

DELAYED ACCESS TO LOCAL SONGS PROLONGS VOCAL DEVELOPMENT IN DIALECT POPULATIONS OF BROWN-HEADED COWBIRDS¹

ADRIAN L. O'LOGHLEN²

Department of Biology, University of California at Santa Barbara, Santa Barbara, CA 93106

Abstract. A recent study by O'Lughlen and Rothstein (1993) found that ontogeny of the Mammoth dialect flight whistle (FW) and repertoires of local perched songs (PS) was not complete by the first breeding season for male Brown-headed Cowbirds (*Molothrus ater artemisiae*) in the eastern Sierra Nevada of California. To determine how typical of the region these results were, I compared adult and yearling vocal behavior in the Convict dialect adjacent to Mammoth and the Round Valley dialect, 55 km south and 900 m lower elevation. In the Convict group, a majority of 20 yearlings produced either incomplete local (35%) or foreign (35%) FWs. In the Round Valley, 15 of 19 yearlings (79%) gave foreign whistles. In both dialects, yearling PS repertoires lacked local song types, and in Convict, repertoires were significantly smaller than those of local adults. As was found in the Mammoth dialect, incomplete FWs of yearlings were resistant to modification during the season, and modification of yearling PS repertoires was also arrested. I propose a scheme for vocal development in these Sierran populations and discuss possible reproductive consequences of delayed vocal learning.

Key words: Songbirds; vocal development; song learning; dialects; cowbirds; *Molothrus ater*.

INTRODUCTION

Most temperate region songbirds are assumed to memorize their species-typical songs during their hatching year and to produce fully developed song by the time they are one year old and beginning their first breeding season (Slater 1983, Konishi 1989). For most birds, these will be the songs they sing for the rest of their lives (Thorpe 1958, Marler 1970, Lemon 1975, Marler and Peters 1982a, Konishi 1989), although subsequent addition of new song or syllable types has been reported to occur in some species (Rice and Thomson 1968, Marler et al. 1972, Payne 1973, Jenkins 1977, Nottebohm and Nottebohm 1978, Lemon et al. 1994). A recent study of wild birds from a migratory population of the brood parasitic Brown-headed Cowbird (*Molothrus ater artemisiae*), in the eastern high Sierra Nevada of California, suggests a novel vocal development (O'Lughlen and Rothstein 1993). The goal of this paper is to determine the extent to which results for this population characterize other cowbird populations in the region.

Male cowbirds possess two types of songs, the flight whistle and the perched song (Rothstein et al. 1988). Flight whistles (FW) show well-defined and often highly divergent dialects (Rothstein and Fleischer 1987). Males usually sing only one FW variant. Generally, perched songs (PS) also vary geographically but always conform to certain structural rules (King et al. 1980), and males have repertoires of two to seven PS variants (Dufty 1985, West and King 1986, Yokel 1987). The previous study of vocal development in wild cowbirds was conducted during the 1989 breeding season in the Mammoth FW dialect (O'Lughlen and Rothstein 1993). Results from the Mammoth study indicated that it takes two years for the great majority of cowbirds to achieve vocal repertoires comparable to those of local adults (two years or older). During their first breeding season, yearling males trapped locally produced incomplete versions of the Mammoth FW given by nearly all local adults. Furthermore, the PS repertoires of yearlings were smaller than and lacked the PS types common to the repertoires of local adults.

The incomplete vocal development of Mammoth yearlings was attributed to limited access to local song models during their hatching year (O'Lughlen and Rothstein 1993). The Mammoth dialect is at an elevation extreme for breeding

¹ Received 1 October 1994. Accepted 19 January 1995.

² Present address: Department of Psychology NI-25, University of Washington, Seattle, WA 98195.

populations of cowbirds in this region (Rothstein et al. 1980). At this elevation (2,380 m), the breeding season is brief (Fleischer et al. 1987) and many if not most young cowbirds are fledged by host species after cowbird breeding activity, including singing, has ceased (Rothstein et al. 1980). In addition, many if not most adult cowbirds migrate from the area before many young cowbirds fledge (Rothstein et al. 1987), a situation unlikely to occur in nonparasitic species.

The first objective of my study was to determine whether the delayed vocal development evident during the 1989 season in the Mammoth dialect is typical of cowbird populations in the eastern Sierra Nevada. Using the procedures of O'Loughlen and Rothstein (1993), I looked for evidence of delayed vocal development in two additional FW dialects in the region: the Convict dialect adjacent to Mammoth and at approximately 220 m lower elevation, and the Round Valley dialect, 55 km south of Mammoth at 900 m lower elevation. The elevation and climate of this latter dialect is more typical of the Great Basin where distribution of the *artemisiae* subspecies is widespread (Rothstein et al. 1980).

The start and duration of the breeding season in the Mammoth and Convict dialects (late-May to mid-July) are similar (Fleischer et al. 1987; pers. observ.), although fledged cowbirds appear several days earlier in the Convict dialect. Thus, opportunities for cowbirds to hear adult singing during their hatching year should be comparable in each dialect, and vocal development in these two populations would not be expected to diverge significantly. In contrast, the breeding season in the Round Valley starts earlier (roughly two weeks) than in Mammoth and Convict but finishes at approximately the same date (second week of July, pers. observ.) or later (Rothstein et al. 1980). Temporal overlap between fledging of young cowbirds and cowbird breeding activity should be greater in the Round Valley, and the limiting effects of access to local song models should be less pronounced than in the higher elevation dialects.

A second objective of this study was to assess the general validity of an unexpected feature of vocal development discovered in the Mammoth dialect. There was no evidence that FWs recorded from yearlings trapped later in the breeding season more closely matched the whistles of local adults than those of different yearlings trapped at the start of the season. Thus, there was an

apparent lack of modification of the incomplete FWs of yearlings as the season progressed due to some unknown constraint (O'Loughlen and Rothstein 1993). However, the number of cowbirds involved in this analysis was small and the possibility of a Type II statistical error was high. In other words, the sample size may have been too small to detect a trend that in fact existed. Moreover, the previous study did not assess whether development of local PS repertoires in yearlings progressed during the course of the breeding season. Using data from all three dialects, this paper assesses whether yearlings show any continued FW and PS development as the season advances.

METHODS

DIALECTS SITES

I trapped male cowbirds in three flight whistle dialects located on the eastern slope of the Sierra Nevada of California during the 1989, 1990, and 1991 breeding seasons. In the Mammoth FW dialect near the town of Mammoth Lakes, Mono County, cowbirds were trapped from 6 May to 11 July 1989 at three sites using seed-baited Potter traps. In 1990, cowbirds were trapped from 6 May to 10 July in a permanent decoy trap (2 × 2 × 2 m) located in riparian habitat where cowbirds commonly breed (Rothstein et al. 1980) along Convict Creek in the Convict dialect, the neighboring dialect south of Mammoth (Rothstein and Fleischer 1987). In addition, six Convict males were captured with seed-baited Potter traps at a site about 200 m from this decoy trap. The Convict and Mammoth dialects are separated by areas of sagebrush up to 10 km wide which are rarely frequented by cowbirds. However, there are small areas of overlap between these dialects, and males in these areas are often bilingual (Rothstein and Fleischer 1987). Cowbirds were trapped in Round Valley, Inyo Co., from 11 May to 9 July 1991 using a decoy trap located in riparian habitat where cowbirds breed.

