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# Fooling the experts: accurate vocal mimicry in the song of the superb lyrebird, *Menura novaehollandiae*

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The degree of resemblance between mimics and models provides valuable insight into the evolutionary dynamics of mimicry signalling systems, but for many systems mimetic resemblance has not been quantified. Superb lyrebirds have a reputation for accurately imitating an astonishing variety of sounds that they incorporate into their sexual displays. We assessed the accuracy with which males imitate the complex song of the grey shrike-thrush, *Colluricincla harmonica*. We measured vocal accuracy by (1) using playback experiments as a bioassay, to determine whether and how shrike-thrushes distinguish between their own song and imitations of shrike-thrush songs by lyrebirds and (2) comparing acoustic properties of mimicked and model songs. Shrike-thrushes reacted just as strongly towards mimetic song as to their own when songs were presented alone. When mimetic song was accompanied by lyrebird song sequences (emulating the lyrebird's natural singing style), shrike-thrushes still usually approached the speaker but less often than when mimetic song was presented alone or when model songs were broadcast. Acoustic analyses showed that imitations were remarkably similar to model songs. However, while lyrebirds maintained the structure and complexity of model songs, they sang fewer repetitions of individual element types. This 'abridging' of model songs is consistent with a trade-off between demonstrating both mimetic accuracy and versatility. Overall, these results indicate strong selection on male lyrebirds to imitate accurately the complex vocalizations of other species, and show that species can integrate contextual information with the signal structure to distinguish between their own signals and imitations.



Mimicry is a classic example of adaptive signal design in which individuals benefit from imitating the signals of other species (Bates 1862; Müller 1878; Vane-Wright 1980) or conspecifics (Dominey 1980; Gross 1996; Norman et al. 1999; Whiting et al. 2009). Despite considerable advances over the last 150 years, many aspects of mimetic signalling systems are only beginning to be understood (Ruxton & Speed 2005; Chittka & Osorio 2007; Vereecken & McNeil 2010). One area attracting recent attention is the accuracy of mimetic signals (McGuire et al. 2006; Chittka & Osorio 2007; Pekár et al. 2011), as it has become clear that the degree of resemblance between mimics and models can provide valuable insight into the selective forces driving mimicry signalling systems (e.g. Holen & Johnstone 2004; Coleman et al. 2007; Stoddard & Stevens 2010).

Traditional theory assumes that selection will always favour mimics that most closely resemble the species or conspecific they imitate, 'the model', but several studies have challenged the simplicity of this view (Johnstone 2002; Sherratt 2002; Holen & Johnstone 2004; Chittka & Osorio 2007; Harper & Pfennig 2007; Cheney & Marshall 2009; Pekár et al. 2011). How closely the mimic resembles the model is a function of the costs and benefits of mimicry among all three protagonists in the mimicry complex: the mimic, the model and the receiver of the signal. The benefits of mimicry include gaining protection from predators, increased access to food and reproductive advantages (Starrett 1993; Cheney 2010). The costs of mimicry include increased detection by predators, conflicting signal requirements and costs imposed by the model (Edmunds 2000; Sherratt 2002; Holen & Johnstone 2004; Estrada & Jiggins 2008; Stoddard & Stevens 2010). Physiological and phylogenetic constraints on the mimic will also limit resemblance. Furthermore, mimetic accuracy can depend on the receiver's ability to discriminate between models and mimics, and inaccurate mimics may evolve as a result of weak selection on the receiver for fine discrimination, or physiological constraints on the receiver (Chittka & Osorio 2007; Cheney & Marshall 2009; Kikuchi & Pfennig 2010). Mimetic accuracy is the outcome of these benefits, costs and constraints. Thus, highly accurate mimicry implies both an

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advantage for accuracy in the mimic as well as strong selection on the receiver to discriminate between models and mimics. The nature of the differences between model and mimic are equally informative about the selection pressures shaping the mimetic signal.

Several species of bird from disparate families habitually mimic the sounds produced by other species with remarkable accuracy (Chisholm 1932), but the evolutionary drivers of vocal mimicry are usually unclear (Baylis 1982; Kroodsma 2004; Garamszegi et al. 2007; Kelley et al. 2008). In some bird species mimicry functions deceptively (Langmore et al. 2003, 2008; Flower 2011) or may provide increased protection from predators (Goodale & Kotagama 2006a,b). Alternatively, mimicry may not be deceptive and instead function to attract mates or repel rivals (Dobkin 1979). This rarely tested hypothesis is plausible in versatile mimics: oscine passerines in which males incorporate imitations of multiple sounds into elaborate, song-like displays (e.g. the northern mockingbird, *Mimus polyglottos*, marsh warbler, *Acrocephalus palustris*, and European starling, *Sturnus vulgaris*: Catchpole & Slater 2008). Here, the conspecific receiver driving the evolution of mimicry gains information about the quality of the singer by evaluating the singer's mimetic song. However, the structures of mimetic songs have seldom been examined.

