Song-type sharing and matching in a bird with very large song repertoires, the tropical mockingbird

J. Jordan Price[1] **& David H. Yuan**
(Department of Biology, St. Mary's College of Maryland, 18952 E. Fisher Road,
St. Mary's City, MD 20686, USA)

(Accepted: 12 March 2011)

Summary

Song-type matching, a behaviour of some songbirds in which one individual replies to another's song with a matching song type, has been studied primarily in birds that have small to moderately sized song repertoires (<15 song types) and that share only a few song types with neighbours. Few previous studies have examined song-type matching in species with very large song repertoires, in which birds can share larger numbers of songs with neighbours and matching particular song types might be more challenging. Here we describe frequent and rapid song-type matching in a population of tropical mockingbirds, *Mimus gilvus*. Males had repertoire sizes of about 133 distinct song types on average which were delivered with high versatility. Territorial neighbours shared significantly more song types than did non-neighbours, and neighbouring males matched each other's songs frequently and often with surprising speed. Overlapping of songs occurred at approximately chance levels. Song-type matching in these birds could indicate more than just aggressive intentions, which is the presumed function of this behaviour in species with smaller repertoires. In tropical mockingbirds, rapidly matching the songs of neighbours could provide information to listeners about a singer's experience or abilities.

Keywords: conventional signals, Mimidae, repertoire sharing, singing versatility, song overlapping, song-type matching, vocal performance.

1. Introduction

Animals can use a variety of methods to direct their signals to particular receivers during communication. For example, in species that have repertoires of functionally redundant signals, a common way for individuals to

---

[1] Corresponding author's e-mail address: jjprice@smcm.edu

DOI:10.1163/000579511X573908

address specific rivals is by immediately replying to the rival's signal using a matching signal type (Bradbury & Vehrencamp, 1998). In acoustic communication systems, such 'type matching' behaviour allows individuals to direct their otherwise omnidirectional signals toward specific receivers (Armstrong, 1973; Krebs et al., 1981; Catchpole & Slater, 2008). Directed signals can convey information about a signaller's current motivation or intentions to particular rivals, in contrast to other conspicuous displays that may advertise a signaller's abilities, status or resource ownership to all potential competitors (Todt & Naguib, 2000; Naguib, 2005). Furthermore, in species that learn their vocalizations, sharing particular portions of their vocal repertoires with neighbours provides insights into the circumstances under which these vocalizations were acquired (Hultsch & Todt, 1981; Ewert & Kroodsma, 1994; Hughes et al., 1998; Kroodsma et al., 1999; Wilson et al., 2000; Grießmann & Naguib, 2002).

Repertoire sharing and song-type matching have been well-studied in songbirds (Catchpole & Slater, 2008). In many of these species, individuals produce more than one distinct song type, territorial neighbours share portions of their song repertoires, and counter-singing birds often reply to each other's songs with identical song types (e.g., Lemon, 1968; Krebs et al., 1981; Payne, 1982; Schroeder & Wiley, 1983; Stoddard et al., 1992; Beecher et al., 2000). Songbirds have been shown to address specific rivals in other complex ways as well. For example, a bird may 'repertoire match' by replying to a neighbour's song with a song type that does not match but is nevertheless shared with that particular neighbour's repertoire (Beecher et al., 1996). Alternatively, a bird may match only a portion of a rival's song rather than producing an exactly matching song type (Anderson et al., 2005) or may adjust the sound frequency of a song to match that of a rival (Mennill & Ratcliffe, 2004). Finally, singers may adjust the timing of their songs in order to either overlap or avoid overlapping the songs of particular neighbours (reviewed by Naguib & Mennill, 2010).

Evidence from a variety of species suggests that song-type matching functions as a graded signal of low-level aggression in birds, indicating a willingness to attack if a contest between countersinging rivals should escalate (Krebs et al., 1981; Beecher et al., 2000; Burt et al., 2001; Searcy & Beecher, 2009). Matching a rival's song type may, therefore, function as a 'conventional signal' of aggressive intent, because it is only arbitrarily connected with a singer's underlying status or condition and presumably conveys specific meaning to receivers solely by convention (Guilford & Dawkins, 1995; Vehrencamp, 2000, 2001). Song matching can increase the probability of attack by rivals (Krebs et al., 1981; Burt et al., 2001), so singers should only match their neighbours if they are willing to escalate. Thus, the honesty of this signal is maintained by receiver retaliation against bluffers rather than by any inherent costs or constraints associated with signal production (Vehrencamp, 2001). Other forms of directed signalling, such as repertoire matching and song overlapping, may play similar roles in regulating agonistic interactions between singing rivals and may function as similar indicators of motivation or intent (Beecher et al., 1996; Mennill & Ratcliffe, 2004; Searcy & Beecher, 2009; Naguib & Mennill, 2010).