PROCEDURES FOR RECORDING BIRDS

Captive males were aged as yearlings or adults based on their plumage (Selander and Giller 1960), subjected to a standardized set of morphological measurements (Fleischer and Rothstein 1988), and uniquely color banded. Mammoth and Convict birds were housed at the University of California's Valentine Reserve at Mammoth Lakes, and Round Valley birds at the

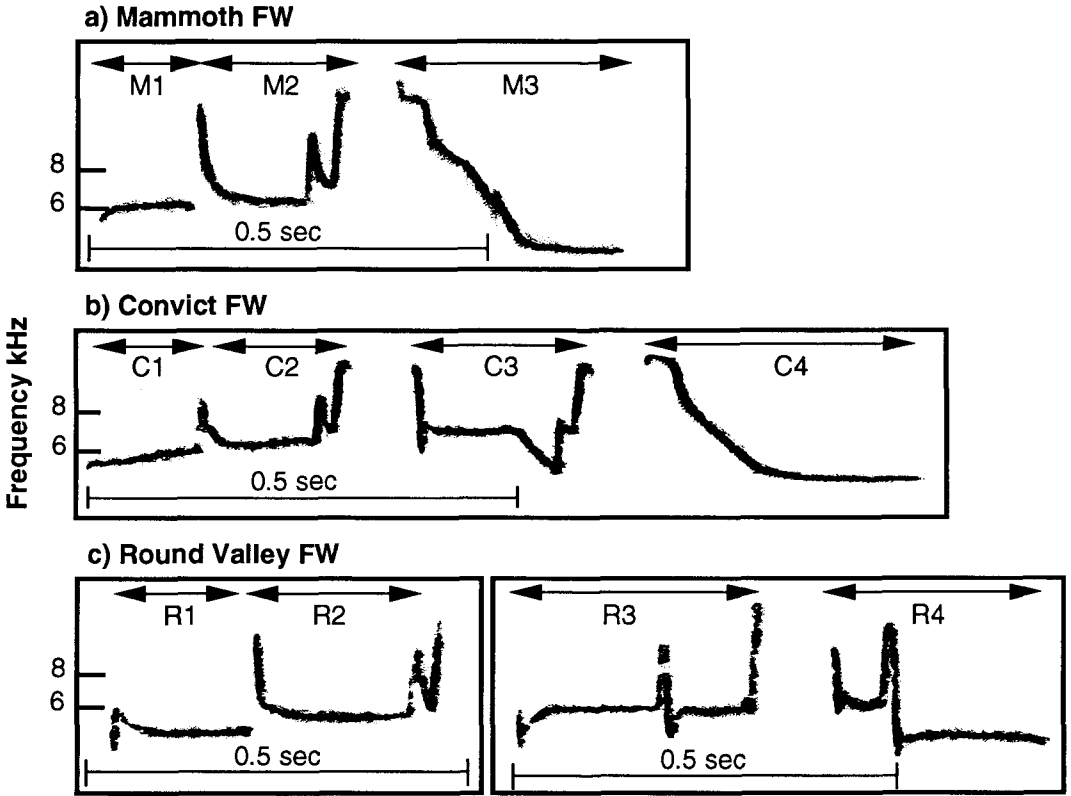


FIGURE 1. Audiospectrograms of the three dialect flight whistles. Round Valley elements R1 and R2 are the most frequently heard whistle in the dialect. Round Valley elements R3 and R4 are given less frequently and are occasionally given in combination with the R1 and R2 whistle. Of the 19 adults trapped in the Round Valley and given testosterone in the present study, 14 produced local FWs and 11 of these 14 adults (78.6%) produced all four elements, although not always in combination.

Sierra Nevada Aquatic Research Laboratory of the University of California 15 km south of Mammoth Lakes. To encourage singing (Balthazart 1983), birds received Silastic implants (Dow Corning, 1.69 mm outer diameter) packed with a 10 mm length of testosterone (Sigma) on either the day of their capture or the following morning. Birds were held in individual cages for five days, out of visual but in audio contact. On the fourth day after receiving their implants, each male was placed in turn in a sound attenuation chamber, and I recorded their responses to playback of the female cowbird call known as 'chatter' (Friedmann 1929) on a Marantz PMD 340 cassette-recorder. On the fifth day, responses to female chatter and to FW and PS playbacks were recorded in the chamber. Later that day, each bird was recorded (Sony Professional Walkman with a Sennheiser Directional ME-80 microphone) out-of-doors as he interacted with the local wild

males (O'Loghlen and Rothstein 1993). I then removed the implants and released the birds at their site of capture. Individual birds were treated with testosterone and tested on only one occasion during a breeding season with the exception of two Convict yearlings that were tested twice.

Vocal behavior in nine of the above birds was studied in both their first and second breeding seasons. As yearlings, these birds gave either incomplete local or foreign whistles. All were located as adults in the same dialect areas in which they were trapped when yearlings. Six were yearlings from the Convict dialect. Four of these males were re-captured and tested as adults, and the remaining two recorded in the wild. Also, at the start of the 1992 breeding season I recorded FWs from three adult males in the wild in the Round Valley that I had implanted and recorded as yearlings in 1991.

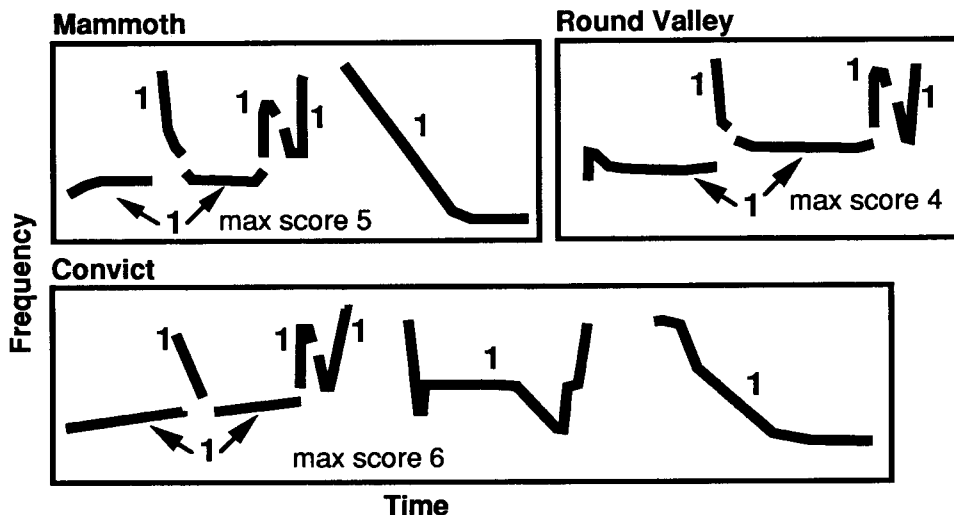


FIGURE 2. Schematic representations of audiospectrograms of the three dialect whistles used to score FWs for completeness drawn approximately to scale from the sonagrams of actual FWs shown in Figure 1. These scoring systems are based on the naturally occurring variation found in the incomplete FWs of yearlings in the respective dialects. No Round Valley yearling ever produced elements R3 and R4 shown in Figure 1. Absence of any of the elements indicated by the arrows reduced the maximum possible score for a whistle by one. Foreign FWs were given scores of zero.

