of skin specimens for myological studies. The photographs are by Victor E. Krantz.

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Brown-headed Cowbirds Learn Flight Whistles after the Juvenile Period

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The ontogeny of songbird vocalizations has become a classic example of the interaction of genetic and environmental factors in the development of complex behavior (Baptista and Petrinovich 1984). In the best-known study, Marler and Tamura (1964) used taped playbacks of song as "tutors" and concluded that White-crowned Sparrows (*Zonotrichia leucophrys*) learn only conspecific song and will do so only if they hear it between about 10–50 days of age. These findings do not apply to all songbirds as many species learn new songs after 50 days of age (Kroodsma 1982). Moreover, by exposing birds to live tutors, Baptista and Petrinovich (1984, 1986) found that White-crowns will learn songs, even of heterospecifics, after 50 days of age (but see Cunningham and Baker 1983, Baker and Cunningham 1985). Besides its importance in basic ontogeny, vocal development in songbirds is critical to understanding possible evolutionary consequences of dialects, about which there has been much recent controversy (Kroodsma et al. 1984, Baker and Cunningham 1985 and accompanying critiques).

We report on the flight whistles (hereafter FWs) developed by captive Brown-headed Cowbirds (*Molothrus ater*) exposed to live, rather than taped, tutors. The behavioral ontogeny of a brood-parasitic species such as the cowbird is especially interesting because the birds have no known contact with their parents. This has led some (e.g. Mayr 1974) to suggest that cowbirds have a closed developmental program resistant to environmental influences to ensure that vital species-specific behavior develops properly. Although there are genetically programmed aspects to

the ontogeny of the vocalization known as the cowbird's song, learning plays a major role in altering song structure (West et al. 1981, King and West 1983).

The FW and song are given only by males, and both function in agonistic male-male and sexual male-female communication (Rothstein et al. in press). Critical differences exist between the two vocalizations, however. Most FWs are given in flight. Because virtually all songs are given while males are perched or are standing on the ground (Friedmann 1929), we call this vocalization perched song (hereafter PS). PSs always begin with brief notes below 3 kHz and then rise rapidly to at least 7 kHz (West et al. 1981, Dufty 1985). By contrast, FWs are mostly pure-tone vocalizations between 4 and 10 kHz (Rothstein and Fleischer 1987, Rothstein et al. in press). Although the PS varies between two cowbird subspecies (King et al. 1980), localized dialects with discrete borders appear to be absent, at least in New York state (Dufty 1985). But discrete dialects occur in the FW in parts of California (Rothstein et al. 1986, Rothstein and Fleischer 1987). Males have repertoires of 2–6 PSs (Dufty 1985, pers. obs.) but most have only one FW type, except that males with 2 FWs are common at borders between FW dialects (Rothstein and Fleischer 1987). Because the PS and FW have different acoustic structures and patterns of variation, work on the ontogeny of the former (West et al. 1981, King and West 1983) cannot be used to make conclusions about the ontogeny of the FW.

All birds cited herein were housed in 3 outdoor aviaries (A, B, C) at the University of California at Santa Barbara. The aviaries had 3 adjoining and parallel cages, each measuring 5.3 × 1.0 × 2.9 m. The 5 subjects of this study were divided into 2 groups. Males 1–4 were captured on the east slope of the Sierra Nevada at Mammoth Lakes, Mono Co., Cali-

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fornia, from 18 July to 8 August 1984. When captured, males 1 and 3 were independent juveniles (<2 months old), male 2 an adult (≥2 yr old), and male 4 a yearling (1 yr old). Males 2 and 4 were aged by the criteria of Selander and Giller (1960). Males 1 and 3 were in the distinctive femalelike juvenile plumage and were captured after nearly all mature birds (adults and yearlings) had migrated from the area. This early departure of mature cowbirds in the Sierra typically occurs in mid-July before the numbers of fledged cowbirds peak (Rothstein et al. 1980, Verner and Ritter 1983). Males 1–4 were placed in the center cage of aviary A with 4 females captured at the same site between 14 July and 8 August 1984 (2 as juveniles and 2 as adults, i.e. ≥1 yr old). One cage of aviary A housed female Shiny Cowbirds (*M. bonariensis*) from Colonia, Uruguay, and the other remained empty.