Assessment of mimetic accuracy could help resolve the debate over which vocal features of versatile mimics are targeted by natural selection. Selection may favour large repertoires rather than mimicry per se, since repertoire size affects mate choice and territory defence in nonmimetic birds (reviewed in Catchpole & Slater 2008). Mimicry would thus evolve as a shortcut to gaining a large repertoire (Howard 1974) or as a by-product of repertoire acquisition itself (Hindmarsh 1986; Kelley et al. 2008). However, highly accurate mimicry provides evidence that mimicry itself is under selection, for two reasons. First, if repertoire size alone is important, accurate resemblance between model and mimetic vocalizations is unlikely to be maintained because accumulated copying errors and differential selection pressures between models and mimics should eventually lead to divergent acoustic structures. Second, it is doubtful that accurate mimicry is selectively neutral given strong evidence that precise vocal production is challenging (reviewed in Podos et al. 2009) and that individual species appear to have physiological adaptations optimized for species-specific vocalizations (Zollinger & Suthers 2004). Versatile mimics, then, are probably under selection for both mimetic accuracy and versatility, a conclusion supported by the only study to investigate the relationship between mating success and both mimetic accuracy and versatility (Coleman et al. 2007). Investigating mimetic accuracy is thus fundamental to elucidating the evolution of mimicry.

Superb lyrebirds are large (880–1100 g) oscine passerines with versatile vocal mimicry and appear to be subject to strong sexual selection (Higgins et al. 2001). Males have extravagant tails while females are cryptic, only females care for the young (Lill 1979), and during the winter breeding season males are geographically clustered in a lek-like pattern (Robinson & Curtis 1996). Males incorporate mimicry into a flamboyant vocal display with approximately 70% of vocalizations consisting of imitations of about 20 different species of local birds (Higgins et al. 2001; Zann & Dunstan 2008). Vocal displays are performed both as a prelude to mating and during territorial interactions with other males, occurring most often during the breeding season (Higgins et al. 2001). These observations strongly suggest that mimetic songs sung by males are a sexually selected trait and the receiver is either a rival male or a potential mate.

Adult superb lyrebirds enjoy a reputation for highly accurate mimicry (e.g. Attenborough 2002; Zoos South Australia 2009), but there has been only one study of mimetic accuracy in this species (Zann & Dunstan 2008). Acoustic analysis revealed that adult males reproduce individual elements from two species of bird with remarkable accuracy. Furthermore, adult males are more accurate mimics than juveniles of indeterminate sex, suggesting that mimetic accuracy improves with age. We built on this introductory investigation into mimetic accuracy in lyrebirds by analysing a complex model sound with multiple elements and by using two methods to measure accuracy: acoustic analysis and a bioassay.

Acoustic analysis is a powerful tool to investigate the accuracy of vocal parameters but an additional approach is to employ a bioassay to use a bird's assessment of mimetic accuracy (Lemaire 1975; Brenowitz 1982). The sensory systems of the model should be attuned to its own song making it a sensitive assessor of mimetic accuracy. Moreover, the model may be under selection to distinguish between conspecifics and mimics to avoid costly, unnecessary responses to mimetic signals. Studies of nonmimetic oscine passerines have shown that birds respond differently to subtle differences in species-specific songs (Stoddard 1996; Illes et al. 2006; Blumenrath et al. 2007; Botero et al. 2007; Nicholls 2008; de Kort et al. 2009). Thus bioassays have the dual advantage of being able to reveal differences between model and mimetic songs that may not be detectable using acoustic analysis, and of providing insight into signal discrimination by model species.

Our aim was to investigate the selective forces acting on mimetic song in lyrebirds by quantifying mimetic resemblance from the perspective of the model using a bioassay, and by directly measuring acoustic features of model and mimetic songs. In addition, we examined how a model species distinguished between model and mimetic songs. The grey shrike-thrush, *Colluricincla harmonica*, produces a complex, multielement song and is regularly imitated by lyrebirds (Zann & Dunstan 2008). Shrike-thrushes are ideal subjects for a bioassay because there is no evidence from our study or published accounts that shrike-thrushes interact directly with lyrebirds, making it unlikely that they select for mimicry in lyrebirds. We conducted two playback experiments. First, we tested whether shrike-thrushes could discriminate between model and mimetic songs. Given the likely costs of unnecessary responses, and the sophisticated auditory systems of oscine passerines, we assumed that shrike-thrushes would respond similarly to model and mimic only if mimicry is highly accurate. Second, since lyrebirds typically imitate several species in succession, we tested whether the model was more alert to acoustic differences if songs were presented with lyrebird mimicry of other species.