FLIGHT WHISTLES

The first two syllables in all three whistles are clearly similar but can be distinguished by quantitative characteristics (Fig. 1). Males in the Round Valley also give whistles consisting of syllables R3 and R4 (Fig. 1) and less frequently, of a full combination of all four syllables. However, no yearlings trapped in the Round Valley ever gave syllables R3 and R4, and these syllables have been excluded from analyses of Round Valley FWs. Thus, comparisons in vocal development between Round Valley adults and yearlings are conservative because the majority of adults gave whistle combinations which included R3 and R4.

Cowbirds recorded in the wild and in captivity occasionally produce FWs in which terminal syllables are entirely absent (Rothstein and Fleischer 1987), and these have been described as "partial" FWs (O'Loughlen and Rothstein 1993). "Incomplete" FWs referred to in the current report differ from partial whistles in that they contain syllables which are themselves incomplete (see Fig. 2, O'Loughlen and Rothstein 1993), or they lack a non-terminal syllable, e.g., syllable C3 of the Convict FW (Fig. 1).

Recordings were analyzed using a Uniscan Real Time Analyzer (Model 4500), and a Kay Digital Sona-graph 7800 Dual Channel Spectrograph and

7900 Sona-graph Printer. Representative audiospectrograms (90 kHz band filter, 0–16 kHz) of all different FW types given by each male were printed. I compared FWs using tracings on acetate sheets taken directly from the Uniscan screen of a still image of the whistle played at half speed.

I classified whistles with reference to the predominant FW type (Fig. 1) in each dialect area and developed a scoring system for each dialect based (Fig. 2) on the incomplete FWs of locally caught yearlings as in O'Loughlen and Rothstein (1993). Note that homologous syllables in different dialects are scored via identical criteria. These scoring systems allowed me to make quantitative comparisons of the differences among individual males and between age classes within each dialect. Although it is not known whether the foreign FWs given by yearlings are complete, there is conclusive evidence that these birds switch to local whistle types by their second season (O'Loughlen and Rothstein 1993; this study). Thus, all foreign whistles were awarded scores of zero.

PERCHED SONGS

The number of different types of PS recorded from each bird was determined using acetate tracings and printed audiospectrograms as de-

scribed for FWs. I placed PSs into different categories based on similarities in all elements visible on the audiospectrograms; these elements included the low-frequency note clusters at the start of the song, middle elements, and the "whistle" phrase at the end (King et al. 1980). There was high agreement (>90%) between mine and another individual's independent categorization of these PSs.

Cowbirds tend to run through their repertoire of different PS types quickly. For eastern cowbirds, a recording session of at least 12 songs is likely to contain a male's full PS repertoire (West and King 1983, Dufty 1986). I used data from males with eight or more PSs recorded to estimate repertoire sizes. Estimating repertoire size on this basis may underestimate true repertoire size. However, O'Loughlen and Rothstein (1993) showed that any underestimate from using an eight song criterion is likely to be slight for the Mammoth sample described in the current report. I will present evidence below that this is probably true for repertoire sizes estimated for birds giving eight or more PSs in the Convict and Round Valley dialects. For consistency in comparisons among dialects, I have used this eight song criterion for males to be included in the analyses of PS repertoire sizes in all dialects.

Perched song types could be classified as "shared," i.e., found in the repertoires of two or more birds of either age class in the local dialect, or "unique," i.e., found exclusively in the repertoire of one bird (O'Loughlen and Rothstein 1993). Analyses of PS sharing within FW dialects was based on all birds giving one or more PSs since number of songs recorded per individual does not affect this property of PSs.

DATA ANALYSES

All non-parametric statistical tests were performed by Abstat (AndersonBell) or Systat (Systat, Inc.). Probabilities are two-tailed unless otherwise stated. I expected to find that yearlings would be less advanced vocally than adults within each dialect based upon previous work (Rothstein and Fleischer 1987), and I used one-tailed probabilities in these comparisons.

RESULTS

FLIGHT WHISTLES

A total of 117 male cowbirds from the three FW dialects were treated with testosterone and their

vocalizations recorded; 50 (42.7%) were adults and 67 (57.3%) yearlings. Flight whistles were recorded from 46 (92.0%) adults and 55 (82.1%) yearlings. There were no significant differences in average number of FWs recorded per bird between the age classes in any of the dialects (O'Loughlen 1993).

Adult vocal behavior was extremely consistent in each of the dialects studied. Most adults (87.0%) gave complete renditions of the FW type most frequently heard from wild males (Rothstein and Fleischer 1987) in the area where they were trapped, and there were no differences among the dialects in the proportion of adults doing so (Fig. 3. $G = 0.520$, $df = 2$, $P > 0.5$). Six adults (13.0%) gave whistle types other than the local FW of the area in which they were trapped.

In contrast to adults, only nine (16.4%) of 55 yearlings from whom FWs were recorded ever gave a complete correct local whistle (Fig. 3. $G = 55.280$, one-tailed $P < 0.001$ for 40 of 46 adults versus 9 of 55 yearlings). The percentage of yearlings who gave complete local whistles ranged from 30.0% in the Convict dialect to 5.3% in the Round Valley and did not vary significantly among the three dialects (Fig. 3. $G = 4.696$, $df = 2$, $P > 0.05$). Yearlings generally produced either incomplete versions of the local whistle (36.4% of all yearlings), or foreign FWs (47.3%, Fig. 3).

Average scores for FWs given by yearlings were significantly below those for adults in each dialect (Table 1). Mean scores for adult FWs ranged from 89.6% to 79.0% of the potential maximum score in the dialects compared to a range of 49.2% to 15.5% for yearlings. In the Mammoth and Convict dialects, mean yearling scores were 54.9% and 53.9% of the respective adult averages, and in Round Valley, the average score for yearling FWs was 19.6% of that for local adults (Table 1).

ARRESTED DEVELOPMENT OF LOCAL FWS IN YEARLINGS

There was no evidence in any of the dialects that yearlings altered their incomplete local whistles or foreign whistle types during the course of the breeding season. There was no association between the date on which yearlings were tested and average FW scores of individual yearlings as a proportion of the total average for adults in each dialect (Fig. 4a). The number of yearlings

