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Relative threat and recognition ability in the responses of tropical mockingbirds to song playback

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Abstract

It has been suggested that individual recognition based on song may be constrained by repertoire size in songbirds with very large song repertoires. This hypothesis has been difficult to test because there are few studies on species with very large repertoires and because traditional experiments based on the dear enemy effect do not provide evidence against recognition. The tropical mockingbird, *Mimus gilvus*, is a cooperative breeder with very large song repertoires and stable territorial neighbourhoods. The social system of this species allowed us to test individual recognition based on song independently from the dear enemy effect by evaluating male response to playback of strangers, neighbours (from shared and unshared boundaries), co-males (i.e. other males in the same social group) and own songs. Although subjects did not show a dear enemy effect, they were less aggressive to co-males than to all other singers. Our results suggest that recognition in tropical mockingbirds (1) does not simply distinguish between familiar and unfamiliar singers, (2) requires a small sample of both songs and song types, (3) does not rely on individual-specific sequences of song types and (4) is not likely to rely on group-specific vocal signatures potentially available in cooperatively breeding groups. We conclude that this is a case of true recognition and suggest that the lack of a dear enemy effect in this and other species with large repertoires may relate to the role of song in mate attraction and the perception of neighbours as a threat to future paternity.

Keywords

dear enemy effect; individual recognition; *Mimus gilvus*; playback experiment; song repertoires; tropical mockingbird

Many animals have evolved conspecific recognition abilities that allow them to direct costly behaviours to the appropriate targets. Individual recognition allows animals to invest preferentially in their own progeny in the presence of unrelated young (Beecher et al. 1981; Seddon & Vanheezik 1993; Leonard et al. 1997; Lefevre et al. 1998; Searby & Jouventin 2003), to find their mates in crowded environments (Lengagne et al. 2004), or to preferentially display altruistic acts towards those who have helped them in the past (Wilkinson 1988; Denault & McFarlane 1995). Individual recognition is important in territorial contexts where territory owners are expected to benefit from behaving less aggressively towards stable neighbours not likely to trespass than towards strangers trying to establish a new territory (dear enemy effect: Fisher 1954). Individual recognition may also allow territory owners to determine quickly when a neighbour has gone outside its typical territorial boundaries and is likely to represent a greater threat.

The ability to recognize individual conspecifics on the basis of song is thought to be widespread among songbirds (Falls 1982; Temeles 1994; Stoddard 1996). Nevertheless, a few species have shown a weak dear enemy effect (Kroodsma 1976), a similar response to neighbours and strangers (Falls & d'Agincourt 1981; Beletsky 1983) or a similar response to neighbours singing from shared versus unshared boundaries (Schroeder & Wiley 1983; Godard 1993). Some of these results were initially interpreted as an indication that an increase in song repertoire size could interfere with the ability to recognize individuals by song (Kroodsma 1976; Krebs & Kroodsma 1980; McGregor & Avery 1986; Clayton 2004). However, there is little evidence to support this hypothesis, and such a conflict may only affect species with very large song repertoires (Stoddard 1996). The conflict between repertoire size and individual recognition is thought to occur because, as conspecific repertoires increase, (1) there is a greater number of options that individuals must learn to discriminate, (2) the assignment of identity could become harder owing to potentially higher levels of song type sharing (but see Hultsch & Todt 1981), and (3) the opportunities for learning how different individuals sing each song type decrease, because singers now sing many song types a few times each instead of singing a few song types many times each (reviewed in Stoddard 1996). In spite of these arguments, large song repertoires do not seem to impair the individual song recognition abilities of European robins, *Erithacus rubecula* (Bremond 1968; Brindley 1991), European starlings, *Sturnus vulgaris* (Gentner & Hulse 1998), or thrush nightingales, *Luscinia luscinia* (Naguib & Todt 1998) and experiments in captivity have shown that birds have the potential to learn more songs than those to which they are exposed in natural conditions (Stoddard et al. 1992). Furthermore, individual recognition may be largely independent of repertoire size if it is based on learning the general characteristics of a singer's voice rather than on learning each of the song types he sings (Weary & Krebs 1992). The issue of a potential conflict between very large repertoire sizes and individual recognition by song highlights a major difficulty in the interpretation of playback experiments based on the dear enemy effect: even if listeners can tell neighbours and strangers apart, they may still respond equally to both stimuli if the different types of simulated singers pose similar threats to territorial tenure or other critical resources (Temeles 1994). Until this possibility is thoroughly explored, the effects of large repertoire sizes on song recognition will remain controversial.