To qualify as a conventional signal, song-type matching should not be especially costly to perform, as in handicap signals (Grafen, 1990), and should not be necessarily linked with an individual's inherent quality, as in index or assessment signals (Vehrencamp, 2000, 2001; Maynard Smith & Harper, 2003). In birds with moderately sized song repertoires of fewer than 15 song types each, which constitute the majority of type-matching species studied to date (Todt & Naguib, 2000; Catchpole & Slater, 2008), replying to a neighbour's song with one of only a few shared song types is thought to require negligible production costs and to indicate little about a singer's vocal abilities (Vehrencamp, 2001). Most of these species sing with 'eventual variety' by repeating each song type multiple times before switching to the next, making this task even easier. Previous research has focused on the potential challenges involved in learning complex song types of neighbours with high accuracy (Nowicki et al., 1998, 2002) or the consequences of having matched songs assessed by eavesdroppers (Payne, 1982; Logue & Forstmeier, 2008). However, the idea that song-type matching itself might involve performance constraints has received relatively little attention.

Song-type matching may not qualify as a conventional signal in all species in which it occurs (Vehrencamp, 2001). For example, matched countersinging should be more challenging in species that have very large song repertoires, especially when singers deliver their songs with 'immediate variety' by rapidly switching from one song type to the next (Kroodsma, 1979; Whitney & Miller, 1983; Todt & Naguib, 2000). It might be exceedingly difficult in such species to match a rival's song, and an ability to do so rapidly could reflect an individual's experience or skill as a singer. Few previous studies, however, have investigated the occurrence of song-type matching in species with large song repertoires (Todt & Naguib, 2000).

Here we describe frequent song-type matching in a population of tropical mockingbirds, *Mimus gilvus*, in which singers produce large repertoires of songs with immediate variety. We estimated the song repertoire sizes of seven territorial males and calculated proportions of shared song types among them to assess whether repertoire sharing differed between neighbouring and non-neighbouring birds. Preliminary observations of countersinging males suggested that individuals in this population regularly type match and overlap the songs of their neighbours; however, both events should be expected to occur at some level by chance alone (Searcy & Beecher, 2009). Therefore, in an effort to establish that these behaviours function as directed signals, we compared their occurrence to levels expected if birds were singing at random. Our aim in this study was to provide a basis for future investigations into the functional significance of the behavioural patterns described here.

2. Methods

2.1. Study site and species

We recorded the songs of seven male tropical mockingbirds on Calabash Caye, an island on the south-eastern edge of Turneffe Atoll, Belize (17°16.414′N, 87°48.674′W). All recordings were made during peak singing activity from 5:00 to 10:00 AM and from 4:30 to 6:30 PM at the beginning of the rainy season in late May and early June 2005. The island is nearly 2 km long and 1 km wide at its widest point and includes terrestrial forest surrounded by a wide fringing margin of mangroves (Piou et al., 2006). Observations over multiple years suggest that tropical mockingbirds on the island maintain stable, year-round territories approximately a hectare in size (Figure 1). Although we did not colour band birds for individual identification, only one bird was ever observed singing in each territory and each individual sang from only one or a few perches throughout our study, so presumably we recorded the songs of one male per territory.

Digital song recordings were made at a sampling rate of 48 kHz and 16 bits per sample using a Marantz PMD670 solid state digital recorder and a Sennheiser ME62 omnidirectional microphone in a Telinga parabolic dish.

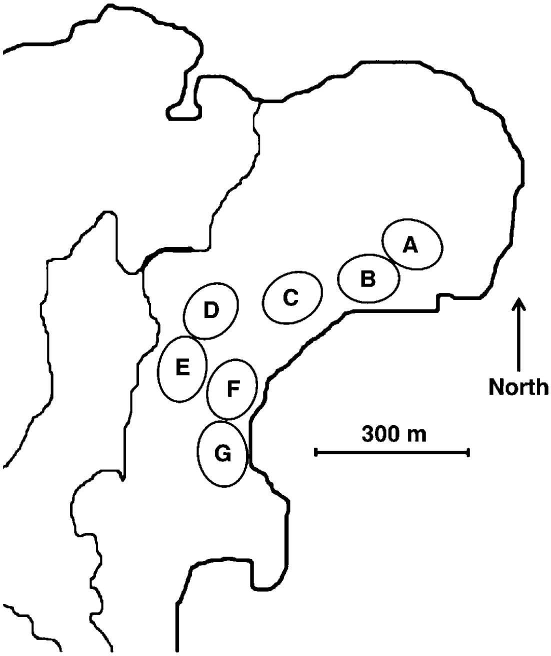

Figure 1. Locations and estimated boundaries of seven tropical mockingbird territories on Calabash Caye, Belize. Mockingbirds on the island occupied a small area of terrestrial forest which was surrounded by a fringing margin of mangroves. Counter-singing interactions were recorded between males A and B, D and E, and G and F during our study.