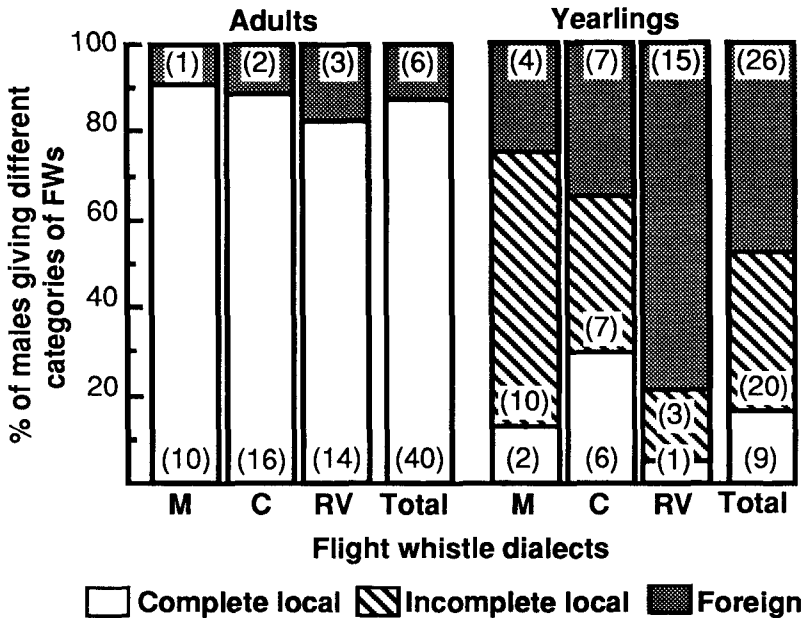


FIGURE 3. Proportion of males giving complete, incomplete local and foreign FWs by age class in each dialect and for all males in each age class. Data are based on all males giving at least one FW. Note that no adults gave incomplete local FWs. Numbers of males are shown in parentheses. M = Mammoth, C = Convict, LV = Lee Vining.

in the Round Valley sample who actually gave the local FW type was insufficient ($n = 4$) to detect any change that might have occurred in whistle score during the season. Nevertheless, Round Valley yearlings with foreign whistles (Fig. 4a, zero scores) were as likely to be trapped during the first half (15 May–13 June) as in the latter half (14 June–13 July) of the breeding season ($G = 0.368, P > 0.5$ for 10 of 12 versus 5 of 7 yearlings with zero FW scores).

In the Round Valley, 13 (54.1%) of the 23 test yearlings were captured more than once in the local decoy trap, and 11 (47.8%) were trapped at least once at the start of the season in May and

again at the end in July. In the Convict dialect, ten (50.0%) of the yearlings were trapped on more than one occasion and six (30.0%) were caught both in May and July. Comparable trapping data for the Mammoth yearlings are not available because the trapping method used in that dialect captured only a small proportion of local birds.

Figure 5 shows the changes that occurred in the whistles of three Round Valley males who were tested as yearlings using testosterone in 1991 and recorded in the wild a year later as adults at the start of the 1992 breeding season. As yearlings all three birds gave non-local FWs. When recorded in May 1992, all three birds gave com-

TABLE 1. Average flight whistle (FW) scores for all cowbirds giving FWs (local and foreign) from the Mammoth, Convict, and Round Valley dialect populations.

Dialect	Adults				Yearlings				
	Mean ¹ (±SE)	Max ² (%)	Median (range)	n	Mean ¹ (±SE)	% max ³	% adult ⁴	Median (range)	n
Mammoth	4.5 (0.5)	5 (89.6)	5.0 (0–5)	11	2.5 (0.4)	49.2	54.9	2.6 (0–5)	16*
Convict	5.2 (0.5)	6 (86.3)	5.9 (0–6)	18	2.8 (0.5)	46.5	53.9	2.9 (0–5.9)	20*
Round Valley	3.2 (0.4)	4 (79.0)	4.0 (0–4)	17	0.6 (0.3)	15.5	19.6	0 (0–3.5)	19*

¹ See text and Figure 2 for explanation of scoring system.

² Potential maximum FW score and mean FW score as a percentage of potential maximum for each dialect.

³ Mean yearling FW score as a percentage of the potential maximum score in each dialect.

⁴ Mean yearling FW score as a percentage of the mean for adults in each dialect.

* Comparisons of adult versus yearling FW scores; Mann-Whitney U-tests, all one-tailed $P_s < 0.002$.

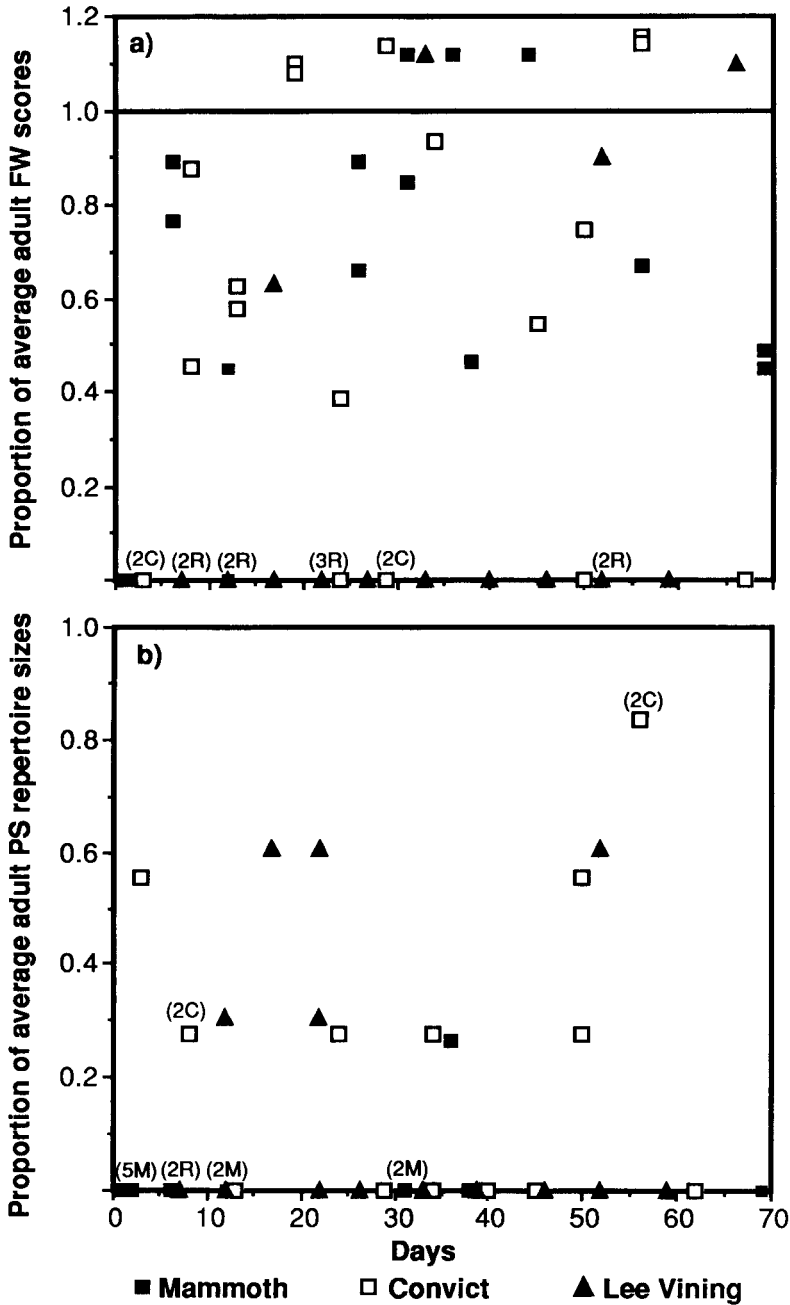


FIGURE 4. The relationship between, (a) average FW scores, and (b) estimated PS repertoire sizes of individual yearlings as a proportion of the total average FW scores and estimated PS repertoire sizes for adults in each dialect, and the number of days lapsed since 9 May (day 0), the earliest date a bird was tested. Some yearlings had average FW scores greater than the average for all adult FWs in their respective dialect, hence the points above the line representing average adult scores in Figure 4a. See text and Figure 2 for an explanation of the scoring systems in each dialect. PS repertoire sizes in Figure 4b are based on local adult-shared songs (songs shared by two or more adults) for all birds with eight or more PSs recorded. Numbers in parentheses are multiple data points. Spearman rank correlations for FW scores; Mammoth $n = 16$, $r_s = 0.30$, $P > 0.1$, Convict $n = 20$, $r_s = 0.20$, $P > 0.1$, Round Valley $n = 19$, $r_s = 0.31$, $P > 0.1$. Spearman rank correlations for PS repertoire sizes; Mammoth $n = 13$, $r_s = 0.31$, one-tailed $P > 0.1$, Convict $n = 15$, $r_s = 0.11$, one-tailed $P > 0.25$, Round Valley $n = 15$, $r_s = -0.09$, one-tailed $P > 0.25$.