Mockingbirds are a group of New World songbirds widely recognized for their large song repertoires and highly territorial nature (Brewer & MacKay 2001). The tropical mockingbird, *Mimus gilvus*, is a common species in open habitats across northern South America, Central America and the Caribbean. In Venezuela (Laurent 1990), Panama (Morton et al. 2004), and Colombia (Botero & Vehrencamp 2007), tropical mockingbirds are known to be cooperative breeders and to live in stable territorial neighbourhoods year round. Co-males (i.e. males that belong to the same social group; Langmore 1998), tolerate each other's presence and engage in joint territorial defence. Male tropical mockingbirds show marked cycles of song output similar to those of the closely related northern mockingbird, *Mimus polyglottos* (Logan 1983), and they sing temporally discrete songs of roughly 1–2 s (Fig. 1). Each song typically includes less than 10 syllables and two or more different syllable types (Botero & Vehrencamp 2007). Our preliminary analyses indicated that adult breeding males in Colombia (N = 6) have an average repertoire size of 130 different syllable types, analogous to the 'song' types of the northern mockingbird (Derrickson 1987). Syllable types are combined in multiple ways to produce a seemingly unlimited number of song types that are commonly delivered with immediate variety (Botero & Vehrencamp 2007).

We took advantage of the unique natural history of the tropical mockingbird to test the ability of a species with very large song repertoires to recognize individuals by song independently from its tendency to show a dear enemy effect. Following Langmore's (1998) study of polyandrous dunnocks, *Prunella modularis*, we compared the responses of adult males to playback of strangers, neighbours (from shared and unshared boundaries) and co-males. Given

that communal breeding in the tropical mockingbird predicts a diminished response to group members relative to outsiders, we hypothesized that this system would allow us to detect an ability for individual song recognition even in the absence of a dear enemy effect. Our experiment was thus set to ask two different questions. (1) Is there a dear enemy effect in the tropical mockingbird? (2) Can male tropical mockingbirds recognize individual conspecifics solely on the basis of song? We present the most likely outcomes for our experiment in terms of relative strength of response to alternative playback treatments, and our interpretation of each, in Table 1.

We also included in our experimental design a treatment in which each focal male heard his own songs. Although this treatment is not necessary for testing song recognition abilities, it offers insight to the relative importance of group membership cues potentially available in the vocal displays of cooperatively breeding groups (e.g. Hopp et al. 2001). If songs of group members converge in acoustic properties, then it could be expected that own songs will be treated as those of co-males. If, on the other hand, birds that hear themselves out of context treat the playback as a stranger while their co-males treat it, at least initially, as a group member, then this treatment will provide yet another line of evidence for individual recognition. Finally, a treatment with a bird's own songs may also be useful for assessing whether birds are simply responding to shared versus unshared songs and for drawing comparisons with studies that have used it in the past (e.g. Gentner & Hulse 1998).

METHODS

Study Site

This experiment was conducted from late October to early December 2004 at Hacienda El Emporio in Villa de Leyva, Colombia (5°36'34"N, 73°32'47"W). The site is located 2100 m above sea level and has a mean annual temperature of 17°C, a bimodal distribution of rainfall (rainy seasons: February-May and October-December) and an average total annual precipitation of 638.1 mm (based on data collected from January 1984 to December 2003). The habitat is very open and is dominated by low grasses, prickly pears (*Opuntia* spp.) and pepper trees (*Schinus molle* L.).

