VOCAL AND BEHAVIORAL RESPONSES OF BROWN-HEADED COWBIRDS TO FLIGHT WHISTLES FROM DIFFERENT DIALECTS[1]

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Abstract. We examined the vocal and behavioral responses of free-living male Brown-headed Cowbirds (*Molothrus ater*) to playbacks of flight whistles (FWs) from local, near-foreign, and distant-foreign dialects. Full, partial, and reverse FWs were broadcast to solitary males. Test males responded with their own FWs and approached playbacks of FWs significantly more than playbacks of control heterospecific vocalizations. This suggests that all three dialects were recognized as conspecific. The strongest responses were elicited by playbacks of local FWs, and there was little behavioral evidence that males distinguished between the near-foreign and distant-foreign dialects. Males responded to playbacks of partial or complete local FWs primarily with the next or missing part of the FW. That is, they avoided matching the playback. The FW responses to playbacks of near-foreign and distant-foreign FWs were not consistent. Males presumably use matching-avoidance within a FW dialect to initiate social interactions with particular conspecific males.

Key words: Brown-headed Cowbird, countersinging, dialects, flight whistles, Molothrus ater, *playbacks, vocalizations.*

INTRODUCTION

It is not unusual for neighboring songbirds to sing similar songs. Depending on the species, songs may be shared among only a few birds in a population (Payne 1981), or may involve a large number of individuals (Baptista 1975, McGregor and Thompson 1988) and can result in geographically-distinct vocal dialects. Song dialects have been documented in species in which most males in a local population sing the same single song, such as the White-crowned Sparrow *Zonotrichia leucophrys* (Marler and Tamura 1962). Distinct dialects sometimes also occur in species with multiple renditions of their species-typical song (European Wren *Troglodytes troglodytes,* Catchpole and Rowell 1993).

Shared songs function in a variety of contexts. For example, males of some species use the degradation of acoustic properties of shared songs to assess the distance of rival singing males (Richards 1981, McGregor and Krebs 1984). In other species, males respond antiphonally by matching (or avoiding matching) shared songs during competitive interactions (Whitney 1991, McGregor et al. 1992, Stoddard et al. 1992), which allows specific birds to establish and maintain contact with one another. Furthermore, the pattern of antiphonal countersinging may re-

flect dominance relationships (Kroodsma 1979, Smith and Norman 1979).

The Brown-headed Cowbird (*Molothrus ater*) has two vocalizations with song-like properties (Thorpe 1961, Krebs and Kroodsma 1980). The "traditional" cowbird song is represented by a set of vocalizations that are shared among local males, with each male possessing a subset of two or more renditions (Dufty 1985). Song characteristics at the subspecies level are important both in intrasexual and intersexual interactions (King et al. 1980, West et al. 1983, 1998). Although there is no clear evidence of dialects in this category of cowbird vocalizations (Dufty 1985) or any indication that specific song types are used in particular kinds of social interactions (West et al. 1981), West and King (1996) indicate that males with a high level of shared songs are more reproductively active.

In contrast, the second song-like vocalization, the flight whistle (FW), does exhibit dialects (Rothstein et al. 1986, Rothstein and Fleischer 1987). Cowbird males usually possess a single FW that is shared with most other males in a population (Rothstein and Fleischer 1987). FWs largely are pure tones, typically contain two or more syllables, and can either be produced in a partial (i.e., missing one or more syllables) or complete form. Furthermore, in our study populations, the order in which syllables are presented is not constant; for example, in a two-part FW the order of presentation may be reversed.

Cowbirds use FWs in a variety of contexts. They are given during copulations (Rothstein et al. 1988, Dufty and McChrystal 1992, West et al. 1998) and, as their name implies, they are associated closely with flight. When given by a perched male, FWs are a strong indicator that the male is about to take flight (Friedmann 1929). FWs also are produced during and at the end of flights, suggesting that they function in long distance communication (Rothstein et al. 1988, pers. observ.).