We recorded individual singing bouts for up to 12 min at a time (mean ± SE recording time = 3.3 ± 0.3 min) to obtain at least 30 min of singing for each male (mean ± SE recording time per male = 47.0 ± 8.5 min; 10.17 h total). We also made stereo recordings of three counter-singing pairs of neighbouring males (mean ± SE recording time per dyad = 17.6 ± 4.0 min), typically using two parabolic microphones connected to the same solid state digital recorder, with one of the microphones on a 15 m lead. In several cases, dense vegetation required us to record these counter-singing males using two recorders simultaneously and then later mix the recordings in Sound Studio 2.1.1 (Felt Tip, New York, NY, USA) to produce stereo files, using a time cue to synchronize the recordings. We focused on just three male pairs for this analysis because these birds had directly adjacent territories and had been observed counter-singing regularly. Males were always within 60 m of each other during these counter-singing interactions. Spectrograms of all songs were generated using Raven Pro 1.4 (Cornell Lab of Ornithology, Ithaca, NY, USA; frequency resolution = 135 Hz; time resolution = 10.7 ms).

Songs generally consisted of short (<1 s), acoustically distinct sounds that were repeated to produce temporally discrete songs, similar to the typical singing pattern of the northern mockingbird (*Mimus polyglottos*; Derrickson & Breitwisch, 1992; Reichard & Price, 2008), the tropical mockingbird's closest phylogenetic relative (Lovette & Rubenstein, 2007). We defined these distinct, repeated units as ‘syllables’ following terminology used in previous studies of tropical mockingbirds (Botero & Vehrencamp, 2007; Botero et al., 2007, 2009a). In our study population, each song consisted of a single syllable type repeated roughly 3–5 times, and different song types were typically delivered with immediate variety during a singing bout (Figure 2). This syllable repetition pattern is different from that reported for tropical mockingbirds in other parts of this species' range (e.g., Bonaire: Botero & Vehrencamp, 2007; Colombia: Botero et al., 2007, 2009a), which often include three or more distinct syllable types in each song.

2.2. *Song repertoire sharing, matching and overlapping*

We estimated the song repertoire size of each male following the methods of Wildenthal (1965) and Howard (1974), which assume that the number of new elements encountered with the number of songs sampled rises to meet an asymptote following an exponential equation: $n = N(1 - \mathrm{e}^{-T/N})$, where n is the number of distinct song types in the sample, T is the total number of songs sampled from an individual, and N is the estimated total number of song types in the repertoire. Fitting the number of songs sampled and the number of new types encountered into this equation enables the total number of song types to be estimated. This equation makes certain assumptions, notably that the repertoire size is constant, that the probability of a new type appearing is proportional to the number of unused types remaining in the repertoire, and that song types are produced in a random sequence. The last of these assumptions is especially unlikely to be true in birds that sing with immediate variety, as such species have been shown to deliver their songs following specific organizational rules (Todt & Naguib, 2000). Because of the potential inaccuracies involved in estimating large repertoire sizes (Botero et al., 2008), all comparisons between individuals in our study used only identified song types rather than estimated repertoire sizes.

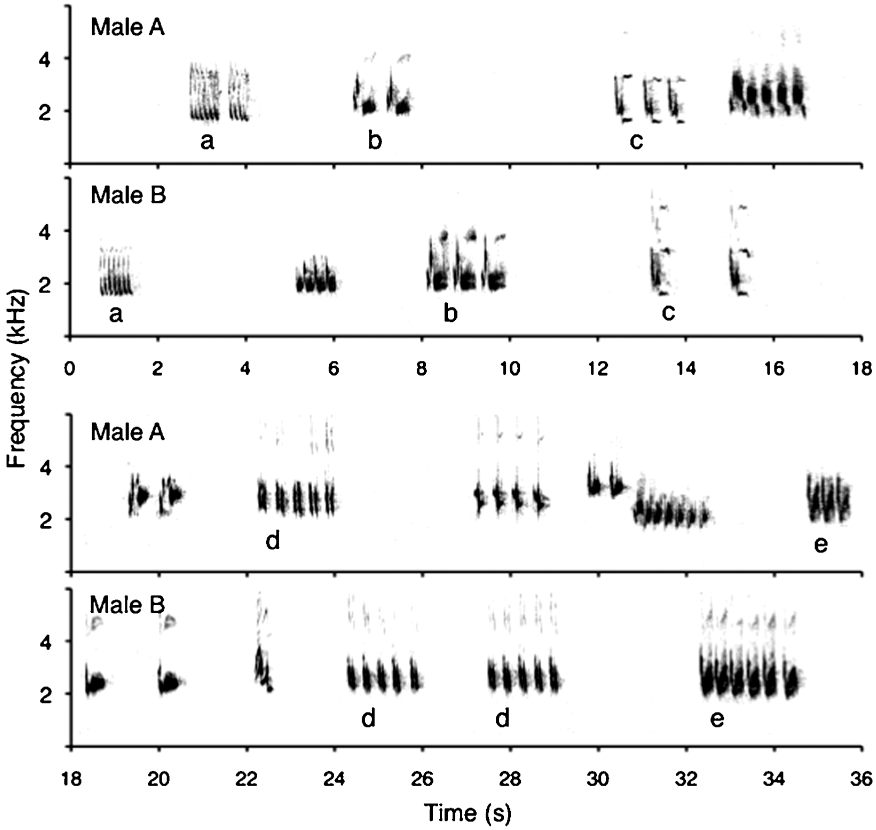

Figure 2. Spectrograms showing natural counter-singing interactions between two neighbouring males (A and B). Lower case letters (a–e) below spectrograms indicate five song types that were matched. Note that the singers often switched roles, with male A sometimes matching B and B sometimes matching A.

