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CONTEXT-SPECIFIC RESPONSE OF FLORIDA SCRUB-JAY PAIRS TO NORTHERN MOCKINGBIRD VOCAL MIMICRY

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Abstract. It is well established that vocal mimicry serves an intraspecific function in birds by increasing repertoire size. On an interspecific level, territorial exclusion of other species by deceptive mimicry may occur if the model (i.e., mimicked) species song is effectively reproduced by the mimicking species. Few studies have effectively demonstrated deceptive mimicry because they did not use the context of the mimic's song as a control stimulus. We addressed this shortcoming by using isolated and context-dependent playback stimuli to assess the response of Florida Scrub-Jay (*Aphelocoma coerulescens*) pairs to Northern Mockingbird (*Mimus polyglottos*) imitation. Scrub-jay pairs responded more aggressively to isolated scrub-jay *weep* calls than to playbacks consisting of either isolated imitation calls, imitated calls embedded in mockingbird song, or control mockingbird song.

These results fail to support the hypothesis that mimicry deceives the model species. Whether mockingbird imitation of scrub-jays deceives other species requires further investigation.

Key words: *Florida Scrub-Jay, mimicry, Northern Mockingbird, playbacks, territoriality, vocalizations.*

Respuesta Contexto-Específica de *Aphelocoma coerulescens* a las Vocalizaciones Miméticas de *Mimus polyglottos*

Resumen. Se conoce que el mimetismo vocal en las aves tiene la función de incrementar el repertorio de vocalización a nivel intraespecífico. A nivel interespecífico, la exclusión territorial de una especie por parte de otra por medio del "mimetismo de engaño" puede suceder si el canto de la especie modelo (i.e., aquella que es imitada) es emulado con precisión. Pocos estudios han demostrado el uso de "mimetismo de engaño" debido a que no han analizado el contexto en el que ocurre la vocalización mimética. En este estudio utilizamos grabaciones de cantos, tanto aislados como dependientes del contexto de la vocalización, para investigar cómo las parejas de *Aphelocoma coerulescens* responden a las emulaciones de *Mimus polyglottos*. Las parejas de *A. coerulescens* respondieron

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de manera más agresiva al escuchar grabaciones de sus propios gemidos que al escuchar imitaciones a sus llamadas, imitaciones mezcladas con vocalizaciones propias de *M. polyglottos*, o vocalizaciones exclusivas de *M. polyglottos* (control). Estos resultados no apoyan la hipótesis del "mimetismo de engaño." Sin embargo, se desconoce si *M. polyglottos* engaña a otras especies cuando imita a *A. coerulescens*.

Many songbirds mimic the vocalizations of other species. The functional significance of vocal mimicry in birds has been reviewed extensively (e.g., Dobkin 1979, Baylis 1982), but few experimental studies have tested the multiple hypotheses. Vocal mimicry has been postulated to serve both intra- and interspecific functions (Harcus 1977, Dobkin 1979, Hindmarsh 1986). It is widely accepted that mimicry functions intraspecifically by enhancing repertoire size, which is important for mate attraction (Yasukawa 1981, Catchpole et al. 1984, Hasselquist et al. 1996). For example, male Northern Mockingbirds (*Mimus polyglottos*) with larger repertoires than other males (1) acquire larger territories and (2) attract females that are prepared to breed earlier than other females in the population (Howard 1974). This form of mimicry, termed vocal appropriation, does not require perfect imitations of the model (mimicked) species, and the appropriator does not gain a selective advantage from sounding like the model (Dobkin 1979).