More recently, Dufty and Pugh (1994) reported that male cowbirds in our population respond antiphonally to FWs. When tape-recordings of partial or complete renditions of the local two-part FW were broadcast to solitary male cowbirds, they elicited predictable vocal and behavioral responses. In short, when males heard all or part of a FW, they responded with the next or missing part of the FW. For example, males responded to playback of the first half of the FW (= FW1) by singing the second half (= FW2), and vice versa. Similarly, if complete FWs were broadcast (i.e., FW1 followed by FW2), then the test males again produced the next part (i.e., FW1). These vocal responses were accompanied by rapid approach to the playback speaker. Dufty and Pugh (1994) suggested that such antiphonal responses are used to designate specific recipients of FW vocalizations. This would facilitate additional intrasexual interactions, in a manner similar to that found in other passerine species (Krebs et al. 1981, Capp 1992, McGregor et al. 1992).

In this study we investigated whether the antiphonal response of male cowbirds is dialect specific. That is, we asked whether male cowbirds respond vocally and behaviorally to foreign FWs, which they themselves do not sing, the same way they respond to FWs from their own dialect. In addition, we examined whether the response of male cowbirds to a near-foreign FW is different from the response to a distant-foreign FW. In other species with song dialects, males distinguish among dialects with which they have different degrees of familiarity (McGregor 1983, Kroodsma et al. 1984).

METHODS

TAPE RECORDINGS AND CONSTRUCTION OF PLAYBACK TAPES

Flight whistle playbacks were conducted during spring and summer of 1994. In spring and summer of 1993, tape recordings were made of male cowbirds in and around Boise, Idaho. This population was the subject of the earlier study on antiphonal responses (Dufty and Pugh 1994), and its FW represented the local dialect. Tape recordings made in 1993 from a second cowbird population, located along the Snake River approximately 85 km from Boise, served as the near-foreign dialect.

Males from both populations were recorded using a Marantz PMD 221 tape recorder, a Sennheiser directional ME-80 microphone and windscreen, and a SME-BA microphone preamplifier. Males were induced to approach and produce FWs by broadcast of tape recordings of the female cowbird chatter vocalization.

High-quality tape recordings of the distant-foreign dialect FWs were obtained from a third cowbird population located approximately 460 km from Boise. Male cowbirds from this population were captured between 10 May and 18 June 1990 and given implants of testosterone to induce singing. Birds were recorded while they were in an outdoor cage as they interacted with free-living conspecifics. Recordings were made using a Sony Professional Walkman and a Sennheiser directional ME-80 microphone. See O'Loghlen and Rothstein (1993) for additional recording details, and Rothstein and Fleischer (1987) for additional audiospectrograms of FWs from this dialect (known as the Convict dialect). All three dialects were from the same cowbird subspecies (*M. a. artemisiae*).

Each of the three dialects (Fig. 1) was represented by a set of four dialect-specific playback tapes. Each set consisted of one tape of complete FWs, two tapes of partial FWs (one FW1 and one FW2), and one tape of reverse FWs. Five different exemplars of the appropriate FW or partial FW were recorded on each tape. Each exemplar was repeated on the tape for 3 min, with 10 sec of silence between each repetition. Thus, for each dialect, all FW types (full, FW1, FW2, and reverse) had five possible renditions, each of which constituted a playback test. Playback vocalizations were standardized to 90 db peak amplitude at 0.6 m on axis from the speaker, using a Realistic sound level meter (C-weighting, fast response). Each FW was used on only one tape, with one exception: the second half of a local FW was used on both the FW2 tape and on the full FW tape.