## METHODS

### *Study Site and Species*

We studied populations of superb lyrebirds and grey shrike-thrushes in Sherbrooke Forest (37°53′, 145°21′), part of the Dandenong Ranges National Park in Victoria, Australia. The population of lyrebirds has been monitored for 50 years by the Sherbrooke Lyrebird Study Group (e.g. Kenyon 1972; N. Carter, unpublished data) and many lyrebirds are individually colour-banded as nestlings. Further individuals are distinguishable by plumage. Lyrebird songs were recorded in June–July 2007 for the playback experiments, and these were supplemented with recordings made in 2008 for the sound analysis. Grey shrike-thrushes are socially monogamous, territorial passerines (Higgins & Peter 2002) and both sexes sing discrete, 3 s songs from what is probably a large repertoire of song types (Higgins & Peter 2002). The sexes can be distinguished by slight differences in plumage (Higgins & Peter 2002) but not by song. Shrike-thrushes are most vocal and territorially active from August to September, just before their breeding season. Thus they sing most when lyrebirds are relatively quiet.

Song types of grey shrike-thrushes can be classed into two different groups: (1) song types beginning with repeated, low-frequency, piping elements (Fig. 1) and (2) high-frequency song types without introductions (Higgins & Peter 2002). Low-frequency song types were more common in both species (unpublished data), so only these were considered in this study. Song types were easily identified by visual inspection of spectrograms (Fig. 1). All recordings of shrike-thrushes were made in August–October 2007.

*General Playback Design*

We carried out two experiments involving the playback of imitations of shrike-thrushes (mimetic songs) to territorial shrike-thrush pairs in Sherbrooke forest from September to October 2007. Both experiments employed a matched design so that the 15 shrike-thrush pairs in each of two experiments received all treatments. Territorial boundaries were determined by observing singing shrike-thrushes before experiments. During some playbacks both sexes responded while in others only one bird responded. Since we could not always identify each sex at all times during playbacks we measured the pair's response to the playback (e.g. the latency of the first bird to approach the speaker and the combined song output). We use the term 'pair' throughout to refer to each replicate. For each pair, the speaker was set up 1–2 m above the ground, at least 30 m inside a territorial boundary and within 30 m of the birds' current location, although birds would sometimes move further away before an experimented started. Per pair, all playbacks were presented from the same location and adjacent locations were no closer than 600 m to reduce the chance that the same pair was sampled more than once. A 15 m radius was flagged around the speaker to facilitate measurements of approach distance (after Vehrencamp et al. 2007). Playbacks were not started until at least 10 min after any aggressive interactions.

Songs used in playback experiments had high signal to noise ratios, and were recorded using a Sennheiser ME66 shotgun microphone and a Marantz PMD670 digital recorder sampling wave files at 44.1 kHz and 16 bits. Recordings were filtered below 400 Hz in Syrinx (J. Burt, http://www.syrinxpc.com). Playback tracks were normalized to 90% using Audacity 1.2.6 (http://audacutt.sourceforge.net). We played back songs at 71 dB at 9 m, which we found to be the mean natural amplitude of shrike-thrushes at that distance. We used a 'Peerless' 4-inch, midrange speaker, attached via an amplifier to a Roland Edirol R-09 HR solid-state digital player.

Each pair of shrike-thrushes was played recordings from one individual lyrebird and one shrike-thrush, both of which were recorded at least 3 km away from the experimental subjects. Pairs received playbacks of a unique set of individuals. Treatments consisted of a silent, 5 min, preplayback period, a 5 min playback period and 5 min of silent, postplayback observation. The playback period contained two sets of identical, 2 min stimuli separated by 1 min of silence. Dictated observations and vocal responses of shrike-thrushes were recorded using the Marantz recorder and shotgun microphone described above.

We assessed the response of shrike-thrushes to each playback treatment by (1) counting the songs sung, (2) determining whether shrike-thrushes type-matched broadcast songs, and (3) scoring whether they approached within 15 m of the speaker. To determine vocal responses we used spectrograms of the sound recordings of the experiment and scored separately for pre-, during and post-playback periods. Differential responses to the two experiments resulted in additional measurements of approach behaviours specific to each experiment (below).

*Experiment 1: Mimic versus Model*

We tested whether shrike-thrushes could distinguish between model and mimicked songs. Each shrike-thrush pair received a shrike-thrush song sung by a shrike-thrush, a lyrebird imitation of a shrike-thrush song and a lyrebird imitation of a an eastern whipbird, *Psophodes olivaceus*, duet. This last treatment controlled for any shrike-thrush response to lyrebird mimicry of other species or to the sounds of ecologically neutral sympatric species. Treatments were played on the same day with at least 10 min between each playback and began when the pair was within 15–50 m of the speaker. Each 2 min stimulus contained 13 repetitions of one song, emulating natural shrike-thrush singing (unpublished data). The sequence of treatments was balanced between pairs to control for

