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Singing and the establishment and maintenance of dominance hierarchies in captive brown-headed cowbirds

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Summary. The importance of singing in the establishment and maintenance of dominance rank was investigated in captive flocks of brown-headed cowbirds (*Molothrus ater*). Each flock consisted of 3 males and 1 female. In one experiment the two largest males in each of 4 flocks were temporarily devocalized by puncturing the interclavicular air sac just before group formation. The third male in each group was sham-operated. There was a significant tendency for the non-devocalized birds to become the dominant member of their group. Only sham-operated males sang immediately after the operation. In a second experiment, dominant males from flocks with established hierarchies were temporarily devocalized. None of these males lost their dominant positions, despite their inability to sing. These results suggest that song is important in the establishment of dominance rank; however, once established, social hierarchies may be maintained by non-vocal means, such as social inertia or individual recognition.

Introduction

Darwin's (1871) theory of sexual selection has as its foundation two processes which may act independently or in concert: First, organisms of one sex, usually males, compete among themselves for access to individuals of the opposite sex (intrasexual selection). Second, females show mating preferences for particular males (intersexual selection). The outcome of these processes is nonrandom mating success for males, and can lead to the development of elaborate male secondary sexual characteristics, including song.

In brood parasitic brown-headed cowbirds (*Molothrus ater*) males outnumber females in the adult population (Fankhauser 1971). Since these birds are largely monogamous in northeastern North America, this skewed sex ratio results in intrasexual competition by males for females (Darley 1982; Dufty 1982a, b).

Female choice may be important in cowbirds. Captive females courted by several males will copulate only with the highest ranking individual, and even then only after several days of courting which presumably allows females to assess social rank accurately (West et al. 1981a). Although these results are also consistent with a mating pattern based on male competition, additional indications of female choice come from the response of female cowbirds to playbacks of recorded male vocalizations. Male cowbirds sing in both intra- and intersexual encounters (Friedmann 1929). Their song consists of several low frequency notes followed by a high frequency whistle. Males usually possess from 2–6 song variants, many of which are unique to a given local population (Dufty 1985). Recent evidence has shown that the amplitude characteristics of a small section of the song serve as a sensitive marker for dominance rank, with playbacks of songs of dominant males eliciting more copulatory responses from females than songs of subordinate males (West et al. 1979, 1981a). Captive males of low social status that sing dominant-like (or 'potent') songs are severely attacked and may be killed by other males. Furthermore, males can vary the potency of their songs in different social situations (West et al. 1981b).

In this study I examined the importance of the ability to sing in establishing and maintaining dominance relationships in brown-headed cowbirds. If song is a primary determinant of social rank, then only males capable of singing should achieve dominant status and mate with females. Once hierarchies are established, however, song may diminish in importance and dominant males that can no longer sing may yet retain their rank by social inertia (Guhl 1964) or individual recognition (Chase 1982). Finally, I examined differences in the behavior of dominant and subordinate males.

Methods

Experiment 1: Singing and the establishment of dominance

Twelve male cowbirds were captured in early spring, individually color-banded, and housed singly in cages. The birds could hear but not see other males. The following day the 4 smallest birds (based on wing length) were each assigned to 1 of 4 different groups. The eight larger males were assigned at random, two to each of the 4 groups. In two of the groups the two larger males were temporarily devocalized under metofane anesthesia following the method described by Smith (1977). Briefly, an incision was made in the skin of the neck between the furculae, just anterior to their point of fusion. The interclavicular air sac was exposed and punctured using fine forceps. The sac was then cut 1–2 cm, and the skin was closed using collodion. The smallest male in each group received a sham operation, with the same surgical procedure as the devocalized males except that the interclavicular air sac was merely touched with the forceps, but not punctured. The devocalized birds showed no signs of respiratory or other stress.

After recovery from anesthesia (approx. 30 min) each group of 3 males, along with 1 female cowbird per group, was placed in a compartment ($2.4 \times 1.8 \times 1.2$ m) of an outdoor aviary. Females were implanted with a subcutaneous silastic capsule of oestradiol (i.d. 0.058 mm, o.d. 0.077 mm, length 12 mm) to facilitate sexual responsiveness. These capsules brought the females into the high physiological range of plasma oestradiol (Dufty, unpublished). The following day the males from the remaining two groups were treated in the same manner as above. Behavioral observations were initiated the day following introduction of the birds into the aviaries.

The largest birds in each flock were chosen for devocalization to prevent male body size from confounding the results. Larger males tend to be dominant in captive flocks of red-winged blackbirds (Searcy 1979) and many other species.