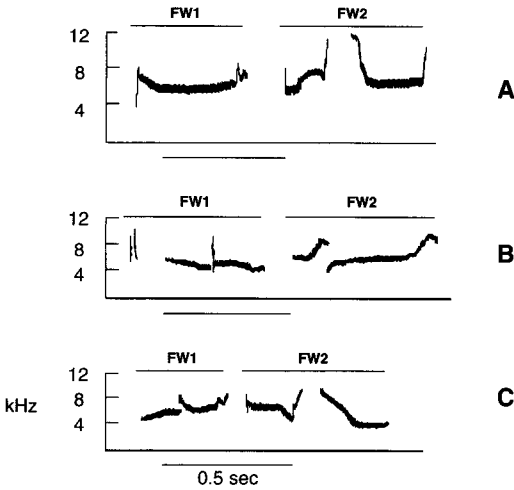A control tape was constructed using heter-

FIGURE 1. Audiospectrograms of full cowbird flight whistles (FW) used in playback experiments. The whistles are from the (A) local, (B) neighboring, and (C) distant dialects. FW1 and FW2 refer to the parts of the flight whistles used in partial flight whistle playbacks. Reverse flight whistles consisted of FW2 followed by FW1.

ospecific avian vocal examples provided by the Cornell Bioacoustics Workstation (version 1.1, Cornell Laboratory of Ornithology, Ithaca, New York). A song from each of five different species was repeated for 3 min with 10 sec between repetitions, as with the FW tapes. The five species included the Common Loon (*Gavia immer*), Western Meadowlark (*Sturnella neglecta*), American Robin (*Turdus migratorius*), Canada Warbler (*Wilsonia canadensis*), and Rufous-sided Towhee (*Pipilo erythrophthalmus*).

PLAYBACK PARADIGM

Playbacks occurred from 9 May through 28 June 1994 at 33 locations in and around Boise. All test sites were within the local FW dialect. Most were approximately 1.61 km apart to reduce the chance of testing the same male at more than one site. Sites that were < 1.61 km apart were known previously to maintain different males (unpubl. data). Playbacks were conducted under the following protocol: at each site up to six FW playbacks were conducted plus one control playback. A maximum of two playbacks from any one dialect were performed at a given site, and playbacks of the same dialect were not of the same general type. For example, two full FWs from the same dialect were not presented at the

same site, but one full and one reverse FW from the same dialect could be presented. Otherwise, the order of dialect presentation and the type of FW to be broadcast were determined randomly for all sites. Similarly, the specific FW to be tested (of the five possible exemplars for each FW type) was assigned randomly.

An average (± SE) of 6.62 ± 0.19 days (range = 3–19 days) intervened between successive FW presentations at a given site to avoid any carryover effects from previous playbacks. Because of logistical considerations, some control playbacks were conducted on the same day as, but prior to, FW playbacks. All tests occurred between 06:20 and 11:35.

Playbacks were presented only to solitary male cowbirds. No vocalizations were used to attract these males. Solitary males were studied because males engaged in intra- or intersexual interactions are unlikely to abandon ongoing exchanges to investigate new acoustic stimuli (Dufty 1982a, Rothstein et al. 1988). Although we attempted to ascertain whether males were accompanied by conspecifics prior to the onset of playbacks, some tests were abandoned because of the detection of additional cowbirds. These tests are not included in the dataset. Replacement tests were conducted at the site after at least three days had passed. Males were unmarked, so we do not know if the same male was tested more than once at a given site.

A record of the test cowbird's vocal responses and a running commentary of its behavioral responses were made on a second tape recorder, which was activated at the onset of each playback. This allowed us to verify vocalizations and to determine accurately the time course of events in the session. We noted whether males responded to playbacks with FWs, the type of the first FW produced in response to a playback (FW1 or FW2), the time from the onset of the playback to the first vocal response, the number of FWs produced, whether the male approached the playback speaker, the closest approach, the time to first flight, the number of flights during the playback, and the amount of time spent in sight (up to 3 min). A Ranging Opti-meter 620 rangefinder was used to estimate distances greater than 15 m. Shorter distances were estimated by eye. Sample sizes vary slightly among variables because occasionally not all measurements were recorded during a playback.

