory experiment Parsons and Baptista (1980) artificially induced early development of white crowns in juveniles. White-crowned juveniles were then placed with (1) other brown-crowned juveniles or (2) a mixed flock of adults and juveniles. In both environments white-crowned juveniles achieved high social status. Parsons and Baptista concluded that "juveniles are conditioned to perceive black-and-white crowned (adult) individuals as aggressive and dominant, avoiding the latter or assuming submissive postures." Our results confirm the observation of (complete) dominance of White-crowned adults over juveniles and suggest that extreme forms of this relationship may lead to abnormal song development.

Prolonged and intense aggressive interactions seen in our experiments and the confinement to small cages are unnatural. Field observations suggest that pre-dispersal juveniles are often protected and even fed by their fathers. Although post-dispersal juveniles engage in territorial behavior with non-parental adults, they escape these situations or minimize such encounters. For example, DeWolfe et al. (1989) recorded in the field the songs of juveniles at approximately 90–120 days of age. In response to neighboring singing adults, these juveniles sang songs similar to normal adult songs. There were many territorial skirmishes and aggressive interactions between adults and juveniles, as juveniles attempted to establish territories among established adults. Presumably these interactions were of short duration compared to our laboratory experiments. DeWolfe et al. (1989) also present evidence of juveniles whose songs changed from one adult-like form to another so as to match the songs of neighboring males (see their Figure 8, p. 403). Therefore, the songs of field-raised juveniles seem enhanced by moderately intense aggressive interactions with adults, whereas songs of laboratory-raised juveniles seem disturbed by higher levels of aggression with adults. Hence, the precise nature of aggressive encounters between adults and juveniles may have important implications in song development.

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DO SWALLOWS SUNBATHE TO CONTROL ECTOPARASITES? AN EXPERIMENTAL TEST¹

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Key words: Violet-green Swallow; *Tachycineta thalassina*; sunbathing; ectoparasites.

Several species of swallows (Hirudinidae) sunbathe in a manner producing the appearance of heat stress (Barlow et al. 1963, Simmons 1986, Blem and Blem 1992). These swallows spread their wings and tails in an obvious attempt to expose those surfaces to the sun. They also gape, pant markedly, and even appear to go into a trance (Hauser 1957, Kennedy 1969, Blem and Blem 1992). This behavior occurs only on bright, sunny days with low wind velocities and high ambient temperatures and has been observed to occur on substrates exceeding 52°C (Blem and Blem 1992). Plausible hy-

potheses explaining this behavior in birds include: (1) acquisition of heat for thermoregulation (e.g., Lustick 1969, Cade 1973), (2) drying of wet plumage (Kennedy 1969, Storer et al. 1975), (3) soothing of feather tracts irritated by molting (Potter and Hauser 1974, Simmons 1986), and (4) deliberate overheating in order to stun or kill tiny ectoparasites, particularly mites (Acarina) and lice (Mallophaga) (see Simmons 1986). The present paper provides experimental evidence supporting the last hypothesis.

STUDY AREA AND METHODS

During the period 20 June-30 June 1992, we mist-netted and color-banded 32 adult (16 male, 16 female) Violet-green Swallows (*Tachycineta thalassina*) at Flathead Lake Biological Station, 30 km north of Polson, Montana (47°41.4'N, 114°09.3'W). The resident swallow population at this site includes at least 50 nesting pairs of Violet-green Swallows as well as several pairs

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