Four additional groups of intact cowbirds were established in the compartments ($3 \times 3 \times 2.5$ m) of another aviary. The groups were similar to those described above (i.e., 1 small and 2 larger males plus an implanted female) except that no surgical manipulations were conducted.

Shortly after the end of experiment 1, a dominant control male, BW, injured his foot. He was replaced by a second male, also identified as BW, 13 days before the onset of experiment 2. Positions in this flock shifted, with the second ranking male, WW, assuming the alpha rank and the new BW at the bottom of the hierarchy. The hierarchy in this flock was well defined by the start of experiment 2, despite its shorter existence.

Experiment 2: Singing and the maintenance of dominance

In a second experiment to examine whether singing is necessary to maintain dominance rank in established flocks, the control groups of experiment 1 became the experimental groups in experiment 2. Dominant males were devocalized and returned to their original groups. Observations were begun on the following day, and a total of five observation sessions were made over the six day period following devocalization. In addition, new sets of individuals were set up as controls. These birds were randomly divided into four flocks of 3 males and 1 female and were housed as such for 13 days prior to the experiment to establish stable hierarchies. The dominant individual in each of these flocks was sham-devocalized; observations were made the following day and four additional times over a total of 10 days.

Observations

Groups were observed for 30-min periods from behind a wooden screen with an eyeslit or from behind one-way glass. Within groups each male was watched for 10 min using focal animal sampling (Altmann 1974) to obtain behavioral data. The sequence of observations within flocks changed daily, with each male advancing one position from the previous order, and the first male moving to the last position (e.g., 1, 2, 3; 2, 3, 1; 3, 1, 2; etc.). The order in which flocks were observed was varied in a similar fashion. All observations were made between 0600 and 1100, and groups were observed with equal frequency in the early and later parts of this time period.

I recorded all aggressive interactions in which the focal animal participated, either as the initiator or the recipient, and all courtship activities. Aggressive behavior included displacements of other males and song spread displays in which the singing male arches his wings, spreads his tail, fluffs his body feathers, and bows forward. The display can be scored as 1 (little or no bowing or arching of wings), 2 (moderate levels) or 3 (wings fully arched, deep bow). A song and its accompanying display were considered to be directed if the singer oriented the display toward a particular individual. Other songs were scored as undirected.

Blood samples (approx. 450 μl) were taken from the wing vein of each male before flocks were established and one (experiment 2) or two (experiment 1) times afterwards. The plasma was assayed for steroid and pituitary hormone levels; these results will be presented elsewhere. Removal of this small amount of blood had no visible effect on the behavior of the birds.

Results

Experiment 1

None of the males with punctured interclavicular air sacs sang during the establishment of social hierarchies. The effect was temporary, and at least one devocalized male in each flock began to sing again 13–20 days after devocalization.

In each experimental group the sham-operated, singing male attained the highest dominance rank, despite being the smallest bird in each case (Tables 1 and 2), In the four control flocks only one of the smallest males became dominant. Under the null hypothesis, the probability of any given male becoming dominant in its flock is $^1/_3$. Therefore, the probability of all four small, singing males attaining dominant rank by chance is $(^1/_3)^4 = 0.012$. The probability of the control result occurring by chance is $^2/_3 \times {}^1/_3 \times 4 = 0.89$.

Dominant males rarely lost encounters with subordinates in either the experimental or control

Table 1. Experiment 1: Initial dominance hierarchies in flocks of cowbirds with two males devocalized prior to grouping. Bold letters represent sham-operated males; others are devocalized

	Loser							
	Flock 1				Flock 2			
		BB	BR	RR		**WR**	YY	WY
Winner	**BB**	–	167	276	**WR**	–	8(207)[a]	31
	BR	0	–	29	YY	1(1)[a]	–	0
	RR	0	5	–	WY	0	0	–
	Flock 3				Flock 4			
		YW	WW	BW		**YB**	RY	RW
	YW	–	157	46	**YB**	–	300	250
	WW	1	–	2	RY	2	–	20
	BW	0	0	–	RW	0	8	–

[a] Male WY escaped after 5 observation sessions. Number in parentheses represents the number of additional interactions between WR and YY after that time

Table 2. Experiment 1: Dominance hierarchies in control flocks of cowbirds, all males intact

	Loser							
	Flock 1				Flock 2			
		RW	BB	RR		RY	YB	BY
Winner	RW	–	47	156	RY	–	147	204
	BB	0	–	13	YB	0	–	32
	RR	3	3	–	BY	0	1	–
	Flock 3				Flock 4			
		YY	WR	WB		BW	WW	YR
	YY	–	68	85(82)[a]	BW	–	144	157
	WR	0	–	6	WW	0	–	43
	WB	0	0	–	YR	0	7	–