STATISTICAL ANALYSES

General responses to playbacks. Our first objective was to determine the general behavioral and vocal responses of male Brown-headed Cowbirds to broadcast of the three FW dialects and to the control vocalizations. Because more than one playback occurred at each site, site was considered a repeated measure. Moreover, for continuous and discrete variables (latency to approach, closest approach, latency to produce a FW, time in sight, number of FWs, number of flights), when a given dialect was played more than once at a site, responses were averaged for that site. Nominal data (approach, produced FWs) were converted to percentages and then averaged. The results were used in subsequent repeated measures analysis of variance (ANOVA), which examined the effect of the treatments on cowbird behavior. Because eight dependent variables were analyzed from each playback site, Type I error probabilities were adjusted using the Bonferroni approach. Consequently, for these analyses $P < 0.006$ was considered significant. If significant effects were detected, then subsequent pairwise means comparisons were made using Tukey's Studentized Range (HSD) Test which controls experiment-wide error rates at the $P = 0.05$ level.

Antiphonal responses to playbacks. Our second objective was to determine whether male cowbirds made the predicted FW response to playbacks of the three FW dialects. Only the first playback of a FW type (ending in either FW1 or FW2) from a given FW dialect is included at each site. To determine whether males produced the predicted vocal response to FW playbacks, the data were analyzed as a logistic regression using generalized estimating equations (GEE; Liang and Zeger 1986). The outcome was whether the test birds avoided matching the last part of the FWs we broadcast. If we broadcast FW1 (or a reverse FW, which ends in FW1), then the predicted response was FW2. Conversely, if we broadcast FW2 (or a full FW, which ends in FW2), then the predicted response was FW1. Explanatory factors were the dialect of the FW (local, near-foreign, or distant-foreign) and the sequence last heard (FW1 or FW2). The GEE approach allows for incomplete treatment sequences at a site and accommodates repeated playbacks at each site by incorporating the variance structure into the model. This is necessary

because the same male may have been tested more than once at a given site. Data analysis was conducted using SAS 6.12 (SAS Institute 1996).

RESULTS

GENERAL RESPONSES TO PLAYBACKS

There was a significant difference in the percent of male Brown-headed Cowbirds that produced FWs during the different playbacks (Table 1). FWs were produced in almost 90% of the FW playbacks, and there was little difference in the response among the different FW dialects. FWs also were produced in over half (57%) of the control playbacks. For the dependent variable "Gave FWs," all three FW dialects differed from the control playbacks but did not differ from each other.

The mean number of FWs produced (by males that gave at least one FW) was significantly different across vocalizations (Table 1). Pairwise comparisons revealed no difference among the three FW dialects in the mean number of FWs produced. The number of FWs produced in response to near-foreign and distant-foreign FWs also did not differ from the number produced during control playbacks. The only pairwise comparison to reach significance was between the response to the local FW dialect and control playbacks. The mean latency to produce a FW was not significantly different among the playback vocalizations (Table 1).

Males strongly differed in their tendency to approach in response to the different playbacks (Table 1). Twice as many males approached in response to their local FW dialect compared to any other vocalization. Indeed, pairwise comparisons revealed significant differences between the percentage of males that approached local FWs and those that approached during any other playback types. Furthermore, significantly more males also approached in response to the distant-foreign FW dialect than to the controls. However, the difference in approach when near-foreign FWs and control vocalizations were broadcast was marginally nonsignificant. Male cowbirds responded similarly to the two foreign FW dialects. For those males that approached the playbacks, there was no significant relationship between the playback type and the mean latency to approach or in the distance of their closest approach (Table 1).

There was a significant difference in the mean

TABLE 1. Vocal and behavioral responses (means ± SD) of male Brown-headed Cowbirds to playbacks of three FW dialects and heterospecific control vocalizations. Sample sizes are given in parentheses. Statistical results refer to the repeated measures ANOVA performed for each variable. Values with different superscripts differ at $P < 0.05$ (Tukey's Studentized Range Test).