We estimated the number of shared song types between individuals by comparing onscreen spectrograms of all recorded song types of each male against all song types of other males. Overall we made 21 pair-wise repertoire comparisons, 6 among neighbouring males and 15 among non-neighbouring males. Songs were identified as the same type if their syllables appeared and sounded identical or nearly so, and five independent referees were employed to ensure that our scoring was consistent. For each pair of males, we calculated an index of repertoire sharing (RS) using the equation: $\mathrm{RS} = Z/((X+Y)-Z)$, where X and Y were the number of song types identified in birds x and y, and Z was the number of shared song types (Hultsch

& Todt, 1981; Grießmann & Naguib, 2002). This index of sharing can vary from 0 (no song types shared between two birds) to 1 (all song types in both repertoires shared) and accounts for the fact that different males can have different numbers of identified song types. We compared repertoire sharing between neighbouring and non-neighbouring dyads using a Mann–Whitney U-test. We also looked at sharing as a function of the approximate distance between the centres of territories using linear regression.

Song-type matching and overlapping behaviours were measured from stereo recordings of three pairs of neighbouring males interacting over multiple days. Males were on singing perches between 30 and 60 m apart during all of these interactions. We defined a song-type match as production of the same song type as that just sung by a neighbour within 5 s of the beginning of the neighbour's song. Some matching should be expected to occur by chance alone if neighbouring birds share song types in their repertoires (Searcy & Beecher, 2009). Therefore, we assessed whether or not each male was matching his neighbour's songs at above-chance levels by calculating the number of song-type matches expected if a bird was singing randomly, given the proportion of types shared with that neighbour, and then comparing this to the number of matches observed. Song overlapping, in which a singer begins a song after the beginning of a neighbour's song but before that song has finished, is also a pattern that can occur by chance alone (Searcy & Beecher, 2009). The probability that one birds' song will begin by chance while another bird is singing is equal to the proportion of time that the other bird spends vocalizing (Ficken et al., 1974; also see Planck et al., 1975). We compared the frequencies of both song-type matching and song overlapping by each male to chance levels using G-tests (Sokal & Rohlf, 1995).

3. Results

3.1. *Repertoire sharing*

Repertoire size estimates for the seven males ranged from 99 to 182 song types (Table 1; mean ± SE $=$ 133.3 ± 10.4 song types), consistent with previous estimates for this species (130 types: Botero et al., 2007) and for northern mockingbirds (45 to 203 types: Derrickson & Breitwisch, 1992). The two birds with the highest and lowest estimated repertoire sizes (birds

Table 1. Estimated song repertoire sizes for the seven birds (A–G) included in the study.

	Individual males						
	A	B	C	D	E	F	G
Identified song types (*n*)	71	122	74	106	93	133	107
Total songs sampled (*T*)	125	289	95	296	149	426	335
Estimated repertoire size (*N*)	99	140	182	115	145	140	112
% repertoire represented in sample	73.4	87.1	40.7	92.2	64.1	95.0	95.5

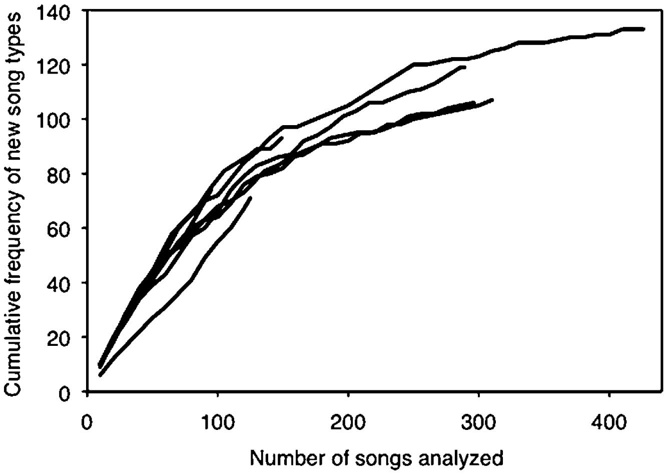

Figure 3. Cumulative curves showing the number of identified song types as a function of songs analyzed for seven tropical mockingbirds.

A and C) were also the birds that had the fewest songs sampled (*T* in Table 1) and so presumably provided the least accurate estimates (Botero et al., 2008), suggesting that the actual range of repertoire sizes in our population was narrower than what was indicated by our calculations. New song types were encountered at progressively slower rates as the total number of songs analyzed increased (Figure 3); however, repertoire sizes were still increasing even after analyzing over 300 songs.