Deceptive, or "true" mimicry occurs when the mimic song is of sufficient quality to deceive (1) the model species or (2) species other than the model that are potential competitors of the mimic (competitive acoustic mimicry; Dobkin 1979). The importance of birdsong for intraspecific territoriality suggests that mimicry may also exclude individuals of competing species that are fooled by the songs of the mimicking species. Lemaire (1975) found that Willow Warblers (*Phylloscopus trochilus*) and Chaffinches (*Fringilla coelebs*) were unable to distinguish between conspecific vocalizations and calls mimicked by Marsh Warblers (*Acrocephalus palustris*). In addition, Brenowitz (1982) documented that male Red-winged Blackbirds (*Agelaius phoeniceus*) did not discriminate between conspecific song and isolated Northern Mockingbird imitation. Hindmarsh (1986) noted, however, that even though these studies suggest that imitation is of high quality, playback stimuli were not presented in the context of the rest of the mimic species song, and therefore reveal little about responses to imitation in the wild. Typically, neither of the above mimic species mimics a particular vocalization at length, but rather cycles rapidly through numerous phrases that form the repertoire.

Catchpole and Baptista (1988) addressed this issue by testing whether territorial male White-crowned Sparrows (*Zonotrichia leucophrys*) could discriminate between conspecific playback and the same song produced by a Song Sparrow (*Melospiza melodia*; the mimic), a species that repeats one song type before switching to another. Even though White-crowned Sparrows can discriminate between different conspecific song types, as well as the same song type sung by different individuals (Baker et al. 1981, Petrinovich

and Patterson 1981, Tomback et al. 1983), males responded equally strongly to playbacks of model and mimic song.

We tested the deceptive mimicry hypothesis (aimed at the model species) by measuring the response of Florida Scrub-Jay (*Aphelocoma coerulescens*) pairs to Northern Mockingbird song imitation using isolated and context-dependent playback stimuli. Northern Mockingbirds are common throughout the oak scrub that defines the limited distribution of Florida Scrub-Jays, and territories of the two species often overlap (Woolfenden and Fitzpatrick 1996). Interspecific interactions between the two species occur (Curry 1990, Woolfenden and Fitzpatrick 1996), but it is not known if they compete for resources. The context in which the imitated call is presented, either alone or with normal mockingbird song, may influence how scrub-jays perceive and respond to the mimic, so we manipulated the context and the frequency at which the imitated call was played. If scrub-jays act aggressively toward the isolated call and the call inserted into a normal mockingbird song as compared to control song (mockingbird song without imitated elements), then the imitation is of good quality and has effectively duped the model species. This finding would clearly support the deceptive mimicry hypothesis. Two other possible outcomes would fail to support this hypothesis: (1) a response to the isolated call but not to the context-dependent call would suggest that scrub-jays use context to distinguish between mimics and conspecifics. This prediction assumes that mockingbirds only sing the imitated call within the context of the rest of their song. (2) Lack of response by scrub-jays to both the isolated call and the context-dependent call would imply that the quality of the imitation is not sufficient to deceive scrub-jays.

METHODS

STUDY SITE

This study was conducted at Archbold Biological Station in south-central Florida (27°10'N, 81°21'W, elevation 38–68 m). The study population occupies the southern half of the station and has been monitored since 1986 (Schoech et al. 1991, 1996, Mumme 1992) and is adjacent to the population that has been studied for over 30 years by Woolfenden and Fitzpatrick (1977, 1984, 1990). Florida Scrub-Jays are cooperative breeders and defend all-purpose territories year round (Woolfenden and Fitzpatrick 1984). Scrub-jay families consist of a monogamous breeding pair and surviving offspring that typically remain at home and help the breeding pair defend the territory and feed young. Scrub-jay territories in our study tract are monitored from February to July every year, and virtually all birds are banded with a unique combination of colored plastic and aluminum (U.S. Fish and Wildlife Service) bands. Sex, reproductive status (breeder vs. nonbreeder), and social affiliation are known using records from previous years or field observations. Age is known for most individuals because they were color banded as 11-day-old nestlings. Northern Mockingbird pairs occur throughout the same tract and often reside in the same territories as scrub-jay families. However, the

TABLE 1. Experimental design of five playback treatments using isolated and context-dependent stimuli from recordings of Florida Scrub-Jays and Northern Mockingbirds at Archbold Biological Station, Florida. Multiple replicates of each playback sample (MB, MBW, or SJW) were recorded from several individuals to prevent pseudoreplication of playback stimuli. Replicates were then assigned randomly to 10-sec blocks for each 1-min playback sample.