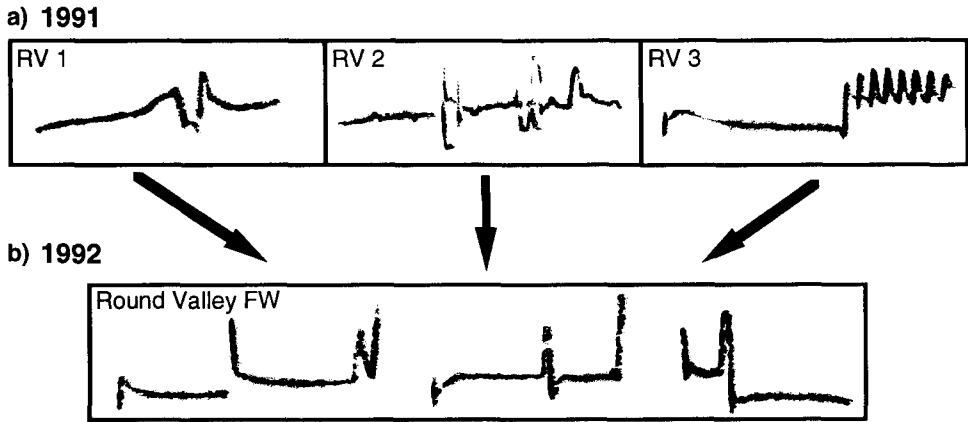


FIGURE 5. (a) Examples of flight whistles of three testosterone-treated yearlings trapped in the Round Valley in 1991. Males RV 1 and 2 showed some variation in their FWs and the most complex produced is shown. (b) Flight whistles recorded from these birds in 1992 when they were adults. As adults, the three birds gave all of the whistle syllables shown (see text and Figure 1 for explanation), although not always as one vocalization.

plete renditions of the two syllable whistle most frequently heard from Round Valley adults (see Fig. 1). These three males also gave the other whistle elements (R3 and R4) commonly heard in the Round Valley area.

PERCHED SONGS

At least one perched song was recorded from 97 (82.9%) of the 117 males trapped during the three-year study period, 54 (55.7%) of whom were yearlings and 43 (44.3%) adults. Yearlings were just as likely to produce at least one PS as adults ($G = 0.598$, $P > 0.1$ for 54 of 67 [80.6%] yearlings versus 43 of 50 [86.0%] adults), and there were no significant differences between dialects in the proportions of each age class that gave PSs (O'Loughlen 1993).

For Mammoth and Round Valley adults, there was no association between estimated repertoire sizes and number of PSs recorded for all birds giving eight or more PSs. For Convict adults with eight or more PSs recorded, estimated repertoire sizes and number of songs were correlated (Spearman rank correlation, $n = 10$, $r_s = 0.692$, one-tailed $P < 0.05$). Fifteen or more PSs were recorded from nine of the adults in this latter sample and there was no correlation between estimated repertoire sizes and number of PSs recorded for these birds (Spearman rank correlation, $n = 9$, $r_s = 0.589$, one-tailed $P < 0.1$). Average repertoire size estimated for Convict adults with eight or more PSs recorded ($n = 10$) was 4.40 ± 0.37 song types; for adults with 15

or more PSs recorded ($n = 9$), the equivalent average was 4.56 ± 0.38 . Thus, any underestimation of repertoire size for Convict adults due to use of the former sample is likely to be small and, therefore, conservative in comparison with the relatively small repertoire sizes of yearlings.

Adults had repertoires of three to seven song types, and means ranged from 4.0 (± 0.3) in Round Valley to 5.5 (± 0.6) types in Mammoth (Fig. 6). Yearlings had one to six song types. Estimated repertoire sizes for yearlings were smaller than those of adults in all three dialects, and the differences between age classes were significant in Mammoth and Convict (Fig. 6). Aged-based differences in repertoire sizes are likely to be conservative for Mammoth and Round Valley males because significantly more PSs were recorded from yearlings than adults taken from these dialects (O'Loughlen 1993, O'Loughlen and Rothstein 1993). There was no difference between Convict adults and yearlings in numbers of PSs recorded (O'Loughlen 1993).

One particular song type was found in the majority of repertoires of both age classes in all dialects. Seventy of the 97 (72.2%) males from whom one or more songs were recorded gave this song, and there was no difference among the dialects or within the age classes in proportions of males with this song. As stated elsewhere (O'Loughlen and Rothstein 1993), this song type occurs throughout the range of the three cowbird subspecies (Rothstein and O'Loughlen, unpubl. ms.). Thus, this song type is less informative than other types in studies of local song learning, and

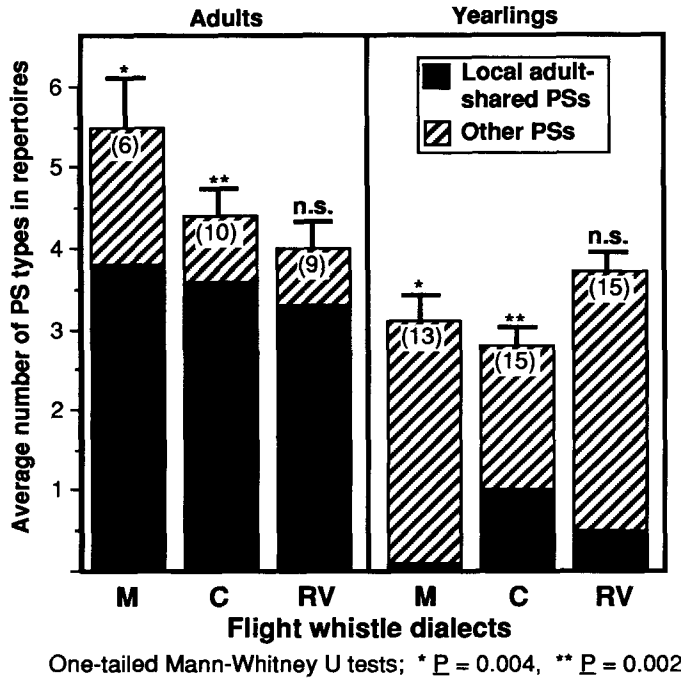


FIGURE 6. Average number (\pm SE) of different PS types given by adults and yearlings for all birds giving eight or more PSs in each dialect. In the Mammoth and Convict dialects, adult and yearling repertoire sizes were significantly different (Mann-Whitney U -tests, $P = 0.004$ and 0.002 respectively). Local adult-shared PS types (solid bars) are songs shared by two or more adults in a dialect. Yearling repertoires of local adult-shared PSs were significantly smaller than equivalent adult repertoires in all dialects (Mann-Whitney U -tests, one-tailed P 's < 0.001). Numbers in parentheses are sample sizes.

it has been excluded from estimates of repertoire sizes used in analyses of local song sharing.