Focal Birds

From August to October 2004, we colour-banded 23 adult males and followed them to establish group affiliations and territorial boundaries. We established dominance relationships by direct observation of agonistic interactions between co-males and by comparison of song output. Dominant males tend to displace their co-males rather than being displaced by them, to perch higher than other males and to sing more during courtship. Our field observations from 2004 to 2006 indicated that some subordinate co-males are the offspring of the breeding female (see also Morton et al. 2004) and others are immigrants to the group.

The 23 focal males belonged to 13 social groups. In 10 of these groups, we collected data on both a dominant and a subordinate co-male; in the other three groups, we collected data only on the dominant male because other co-males were not banded (two groups) or because only one male was in the group (one group). Four of the groups with two focal males included a subordinate focal male or a breeding female that had immigrated into the group during the 3 months of observations before our playback experiment. In these four groups, focal subordinates were observed challenging their dominant co-males before egg laying by singing at high rates, usually while countersinging with the dominant male from opposite ends of the territory, and by attempting to build a nest (this behaviour was not observed in other groups). Despite the internal competition for reproduction, co-males in these groups still kept responding together to territorial challenges and were not as aggressive to each other as they

were to conspecific intruders. Countersinging between co-males became extremely rare once the female laid eggs and started incubating.

Experimental Design

Playback trials took place between 15 October and 9 December 2004, a period of moderately high breeding activity at El Emporio (males in 11 of the 13 groups initiated one or two breeding attempts during this experiment). We exposed each focal bird to five playback treatments: (1) stranger, (2) neighbour from a shared boundary, (3) neighbour from an unshared boundary (this treatment involved the same playback sequence in the other neighbour treatment), (4) co-male and (5) bird's own songs. Different playback trials for the same focal bird were scored by the same human observer. We defined neighbours as dominant males that held a territory adjacent to a focal bird and strangers as dominant males that held a territory three or more territories away. The co-male treatment refers to songs of a male, different from himself, belonging to the same social group as the focal individual. When testing subordinate co-males, we used the songs of their dominant co-males as the source of the co-male treatment, and vice versa. All subordinate co-males included in this study were adult birds whose songs did not differ in any conspicuous parameter with regard to the songs of their dominant co-males. Subjects were exposed to a single trial per day and were tested again only after a period of two or more days without playback. The order of presentation of treatments was balanced across birds.

Our analyses do not include data from trials in which the focal bird went more than 100 m away from the speaker during the preplayback period, trials in which birds outside the focal group interfered and might have influenced the response of the focal male and trials that were interrupted by human activity (e.g. herding of cattle or loud trucks passing by close to the speaker). On average, focal males were successfully exposed to three different treatments (two subjects had successful trials for all five treatments and four had only one). We included 74 observations in our statistical analyses.

To evaluate the effects of co-males on each other's response to playback, two of us collected data simultaneously on different co-males in a subset of the trials performed on the 10 groups with two focal males. Discounting the observations that were not included in our statistical analyses for the reasons described above, 26 observations came from 13 trials in which we successfully collected data on both focal males (i.e. 40% of the observations for groups with two focal males and 35% of the total number of observations included in our statistical analyses).

Playback Stimuli

We used a different neighbour and stranger playback sequence for every social group ($N = 13$ groups). In nine of the 10 groups in which two co-males tested, we chose one of these males as the source of the within-group playback sequence (i.e. own-songs treatment for that focal bird and co-male treatment for the other). Four of these playback sequences came from dominant birds and five from subordinate birds. In the remaining group where two co-males were tested, we performed one trial using the songs of one co-male and another trial using the songs of the other. All songs used to generate the playback sequences were recorded in 2004 at close range, with good signal-to-noise ratio, no overlapping sounds and little to no detectable reverberation. Digital recordings were made in Wave file format at 48 kHz and 16 bits per sample using a Marantz portable PC card recorder PMD690 and a Sennheiser ME67 directional microphone. Each playback sequence consisted of seven repetitions of five song types from a single individual, presented with immediate variety and played in the same order every time (1, 2, 3, 4, 5, 1, 2, 3...). The song rates and switching rates of all our playback stimuli were well within the range of natural solo singing patterns in our population. The initial ordering of

song types within each sequence was created at random and was deliberately not intended to reflect a sequence of types heard in the wild. To avoid confounding effects of variation in song continuity and versatility (Derrickson 1988; Botero & Vehrencamp 2007), we standardized song duration, number of syllables per song, number of syllable types per song and intersong intervals at each position of the playback sequence for all the treatments heard by each social group (mean $\pm$ SD duration of playback sequences presented to birds in different social groups = 4.16 ± 0.17 min, range 3.92–4.52 min).