Playback stimuli	Sequence of 10-sec blocks in playback sample					
	1	2	3	4	5	6
Mockingbird bout, lacking mimicked elements (MB)	MB	MB	MB	MB	MB	MB
Imitated <i>weep</i> inserted into a mockingbird bout (MB + MBW)	MBW	MB	MBW	MB	MBW	MB
Scrub-jay <i>weep</i> call inserted into a mockingbird bout (MB + SJW)	SJW	MB	SJW	MB	SJW	MB
Isolated imitated <i>weep</i> call (MBW)	MBW	silence	MBW	silence	MBW	silence
Isolated scrub-jay <i>weep</i> call (SJW)	SJW	silence	SJW	silence	SJW	silence

density and distribution of mockingbirds at Archbold Biological Station has not been determined.

SONG STIMULI

We recorded both mockingbird and scrub-jay vocalizations between 06:00 and 12:00 EDT from 6–10 June 1998 using a Marantz (Itasca, Illinois) PMD-221 cassette tape recorder, TDK high bias audio tapes, and a Sennheiser (Old Lyme, Connecticut) ME88 shotgun microphone. Mockingbirds in the study tract imitate at least three stereotypic scrub-jay vocalizations: the *weep* call, the screech scold, and the female-specific hiccup call (NTO, pers. obs.). All three vocalizations are used by jays primarily in intraspecific agonistic encounters, and playback experiments using these calls are very effective in eliciting an aggressive response (Barbour 1977). We observed Northern Mockingbirds producing only one jay call type for a given song bout; there were no cases of mockingbirds incorporating different scrub-jay imitations into a single song bout. Because the *weep* vocalization was the most frequently imitated call by mockingbirds in the study tract (Owen-Ashley, unpubl. data), only the imitated *weep* vocalization was used in playbacks in this study.

To create standardized playback stimuli and to minimize the likelihood of pseudoreplication of playback trials, two different *weep* vocalizations from three different individuals of the mimic and model species were used (Kroodsma 1989). Additionally, complete song bouts from three different mockingbirds were recorded as a contextual stimulus. All replicates were digitized at 44 000 Hz with 16-bit accuracy. The samples were then filtered, amplified to similar levels, and cropped or expanded into 10-sec blocks using SoundEdit 16 V. 2.0 (Macromedia, Inc. 1996), a sound analysis program. Using these replicates, five different 1-min playback stimuli were synthesized (Table 1): isolated *weep* calls of mockingbirds (MBW) and scrub-jays (SJW; the positive control), isolated calls of mockingbirds or scrub-jays inserted into a mockingbird song (MB + MBW, MB + SJW, respectively), and mockingbird song without *weep* calls (MB; the negative control). For each recording, replicates for each sample type were chosen randomly, and used only once. Instead of using playback tapes, each finalized playback was re-

corded onto a compact disc as a song track, thus allowing for near-immediate access to playback stimuli.

PLAYBACK TRIALS

Song playback experiments were performed on 25 scrub-jay territories from 13–23 June 1998. Playback experiments were performed either in the morning (07:00–12:00 EDT) or occasionally in the late afternoon to early evening (15:00–19:00 EDT). A random-block design was used where scrub-jay pairs were played one song stimulus per day for five days. Song stimulus order for the five-day period was determined by random number generation for each scrub-jay pair being tested. This method ensured that responses to playback would not be influenced by the carryover effect introduced by two or more sequential playback trials. To assure that scrub-jays being tested were not familiar with the calls of either the conspecific or mimic, vocalizations recorded from adjacent territories were not used. Occasionally, song stimuli attracted other individuals from neighboring territories during the playback trials. In these cases, it was impossible to distinguish whether the focal birds were responding to concurrent playback stimuli or to the presence of another bird on their territory. As a result, these playback trials were stopped and not incorporated into the analysis. Scrub-jay pairs that were interrupted by intruding birds were retested another day.