Males 1–4 were *M. a. artemisiae* (Grinnell and Miller 1944). The remaining male, number 5, was a *M. a. obscurus* removed from a large decoy trap in northern Santa Barbara Co., California, on 24 September 1984. Male 5 had been in the trap 0–7 days and was still partially in juvenile plumage. He and 3 other juvenile males removed from the decoy trap at the same time were placed in one cage of aviary B, which was 10 m from the closest part of aviary A. The other 3 males died before recordings began. Aviary B had no other birds until March 1985, when male and female Shiny Cowbirds from partido de Gral. Lavalle, Buenos Aires Province, Argentina, were placed in the other two cages. The third aviary, C, housed cowbirds captured on the west slope of the Sierra Nevada at Dinkey Creek, Fresno Co., California, in 1981. Aviary C was 5 m from aviary A and 4 m from aviary B. Birds in the 3 aviaries were isolated visually by walls and dense shrubbery but could hear one another. All birds were maintained on a natural photoperiod and given a diet of game-bird starter and mixed bird seed, with mealworms available *ad libitum* once a week.

No recordings were made in 1985. Male 1 gave 24 FWs and the other three males only 1 during 32 min of observation on 27–28 March 1986. At this time wild birds in Santa Barbara were also beginning to whistle. Male 1 was dominant by the criteria in Rothstein et al. (1986), e.g. he gave 25 PSs, compared with 9 for the three other males combined. Because it seemed likely that male 1 was inhibiting the other males from vocalizing (Rothstein et al. 1986), he was removed on 28 March. FWs were eventually recorded from the remaining males (numbered according to the dominance hierarchy) between 29 March and 21 June by successively removing the dominant male, although no other male was as vocal as male 1. Male 4 never whistled while in the cage but did so while held in the hand. FWs given by free-flying birds do not differ from those of birds being held (Rothstein and Fleischer 1987).

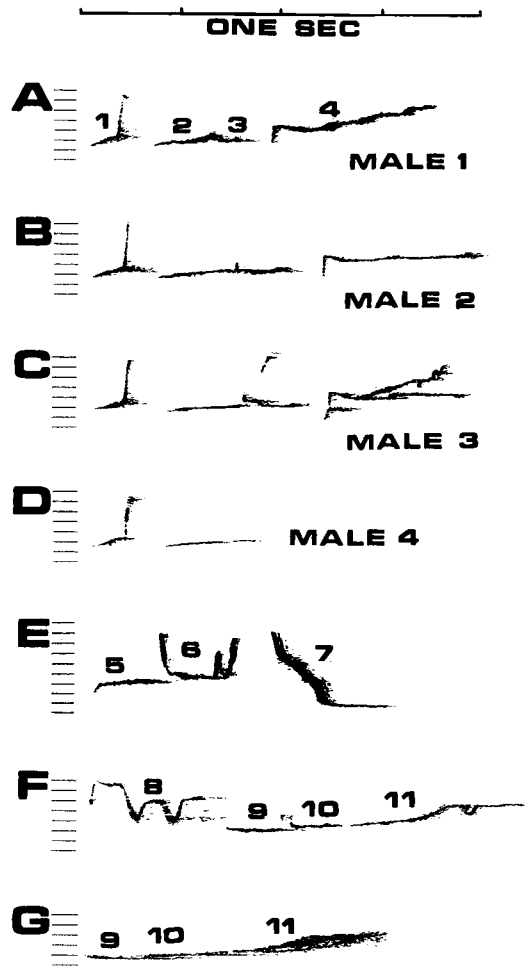We analyzed 24 of male 1's FWs with a Kay Elemetric Corporation Sonagraph machine (model 6061-

Fig. 1.   Narrow-band (45 Hz) spectrograms of flight whistles (FWs) of Brown-headed Cowbirds. Frequency scales start at 3 kHz. A–D are FWs by male cowbirds 1–4, who were caught in Mono Co., California, and caged together from August 1984 until March 1986. E is the type of FW given in the area where the males were caught. F is the FW by birds caught at Dinkey Creek, Fresno Co., California, and caged 5 m from males 1–4. G is a degraded version of F (without element 8, which was often deleted) recorded from the cage that contained males 1–4.