Trial Procedures

We used a Nomad Jukebox digital player (Creative Technology Ltd., www.creative.com, Milpitas, California, U.S.A.) to play back prerecorded song sequences from a single speaker (Anchor Audio Mini-box PB-25, www.anchoraudio.com, Torrance, California, U.S.A.) hidden in a bush at a known boundary of the test subject's territory. Stranger, neighbour from shared boundary, co-male and bird's own-song treatments were played from the same location and the neighbour from unshared boundary treatment was played from the directly opposite side of the territory. Playback intensity was standardized to 70 dB SPL measured at 3 m. We used flagging tape to mark concentric rings that defined distance bins at distances of 15, 30 and 45 m from the speaker. Trials were conducted between 0600 and 1100 hours and started after the subject was seen within 100 m from the speaker (territory diameter of our focal groups ranged from 200 to 350 m). Each trial included 4 min of preplayback observation, a playback sequence unknown to the observers at the time of the experiment and 10 min of postplayback observation. The observers scored the subjects' responses with a personal digital assistant (Palm m105, Palm Inc., Sunnyvale, California U.S.A.) with custom event recording software (J. M. Burt, University of Washington at Seattle). Data collected in real time included the times when the bird sang or crossed one of the distance markers (specifying whether he was going towards or away from the speaker). From these data, we computed the following six response variables, adding during- and postplayback observations: (1) latency to sing, (2) latency to approach within 45 m of the speaker (3) song rate (songs/s), and proportion of time spent (4) within 15 m of the speaker, (5) between 15 and 30 m from the speaker and (6) between 30 and 45 m from the speaker.

Statistical Analyses

It is generally desirable to minimize the number of statistical tests performed in the analysis of a playback experiment by reducing the responses measured originally to a few composite variables using multivariate techniques (McGregor 1992). We used factor analysis (Tabachnick & Fidell 2001) to reduce the song rate and the proportion of time spent at each of the three distance bins to two orthogonal composite response scores that can be described as weak and intense responses (Factor1 and Factor2, respectively, in Table 2). A high weak-response score implies that the bird tended to stay more than 30 m away from the speaker, and a high intense-response score implies that it spent a high proportion of time close to the speaker singing at a high rate. We tested for differences across treatments in these composite variables with general linear mixed models (GLMM) that included social group and focal bird nested within social group as random factors. Intense-response scores were log-transformed to meet normality assumptions (Osborne 2002). Every model was initially fitted to correct for the number of songs sung during preplayback, the closest range of approach before initiation of playback (1 = 0–15 m, 4 = > 45 m), the focal bird's rank within his social unit (dominant or subordinate) and the order of presentation of the treatment (i.e. n_{th} trial performed at that territory). As a conservative way to correct for the effects of biologically meaningful factors while avoiding overparameterization of statistical models, we removed covariates from the final models when their P value was above 0.50 (note that dropping these same factors at the 0.05 level did not alter the statistical conclusions reported here). All reported pairwise

comparisons were done as a posteriori tests with the command LSMEANS in SAS (SAS Institute, Cary, North Carolina, U.S.A., 2003).

The latencies to sing and to approach could not be included in the previous analyses, because in some trials the subjects did not perform those behaviours during the period sampled, and thus no values could be entered in the factor analysis. Discarding these observations (known as censored observations) or replacing them with arbitrary values (e.g. the duration of the trial) would have led to an alteration of the real distribution of the data and subsequent bias in our results (Botero & Vehrencamp 2007). Analysing latency variables separately from other responses also allowed us to distinguish between first reactions to playback and subsequent responses, something highly desirable when testing for recognition abilities. We used tobit regression models to test for differences in latency of response between treatments (Long 1997). The tobit regression models dealt with our censored observations and allowed us to define focal bird as a random factor. We included the same covariates in these models as the ones described for the GLMM (removing them from the final models when their p -value was above 0.50), and used Wald tests (Agresti 1990; Polit 1996) to test for the overall significance of categorical factors with more than two levels (e.g., playback treatment). A posteriori pair-wise comparisons in our tobit models were computed with the command TEST in STATA (Statacorp, College Station, Texas, U.S.A., Release 8, 2005).