Since Florida Scrub-Jays often become extremely tame and can be trained to come to food (Woolfenden and Fitzpatrick 1984, Fitzpatrick and Woolfenden 1996), location of pairs for playback trials was not difficult. Typically, when we arrived at a specific territory, resident scrub-jays were quickly attracted to our presence, perching within 15 m. Less frequently, we called or whistled for jays. If birds were not present, we threw peanuts on the ground to attract them to the playback area. Because we were measuring the response of both individuals within a breeding pair, if either the breeding male or female were absent, we suspended the playback trial until the following day. Of the 25 scrub-jay pairs analyzed, 10 pairs had additional family members (nonbreeders). We did not measure the responses of nonbreeders.

After setting up the sound equipment, we initiated playback trials when scrub-jay pairs were within 20 m of the speaker. The song stimuli were broadcast through a microphone speaker mounted on a 1.5-m metal pole using a compact disc player linked to a mini-amplifier. All stimuli were standardized at a peak amplitude of 88 dB 20 μ Pa at 1 m. The cable between the speaker and the disc player was sufficiently long to allow concurrent operation of the compact disc player and observation of the behavior of the test subjects. Each playback trial consisted of a 2-min prestimulus period where scrub-jays were allowed to acclimate to human presence and sound equipment, a 1-min stimulus period using one of the five synthesized sound samples, and a 2-min poststimulus period. Responses of both resident male and female scrub-jays were measured during the 1-min stimulus period and the 2-min period after playback. Behavioral observations for each member of a pair were recorded with a handheld tape recorder. All trials were conducted by NTO.

We assessed the response of scrub-jay pairs to playback trials by recording a series of stereotypic behaviors commonly expressed during territorial intrusion by conspecifics. Both sexes perform bobbing motions ("flight-intent bobs") when they detect a conspecific intruder (Woolfenden and Fitzpatrick 1996). Florida Scrub-Jays also give a variety of vocalizations during agonistic interactions. Both males and females deliver rapid, multiple *weep* calls (Woolfenden and Fitzpatrick 1996), while performing stereotypic undulating flight displays or bobbing on a perch. Aggressive jays use screech scolds during intense territorial disputes (Woolfenden and Fitzpatrick 1996). An additional vocalization, the "hiccup" call, is given only by females and is generally delivered from the perch or ground, in conjunction with flight-intent bobs (Woolfenden and Fitzpatrick 1996). We used four behavior patterns to measure the response of both members of a pair to recorded stimuli: (1) number of flight-intent bobs, (2) number of *weep* calls, (3) number of screech scolds, and (4) number of female hiccup calls.

VOCAL AND STATISTICAL ANALYSES

To assess the quality of the imitated *weep* call to that of the real *weep* call, we made sound spectrograms of each scrub-jay and mockingbird *weep* vocalization from the above recordings using Canary 1.2 (Charif et al. 1995). From the spectrograms, we measured the number of *weeps* per bout, maximum and minimum frequencies, frequency at maximum amplitude (FMA), and duration (msec) of individual *weep* calls. For each recording, three *weep* calls were selected randomly for spectrographic analysis, and the temporal and frequency characteristics of each call were averaged to produce a single value per recording. Unpaired *t*-tests (two-tailed) were used to compare differences in spectrogram characteristics between the scrub-jay and imitated *weep* recordings. Mann-Whitney *U*-tests were conducted when spectrogram characteristics did not conform to normality.

Behavioral data were highly skewed toward zero. To assess territorial responses to playback, we log-transformed the behavioral variables and then combined them into a single response index using a principal components analysis (PCA) extracted from a Pearson

TABLE 2. Factor loadings, eigenvalues, and percentage of variance explained for principal components analysis (PCA) of the responses of male and female Florida Scrub-Jays to playback stimuli. Factor loadings >0.70 are shown in bold.