Variable	Vocalization				F	df	P
	Local	Near-foreign	Distant-foreign	Control			
Gave FWs (%)	94 ± 24ᵃ (31)	87 ± 29ᵃ (29)	80 ± 28ᵃ (30)	57 ± 50ᵇ (21)	7.57	3, 75	0.001
Number of FWs	5.9 ± 4.7ᵃ (30)	4.9 ± 2.6ᵃˑᵇ (27)	4.2 ± 2.6ᵃˑᵇ (29)	2.7 ± 1.4ᵇ (13)	5.89	3, 63	0.001
Latency to 1st FW (sec)	18 ± 27 (30)	18 ± 25 (27)	22 ± 27 (29)	27 ± 43 (13)	0.64	3, 63	0.59
Approach (%)	68 ± 38ᵃ (31)	23 ± 29ᵇˑᶜ (29)	33 ± 36ᵇ (30)	5 ± 23ᶜ (19)	23.18	3, 73	0.001
Latency to approach (sec)	59.4 ± 53.0 (26)	43.9 ± 35.5 (12)	45.7 ± 30.4 (16)	32.0 (1)	0.22	3, 23	0.88
Closest approach (m)	14.5 ± 8.9 (26)	12.9 ± 10.2 (12)	14.9 ± 7.8 (16)	10.0 (1)	0.90	3, 23	0.45
Number of flights	2.4 ± 1.4ᵃ (31)	1.4 ± 1.0ᵇ (29)	1.5 ± 0.7ᵇ (30)	1.0 ± 0.6ᵇ (21)	14.01	3, 75	0.001
Time in sight (sec)	136 ± 48.7ᵃ (31)	118 ± 54ᵃ (29)	127 ± 48ᵃ (30)	76 ± 13ᵇ (21)	5.40	3, 75	0.002

number of flights made by male cowbirds in response to the playbacks (Table 1). Pairwise comparisons showed that the mean number of flights in response to the local FW dialect was significantly greater than to the controls or to either of the other two FW dialects. No other pairwise comparisons differed significantly. Finally, males remained in sight significantly longer when FWs were broadcast than when control vocalizations were broadcast (Table 1). There were no differences among the three dialects in the amount of time males remained in sight.

ANTIPHONAL RESPONSES

An initial logistic regression model, with an interaction between dialect and sequence (whether the birds heard FW1 or FW2), was fit to determine whether order differed within a dialect. This interaction was nonsignificant, so a final model was fit without this interaction term. The adequacy of the model fitting procedure was assessed by calculating Pearson Chi-square ($\chi^2_{143} = 118.49$, $P > 0.35$). This nonsignificant probability value indicates that the model fit is adequate, relative to the saturated model. Dialect was a significant variable in this model for predicting outcomes (Wald $\chi^2_2 = 12.62$, $P < 0.002$), while sequence was not (Wald $\chi^2_1 = 0.80$, $P = 0.37$).

The initial FW responses of male cowbirds to playbacks of FWs from the three dialects are shown in Table 2. Male cowbirds were over five times more likely to respond with the predicted FW to FWs from their local dialect than to FWs from the near-foreign dialect (Table 3). Similarly, males were approximately three times more likely to respond with the predicted FW to FWs from the local dialect than to FWs from the distant-foreign dialect (Table 3). Both differences are significant and indicate that male cowbirds tend to respond to the first part (FW1) of the local dialect (either alone or as the last section of a reverse FW) with FW2, and to the second part (FW2) of the local dialect (either alone or as the last section of a full FW) with FW1. In contrast, upon hearing FW1 or FW2 of the near-foreign or distant-foreign dialect, local male cowbirds were as likely to respond with the first half of their own FW as with the second half. Finally, the near-foreign and distant-foreign FW dialects were equally likely to elicit the predicted FW responses (Table 3).

TABLE 2. First FW response of male Brown-headed Cowbirds to playbacks of three FW dialects and hetero-specific control vocalizations.

1st response	Local		Near-foreign		Distant-foreign		Control
	FW1	FW2	FW1	FW2	FW1	FW2	
FW1	6	17	9	4	8	10	7
FW2	16	5	11	15	8	9	5

DISCUSSION

GENERAL RESPONSES TO PLAYBACKS

The results suggest that our local male cowbirds recognize FWs from other dialects, even those they are unlikely to have encountered previously. Males responded similarly to FWs from all three dialects for several of the responses we measured. This suggests that there are acoustic parameters common to FWs from a wide geographic range that render them recognizable as such to male cowbirds.