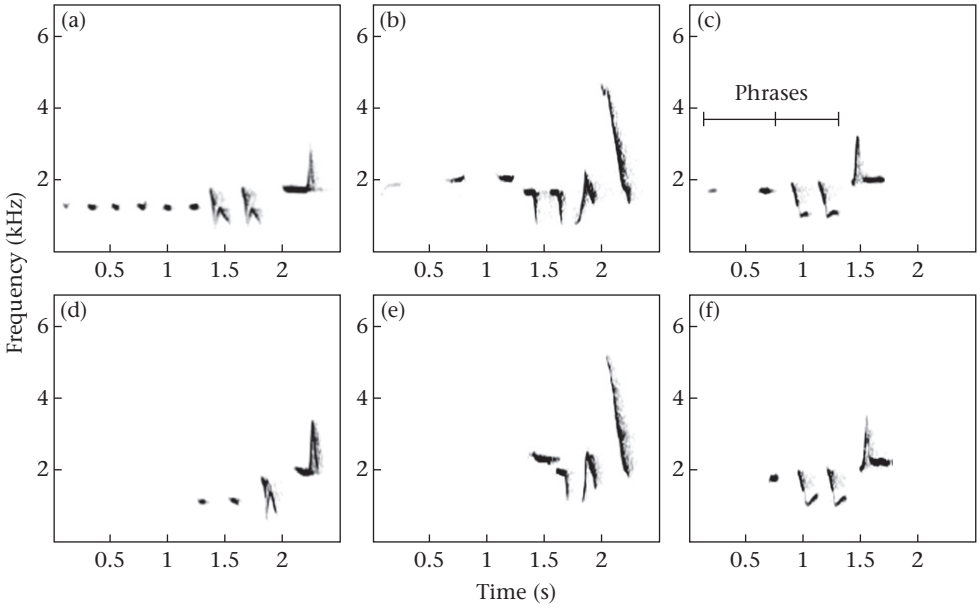


**Figure 1.** (a–c) Three different grey shrike-thrush song types sung by grey shrike-thrushes and (d–f) the same song types imitated by superb lyrebirds. Songs are subdivided into phrases containing repeats of one element type (c).

potential order effects. We also measured (4) the shrike-thrush's latency to approach within 15 m of the speaker, (5) the latency to retreat from a 15 m radius circle, (6) the closest approach to the speaker and (7) the time spent within the circle.

*Experiment 2: Song Context*

We tested whether the presence of lyrebird song caused shrike-thrushes to respond differently to playbacks of either their own species' song or imitations of their song. Each shrike-thrush pair was played four playback treatments that differed in both the species singing the song (shrike-thrush or lyrebird) and the acoustic context of the song (with additional lyrebird song or alone). Each playback consisted of a clip of one song repeated approximately every 20 s, reflecting the song rate of shrike-thrushes and the rate shrike-thrush songs were sung by lyrebirds. Playbacks presented 'alone' consisted of songs separated by periods of silence (Fig. 2a). Playbacks with a 'lyrebird context' consisted of songs separated by an approximately 18 s period of lyrebird song (Fig. 2b): a natural sequence of mimicked sounds of different species of bird interspersed with vocalizations unique to lyrebirds. These periods were edited to exclude vocalizations of shrike-thrushes and extremely loud sounds. The sequence was then amplified so that the amplitude of the shrike-thrush song was similar to the majority of sounds in the sequence of mimicry.

The four playbacks were presented using a split-plot design and were played over 2 days. Day A consisted of the two 'shrike-thrush' treatments: a model song presented (1) alone and (2) in a 'lyrebird context'. Similarly, day B consisted of the two 'imitation' treatments. The order of the tracks within days and the order of the 2 days themselves were balanced among pairs. This design limited the number of days required to complete a set of treatments (and thus avoiding long gaps between treatments caused by unsuitable weather) while minimizing potential order effects. Within a day, tracks were separated by at least 15 min and playbacks of groups A and B were separated by 1–3 days. Pairs had to be between 25 and 40 m from the speaker before the playback started. In addition to the three measurements outlined above (see General playback design) we also measured whether pairs moved at least 5 m towards the speaker because, unlike the previous experiment, some shrike-thrushes flew towards the speaker but did not come within 15 m of it ($N = 9$ of 60 playbacks).

*Quantifying Differences in Vocal Parameters*

We quantified acoustic differences between model and mimetic songs by spectrographic analyses of 38 songs with the highest signal to noise ratio and with one song from each individual. This sample included 19 different song types with an example of each song type from both the mimic and the model. We used this design because in our sample of recordings shrike-thrushes very rarely shared song types and there was a large repertoire of shrike-thrush song types in both model and mimic (72 types sung by shrike-thrushes of which 25 were imitated by lyrebirds). In two cases, there were two songs with signal to noise ratios that were indistinguishable and here we used a random number generator to choose between examples of a particular type.