Excluding the above song type, the Convict dialect had eight song types that were shared by two or more local adults; Mammoth had seven and Round Valley, six. As a measure of local song matching, I compared average size of repertoires for birds meeting the eight song criterion, based solely on these local adult-shared song types. Whereas 31 of 43 (72.1%) adults had repertoires based entirely on these local adult-shared songs, only 5 of 54 (9.3%) yearlings did so ($G = 43.718$, $P < 0.001$), and in all three dialects, adults had significantly larger adult-shared repertoires than yearlings (Fig. 6. Mann-Whitney U -tests, all one-tailed P 's < 0.001).

ARRESTED DEVELOPMENT OF LOCAL PS REPERTOIRES IN YEARLINGS

There was no evidence that yearling males in any of the dialects altered either the size or content of their PS repertoires during the breeding season to better match the repertoires of local adults.

There was no correlation between date tested and estimated repertoire sizes for yearlings with eight or more PSs recorded in any of the dialects (Spearman rank correlations. Mammoth, $n = 13$, $r_s = -0.082$, $P > 0.25$; Convict, $n = 15$, $r_s = -0.091$, $P > 0.25$; Round Valley, $n = 15$, $r_s = -0.380$, $P > 0.05$). Yearling repertoires showed no increase in the number of local adult-shared songs as the season progressed. There was no correlation between individual yearling repertoire sizes based on these shared songs as a proportion of the average repertoire size for all local adults and date when tested in any dialect (Fig. 4b. Spearman rank correlations, all P 's > 0.1).

Perched songs were recorded from six males trapped as yearlings in Convict in 1990 and again in 1991 when these birds were adults. All were treated with testosterone in 1990, and four received testosterone in 1991; the remaining two were recorded as free-living adults in the wild. In 1990, all six males met the criterion of eight or more PSs recorded for estimating repertoire sizes, and in 1991 only four did, so comparisons

TABLE 2. Total numbers of perched songs (PSs) and numbers of different PS types recorded from Convict dialect males as yearlings and as adults in two consecutive years.

	Yearling in 1990				Adult in 1991			
	Date of 1st test	Total PSs rec'd	Number of PS types		Date tested	Total PSs rec'd	Number of PS types	
			Total (unique)	Adult-shared ¹			Total	Adult-shared ¹
Convict 1	16 May	54	3 (1)	1	9 May	38	6	5
Convict 2	21 May	55	4 (3)	0	9 May	5	4	4
Convict 3	22 Jun	20	2 (1)	0	9 May	4	3	2
Convict 4	27 Jun	11	2 (0)	2	19 May	16	3	3
Convict 5	3 Jul	139	3 (0)	3	12 Jul	41	3	3
Convict 6	3 Jul	8	4 (0)	3	10 Jun	9	6	5

¹ Based on PS types shared by two or more Convict adults in 1990 and excluding the PS found throughout the species range. Wilcoxon test, $P = 0.02$ for numbers of adult-shared PSs in 1990 versus 1991.

are conservative. Average repertoire sizes for these males based on all songs recorded increased between their first and second breeding seasons (Table 2). Repertoire sizes based on 1990 local adult-shared song types increased significantly from an average of 1.50 (± 0.56) songs in 1990 to 3.67 (± 0.49) in 1991 (Table 2, Wilcoxon test, one-tailed $P = 0.02$).

Qualitative changes were apparent in the adult repertoires of these Convict males when compared with their yearling repertoires. With the exception of males Con 2 and 5, all had increased their repertoire size by adding local adult-shared songs. However, the adult repertoire of Con 2 contained four adult-shared types not found in his yearling repertoire. There were two new adult-shared songs in the adult repertoire of Con 5. These new songs were types shared exclusively by adults in 1990 and apparently replaced two types found in both adult and yearling repertoires. The three males who gave unique songs in 1990 appeared to have dropped them from their adult repertoires. Thus, all songs given by the six males in 1991 were types shared by two or more adults in 1990.

DISCUSSION

The delayed vocal development shown by the majority of cowbirds in the Mammoth dialect (O'Loughlen and Rothstein 1993) is not confined to that dialect. In the Convict and Round Valley dialects, vocal ontogeny was also not complete by the first breeding season, and most males did not appear to achieve typical adult repertoires until the start of their second season.

Results from the Convict dialect corroborate those of the earlier Mammoth study (O'Loughlen and Rothstein 1993), and as predicted there was

no significant distinction between these two dialects in numbers of yearlings giving different categories of FWs. Furthermore, Convict yearlings did not appear to alter their incomplete local whistles during the course of the season to more closely match the FWs of local adults. This occurred despite the fact that many of these yearlings were exposed to the singing of local adults throughout the season as suggested by repeated trapping of these individuals. In the Round Valley where the majority of yearlings produced foreign whistle types, there was also no evidence of birds switching to the local FW type as the season progressed. Data on repeated trapping of individuals also argue against differential immigration of foreign yearlings during the season as an explanation for the latter finding. Lack of change in size or content of yearling PS repertoires during the course of the season in all three dialects supports the premise that the above constraint on FW modification is a general restriction on production that affects the entire vocal repertoire of individuals in these populations.

Two characteristics distinguished the Round Valley dialect from the two higher elevation dialects; the proportion of yearlings with foreign FW types and the relatively large size of yearling PS repertoires compared with that of local adults. It is not known how these differences between the dialect populations arose, but they may both relate to prior experience in other dialects by Round Valley yearlings. Round Valley yearlings may have been fledged in dialects located at low elevations where exposure to local FW and PS types was not as restricted during their hatching year. The composition of the yearling PS repertoires supports this proposition. Perched song repertoires of Round Valley yearlings contained

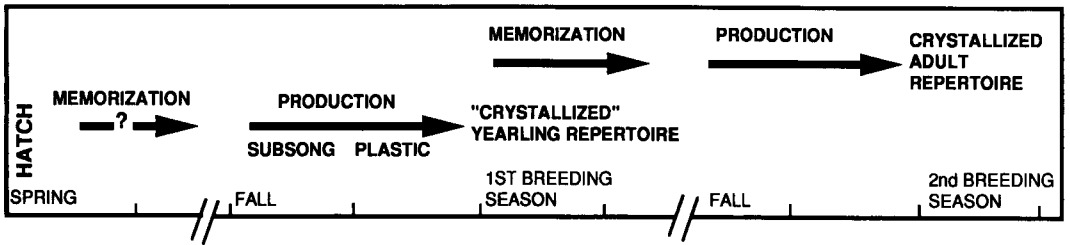


FIGURE 7. A proposed scheme for development of an adult vocal repertoire based on local song types in eastern Sierra Nevada flight whistle (FW) dialect populations. The "crystallized" vocal repertoires of yearlings are distinguished from adult repertoires by their incomplete local or foreign FWs and by their smaller perched song (PS) repertoires and lack of local PS types. Young cowbirds do not appear to modify their vocal repertoires during the course of their first breeding season. When males return from wintering for their second season, they have complete local FWs and enlarged PS repertoires based on the local PS types of the dialect area where they spent their first breeding season.

mostly non-local PS types, and yearling repertoires based solely on local adult-shared types were significantly smaller than adults.