Male cowbirds responded to most FW playbacks with their own FWs, regardless of the FW dialect presented. The distant-foreign dialect, to which local males responded least, nonetheless evoked FW responses in 80% of playbacks. Solitary control males also produced FW vocalizations in over half of the control playbacks. However, these males appeared to be scanning the area, usually from a high, exposed perch. FWs given in this context probably represent attempts at long-range communication with other, unseen male cowbirds (Rothstein et al. 1988, Dufty and Pugh 1994). The frequent use of such a signal is not surprising, given the lack of territorial behavior by male cowbirds (Dufty 1982a, Yokel 1989), their large home ranges (Darley 1982, Dufty 1982b, Rothstein et al. 1984), and their highly social intrasexual interactions (Friedmann 1929, Darley 1982, Dufty 1982a).

Despite the high level of responsiveness to all FWs, there also was a clear difference in the response of male cowbirds to local and foreign FWs. However, there was little indication that males differentiated between the near-foreign and the distant-foreign dialects. In measures such as approach and number of flights, the response to local FWs was significantly stronger than to either the near-foreign or distant-foreign FW dialects, and the responses to the latter two dialects were indistinguishable from each other. Taken together, these data suggest that local males respond most strongly to FW dialects with which they are most familiar. Similar results have been found in other species, where males respond to local conspecific songs more than to songs recorded from distant populations (McGregor 1983, Tomback et al. 1983), although the opposite result (i.e., stronger response to distant vocalizations) also has been found (Hansen 1984).

The general failure of local males to make fine grain distinctions between the two foreign dialects may stem from the fact that the near-foreign cowbird population was 85 km from the local population and separated from the latter by

TABLE 3. GEE parameter estimates and probability values with the near-foreign FW and the distant-foreign dialect as the referent. Odds ratios represent chances of obtaining the predicted FW response with a given dialect relative to the referent dialect.

Referent dialect	Estimate	Empirical SE	Z	P	Odds Ratio[a]
Near-foreign					
Intercept	−0.68	0.38	−1.79	0.07	
Local FW	1.62	0.46	2.51	0.001	5.05 (Local vs. Near-foreign)
Distant-foreign FW	0.55	0.39	1.31	0.16	1.73 (Distant- vs. Near-foreign)
Distant-foreign					
Intercept	−0.13	0.34	−0.38	0.70	
Local FW	1.07	0.44	2.44	0.02	2.92 (Local vs. Distant-foreign)

[a] Odds ratios are calculated by exponentiating the parameter estimates.

desert-scrub habitat that is unsuitable for cow-
birds. Thus, both foreign dialects may have been
largely unfamiliar to test male cowbirds, despite
their differences in absolute distance from the
local birds.

The reason for the variation in cowbird re-
sponses to FWs from different dialects is un-
clear, given that foreign FWs apparently are rec-
ognized as conspecific vocalizations. One expla-
nation is that the signal value of foreign FWs
may be less effective in eliciting a vocal or be-
havioral response than that of local FWs. That
is, male cowbirds that give foreign FWs may
represent less of a threat to local adult males
than males that produce the local dialect, and the
response to the former may be dampened.

Rothstein and Fleischer (1987) showed that
many males within a FW dialect exhibit differ-
ences in their FWs that could be used for indi-
vidual recognition. Overlap of male home rang-
es (Darley 1982) results in many opportunities
for males to engage in agonistic social encoun-
ters, and recognition of individuals or their dom-
inance rank from afar through their FWs could
help to stabilize the local dominance hierarchy.
However, to our knowledge, no one has yet ex-
amined whether male cowbirds recognize each
other using FWs.