[a] Male WR died after 9 observation sessions. Number in parentheses represents the additional interactions between YY and WB after that time

Table 3. Experiment 1: The number of songs produced by each male in the experimental group, and classified according to recipient (female, male or undirected). Bold letters represent sham-operated males; all others are devocalized

Bird	Total songs	Recipient:			No. obs. sessions	Flock no.
		female	male	undirected		
BB	780	103	635	42	23	1
BR	11	0	1	10	23	
RR	0	–	–	–	23	
WR	415	44	26	345	20	2
YY	1	–	–	1	20	
WY	0	–	–	–	5	
YW	70	31	23	16	17	3
WW	12	2	2	8	17	
BW	0	–	–	–	17	
YB	283	112	145	26	23	4
RY	156	1	3	152	23	
RW	34	0	10	24	23	

Table 4. Experiment 1: The number of songs produced by each male of the control group, and classified according to recipient (female, male or undirected)

Bird	Total songs	Recipient:			No. obs. sessions	Flock no.
		female	male	undirected		
RW	198	87	48	63	16	1
RR	64	3	32	29	16	
BB	47	2	20	25	16	
RY	239	67	107	65	16	2
YB	114	0	22	92	16	
BY	1	0	0	1	16	
YY	405	49	243	113	14	3
WR	34	3	15	16	9	
WB	13	1	2	10	14	
BW	276	70	148	58	14	4
YR	36	11	18	7	14	
WW	35	6	26	3	14	

groups, and were the only birds to guard females successfully. Many of the interactions between dominants and subordinates occurred as the former followed the females throughout the aviaries. Subordinates interacted infrequently and their relationships were less obvious. Nonetheless, patterns emerged in most cases, with one subordinate able to displace the other. Three copulations were observed, two in the experimental group and one in the control, all performed by dominant males.

The amount each male sang is shown in Tables 3 and 4. Subordinate males in the experimental group were not heard to sing until 13–20 days after devocalization. Subordinates in control groups sang from the first day of observation and continued thereafter. Most (108/133) songs of these subordinates that were directed to a male were given to the other subordinate rather than to the dominant male ($\chi^2_1 = 51.80$, $P < 0.001$). Similarly, when the muted subordinates of the experimental groups eventually began to sing, they also avoided singing to the dominant, giving 13 of their

16 male-directed songs to the other subordinate ($\chi_1^2=6.25$, $P<0.02$). Dominant males sang more than subordinates in all four control flocks (Mann Whitney-$U=0$, $P=0.002$). There was no relationship between dominant rank and the distribution of songs (i.e., to females, to males, or undirected) (Friedman 2-way ANOVA: experimental group – $\chi_r^2=1.5$, $df=2$, $P=0.653$; control group – $\chi_r^2=2.0$, $df=2$, $P=0.431$). However, subordinate males (that sang 10 or more songs) tended to avoid singing to females and either sang undirected songs or sang to other males (experimental – $\chi_r^2=7.125$, $df=2$, $P<0.05$; control – $\chi_r^2=5.43$, $df=2$, $P=0.085$).

Dominant males in the experimental and control groups sang similar numbers of songs per observation session (median test: $\chi_1^2=0.60$, NS) and gave primarily high intensity (type 3) displays when singing to other males (experimental: $\chi_r^2=9.0$, $df=2$, $P=0.0099$; control: $\chi_r^2=14.25$, $df=2$, $P=0.000061$). Songs to females tended to be accompanied by type 1 or type 2 displays in the experimental groups ($\chi_r^2=6.0$, $df=2$, $P=0.069$); this relationship was not significant in the control males ($\chi_r^2=1.63$, $df=2$, NS), although 3 of the 4 dominant males gave type 1 displays most often when singing to females.

Reversal. One reversal of dominance rank eventually occurred in the experimental group. The sham-operated male YW, initially a dominant, was replaced by male WW sometime between observation sessions 17 and 18 of the experiment, made on days 36 and 45, respectively. Male WW began singing on day 19 but continued to be displaced by YW ($n=48$) through day 36. None of WW's 11 songs during this period were directed to YW. Male YW continued to sing through day 36, and was seen to copulate with the female on day 28, nine days after WW had begun to sing. It may be noteworthy that male YW sang the fewest songs of any of the dominant males (Table 3), with only seven songs directed to WW by day 36 and only one of these occurring after WW had begun to sing. By day 45 the reversal was complete: Male YW did not sing at all during the remaining six observation sessions (9 days) while male WW sang 200 songs (Table 3) and totally dominated both YW and the third male, BW (Table 5).