We used three different approaches to quantify differences between model and mimetic songs. First, we compared model and mimetic songs in seven characteristics of the entire song: the number of different elements, the length of the song, the sound duration (sum of the duration of all elements), the average element duration, the number of different element types, the rate of elements and the peak frequency (the frequency with maximum power). Second, we compared model and mimetic songs in five characteristics of element structure including the duration, maximum frequency, frequency difference, peak frequency and the RMS amplitude (the root-mean-square amplitude across the duration of the element). Third, we tested for differences between the two species in how consistently they produced repeated song elements. Here we chose a subset of 16 song types in which both lyrebirds and shrike-thrushes produced at least one repeat of the first element in the song (e.g. Fig. 1a and d). We then compared the last two elements in the first phrase (Fig. 1) using the spectrographic cross-correlation analysis (SPCC) to obtain a peak correlation score for each song. We tested whether correlation scores

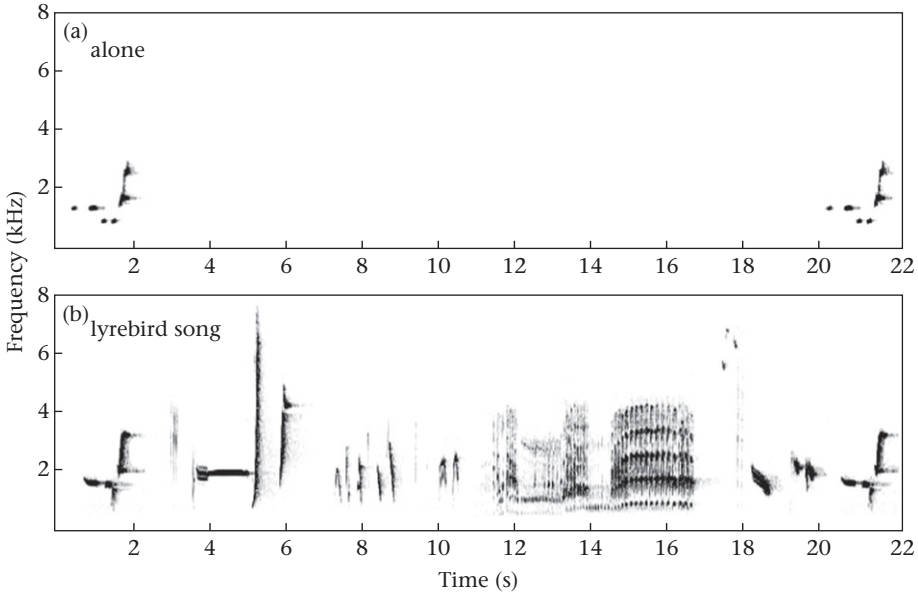


**Figure 2.** Sections from playback stimuli used in experiment 2 on song context. Playback songs were presented in (a) the grey shrike-thrush's singing style (alone) and (b) the superb lyrebird's singing style (lyrebird song context). For the lyrebird song context, each shrike-thrush song (at 1 and 21 s) is interspersed with mimicry and lyrebird-specific vocalizations. Depicted at the beginning and the end of each sequence is (a) a song sung by a shrike-thrush and (b) an imitation of a shrike-thrush by a lyrebird.

differed between species and within song types. SPCC was not used in the other two analyses because of its unsuitability for analyses involving sequences of elements and sensitivity to small transpositions in frequency (Charif et al. 1995).

All vocal parameters were quantified in Raven Pro 1.3 (Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.). Analyses were conducted on a spectrogram display type 'Blackman' (filter bandwidth: 70.7 Hz; size: 1024 samples; grid resolution: 11.3 ms, 43.1 Hz). Amplitudes of whole songs were maximized in Syrinx before analyses. SPCC analysis was performed in Raven using a 'biased' normalization procedure, a band-pass filter of 400–10 000 Hz and a linear power spectrograph of the 'Blackman' type (filter bandwidth: 120 Hz; frame length: 603 samples; grid resolution: 3.42 ms, 43.1 Hz).

### *Statistical Analyses*

Generalized linear models (GLM) using a logit link function and assuming a binomial distribution of error were constructed for approach behaviours in both experiments, while a Poisson distribution with a logarithmic link function was used to model the number of birds that approached the speaker and the number of songs shrike-thrushes sang during the playbacks. Dispersion parameters for Poisson distribution models were estimated in GenStat (Payne 2010a). Final models were chosen by first fitting a saturated model. We then discarded nonsignificant interaction terms, followed by other nonsignificant terms unless there was an a priori reason to retain control variables such as those accounting for the structure in the data. Since Genstat employs a sequential sums of squares approach, we built the saturated model by first entering control variables into the model before the variables of interest. Control variables included the distance of the closest shrike-thrush to the speaker before the playback started and the presentation order of the treatments, and are reported only when significant. Models of the number of songs sung also controlled for the number of songs sung during the 5 min before the playback. For all GLMs, residual plots were used to check that the assumptions of linear models were met (Grafen & Hails 2002) and variates were transformed as appropriate.