RESULTS

Factor Analysis

Intense-response scores differed significantly between treatments (GLMM, factor 2: $F_{4, 47} = 2.82$, $P = 0.036$; trial order, closest approach before playback and number of songs before playback were removed from the final model) and showed a tendency to be higher in dominant individuals (GLMM, rank: $F_{1, 47} = 3.87$, $P = 0.055$). Subjects were more aggressive to neighbours (regardless of the location of playback) and strangers than to co-males (Fig. 2, Table 3). Intense-response scores to own songs were intermediate and did not differ significantly from any other treatment (Table 3). Weak-response scores were not significantly different between treatments (GLMM, factor 1: $F_{4, 45} = 0.42$, $P = 0.794$; rank and trial order were removed from final model).

Analyses of Latencies to Respond

The latency to sing after the initiation of playback also differed significantly across treatments (Wald test after random-effects tobit regression with 10 right-censored observations: $X^2_3 = 17.12$, $P = 0.001$; rank was removed from the final model; Fig. 3a). Subjects took longer to reply to the songs of their co-males than to those of any other playback type ($P \leq 0.003$ for all a posteriori pairwise comparisons with the co-male treatment). Song latencies in response to neighbours (regardless of location of playback), strangers and own songs were not significantly different from each other. The latency to sing after the initiation of playback was not affected by dominance rank, trial order or preplayback behaviour ($P > 0.274$). Latency to approach did not differ significantly between treatments (Wald test after random-effects tobit regression with 27 right-censored observations: $X^2_3 = 5.05$, $P = 0.168$; rank and number of songs before playback were removed from the final model; Fig. 3b).

Co-male Effects on Response to Playback

We explored the possibility that a bird's response could be dependent on the response of his co-males by correlating co-male responses in the subset of trials in which we scored both birds simultaneously. There was no significant correlation in the co-males' intense-response scores (Pearson's correlation: $r_{13} = 0.077$, $P = 0.802$), latencies to sing ($r_{13} = -0.363$, $P = 0.223$) or

latencies to approach ($r_{13} = 0.228$, $P = 0.454$). Weak-response scores were correlated ($r_{13} = 0.847$, $P < 0.001$), but this variable did not vary across treatments.

Given that natural countersinging interactions between co-males were more prevalent in groups in which both co-males were apparently unrelated to the breeding female, we also asked whether male response to co-male songs was different in these groups than in those with lower potential of within-group competition for breeding. As our observations suggested, in groups in which both co-males were apparently unrelated to the breeding female, latency to sing was shorter (tobit regression with 5 right-censored observations: $t_7 = -4.99$, $P = 0.001$; rank was removed from the final model), intense-response scores were higher (Mann-Whitney U test: $U = 30$, $N_1 = 7$, $N_2 = 4$, $P = 0.030$) and latency to approach was marginally shorter (tobit regression with 5 right-censored observations: $t_8 = -2.28$, $P = 0.052$; closest approach before playback and number of songs before playback were removed from the final model) than in the other groups. Weak-response scores to co-males did not differ significantly between these two types of groups (Mann-Whitney U test: $U = 38$, $N_1 = 7$, $N_2 = 4$, $P = 0.508$).