Table 5. Experiment 1: Dominance hierarchy and number of songs produced in flock 3 after the reversal of dominance rank. Bold letters represent a sham-operated male; all others are devocalized

		Loser Flock 3		
		YW	WW	BW
Winner	**YW**	–	0	1
	WW	58	–	48
	BW	0	0	–

Bird	Total songs	Recipient: female	male	undirected	No. obs. sessions	Flock no.
YW	0	–	–	–	6	3
WW	200	6	171	23	6	
BW	0	–	–	–	6	

Table 6. Experiment 2: Dominance hierarchies in established flocks of cowbirds with the dominant male devocalized. Bold letters represent devocalized males

		Loser Flock 1				Flock 2		
		RW	BB	RR		**RY**	YB	BY
Winner	**RW**	–	7	9	**RY**	–	13	45
	BB	0	–	1	YB	0	–	2
	RR	0	0	–	BY	0	1	–
		Flock 3				Flock 4		
		YY	WB	WR		**WW**	YR	BW
	YY	–	19	17	**WW**	–	9	9
	WB	0	–	3	YR	1	–	1
	WR	0	0	–	BW	0	1	–

Experiment 2

None of the dominant males in the experimental and control groups changed status after devocalization or sham-devocalization (Tables 6 and 7). Nonetheless, there was an effect of devocalization. Subordinate males in groups with a devocalized dominant were more likely to sing than those in the control group ($P=0.056$, Fisher exact, Tables 8 and 9). The singing of these experimental subordinates differed from that of control dominant males: considering only individuals that sang 10 or more songs, subordinates sang a lower percentage of their songs to females than dominants, ($U=1$, $P=0.036$) and were less likely to sing to females at all ($P=0.071$, Fisher exact). In addition, subordinates in the devocalized group sang to the dominant male and the other subordinate with equal frequencies ($P=0.5$, median test). In Experiment 1, on the other hand, subordinates avoided singing to the (sham-operated) dominants. The one subor-

Table 7. Experiment 2: Dominance hierarchies in established flocks of cowbirds with the dominant male sham-devocalized. Bold letters represent sham-devocalized males

	Loser							
	Flock 1				Flock 2			
		BF	WW	BR		**BW**	YF	YW
Winner	**BF**	–	290	302	**BW**	–	336	324
	WW	12	–	12	YF	0	–	24
	BR	0	1	–	YW	0	16	–
	Flock 3				Flock 4			
		WF	BY	RF		**WR**	RB	RY
	WF	–	228	73	**WR**	–	101	100
	BY	0	–	16	RB	5	–	11
	RF	0	4	–	RY	0	11	–

Table 8. Experiment 2: The number of songs produced by each male of the experimental group, and classified according to recipient (female, male or undirected). Bold letters represent devocalized males

Bird	Total songs	Recipient: female	male	undirected	No. obs. sessions	Flock no.
RW	–	–	–	–	5	1
BB	24	0	16	8	5	
RR	0	0	0	0	5	
RY	–	–	–	–	5	2
YB	51	0	20	31	5	
BY	14	0	13	1	5	
YY	–	–	–	–	5	3
WB	14	2	12	0	5	
WR	0	0	0	0	5	
WW	–	–	–	–	5	4
YR	155	0	21	134	5	
BW	0	0	0	0	5	

Table 9. Experiment 2: The number of songs produced by each male of the control group, and classified according to recipient (female, male or undirected)

Bird	Total songs	Recipient: female	male	undirected	No. obs. sessions	Flock no.
BF	73	55	13	5	11	1
WW	0	0	0	0	11	
BR	0	0	0	0	11	
BW	290	130	149	11	11	2
YF	20	0	10	10	11	
YW	0	0	0	0	11	
WF	65	7	47	11	11	3
BY	0	0	0	0	11	
RF	0	0	0	0	11	
WR	1	1	0	0	11	4
RY	0	0	0	0	11	
RB	0	0	0	0	11	

dinate control bird that sang in Experiment 2 gave all 10 of its male-directed songs to the other subordinate and none to the dominant.

In order to maintain their rank, devocalized males might compensate for the loss of acoustic signaling capacity with an increase in overt aggression, but there was no evidence of this. No attacks by dominants were observed in the control group. Indeed, one subordinate individual pecked a dominant male on two separate occasions during the first observation session; no other attacks were noted in the control group. Two of the four devocalized dominants did attack subordinates: Male RW attacked BB once and WW attacked YR four different times. However, supplanting rates of these devocalized dominant males were still much lower than those of control dominants ($U=0$, $P=0.014$). The results suggest that devocalization may somehow affect the ways in which dominance relationships are expressed in established hierarchies, although it does not cause changes in rank.