Altogether we identified 479 distinct song types in the repertoires of the seven males. Pair-wise comparisons of these repertoires (Figure 4) showed that individuals shared between 1.9% (2 of 107 song types) and 32.4% (23 of 71 song types) of their song repertoires with other members of the population (mean ± SE = 10.3 ± 1.2%). Repertoire sharing (RS) scores, which

Number of song types shared

Index of repertoire sharing (RS)

	A	B	C	D	E	F	G	*n*
A	X	23	3	7	2	7	2	71
B	0.14	X	12	10	13	15	7	122
C	0.02	0.07	X	6	4	7	4	74
D	0.04	0.05	0.03	X	29	17	7	106
E	0.01	0.06	0.02	0.17	X	21	3	93
F	0.04	0.06	0.03	0.08	0.10	X	20	133
G	0.01	0.03	0.02	0.03	0.02	0.09	X	107

Figure 4. Number of song types shared (above diagonal) and calculated indices of repertoire sharing (RS, below diagonal) between seven tropical mockingbirds (A–G). Individuals beside each other in the matrix were closest neighbours. The far right column shows the number of identified song types (*n*) recorded from each individual.

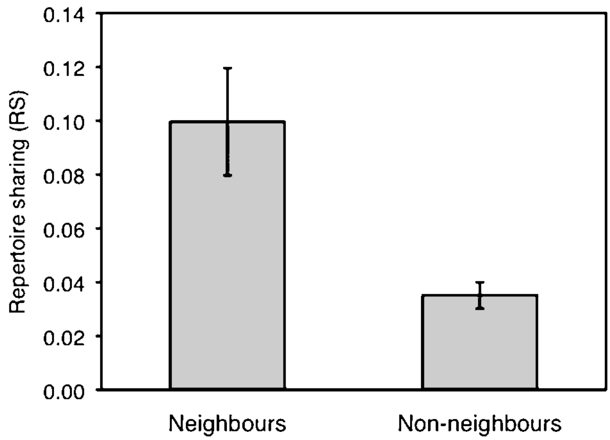

Figure 5. Mean (± SE) repertoire sharing between neighbouring ($N = 6$) and non-neighbouring ($N = 15$) males.

account for differences between individuals in numbers of identified song types, ranged from 0.01 to 0.17 (Figure 4). Neighbouring males shared significantly more song types (RS = 0.10 ± 0.02) than did non-neighbouring males (RS = 0.036 ± 0.005) (Figure 5; Mann–Whitney U-test: $U = 8.0$, $N_1 = 6$, $N_2 = 21$, $p = 0.004$). Song type sharing also decreased with distance between territory centres (ANOVA: $F_{1,19} = 7.74$, $R^2 = -0.27$, $p = 0.012$).

3.2. Song matching and overlapping

Stereo recordings of counter-singing males (Figure 2) showed that birds matched the song types of their neighbours at rates far above what would be expected to occur by chance, given the levels of repertoire sharing within each dyad (observed = 11.3% of song types matched, expected = 0.2% song types matched; G-test: $G = 70.6$, df = 1, $p < 0.0001$). On average (± SE), territorial males produced 11.5 ± 1.3 song types per minute and matched their neighbour's songs 1.3 ± 0.2 times per minute during countersinging bouts. Thus, birds matched approximately every ninth song type that their neighbour produced. Furthermore, within each countersinging pair, males appeared to match each other's songs at similar rates (G-tests: $G < 0.66$, df = 1, $p > 0.42$) and often reciprocally, with a song-type match by one bird often shortly followed by a match by the other (Figure 2). We did not observe any other potentially aggressive behaviours, such as approaches or territorial intrusions, during these counter-singing bouts. Matching song types were generally delivered within 2 s of the beginning of the first bird's song (mean ± SE = 1.76 ± 0.09 s; $N = 95$ matches) and occasionally occurred within 0.5 s.

Song overlapping, in contrast, occurred at frequencies similar to those expected by chance (G-test: $G = 0.10$, df = 1, $p = 0.75$). Males overlapped the songs of their neighbours 28.7% of the time (range = 25.0–38.9%), similar to what would be expected to occur at random given the proportion of time that birds spend vocalizing during singing bouts (30.1% overall; range = 25.6–37.7%; mean ± SE song durations = 1.24 ± 0.03 s, intervals between songs = 2.9 ± 0.1 s). Males within dyads also did not differ from each other in their rates of overlapping (G-tests: $G < 0.33$, df = 1, $p > 0.56$). Thus, although males frequently and often rapidly matched their neighbour's song types, they did not appear to consistently overlap or avoid overlapping their neighbours' songs while countersinging.

4. Discussion

For birds with large repertoires of over 100 song types, such as the tropical mockingbirds described here, rapidly matching the songs of neighbours must be a relatively challenging task in comparison to species with much smaller song repertoires. For example, male song sparrows (*Melospiza melodia*) produce just 5 to 12 song types each and share only a few of their songs with neighbours (Hughes et al., 1998; Beecher et al., 2000; Wilson et al., 2000), so song matching in this species presumably indicates little about a singer's vocal or memory retrieval abilities. Tropical mockingbirds, in contrast, must choose from among a large array of memorized song types in order to match a neighbour, and they usually did so in our study with surprising speed (<2 s). Furthermore, rivals regularly switched roles during counter-singing bouts by reciprocally matching each other's songs (Figure 2). Song matching during such 'vocal duels' could convey more than just aggressive intentions, which is the principal signal function of this behaviour in song sparrows (Vehrencamp, 2001; Searcy & Beecher, 2009). In tropical mockingbirds, an ability to rapidly and accurately match the versatile singing of neighbours could provide information to listeners about such factors as a singer's long-term tenure on a territory, his song learning abilities, or his vocal skill (Kroodsma, 1979; Payne, 1982; Kroodsma et al., 1999; Nowicki et al., 2002; Logue & Forstmeier, 2008). Previous studies of tropical mockingbirds have shown that the production of syllables with high within-individual consistency is associated with a bird's age and reproductive success (Botero et al., 2009a). Perhaps producing songs that are highly similar between individuals is just as biologically relevant.