We employed GLMs instead of GLM mixed models because the latter failed to converge. Instead, we controlled for repeated sampling of pairs by incorporating the blocking term 'pair' into GLMs as the first term. The split-plot design of the song context experiment (experiment 2) resulted in nesting of the context of the playback (lyrebird or alone) in species (shrike-thrush or lyrebird), which was in turn nested in pair. We controlled for this further level of structure by fitting an interaction term between 'pair' and 'species' before fitting the context of the playback (lyrebird or alone), and the interaction between context and 'species'. In both experiments, we used nonparametric tests if data failed to conform to diagnostic tests for a normal distribution of residuals.

Differences between the acoustic structures of model and mimetic songs were analysed using univariate models of individual parameters. Continuous measures of whole songs were first modelled using a mixed models approach with species fitted as a fixed effect and 'song type' modelled as a random term. In several models, the error of this random term was large, and the variance was small, relative to the fixed effect. Therefore, we conducted a likelihood ratio test of the difference in deviance between a model containing song type and one without (Payne 2010b). If the test statistic approached zero, song type was dropped from the model to permit more accurate estimates. The measurement 'song complexity' contained just three levels and was thus analysed using a Wilcoxon signed-ranks test with the data paired according to song type. For analyses of element structure, the random components consisted of the phrase within the song nested in song type to account for the structure in the data (elements, nested within phrases, nested within song types, Fig. 1).

Performing multiple statistical tests can increase the probability of falsely rejecting the null hypothesis (Grafen & Hails 2002) but we were also concerned with type II errors. To balance these two inversely related errors, we emphasize stronger effects in the discussion ($P < 0.01$) and report least significant differences (LSD) and 95% confidence intervals (CI) of effect sizes where possible. In line with recent theory (Colegrave & Ruxton 2003), our conclusions regarding the similarity between model and mimetic song rely most heavily on measurements with smaller confidence intervals of the effect size (or LSD).

All statistical tests were carried out using GenStat 11.1 (VSN International, Hemel Hempstead, U.K.) except for Wilcoxon signed-ranks tests and associated CI, which were calculated using StatsDirect 2.7.8 (StatsDirect Ltd, Altrincham, U.K.).

### *Ethical Note*

This research was conducted under permits from the Animal Experimentation Ethics Committee of the Australian National University and the Victorian Department of Sustainability and Environment.

## RESULTS

### *Experiment 1: Mimic versus Model*

There was no difference between the behaviour of grey shrike-thrushes towards mimetic and model songs in any measure of speaker approach. Shrike-thrushes were equally likely to approach within 15 m of a speaker broadcasting model songs as mimetic songs (12/15 pairs in each case), but only 1/15 came within 15 m of the lyrebird imitation of whipbirds (Fig. 3; GLM: $\chi_2 = 19.3$, $P < 0.001$). Similarly, the number of birds approaching within 15 m of the speaker was identical after playback of model and mimetic songs, but lower following playback of an imitation whipbird duet

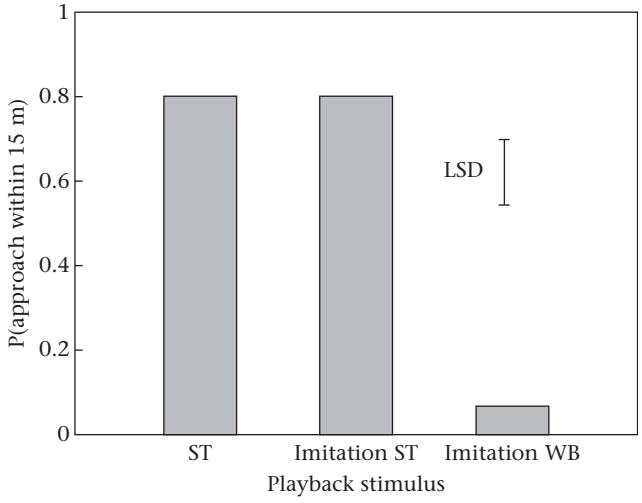


**Figure 3.** Experiment 1, mimic versus model: the proportion of grey shrike-thrush pairs that approached within 15 m of a speaker broadcasting a song sung by an actual shrike-thrush (ST), an imitation of an ST song by a superb lyrebird (imitation ST) or a lyrebird imitating an eastern whipbird duet (imitation WB). Columns show predicted means generated from the model and the bar indicates the average least significant difference (LSD) of the means at the 5% level; $N = 15$ pairs. Statistics are reported in the text.

(GLM: $F_{2,28} = 13.1$, $P < 0.001$; imitation shrike-thrush: mean = 1.13; shrike-thrush: mean = 1.13; imitation whipbird: mean = 0.13; average LSD = 0.53). We did not detect any subtle differences in the approach responses of shrike-thrushes to playbacks of imitations or shrike-thrush songs after excluding the control playback (Table 1), suggesting that shrike-thrushes did not distinguish between model and mimetic songs; however, given the broad confidence intervals for some measurements, there was still room for smaller, undetected differences in responses.