WHEN DO SIERRAN COWBIRDS LEARN THEIR ADULT REPERTOIRES?

Generally, cowbirds overwinter in large flocks with other icterine species drawn from a wide geographic area (Dolbeer 1982, Rothstein et al. 1989). Banded males from the study dialects have been found to winter in locations as far apart as Santa Cruz, CA and Yuma, AZ (S. I. Rothstein, pers. comm.). In addition, wintering cowbirds seldom give well articulated FWs (O'Loughlen and Rothstein 1993), and in general, their PSs are poorly structured (King and West 1988). Thus, while young cowbirds may practice vocalizations during the winter (King and West 1988), there is practically no opportunity to acquire local songs. Whatever learning may occur in a dialect prior to the start of their first breeding season, it is clearly limited and insufficient for the majority of yearlings to produce the local songs.

Learning at the start of the breeding season is also a possible explanation for the complete local vocalizations of two-year-old males returning for their second season. However, the period during which birds could acquire and learn to produce local songs prior to the beginning of the season is limited because cowbirds from these high elevation populations return from wintering in mid to late April (Yokel 1986), and breeding activity begins early to late May depending on the dialect (Fleischer et al. 1987, Yokel 1986). Also, there was no indication of learning, e.g., plastic song, in the vocalizations of adult cowbirds trapped in early May, including birds who had been re-

corded as yearlings with incomplete vocal development the previous year.

In Figure 7, I present a proposed outline for development of an adult repertoire of local songs based on the results of this study. Sierran cowbirds appear to memorize much of their adult repertoires during their first breeding season, but they do not produce these adult songs until later prior to the start of their second season. Thus, these results appear to provide a natural demonstration of the segregation of the memorization and production phases of song learning. Once in full adult song, cowbirds in the wild are not known to change FW type (S. I. Rothstein, pers. comm.) or alter the content of their PS repertoires (Dufty 1985).

I tentatively describe yearling vocal repertoires as "crystallized" because frequently they contain songs with properties not fully consistent with the concept of crystallized song. Crystallization is generally considered as the final stage in development of full song and is characterized by high levels of stereotypy (Marler and Peters 1982b). At this stage, songs are assumed to be complete and not liable to further modification (Marler 1970, Marler and Peters 1982b, Konishi 1989). The local FWs of Mammoth and Convict yearlings were stereotyped (O'Loughlen and Rothstein 1993, unpubl. data), and these FWs appeared resistant to change but were also often incomplete, although not permanently so.

Changes that occur in the FWs of cowbirds from these dialects between their first breeding season and the start of their second have been described in a previous report on four testosterone-treated Convict birds (males Con 1, 2, 3, 4, Table 2 in the present report) and one free-living

Mammoth cowbird (O'Loghlen and Rothstein 1993). These birds learned either to complete their incorrect renditions of the local whistle or to switch whistle type completely from a foreign to the local type. Equivalent changes in the FWs of three Round Valley yearlings are presented in Figure 5. All three males gave only foreign whistles when tested in 1991 as yearlings. In 1992 as free-living adults, they gave all of the whistle combinations (Fig. 1) typically heard in the wild in the Round Valley area. Changes also occurred in the PS repertoires of all six Convict birds recorded as yearlings and a year later as adults. Some of these changes were extensive (Table 2) and involved both addition and deletion of song types.

REPRODUCTIVE CONSEQUENCES OF ARRESTED VOCAL DEVELOPMENT

There is evidence that the arrested vocal development shown by yearling cowbirds during their first breeding season could have detrimental consequences on their reproductive success. Estradiol-primed female cowbirds from these dialect areas are less likely to adopt the precopulatory lordosis posture (King and West 1977, Ratcliffe and Weisman 1987) in response to playback of foreign FWs, and this may also be true for incomplete local whistles (O'Loghlen and Rothstein, in press). Captive females from eastern US populations of cowbirds adopt the lordosis posture more frequently for certain PS types, and males whose repertoires contain these types are more likely to obtain copulations (West et al. 1981). Although yearling cowbirds in the study region are sexually mature, they rarely obtain copulations (Yokel 1986), and lack of the appropriate FW and PSs may play a part in this failure (O'Loghlen and Rothstein 1993). The PS repertoires of adult and yearling cowbirds are indistinguishable in eastern populations studied by Dufty (1985), and yearlings in eastern populations have equal success in competing for females (Dufty 1982). However, it is not known whether eastern birds show adult-yearling differences in FWs.

In other species with correlations between vocal behavior, age and mating success (Yasukawa et al. 1980, Loffredo and Borgia 1986, Eens et al. 1991), a restriction on vocal modification during the breeding season could be an important mechanism maintaining differences between age classes. In populations where there are age-re-

lated vocal differences, such a restriction may make vocal behavior a signal of age and experience resistant to cheating.

ACKNOWLEDGMENTS

I thank Steve Rothstein for his guidance and encouragement throughout this project and for his comments on various drafts of this manuscript. This research was supported by awards from the R. A. Schreiber Memorial Fund of the Los Angeles Audubon Society, the University of California Natural Reserve System, the Frank M. Chapman Memorial Fund of the American Museum of Natural History, and the Josselyn Van Tyne Memorial Fund of the American Ornithological Society and by NSF grant BNS-8616922 to S. I. Rothstein. My thanks to V. Morena and E. Mullen for their assistance in the field and to the Vertebrate Museum at the University of California, Santa Barbara for providing recording and trapping equipment. I am specially appreciative of the facilities and services provided by Dan Dawson and all the staff at the University of California Valentine Reserve. The manuscript also benefitted from the comments of Luis Baptista, Mike Beecher, Eliot Brenowitz, Bob Warner, Ken Yasukawa, and an anonymous reviewer. The procedures followed in this study were approved by the Animal Care Council at the University of California, Santa Barbara (Protocol 185). Birds used in this study were trapped, banded, and maintained in captivity under appropriate Federal and State permits.

LITERATURE CITED

- BALTHAZART, J. 1983. Hormonal correlates of behavior, p. 221-236. *In* S. Farner, J. R. King, and K. S. Parkes [eds.], *Avian biology*, VII. Academic Press, New York.
- DOLBEER, R. A. 1982. Migration patterns for age and sex classes of blackbirds and starlings. *J. Field Ornithol.* 53:28-46.
- DUFTY, A. M., JR. 1982. Response of Brown-headed Cowbirds to simulated conspecific intruders. *Anim. Behav.* 30:1034-1052.
- DUFTY, A. M., JR. 1985. Song sharing in the Brown-headed Cowbird (*Molothrus ater*). *Z. Tierpsychol.* 69:177-190.
- DUFTY, A. M., JR. 1986. Singing and the establishment and maintenance of dominance hierarchies in captive Brown-headed Cowbirds. *Behav. Ecol. Sociobiol.* 19:49-55.
- EENS, M., R. PINXTEN, AND R. F. VERHEYEN. 1991. Male song as a cue for mate choice in the European Starling. *Behaviour* 116:210-238.
- FLEISCHER, R. A., AND S. I. ROTHSTEIN. 1988. Known secondary contact and rapid gene flow among subspecies and dialects in the Brown-headed Cowbird. *Evolution* 42:1146-1158.
- FLEISCHER, R. A., A. P. SMYTH, AND S. I. ROTHSTEIN. 1987. Temporal and age-related variation in the laying rate of the parasitic Brown-headed Cowbird in the eastern Sierra Nevada, California. *Can. J. Zool.* 65:2724-2730.