Matched counter-singing has been examined in relatively few other species that deliver large repertoires of song types with immediate variety (Todt & Naguib, 2000). Frequent song matching has been reported in marsh wrens (*Cistothorus palustris*; Kroodsma, 1979) and in neotropical populations of sedge wrens (*C. platensis*; Kroodsma et al., 1999), both of which can have repertoires of over 100 song types. Complex vocal interactions including song matching have also been studied extensively in nightingales (*Luscinia megarhynchos*), which produce substantial repertoires of up to several hundred song types (reviewed by Todt & Naguib, 2000). These studies show that singers often follow specific rules in transitioning from one song type to the next during vocal interactions and may deliver their songs in highly stereotyped sequences (Kroodsma & Verner, 1978; Kroodsma, 1979; Todt & Naguib, 2000). Although we did not investigate such patterns in tropical mockingbirds, we did note that some song types appeared to regularly follow others during singing bouts, raising the possibility that birds were able to anticipate some of their neighbour's song types before matching them. Individuals also sometimes appeared to 'repertoire match' by producing non-matching song types that were shared with a neighbour, suggesting complex levels of communication beyond just song-type matching (Beecher et al., 1996; Todt & Naguib, 2000; Naguib, 2005).

Although the birds in our study were clearly directing at least some of their songs towards neighbouring males, it is worth noting that these vocal interactions occurred at long range in the absence of any overt aggressive behaviours as would occur during a close-range territorial conflict. Moreover, although our subjects overlapped each other's songs no more or less than expected by chance, this may not necessarily indicate that overlapping does not have an agonistic function in these birds (see Naguib & Mennill, 2010; Searcy & Beecher, 2011). We studied only a relatively small number of interacting neighbours over just a few weeks, and a larger sample may provide more statistical power to reveal patterns not apparent in our analysis. Further studies, including the use of interactive playback experiments (e.g., Naguib & Kipper, 2006), will be required to investigate the signal value of the behavioural patterns described here.

Higher levels of repertoire sharing between neighbours than between non-neighbours in our population could be a product of how individuals tend to acquire their songs. Like the closely related northern mockingbird (Derrickson & Breitwisch, 1992), tropical mockingbirds are presumably open-ended learners that continue to acquire new songs throughout life, and individuals on year-round territories should be expected to learn a portion of their repertoires from long-term neighbours. Nevertheless, the prevalence of song-type matching in this species suggests that repertoire sharing is not just a byproduct of vocal learning but rather has a function in communication by allowing birds to match the song types of neighbouring rivals. Sharing song types with immediate neighbours may have important consequences for a bird's long-term fitness (Hultsch & Todt, 1981; Payne, 1982; Wilson et al., 2000).

Interestingly, the songs of our Belizean study population were much more similar to those of northern mockingbirds, which typically consist of 4–5 repetitions of a single syllable type (Wildenthal, 1965; Reichard & Price, 2008), than to the songs of previously studied South American tropical mockingbirds, which often include three or more distinct syllable types in each song (Botero & Vehrencamp, 2007; Botero et al., 2007, 2009a,b). Although South American birds are known to occasionally increase the repetitiveness of their syllable sequences during territorial interactions, presumably as a sign of aggression (Botero & Vehrencamp, 2007), their typical syllable patterns are very different from those presented here. Our study birds also resembled northern mockingbirds in their average levels of within-population song type sharing (approx. 10%: Wildenthal, 1965; Howard, 1974), in comparison to South American tropical mockingbirds which share approximately 70% of their syllables with neighbours (Botero et al., 2007). Tropical mockingbirds in other areas of northern Central America appear to sing in much the same way as the birds described in our study (unpublished data), suggesting that this part of the species' range is behaviourally distinct from populations farther south. Whether these differences are a product of genetic isolation, hybridization with northern mockingbirds (known to occur in sympatry, Howell & Webb, 1995), selection for different levels of versatility along a latitudinal environmental gradient (Botero et al., 2009b), or a combination of such factors remains to be investigated.

For all their similarities, however, northern mockingbirds and tropical mockingbirds exhibit some intriguing behavioural differences. To our knowledge, no previous studies of northern mockingbirds have suggested that males match each other's songs at above-chance levels or that they share significantly more song types with immediate neighbours than with other local males. Tropical mockingbirds, in contrast, appear to song-type match throughout their range (C.A. Botero, pers. commun.) and use songs in a variety of other complex ways during vocal interactions with neighbors (e.g., Botero & Vehrencamp, 2007; Botero et al., 2007). Thus, in general, the songs of tropical mockingbirds appear to have relatively important functions in intrasexual communication between territorial males, in comparison to the songs of northern mockingbirds which are thought to function primarily in intersexual communication with potential or current mates (Derrickson & Breitwisch, 1992). Given that the ancestors of northern mockingbirds were likely tropical (Lovette & Rubenstein, 2007), such latitudinal differences in vocal behaviour may provide valuable insights into the evolutionary factors selecting for large and diverse song repertoires in these and perhaps other songbirds.