B) and a Unigon real time spectrum analyzer (model 4500). All were identical to Fig. 1A. Five whistles by male 2 were identical to Fig. 1B; another 2 consisted only of elements 1–3. Birds in nature also occasionally delete the final element(s) of a FW (pers. obs., Darley 1968). Only one FW was recorded from male 3 (Fig. 1C). Element 4 in male 3's FW combined the features present in the versions of element 4 by males 1 and 2, i.e. steep and gradual rises in frequency, respec-
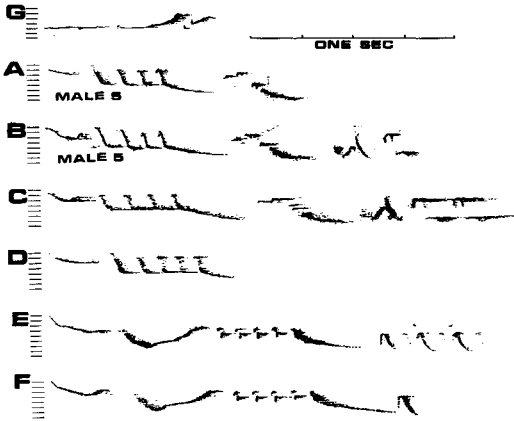
Fig. 2.   Narrow-band (45 Hz) spectrograms of flight whistles (FWs) by a Brown-headed Cowbird and by 4 Shiny Cowbirds. Frequency scales start at 3 kHz. A and B are FWs by male 5, a Brown-headed Cowbird that was caught in Santa Barbara Co., California. C–F are FWs by 4 Shiny Cowbirds caught in Buenos Aires Province, Argentina, and housed next to male 5. G is the type of FW given in the area where male 5 was captured.

tively. The two harmonically independent parts of element 4 in male 3's FW are a clear example of the two-voice phenomenon (Brackenbury 1982). Three of 4 FWs by male 4 were identical to the one in Fig. 1D, i.e. they consisted of elements 1 and 2. The remaining FW was similar, but it had a downward frequency sweep after the upward sweep in element 1.

Males 1–4 shared a FW type that bears little relation to the "Mammoth dialect" FW, the predominant one at their capture site (Fig. 1E; Rothstein and Fleischer 1987). Element 5 (Fig. 1E) could be comparable to element 2 (Fig. 1A), but this has little significance because many FWs have similar, nearly monotonic elements at or near their beginnings. The diagnostic parts of the FW in Fig. 1E, elements 6 and 7, have no counterparts in Fig. 1A. Three possible explanations for the origin of the FW elements of males 1–4 are as follows. (1) We believe most of the FW is a copy of FWs given frequently by the caged males from Dinkey Creek (Fig. 1F and G). Elements 2–4 (Fig. 1A) are similar to 9–11 (Fig. 1F) in that both series have two nearly monotonic syllables followed by a longer syllable at a higher and increasing frequency. The syllable matching is not perfect for elements 4 and 11, possibly because males 1–4 heard only a degraded version of the Dinkey Creek FW (see Fig. 1G). Besides the degradation caused by walls between aviaries, the entire complex was surrounded on three sides by large buildings. Element 1 (Fig. 1A) had no relation to element 8 (Fig. 1F), which was not a fixed part of the Dinkey Creek FWs. Thus, element 1 may have been improvised by males 1–4. Because of its extreme fre-

quency sweeps, element 8 probably was subjected to more degradation via reverberation than elements 9–11, and this, as well as more frequent presentation, may have made the latter elements more effective as learning stimuli (see Morton et al. 1986). The Dinkey Creek birds often whistled in response to FWs by males 1–4, and such social interaction may have induced the latter males to copy the Dinkey Creek FWs.

(2) The entire FW given by males 1–4 may be an improvisation with no relation to FWs given by other males. We doubt this explanation because the FW in Fig. 1A sounded nearly identical to elements 9–11 in Fig. 1F.

(3) One of the males among 1–4 may have heard the FW before being captured, and the other males may have learned it from him. This is unlikely because this FW did not occur in the 300 km north–south span in the Sierra from which we analyzed over 700 FWs by at least 250 males. Whistle variation in this region is organized spatially into dialects that are 5–30 km across at their widest points (Rothstein and Fleischer 1987). We cannot exclude the possibility that the FW in Fig. 1A originated in some distant dialect unknown to us and that one of males 1–4 was a migrant from that dialect. However, we exclude the possibility that 2 or more of the males were migrants from the same distant dialect; this is too improbable a coincidence to consider seriously, especially because males 1–4 were caught on different days (3 August, 30 July, 8 August, and 18 July, respectively).

Regardless of which explanation is correct, 4 of 4 (explanations 1 or 2) or 3 of 4 males (explanation 3) learned a FW they did not hear until after the juvenile stage. Although other explanations are possible, all necessitate FW learning after the juvenile stage.