Discussion

Avian vocalizations are thought to have evolved under the dual pressures of intra- and intersexual selection. Although vocalizations of individual species may have been influenced primarily by one or the other of these forces (see Catchpole 1982 for review), in most species, including the brown-headed cowbird, both factors probably are important.

Dominant male cowbirds are known to have song characteristics that differ from those of subordinate males (West et al. 1981a). These differences have direct effects on females in captivity who, in the absence of males, assume copulatory postures in response to playbacks of potent songs (King and West 1977; West et al. 1979). Dominant males are most successful in guarding females, both in captivity (Rothstein 1972; Darley 1978) and in the wild (Darley 1982; Dufty 1982a), and are also successful in obtaining copulations (West et al. 1981a). Males may themselves be sensitive to song parameters (West and King 1980), although the importance of song (or other factors) in the *establishment* of dominance rank in cowbirds has not previously been explored.

Present results indicate that singing ability is an excellent predictor of dominance during the establishment of intrasexual relationships in male brown-headed cowbirds. Muted males were subordinate to singing males in all four flocks. The dominant singing males, although smaller than the muted males, and thus normally destined to have been subordinate to them, behaved no differently than dominant males in control flocks, courting and guarding females and supplanting other males. Although actual copulations were rare, these, too, were performed only by dominant individuals. The muted subordinate males, even after they resumed singing, directed their songs primarily to each other and, for the most part, remained subordinate despite their larger size. The one reversal occurred 36–45 days after devocalization in the flock with the least-vocal of the dominant males, and was accomplished by a subordinate 17 days or more after its ability to sing had returned.

These data demonstrate a direct effect of male song on the establishment of dominance hierarchies. Muted males appear to be faced with a twofold dilemma: they are unable to compete vocally for the dominant position, yet they are receivers of directed songs from others. Unanswered songs may well be a precursor or indicator of subordination by the recipient. Left unchallenged, the singing male assumes the most dominant rank and guards and courts the female. In terms of sexual selection theory the data thus suggest a double role for cowbird song, both in determining the outcome of male competition for access to females and in female mate choice. Male cowbirds control no resources essential to females (Darley 1982; Dufty 1982a) and, as brood parasites, offer no parental care. Consequently, assessment of males by females depends largely on phenotypic characteristics of the former, particularly the ability of sing attractive songs (West et al. 1981a). However, in order to court females, males must first achieve high social rank, and, as shown above, song is critical to this process. Thus, intersexual selection in cowbirds is greatly affected by the results of intrasexual selection among males, just as it is in the related red-winged blackbird (Searcy and Yasukawa 1983).

The data also show that dominance hierarchies, once established, can be maintined without the use of song. Dominant males muted after group establishment continued to follow females and to supplant subordinates, although the rate of supplanting was reduced relative to controls. Devocalized dominant males also received a higher rate of song displays from subordinates than did dominant control males in either experiment, yet none lost its dominant position. The importance of song in male-male relations in free-ranging birds has also been demonstrated by Peek (1972) and Smith (1979), who found that muted territorial male red-winged blackbirds (*Agelaius phoeniceus*) suffered more intrusions than did control males, although here, too, males retained their social rank. Similarly, others have noted that playbacks of song are effective in delaying reoccupation of areas from which territorial males have been removed (Krebs 1977; Yasukawa 1981).

Somewhat surprisingly, there is no evidence that devocalized dominants in an established group exhibit an increase in overt aggression to compensate for the loss of song. This suggests that social inertia (Guhl 1964) or individual recognition (Chase 1982) suffice to maintain already existing relationships, even after a major cue used in establishing those relationships is removed.

There may be a physiological factor involved in the diminution of the importance of singing in the maintenance of social relationships. The gonadal steroid hormone testosterone (T) is known to influence singing activity (Arnold 1975) as well as a wide range of other agonistic behaviors in birds (e.g., Adkins-Regan 1981; Harding 1981; Balthazart 1983; Wingfield 1985). Circulating levels of T have been shown to correlate with dominance rank during initial encounters between males in mammals and in birds, but once dominance relationships have been established, the correlation between T and dominance disappears (Schuurman 1980; Sapolsky 1983; Ramenofsky 1984). A similar transitory relationship between plasma T-levels and the establishment of dominance rank occurs in the brown-headed cowbird (Dufty and Wingfield, unpubl. data). Thus, a hormonal mechanism may underlie the importance of singing in the establishment of social rank during initial encounters between males, while other social factors are used in the maintenance of stable hierarchies.

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