Acknowledgements

We thank Elizabeth Price for invaluable assistance in the field and the University of Belize Institute of Marine Studies for providing logistical assistance and accommodations on Calabash

Caye. Clivus provided inspiration. Dustin Reichard, Henrik Brumm, and two anonymous reviewers provided helpful comments that improved the manuscript. Funding was provided by a Faculty Development Grant to J.J.P. from St. Mary's College of Maryland.

References

Anderson, R.C., Searcy, W.A. & Nowicki, S. (2005). Partial song matching in an eastern population of song sparrows, *Melospiza melodia*. — Anim. Behav. 69: 189-196.

Armstrong, E.A. (1973). A study of bird song. — Dover, New York.

Beecher, M.D., Campbell, S.E., Burt, J.M., Hill, C.E. & Nordby, J.C. (2000). Song-type matching between neighbouring song sparrows. — Anim. Behav. 59: 21-27.

Beecher, M.D., Stoddard, P.K., Campbell, S.E. & Horning, C.L. (1996). Repertoire matching between neighbouring song sparrows. — Anim. Behav. 51: 917-923.

Botero, C.A., Boogert, N.J., Vehrencamp, S.L. & Lovette, I.J. (2009b). Climatic patterns predict the elaboration of song displays in mockingbirds. — Curr. Biol. 19: 1151-1155.

Botero, C.A., Mudge, A.E., Koltz, A.M., Hochachka, W.M. & Vehrencamp, S.L. (2008). How reliable are the methods for estimating repertoire size? — Ethology 114: 1227-1238.

Botero, C.A., Riveros, J.M. & Vehrencamp, S.L. (2007). Relative threat and recognition ability in the responses of tropical mockingbirds to song playback. — Anim. Behav. 73: 661-669.

Botero, C.A., Rossman, R.J., Caro, L.M., Stenzler, L.M., Lovette, I.J., De Kort, S.R. & Vehrencamp, S.L. (2009a). Syllable type consistency is related to age, social status, and reproductive success in the tropical mockingbird. — Anim. Behav. 77: 701-706.

Botero, C.A. & Vehrencamp, S.L. (2007). Responses of male Tropical Mockingbirds to variation in within-song and between-song versatility. — Auk 124: 185-196.

Bradbury, J.W. & Vehrencamp, S.L. (1998). Principles of animal communication. — Sinauer Associates, Sunderland, MA.

Burt, J.M., Campbell, S.E. & Beecher, M.D. (2001). Song type matching as threat: a test using interactive playback. — Anim. Behav. 62: 1163-1170.

Catchpole, C.K. & Slater, P.J.B. (2008). Bird song, biological themes and variations. — Cambridge University Press, Cambridge.

Derrickson, K.C. & Breitwisch, R. (1992). Northern Mockingbird (*Mimus polyglottos*). — In: The birds of North America online (Poole, A., ed.). Cornell Lab of Ornithology, Ithaca, NY.

Ewert, D.N. & Kroodsma, D.E. (1994). Song sharing and repertoires among migratory and resident Rufous-sided Towhees. — Condor 96: 190-196.

Ficken, R.W., Ficken, M.S. & Hailman, J.P. (1974). Temporal pattern shifts to avoid acoustic interference in singing birds. — Science 183: 762-763.

Grafen, A. (1990). Biological signals as handicaps. — J. Theor. Biol. 144: 517-546.

Grießmann, B. & Naguib, M. (2002). Song sharing in neighboring and non-neighboring thrush nightingales (*Luscinia luscinia*) and its implications for communication. — Ethology 108: 377-387.

Guilford, T. & Dawkins, M.S. (1995). What are conventional signals? — Anim. Behav. 49: 1689-1695.

Howard, R.D. (1974). The influence of sexual selection and interspecific competition on mockingbird song (*Mimus polyglottos*). — Evolution 28: 428-438.

Howell, S.N.G. & Webb, S. (1995). A guide to the birds of Mexico and northern Central America. — Oxford University Press, Oxford.

Hughes, M., Nowicki, S., Searcy, W.A. & Peters, S. (1998). Song-type sharing in song sparrows: implications for repertoire function and song learning. — Behav. Ecol. Sociobiol. 42: 437-446.

Hultsch, H. & Todt, D. (1981). Repertoire sharing and song-post distance in nightingales (*Luscinia megarhynchos* B.). — Behav. Ecol. Sociobiol. 8: 183-188.

Krebs, J.R., Ashcroft, R. & Van Orsdol, K. (1981). Song matching in the great tit *Parus major* L. — Anim. Behav. 29: 918-923.

Kroodsma, D.E. (1979). Vocal dueling among male Marsh Wrens: evidence for ritualized expressions of dominance/subordinance. — Auk 96: 506-515.