Male 5 gave a FW (Fig. 2B) that was nearly a perfect copy of FWs given by at least one Shiny Cowbird (Fig. 2C) in the adjoining cage. This FW was unlike any recorded in the field from Brown-headed Cowbirds. We heard and often recorded more than 50 FWs by male 5, all of which were of the type in Fig. 2B. None of male 5's FWs resembled FWs given at his capture site (Fig. 2G). The only variation shown by male 5 was a failure to sometimes complete the FW (e.g. Fig. 1A). The Shiny Cowbirds also gave incomplete FWs (e.g. Fig. 2D). Male 5 may have been able to adopt a nearly perfect copy of a Shiny Cowbird FW because the latter reached him in undegraded form. There was only wire mesh between male 5 and the Shiny Cowbirds, and the latter often whistled less than 1 m from male 5. Male 5 occasionally directed perched songs to a female Shiny Cowbird; such social interaction may be one reason he learned the FW of another species despite the fact that he could hear conspecific FWs from other aviaries. Social interaction is an important influence in the ontogeny of the cowbird's perched song (King and West 1983) and in the songs of other species (Payne 1981a; Kroodsma and Pickert 1984; Baptista and Petrinovich 1984, 1986).

Because males 1–4 had conspecific females caged with them, we presume that there was no motivation for them to interact with the heterospecific Uruguayan female Shiny Cowbirds housed in the adjacent cage. We never saw these males singing to the Shiny Cowbirds. Furthermore, there is no evidence that the female Shiny Cowbirds influenced males 1–4 because FWs by the latter males bore no resemblance to those of Uruguayan males, which are similar to those given by male Shiny Cowbirds from Argentina (see Fig. 2).

Males 1–5 gave FWs totally unlike those that occurred at their capture sites. By contrast, the Dinkey Creek males continued in 1986 to give FWs that matched those we recorded at their capture site from 1979 to 1981. The Dinkey Creek males present in 1986 were the last survivors of an original group of 37 males (20 yearlings, 17 adults) and 14 females captured at a single pack station and brought to Santa Barbara in 1981. We presume that they did not change their FWs because their initial group size was large and no other cowbirds were present in our aviaries. The FW stability shown by the Dinkey Creek males demonstrates that captivity did not produce artifacts that caused the birds to invariably develop vocalizations divergent from those given at their capture sites.

Although our sample size was small, the uniformity of the results demonstrates that male Brown-headed Cowbirds can learn a FW if exposed to a live tutor after the juvenile stage. Given our sample of 5 individuals, the frequency of cowbird males, in the overall population, that can learn a new FW after the juvenile period is 48–100% (95% confidence interval for 5 of 5; Rohlf and Sokal 1969). Indigo Buntings (*Passerina cyanea*; Payne 1981a) and White-crowned Sparrows (Baptista and Petrinovich 1984) also learn songs if exposed experimentally to live tutors after the juvenile stage or after 50 days of age. Baptista and Petrinovich (1984) isolated sparrows from all adult songs for the first 50 days, and Baker and Cunningham (1985) suggested that such "auditory deprivation" could have extended artificially the sensitive period. The criticism of auditory deprivation does not apply to our study. Both males 2 and 4, captured as an adult and a yearling, respectively, had normal juvenile periods and at least one full breeding season in nature. Males 1, 3, and 5 were captured as juveniles but after local birds had ceased giving FWs. Thus, none of our birds were subjected to unnatural sensory deprivation during their juvenile periods.

Baker and Cunningham (1985) also criticized Baptista and Petrinovich's (1984) study by suggesting that some birds in that study may have experienced abnormal hormonal conditions when caged with dominant adults that inflicted strong aggression from which there was no escape. (For counterarguments see Baptista 1985a, Petrinovich 1985, Baptista and Petrinovich 1986.) Regardless of who is correct, the criticism of "aggression with no escape" does not apply to our birds. Although male cowbirds frequently exchange agonistic displays, they do not maintain mutually exclusive territories (Dufty 1982, Rothstein et al. 1986). Thus, they show only low levels of aggression, and chases are rare in captivity (Rothstein et al. 1986) and in the field (Dufty 1982, Darley 1982, Rothstein et al. 1984). Moreover, male 5 was caged separately from his tutor(s), as were males 1–4 from their apparent tutor(s) (the Dinkey Creek males).

We suggest that our study closely simulated natural dispersal events in which cowbirds from one FW dialect move to another dialect or found a new population. Such dispersal seems to be a common event (Rothstein and Fleischer 1987, Fleischer and Rothstein MS). The postjuvenile development of FWs we observed is expected under the new social-adaptation hypothesis we have developed to explain the maintenance of dialects (Rothstein and Fleischer 1987; see Payne 1981b and Baptista 1985b for further discussion of social adaptation and dialect maintenance).

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