Variable	PC1		PC2 ^a
	Males	Females	Females
Flight-intent bobs	0.88	0.79	-0.21
<i>Weeps</i>	0.58	0.74	0.44
Screech scolds	0.75	0.49	0.83
Hiccup calls	—	0.80	0.11
Eigenvalue	1.7	2.0	0.9
% variance explained	56	51	23

^a Male response was explained only by the first component of the PCA analysis.

correlation matrix (Martin et al. 1996, SAS Institute, Inc. 1998). The character loadings from the analyses were used to compute the response scores for each individual (Table 2). We conducted separate PCAs for male and female jays because females produced an additional vocalization, the hiccup call, which could not be compared with males, and it is possible that the variables conveyed different behavioral information for each sex when combined into a single index.

Friedman's test, a nonparametric version of a repeated-measures ANOVA, was used to assess the effect of treatment upon scrub-jay territorial responses (PC1 for males and PC1 and PC2 for females, Zar 1999). When significant differences were detected, Wilcoxon signed-rank tests were used to compare groups with both positive (SJW) and negative (MB) controls. Sequential Bonferroni tests were then conducted to adjust Type I error probabilities for multiple comparisons (Sokal and Rohlf 1995). Values reported are means \pm SE. Unless indicated otherwise, significance was designated at the $P < 0.05$ level.

RESULTS

QUALITY OF MOCKINGBIRD IMITATION

Florida Scrub-Jay *weep* vocalizations recorded at Archbold Biological Station (Fig. 1a–d) were similar to calls recorded previously at the station (see spectrograms in Barbour 1977, Woolfenden and Fitzpatrick 1996): the base frequency was 1.75 kHz with the dominant frequency between 1.75 and 3.75 kHz; single notes within each series measured 0.185–0.211 sec (Table 3). The notes were delivered at a rate of 4 sec⁻¹, with harmonic overtones apparent (Fig. 1a–d). Fundamental frequencies of imitated *weep* calls by mockingbirds (Fig. 1e–h) were similar in range and distribution to the scrub-jay *weep* call (1.75–4 kHz), although there was some variation in cadence and overall structure between the imitation calls (Fig. 1e, f). Imitated calls did not differ significantly from scrub-jay *weep* calls in maximum or minimum frequency, frequency at maximum amplitude (FMA), or the number of calls per bout (Table 3). However, imitated calls were shorter than scrub-jay calls (Table 3). In most cases, mockingbirds imitated the *weep* call at rates that