Shrike-thrushes sang a similar number of songs during playback of mimetic songs as model songs and responded with fewer songs to playback of an imitation whipbird duet (Fig. 4, Table 2). This result was independent of an increase in the number of songs when more birds were singing, and the tendency of some pairs to sing consistently more than others (Table 2). Shrike-thrushes also responded with more songs after playback of mimetic and model songs than after a whipbird duet during the 5 min after the playback had ended (Table 2).

The only measure of shrike-thrush response that differed between model and mimetic songs was that shrike-thrushes were more likely to type-match model songs (two-tailed binomial test: $H_0$ model = mimic; model: 7/15; mimic: 1/15; $P = 0.013$), although the number of type matches after playback of model sounds varied greatly (1–36).

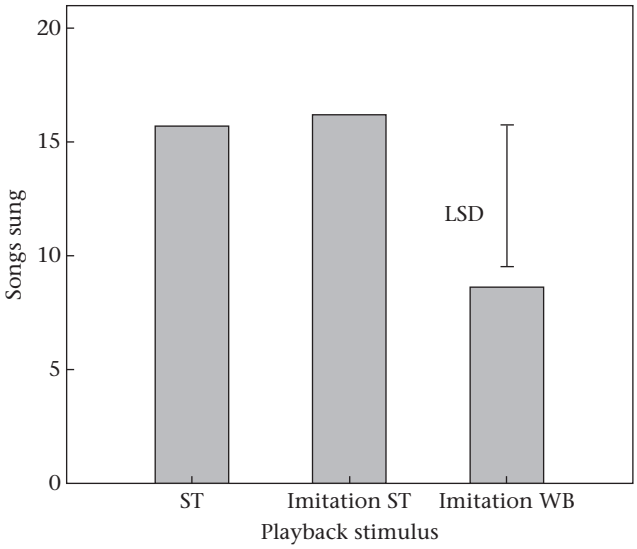


**Figure 4.** Experiment 1, mimic versus model: the predicted means of the number of songs sung by grey shrike-thrushes during the 5 min playback period in response to playback of a song sung by an actual shrike-thrush (ST), an imitation of a ST song by a superb lyrebird (imitation ST) or a lyrebird imitating an eastern whipbird duet (imitation WB). The bar indicates the average least significant difference (LSD) of the means at the 5% level; $N = 15$ pairs. Statistics are shown in Table 2.

*Experiment 2: Song Context*

Shrike-thrush pairs were less likely to approach a speaker broadcasting a mimetic song when it was embedded within a lyrebird's natural song sequence than when it was presented alone, but they nearly always approached model songs regardless of context (Fig. 5, Table 3). The number of birds approaching the speaker was not affected by the type of playback or any other of the modelled variables ($P > 0.1$).

Shrike-thrushes sang more songs during playback of model songs than mimetic songs (model mean = 22.0 songs; mimic mean = 14.1; LSD = 6.72; Table 4) but there was no effect of the context of the song (context: $P = 0.2$; interaction: $P = 0.6$). Shrike-thrushes continued to sing more songs during the 5 min after a playback of model songs than mimetic songs (model mean = 20.6 songs; mimic mean = 14.0; LSD = 6.90; Table 4) after we controlled for a greater song rate among pairs associated with closer proximity to the speaker before the beginning of the playback (Table 4). Again, there was no effect of the context of the song (context: $P = 0.6$; interaction: $P = 0.1$). Unsurprisingly, the total number of songs sung increased with the number of birds singing in both playback periods (Table 4). There was no evidence that shrike-thrushes were more likely to type-match some playback treatments more than others (species singing the song: models = 6/15; mimetic = 2/15; two-tailed binomial test: $H_0$ model = mimic: $P = 0.10$; song context: alone = 5/15; song sequence = 4/15; two-tailed binomial test: $H_0$ alone = song sequence: $P = 0.69$).

*Acoustic Analyses*

Of 13 measures of acoustic properties, only three differed between model and mimetic songs. We detected no differences between model and mimetic element structures (Table 5) suggesting that lyrebirds accurately reproduced the structure of elements within shrike-thrush songs. In addition, spectrographic cross-correlation analysis showed that lyrebirds produced the elements in the first phrase of imitations just as consistently as shrike-thrushes (lyrebird median = 0.93; shrike-thrush median = 0.95; pairwise median difference = 0.015; 95.6% CI = −0.050–0.11; Wilcoxon signed-ranks test: $T = 88$, $N = 16$, $P = 0.3$). The only differences between mimetic and model songs were found in measures of length (Table 5); for example, mimetic songs had fewer elements than model songs. However, the distribution of the number of elements in the songs of both species still overlapped (Fig. 6). Mimetic songs did not differ from model songs in the number of different types of elements (Wilcoxon signed-ranks test: $T = 4$,