Many yearling male cowbirds produce foreign
FWs (O'Loghlen 1995), having apparently dis-
persed from other areas. Furthermore, in some
populations yearling cowbirds obtain few copu-
lations (Yokel 1986). Whereas the FW charac-
teristics of successful and unsuccessful yearlings
are unknown, female cowbirds prefer FWs from
their own dialect in some populations
(O'Loghlen and Rothstein 1995), although not
in others (West et al. 1998). This suggests that,
in some populations, males that produce foreign
FWs may have reduced breeding success com-
pared to males possessing the local FW. A sim-
ilar phenomenon occurs in Indigo Buntings
(*Passerina cyanea*) where matching the song of
older, local males enhances the breeding success
of yearlings (Payne 1982). Young cowbirds that
produce foreign FWs during their first breeding
season can learn the local FW and produce it the
subsequent year (O'Loghlen 1995) which pre-
sumably would enhance their potential repro-
ductive success and the signal value of their
FWs.

ANTIPHONAL RESPONSES

These results confirm and extend the earlier ob-
servation (Dufty and Pugh 1994) that male
Brown-headed Cowbirds respond antiphonally
to flight whistles, and that responding males usu-
ally avoid matching the last part of the FW they
heard. As in that earlier study, FW2 and full
FWs (which end in FW2) from the local dialect
elicited FW1 in response. We presented reverse
FWs (which end in FW1) along with playbacks
of FW1 in the current study, and these evoked
the predicted FW2 in response.

The present results demonstrate that this an-
tiphonal response is dialect-specific. Although
local males produced FWs in response to play-
backs of the near-foreign and distant-foreign di-
alects, the precise nature of the vocal response
was not consistent. That is, local males were just
as likely to produce FW1 as FW2, regardless of
which part of the FW ended the playback of a
foreign FW.

These differences in the precise FW responses
to local and foreign dialects do not appear to be
due to a failure of the males to recognize the
near-foreign and distant-foreign FWs as conspe-
cific vocalizations (see above). One possible ex-
planation is that males recognize foreign dialects
as conspecific vocalizations, but they cannot de-
termine the first and second parts of foreign FWs
with which they have limited or no prior expe-
rience. We do not know what percentage of local
male cowbirds produce foreign FWs, but such
FWs are heard rarely (A. M. Dufty, pers. ob-
serv.), and none of our test males produced for-
eign FWs. Yearling males in other cowbird pop-
ulations are more likely than adults to produce
foreign FWs (O'Loghlen and Rothstein 1995),
presumably because they learn the FW from
their natal area prior to dispersing to a breeding
area with a different FW. However, banding data
indicate that over 70% of cowbirds banded in
their hatching year are recovered in subsequent
years within 36 km of their site of banding (Duf-
ty 1985). For cowbird populations such as ours,
which are somewhat isolated from nearby pop-
ulations by unsuitable habitat, this could result
in limited experience with foreign FWs and
would make it difficult for local males to pro-
duce an appropriate antiphonal response, even to
near-foreign FWs.

If, as we suggest, producing the next or miss-
ing part of a FW during antiphonal interactions

facilitates the establishment and maintenance of social interactions, then the inability to do so should hinder this process. The diminished approach response and the reduced number of flights in response to the two foreign FW are consistent with this idea.

It would be interesting to repeat this experiment in an area where cowbird FW dialects abut, to determine whether males that do have experience with nearby dialects respond to those dialects in the same way as they respond to their own. Beecher et al. (1996) noted that Song Sparrows (*Melospiza melodia*) avoid matching a neighbor with the same song type sung by the neighbor, although they will match song types with a stranger.

Although we have not quantified the occurrence of natural antiphonal responses in our population, we have observed such antiphonal responses to both partial and complete FWs. Indeed, these observations were the impetus for the present investigation. Also, cowbirds exhibit geographic variation in their vocal behavior (King and West 1983), and we do not know the extent to which cowbirds in other populations respond antiphonally to FWs. However, one of us (A. M. Dufty) has observed such responses in a cowbird population of a different subspecies in upstate New York. Clearly, more work on the use of FWs in intrasexual and intersexual interactions is warranted.

ACKNOWLEDGMENTS

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