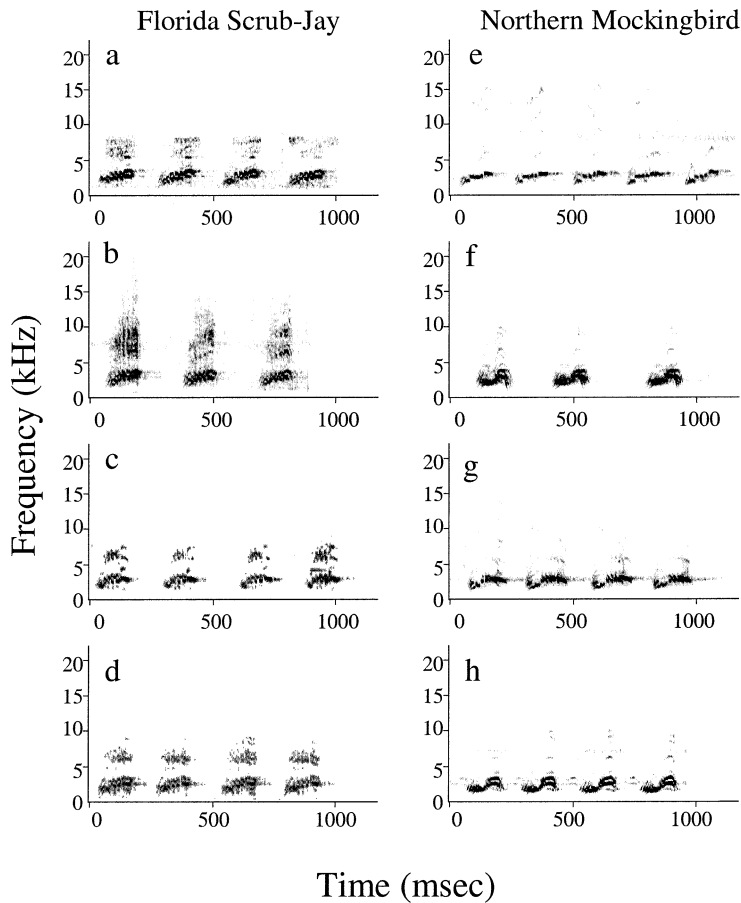


FIGURE 1. Sound spectrograms comparing Florida Scrub-Jay *weep* vocalizations (a–d) and Northern Mockingbird imitations (e–h) from four individuals of each species. Spectrograms were made from calls recorded at Archbold Biological Station.

were similar to scrub-jay rapid *weep* calls (Fig. 1). Overtones were noticeably diminished or absent in mockingbird imitation calls compared to scrub-jay *weep* calls.

RESPONSE TO PLAYBACK

PCA analyses. The first principal component (PC1) explained the majority of the variance in response to playback for both males (56%) and females (51%). All

TABLE 3. Mean \pm SE temporal and frequency characteristics of Florida Scrub-Jay *weep* calls (SJW) and imitated *weep* calls recorded from Northern Mockingbirds (MBW). Six individuals of each species were recorded; three calls per recording were analyzed and then averaged into one value. The two call types were compared using *t*-tests, or Mann-Whitney *U*-tests where indicated.

	SJW	MBW	t_{10} (<i>U</i>)	<i>P</i>
Calls in a bout	6.2 \pm 1.3	8.5 \pm 1.2	1.3	0.22
Min. frequency	1.2 \pm 0.15	1.3 \pm 0.03	0.7	0.53
Max. frequency	14.3 \pm 1.57	14.7 \pm 1.65	16 ^a	0.75
Frequency at maximum amplitude	2.8 \pm 0.06	2.5 \pm 0.16	11 ^a	0.26
Duration (msec)	203.7 \pm 10.4	174.7 \pm 7.6	–2.3	0.05

^a Mann-Whitney *U*-tests.

behavioral variables loaded positively onto this component, suggesting that PC1 describes aggressive or territorial behavior (Table 2). A second principal component (PC2) explained 23% of the variance in female behavioral response to playback. Since several PC2 loadings were inversely correlated, and since these loadings explained less than a quarter of the variance in total response, we do not know what behavior this particular component represents. PC2 loadings did not differ significantly among the different playback stimuli (Friedman's test: $\chi^2_4 = 2.4$, $P > 0.6$). Therefore, only PC1 loadings (hereafter "response index") were considered appropriate indicators of response to playback.

Response index. Male and female jays responded differently to the five playback stimuli (Friedman's test: males, $\chi^2_4 = 66.4$, $P < 0.001$; females, $\chi^2_4 = 41.0$, $P < 0.001$; Fig. 2a, b). Both male and female jays responded more aggressively to the isolated scrub-jay *weep* playback (SJW, positive control) than all other playbacks (Wilcoxon signed-ranks tests: males, all comparisons, $Z < -2.6$, $P < 0.01$; females, all comparisons, $Z < -2.7$, $P < 0.001$). Responses directed toward the mimicked *weep* call embedded in a mockingbird song (MB + MBW) were not significantly different from responses directed toward the negative control mockingbird song (MB) for both males (Wilcoxon signed-ranks test, $Z = -1.5$, $P > 0.1$) and females ($Z = -0.4$; $P > 0.6$). Male and female jays did not respond differently to the isolated mimicked *weep* playback (MBW) compared to the mockingbird (MB) control song (Wilcoxon signed-ranks test: males, $Z = -2.0$, $P = 0.06$, corrected $\alpha = 0.025$; females, $Z = -1.7$, $P = 0.11$). Both male and female scrub-jays responded less to the scrub-jay *weep* vocalizations embedded in a mockingbird song (MB + SJW) than to isolated scrub-jay *weep* playback (Wilcoxon signed-ranks test: males, $Z = -2.7$, $P < 0.01$, corrected $\alpha = 0.02$; females, $Z = -2.8$, $P < 0.01$, corrected $\alpha = 0.02$).