Kroodsma, D.E., Sanchez, J., Stemple, D.W., Goodwin, E., Da Silva, M.L. & Vielliard, J.M. (1999). Sedentary life style of Neotropical sedge wrens promotes song imitation. — Anim. Behav. 57: 855-863.

Kroodsma, D.E. & Verner, J. (1978). Complex singing behaviors among *Cistothorus* wrens. — Auk 95: 703-716.

Lemon, R.E. (1968). The relation between organization and function of song in cardinals. — Behaviour 32: 158-178.

Logue, D.M. & Forstmeier, W. (2008). Constrained performance in a communication network: implications for the function of song-type matching and for the evolution of multiple ornaments. — Am. Nat. 172: 34-41.

Lovette, I.J. & Rubenstein, D.R. (2007). A comprehensive molecular phylogeny of the starlings (Aves: Sturnidae) and mockingbirds (Aves: Mimidae): congruent mtDNA and nuclear trees for a cosmopolitan avian radiation. — Mol. Phylogenet. Evol. 44: 1031-1056.

Maynard Smith, J. & Harper, D. (2003). Animal signals. — Oxford University Press, Oxford.

Mennill, D.J. & Ratcliffe, L.M. (2004). Overlapping and matching in the song contests of black-capped chickadees. — Anim. Behav. 67: 441-450.

Naguib, M. (2005). Singing interactions in song birds: implications for social relations, territoriality and territorial settlement. — In: Animal communication networks (McGregor, P.K., ed.). Cambridge University Press, Cambridge, p. 300-319.

Naguib, M. & Kipper, S. (2006). Effects of different levels of song overlapping on singing behaviour in male territorial nightingales (*Luscinia megarhynchos*). — Behav. Ecol. Sociobiol. 59: 419-426.

Naguib, M. & Mennill, D.J. (2010). The signal value of birdsong: empirical evidence suggests song overlapping is a signal. — Anim. Behav. 80: e11-e15.

Nowicki, S., Peters, S. & Podos, J. (1998). Song learning, early nutrition and sexual selection in songbirds. — Am. Zool. 38: 179-190.

Nowicki, S., Searcy, W.A. & Peters, S. (2002). Quality of song learning affects female response to male bird song. — Proc. Roy. Soc. Lond. B: Biol. 269: 1949-1954.

Payne, R.B. (1982). Ecological consequences of song matching: breeding success and intraspecific song mimicry in indigo buntings. — Ecology 63: 401-411.

Piou, C., Feller, I.C., Berger, U. & Chi, F. (2006). Zonation patterns of Belizean offshore mangrove forests 41 years after a catastrophic hurricane. — Biotropica 38: 365-374.

Planck, R.J., McLaren, G. & Konishi, M. (1975). Temporal pattern shifts in singing birds: a critique. — Science 190: 292.

Reichard, D.G. & Price, J.J. (2008). Species recognition in a vocal mimic: repetition pattern not the only cue used by Northern Mockingbirds in discriminating songs of conspecifics and Brown Thrashers. — Wilson J. Ornithol. 120: 717-724.

Schroeder, D.J. & Wiley, R.H. (1983). Communication with shared song themes in tufted titmice. — Auk 100: 414-424.

Searcy, W.A. & Beecher, M.D. (2009). Song as an aggressive signal in songbirds. — Anim. Behav. 78: 1281-1292.

Searcy, W.A. & Beecher, M.D. (2011). Continued skepticism that song overlapping is a signal. — Anim. Behav. 81: e1-e4.

Sokal, R.R. & Rohlf, F.J. (1995). Biometry: the principles and practice of statistics in biological research. — W.H. Freeman, New York, NY.

Stoddard, P.K., Beecher, M.D., Campbell, S.E. & Horning, C.L. (1992). Song-type matching in the song sparrow. — Can. J. Zool. 70: 1440-1444.

Todt, D. & Naguib, M. (2000). Vocal interactions in birds: the use of song as a model in communication. — In: Advances in the study of behavior (Slater, P.J.B., Rosenblatt, J.S., Snowdon, C.T. & Roper, T.J., eds). Academic Press, New York, NY, p. 247-296.

Vehrencamp, S.L. (2000). Handicap, index, and conventional signal elements of bird song. — In: Animal signals: signalling and signal design in animal communication (Espmark, Y., Amundsen, T. & Rosenqvist, G., eds). Tapir Academic Press, Trondheim, p. 277-300.

Vehrencamp, S.L. (2001). Is song-type matching a conventional signal of aggressive intentions? — Proc. Roy. Soc. Lond. B: Biol. 268: 1637-1642.

Whitney, C.L. & Miller, J. (1983). Song matching in the wood thrush (*Hylocichla mustelina*): a function of song dissimilarity. — Anim. Behav. 31: 457-461.

Wildenthal, J.L. (1965). Structure in primary song of the mockingbird (*Mimus polyglottos*). — Auk 82: 161-189.

Wilson, P.L., Towner, M.C. & Vehrencamp, S.L. (2000). Survival and song-type sharing in a sedentary subspecies of the song sparrow. — Condor 102: 355-363.