DISCUSSION

Male tropical mockingbirds do not show a dear enemy effect and are equally aggressive towards neighbours that sing from shared versus unshared boundaries. Nevertheless, their clearly diminished response to co-male songs suggests that they are capable of recognizing group members by song (outcome 4 in Table 1). Given that the songs of neighbours and co-males represent two types of familiar stimuli, we conclude that the differential response to these treatments was not a product of habituation but rather a case of true recognition (see Langmore 1998). We also conclude that recognition in the tropical mockingbird requires a remarkably small sample of songs and song types because differences across treatments occurred within seconds of initiating playback (Fig. 3), and because our playback sequences included only five of the hundreds of song types available per singer. It is unlikely that co-male recognition was achieved solely on the basis of group-specific vocal tags, because our focal birds responded to their own songs faster than to the songs of their co-males (Fig. 3), even though these two types of stimuli had a similar probability of including group-specific vocal tags. Indeed, highly standardized acoustic group signatures like the ones observed in the budgerigar, *Melopsittacus undulatus* (Hile & Striedter 2000) or the Mexican jay, *Aphelocoma ultramarina* (Hopp et al. 2001) would seem more likely to occur in the contact calls of the tropical mockingbird than in its highly variable songs. It is also unlikely that male mockingbirds recognize their conspecifics based on individually specific song type sequences (Weary & Krebs 1992; Langmore 1998; Naguib & Todt 1998; Todt & Hultsch 1998), because the order of presentation of song types in our playback was initially generated at random and did not mimic any particular sequence heard in the wild.

Another possibility is that our results are a product of a differential response to shared versus unshared song types rather than of a recognition of individual identity (McGregor & Avery 1986). Individuals may share more song types with their co-males than with extraterritorial males, and thus it is possible that our co-male playback sequences could have a higher proportion of shared types than the sequences in other treatments (at this point we do not have enough information on sharing levels between co-males to determine whether this is true). Nevertheless, if males were responding only to shared versus unshared types, then responses to own songs would have been expected to be less rather than more aggressive than those to co-males. Furthermore, our ongoing analyses indicate that males from nearby territories may share on average 70% of their syllable types, indicating that there was also a relatively high probability of including shared types in our neighbour treatment. Finally, given that the sources for co-male sequences in this experiment included both dominant and subordinate birds in

roughly similar proportions, it is unlikely that the overall diminished response to the co-male treatment was a product of differences in the quality of the songs it included.

The lack of a dear enemy effect in this experiment suggests that tropical mockingbirds perceive neighbours and strangers as similar threats to a valuable resource (Fisher 1954; Temeles 1994). With regard to territory, however, neighbouring mockingbirds seem to be less of a threat than strangers, because, in 2004, territorial boundaries and group composition showed little or no variation and almost all the identified intruders were unbanded strangers. It is nevertheless possible that mockingbirds perceive neighbours as significant territorial threats over longer periods. For example, if social groups engage in cyclic changes in territory size like the ones described for the northern mockingbird (Biedenweg 1983) or if territory budding (Woelfenden & Fitzpatrick 1978; 1984) and other forms of parental facilitation in the acquisition of territories (Brown 1987) play an important role in this system, then a neighbour's presence at the border may be equally threatening to territorial tenure as that of a stranger. Another possibility is that male mockingbirds evaluate the threats posed by different singers considering not only potential losses in territorial tenure but also potential losses in future paternity (see Ferkin 1988; Temeles 1994; Howard & Young 1998). Male-male vocal interactions like the ones simulated in our experiment are known to influence female reproductive decisions in some bird species (Payne & Payne 1977; West et al. 1981; Otter et al. 1999; Mennill et al. 2002; van Dongen 2006), and such behaviour would be especially likely in mockingbirds and other species that use song primarily for attracting or stimulating mates into new reproductive events (e.g. those with very large song repertoires, high vocal versatility and marked association between song output and breeding stage: Catchpole & Slater 1995). Given that local neighbourhoods of tropical mockingbirds are relatively stable and that neighbours are an important source of extrapair paternity (Gibbs et al. 1990; Olendorf et al. 2004), it is possible that a highly aggressive and sustained response to neighbours was selected as a mechanism for paternity assurance, even if neighbours truly pose a relatively small threat to territorial tenure.