DISCUSSION

The finding that Florida Scrub-Jays respond differently to conspecific and imitated vocalizations, regardless of context, does not support the deceptive mimicry hypothesis. Seemingly, the imitation call was not of sufficient quality to deceive scrub-jays. Both male and female scrub-jays of a pair showed little or no response to playbacks incorporating mimicked *weep* calls compared to isolated conspecific playback. This is perhaps due to the lack of harmonic structure in the mockingbirds' version of the *weep* call. An interesting contrast was noted by Brenowitz (1982), who found that Red-winged Blackbirds responded aggressively to a Northern Mockingbird's rendition of Red-winged Blackbird song despite the imitation lacking high-frequency components of the true song. This implies that vocal deception by mockingbirds, or the importance of mimicked song having full harmonic structure, can vary depending upon the particular model species.

There was also individual variation in song structure of the imitated call by mockingbirds, suggesting that each mimic imparted its own unique signature to the imitation. Several authors have noted that mimics tend

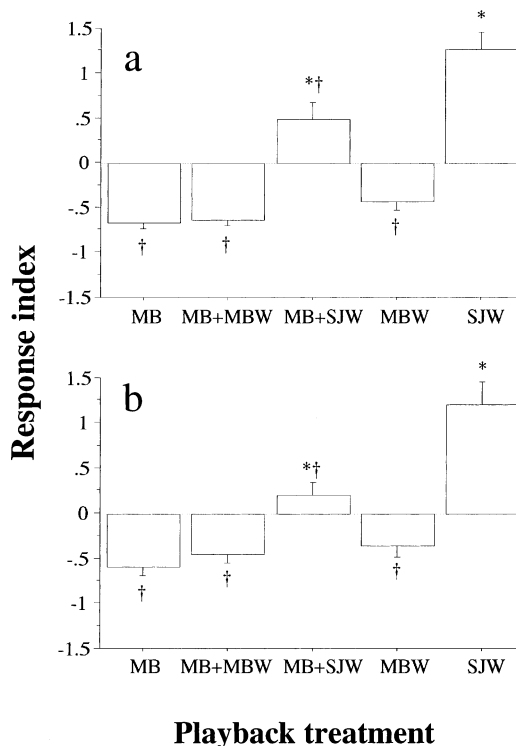


FIGURE 2. Florida Scrub-Jay response (mean \pm SE, $n = 25$) to five different 1-min playback treatments incorporating (1) Northern Mockingbird song without mimicked elements (MB), (2) imitated *weep* calls inserted into Northern Mockingbird song (MB + MBW), (3) scrub-jay *weep* calls inserted into normal mockingbird song (MB + SJW), (4) imitated *weep* calls alone (MBW), and (5) isolated scrub-jay *weep* vocalizations (SJW; see Table 1). Responses to playback were measured for both males (A) and females (B) of a pair during and 2 min after playback. Response index is a cumulative score extracted from a principal components analysis of several behavioral variables (Table 2). Positive scores indicate more aggressive responses; negative scores indicate less aggressive or no responses. Asterisks indicate significant differences between the specified group and the MB negative control; daggers indicate significant differences between the specified group and the SJW positive control.

to alter some component of the song, either the context, tonal quality, or temporal pattern, and this allows for models and mimics alike to distinguish individual singers (Dobkin 1979, Hindmarsh 1986). The alteration of components of song is commonly seen between neighbors of the same species and allows ready identification of neighbors, as compared with an unknown intruder (Baker et al. 1981, Stoddard et al. 1990). As cooperative breeders that live in family groups, Florida Scrub-Jays have been observed to differentiate between familial and nonfamilial jays using vocal recognition, especially during territorial disputes

(Barbour 1977). Further evidence of the ability of Florida Scrub-Jays to discriminate between aural cues was found by Barg and Mumme (1994) who noted that scrub-jays discriminate between the begging vocalizations of their own young and those of unrelated young. Given that the mockingbird *weep* call is of relatively low quality and that scrub-jays can discriminate between conspecific vocalizations, it is not surprising that Florida Scrub-Jays are not deceived by the mimicked calls of mockingbirds.