- FRIEDMANN, H. 1929. The cowbirds, a study in the biology of social parasitism. C. C. Thomas, Springfield, IL.
- JENKINS, P. F. 1977. Cultural transmission of song patterns and dialect development in a free-living bird population. *Anim. Behav.* 5:50-78.
- KING, A. P., AND M. J. WEST. 1977. Species identification in the North American cowbird: appropriate responses to abnormal song. *Science* 195:1002-1004.
- KING, A. P., AND M. J. WEST. 1988. Searching for the functional origins of song in eastern Brown-headed Cowbirds, *Molothrus ater ater*. *Anim. Behav.* 36:1575-1588.
- KING, A. P., M. J. WEST, AND D. H. EASTZER. 1980. Song structure and song development as potential contributors to reproductive isolation in cowbirds (*Molothrus ater*). *J. Comp. Physiol. Psychol.* 94:1028-1036.
- KONISHI, M. 1989. Birdsong for neurobiologists. *Neuron* 3:541-549.
- LEMON, R. E. 1975. How birds develop dialects. *Condor* 77:385-406.
- LEMON, R. E., S. PERREAULT, AND D. M. WEARY. 1994. Dual strategies of song development in American Redstarts, *Setophaga ruticilla*. *Anim. Behav.* 47:317-329.
- LOFFREDO, C. A., AND G. BORGIA. 1986. Male courtship vocalizations as cues for mate choice in the Satin Bowerbird (*Ptilonorhynchus violaceus*). *Auk* 103:189-195.
- MARLER, P. 1970. A comparative approach to vocal learning: song development in White-crowned Sparrows. *J. Comp. Physiol. Psychol.* 71:1-25.
- MARLER, P., P. MUNDINGER, M. S. WASER, AND A. LUTJEN. 1972. Effects of acoustic stimulation and deprivation on song development in the Red-winged Blackbird (*Agelaius phoeniceus*). *Anim. Behav.* 20:586-606.
- MARLER, P., AND S. PETERS. 1982a. Subsong and plastic song: their role in the vocal learning process, p. 1-19. *In* D. E. Kroodsma, E. H. Miller, and H. Ouellet [eds.], *Acoustic communication in birds*, Vol. 2. Academic Press, New York.
- MARLER, P., AND S. PETERS. 1982b. Structural changes in song ontogeny in the Swamp Sparrow *Melospiza georgiana*. *Auk* 99:446-458.
- NOTTEBOHM, F., AND M. E. NOTTEBOHM. 1978. Relationship between song repertoire and age in the canary, *Serinus canarius*. *Z. Tierpsychol.* 46:445-471.
- O'LOGHLEN, A. L. 1993. Vocal ontogeny and the maintenance of dialects in wild populations of Brown-headed Cowbirds. Ph.D. diss., Univ. of California, Santa Barbara, CA.
- O'LOGHLEN, A. L., AND S. I. ROTHSTEIN. 1993. An extreme example of delayed vocal development: song learning in a population of wild Brown-headed Cowbirds. *Anim. Behav.* 46:293-304.
- O'LOGHLEN, A. L., AND S. I. ROTHSTEIN. In press. Culturally correct song dialects are correlated with male age and female preferences in wild populations of Brown-headed Cowbirds. *Behav. Ecol. Sociobiol.*
- PAYNE, R. B. 1973. Behavior, mimetic songs and song dialects, and relationships of the parasitic indigo-birds (*Vidua*) of Africa. *Ornithol. Monogr.* 11:1-33.
- RATCLIFFE, L., AND R. WEISMAN. 1987. Phase order recognition by Brown-headed Cowbirds. *Anim. Behav.* 35:1260-1262.
- RICE, J. O., AND W. L. THOMPSON. 1968. Song development in the Indigo Bunting. *Anim. Behav.* 6:462-469.
- ROTHSTEIN, S. I., AND R. C. FLEISCHER. 1987. Vocal dialects and their possible relation to honest status signalling in the Brown-headed Cowbird. *Condor* 89:1-23.
- ROTHSTEIN, S. I., J. VERNER, AND E. STEVENS. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the eastern Sierra Nevada. *Auk* 97:253-267.
- ROTHSTEIN, S. I., J. VERNER, E. STEVENS, AND L. V. RITTER. 1987. Behavioral differences among sex and age classes of the Brown-headed Cowbird and their relation to the efficacy of a control program. *Wilson Bull.* 99:322-337.
- ROTHSTEIN, S. I., J. C. ORTEGA, AND A. L. O'LOGHLEN. 1989. Cowbird song. *Nature, Lond.* 339:21-22.
- ROTHSTEIN, S. I., D. A. YOKEL, AND R. C. FLEISCHER. 1988. The agonistic and sexual functions of vocalizations of male Brown-headed Cowbirds, *Molothrus ater*. *Anim. Behav.* 36:73-86.
- SELANDER, R. K., AND D. R. GILLER. 1960. First year plumages of the Brown-headed Cowbird and red-winged blackbird. *Condor* 62:202-214.
- SLATER, P.J.B. 1983. Bird song learning: theme and variation, p. 475-511. *In* A. H. Bush and G. A. Clark [eds.], *Perspectives in ornithology*. Cambridge Univ. Press, Cambridge.
- THORPE, W. H. 1958. The learning of song patterns by birds with especial reference to the song of the Chaffinch *Fringilla coelebs*. *Ibis* 100:535-570.
- WEST, M. J., AND A. P. KING. 1983. Epigenesis of cowbird song: a joint endeavour of males and females. *Nature, Lond.* 305:704-706.
- WEST, M. J., AND A. P. KING. 1986. Song repertoire development in male cowbirds (*Molothrus ater*): its relation to female assessment of song potency. *J. Comp. Psychol.* 100:296-303.
- WEST, M. J., A. P. KING, AND D. H. EASTZER. 1981. Validating the female bioassay of cowbird song: relating differences in song potency to mating success. *Anim. Behav.* 29:490-501.
- YASUKAWA, K., J. L. BLANK, AND C. B. PATTERSON. 1980. Song repertoires and sexual selection in the Red-winged Blackbird. *Behav. Ecol. Sociobiol.* 7:223-238.
- YOKEL, D. A. 1986. The social organization of the Brown-headed Cowbird in the Owens Valley, California, p. 164-172. *In* C. A. Hall and D. J. Young [eds.], *Natural history of the White-Inyo Range, eastern California and western Nevada and high altitude physiology*. White Mountain Research Station Symposium, Vol. 1. Univ. of California, Los Angeles.
- YOKEL, D. A. 1987. Sexual selection and the mating system of the Brown-headed Cowbird (*Molothrus ater*) in eastern California. Ph.D. diss., Univ. of California, Santa Barbara, CA.