The hypothesis that mockingbirds consider consequences to future paternity in their response to conspecific singers predicts stronger responses to co-males in groups where there is internal competition over the access to a breeding female. Our field observations indicate that social groups vary in the potential for internal competition for paternity, because in some groups, subordinate males are the offspring of the breeding female, whereas in others they are potentially unrelated to her because of immigration (see also Morton et al. 2004). Thus, we suggest the following explanation for the stronger responses to co-male songs in the groups in which both males were not likely to be related to the breeding female and appeared to compete for reproduction: the intensity of a male's response to conspecific singers may be partially related to the prevention of extrapair copulation with his own mate or the search for extrapair mating opportunities elsewhere. Three of four variables analysed in this experiment (including the two that showed significant variation across treatments) were not correlated between co-males; this result could be explained if males differ in their assessment of the paternity that they stand to lose or gain from these encounters. The alternative explanation to this result (i.e. that male response varies as a result of intrinsic differences in male quality) is not supported by the finding that dominant males did not respond significantly differently to playback than subordinates. It is possible, then, that the overall moderation in aggressive response to group members in times of conflict (e.g. when co-males compete internally for access to the breeding female) is an adaptation for group living favoured by the same evolutionary forces that led to cooperative breeding in the tropical mockingbird. If molecular analyses confirm that subordinate males do sometimes father a portion of the young at the nest, then co-male tropical mockingbirds could be regarded as an atypical case of true 'dear enemies'.

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Figure 1.

Four typical songs of a male tropical mockingbird from Villa de Leyva, Colombia. Each song represents a different song type, based on differences in syllable (sensu Wildenthal 1965) composition.

Figure 2.

Least squares means $\pm$ SE for weak- and intense-response scores during playback trials (see Table 3 for pairwise comparisons). Playback treatments as in Table 1.

Figure 3.

Nonparametric cumulative failure plots (Kaplan-Meier method) for (a) the latency to sing and (b) the latency to approach. The profile for each line reflects the cumulative percentage of subjects that sang or approached within a given time frame. Playback treatments as in Table 1. B stands for the bird's own-songs treatment.

Table 1

Most likely outcome patterns for relative strength of response to alternative playback treatments and biological interpretation

Possible outcome*	Interpretation
(1) $S \approx NU \approx NS \approx C$	No recognition, or all types of males considered equal threat
(2) $S > NU \approx NS \approx C$	Distinction between familiar versus unfamiliar singers
(3) $S > NU > NS > C$	True recognition, neighbours are considered dear enemies when they sing from typical locations
(4) $S \approx NU \approx NS > C$	True recognition, neighbours represent strong threat and group members are less of a threat than all others

* S = stranger; NU = neighbour played back from an unshared boundary; NS = neighbour played back from a shared boundary; C = co-male.

Table 2

Factor analysis of nonlatency variables with varimax rotation

Variable	Factor1 (weak response)*	Factor2 (intense response)*	Communality
Song rate (songs/s)	0.139 (0.183)	0.820 (0.708)	0.692
% Time at 0-15 m bin	-0.258 (-0.164)	0.684 (0.561)	0.535
% Time at 15-30 m bin	-0.802 (-0.687)	-0.099 (-0.148)	0.653
% Time at 30-45 m bin	0.680 (0.561)	-0.188 (-0.106)	0.497
% Variance explained	0.298	0.297	0.594

* Factor loading (score coefficient).

Table 3

Differences of least square means in the final GLMM for Intense response

Difference [*]	Estimate $\pm$ SE	<i>t</i> 47	<i>P</i> [†]
C – B	-0.148 $\pm$ 0.147	1.00	0.322
C – NS	-0.385 $\pm$ 0.141	2.73	0.009
C – NU	-0.352 $\pm$ 0.141	2.5	0.016
C – S	-0.372 $\pm$ 0.130	-2.87	0.006
B – NS	-0.238 $\pm$ 0.143	-1.66	0.104
B – NU	-0.205 $\pm$ 0.143	-1.43	0.160
B – S	-0.225 $\pm$ 0.131	-1.72	0.093
NS – NU	0.033 $\pm$ 0.126	0.26	0.795
NS – S	0.013 $\pm$ 0.117	0.11	0.913
NS – B	-0.020 $\pm$ 0.117	-0.17	0.865

* Playback treatments follow same convention as in Table 1

[†] Posteriori pairwise comparison.