Scrub-jays responded less aggressively to a conspecific *weep* call inserted into a mockingbird song than to playback consisting of isolated scrub-jay *weep* calls. One possible explanation for this context-specific response is that scrub-jay pairs were confused by playback of conspecific calls inserted into a mockingbird song. Scrub-jays may have "tuned-out" the composite playback if they perceived the stimulus as originating from a mockingbird rather than a scrub-jay. The effect of context on vocal recognition has been documented in other species as well. Lemaire (1975) found that playback of imitated Marsh Warbler calls deceived several model species when presented in the absence of the complete song. However, when the same model species were tested with the mimicked song in context (i.e., when the complete Marsh Warbler song was presented), the playbacks were ignored. In our study, scrub-jays showed little or no response to mimicked *weep* calls that were either isolated or embedded within a mockingbird song, indicating that context was unimportant. However, scrub-jays responded less aggressively to playback consisting of conspecific *weep* calls embedded into mockingbird song compared to isolated conspecific calls. This suggests that contextual information can improve or obfuscate vocal recognition in birds depending upon how effective the mimic is in deceiving the model species.

Both male and female scrub-jays were able to distinguish between conspecific calls and mimicked calls from mockingbirds. In contrast, Searcy and Brenowitz (1988) found that female Red-winged Blackbirds discriminated between a mockingbird imitation and actual Red-winged Blackbird song, while males did not (Brenowitz 1982). The authors speculated that selection acts to minimize females from committing a Type II recognition error (analogous to statistical errors) where an individual accepts a stimulus from a different species (Searcy and Brenowitz 1988). Female response is often measured by playing songs to captive subjects and observing their courtship display. A Type II error would be costly for females, leading to hybrid matings and lower reproductive success (Searcy and Brenowitz 1988). Type II recognition errors should not occur in cooperative breeders such as scrub-jays where selection favors the ability of both sexes to discriminate between vocalizations from kin and nonkin (Barg and Mumme 1994, Price 1999, Hatchwell et al. 2001). Thus, we should expect no sexual difference in how scrub-jays perceive and respond to mockingbird mimicry, since this requires less discriminatory ability than kin recognition.

Our findings suggest that vocal mimicry of Florida Scrub-Jays by mockingbirds does not serve an interspecific function by deceiving scrub jays. Even though

scrub-jays are not fooled by mockingbird mimicry, this does not necessarily refute the deceptive mimicry hypothesis. Other model species may be deceived by mockingbird mimicry, such as the Red-winged Blackbird in Brenowitz's (1982) study. In this view, deception of model species by Northern Mockingbirds is likely species-specific, depending upon the ability of the model to differentiate between conspecific and mimicked calls as discussed above.

Mimicry could also function interspecifically as a "Beau Geste" territorial exclusion strategy by deceiving individuals of species other than the model (Krebs 1977, Rechten 1978). By mimicking scrub-jays, mockingbirds may fool other competing species at the study site given that jays are potential nest predators (Woolfenden and Fitzpatrick 1996). A simple test of the Beau Geste hypothesis would require presentation of the playbacks used in this study to a member of a third species that resides in the same habitat as the model and mimic species. This would necessitate careful selection of a species that is a potential competitor of the model and mimic species.

In conclusion, we found that Florida Scrub-Jay pairs responded differently to conspecific vocalizations and imitations by Northern Mockingbirds regardless of the context in which the playbacks were presented. This suggests that mimetic elements in mockingbird song are not likely to play a large role in interspecific interactions between the two species. Vocal mimicry in Northern Mockingbirds is more likely driven by sexual selection through male-male competition and female choice to enhance male repertoire size (Howard 1974). Future studies need to systematically test the alternative hypotheses to determine if vocal mimicry has both intra- and interspecific functions.

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