**Table 1**
Experiment 1, mimic versus model: paired comparisons of speaker approach behaviours by grey shrike-thrushes during playback of model and mimetic songs

| Dependent variable | Test | *T*/*t* | *P* | Mean/median (95% CI) of difference (shrike-thrush–lyrebird)* |
|---|---|---|---|---|
| Closest approach (m) | *T* | 50.5 | 0.77 | 0.15 (−5.4 – 11.6) |
| Latency to approach (s) | *T* | 54 | 0.95 | 1.44 (−149 – 56.3) |
| Time within 15 m (s) | *t* | 0.57 | 0.58 | 80.7 (−224 – 385) |
| Latency to approach within 15 m (s) | *t* | 0.25 | 0.81 | 16.8 (−128 – 162) |
| Latency to retreat further than 15 m (s) | *t* | 0.39 | 0.70 | 50.1 (−225 – 326) |

Wilcoxon signed-ranks tests (*T*) were used instead of paired *t* tests (*t*) where data were not normally distributed. $N = 15$.
* Median differences are shown for Wilcoxon signed-ranks tests and approximate 95% CI. Means and exact 95% CI are shown for *t* tests.

**Table 2**
Experiment 1, mimic versus model: significant effects on the number of songs grey shrike-thrushes sang in response to playback of their own song, an imitation of their song by a superb lyrebird and an imitation of an eastern whipbird duet by a superb lyrebird ('playback type')

| Dependent variable | Effects | *df* | Approximate *F* | *P* |
|---|---|---|---|---|
| Songs during 5 min playback | Whole model | 17, 27 | 5.43 | <0.001 |
| | Pair | 14, 27 | 4.64 | <0.001 |
| | Playback type* | 2, 27 | 8.93 | 0.001 |
| | No. of birds singing | 1, 27 | 9.47 | 0.005 |
| Songs 5 min after playback | Whole model | 16, 28 | 5.20 | <0.001 |
| | Pair | 14, 28 | 5.04 | <0.001 |
| | Playback type | 2, 28 | 6.29 | 0.006 |

* Model predictions are shown in Fig. 4.

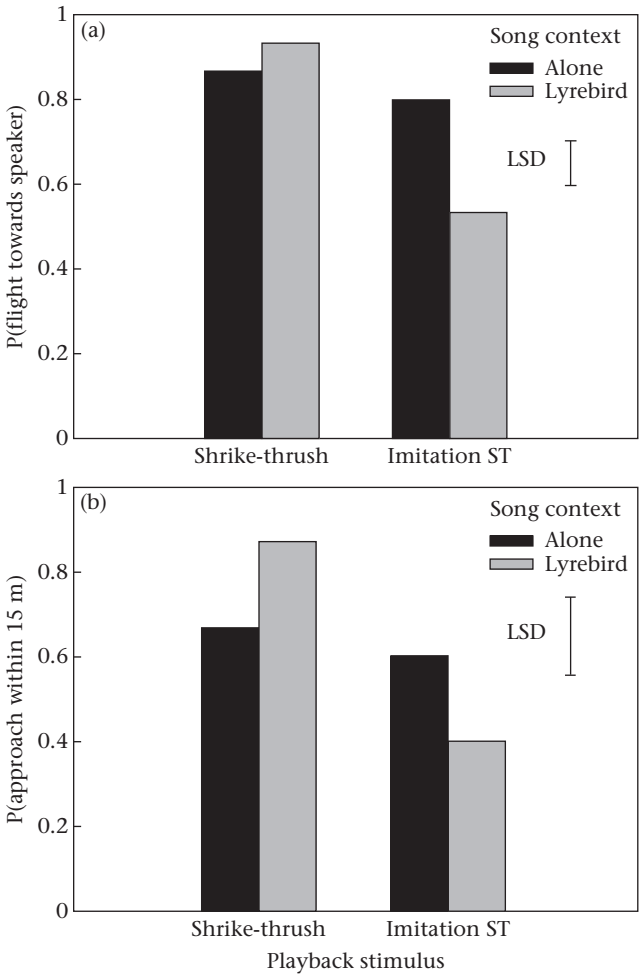


**Figure 5.** Experiment 2, song context: the proportion of grey shrike-thrush pairs that (a) flew at least 5 m towards the speaker or (b) approached within 15 m of a speaker, broadcasting a song sung by an actual shrike-thrush (shrike-thrush) or an imitation of a shrike-thrush song by a superb lyrebird (imitation ST). Each song was either embedded in a stream of mimicry sung by a lyrebird (lyrebird song context) or presented in isolation (alone). Columns show model predictions and the average least-significant difference (LSD) of the means at the 5% level are shown; $N = 15$ pairs. Statistics are shown in Table 3.

**Table 3**
Experiment 2, song context: final generalized linear models of grey shrike-thrush approach behaviours in response to playback of shrike-thrush song sung by either a superb lyrebird or a shrike-thrush ('species'), embedded in either a period of silence or a sequence of lyrebird song ('context')

| Dependent variable | Effects | *df* | Approximate $\chi^2$ | *P* |
|---|---|---|---|---|
| Flight ≥ 5 m towards the speaker | Whole model | 31 | 1.78 | 0.005 |
| | Pair | 14 | 1.68 | 0.051 |
| | Species | 1 | 7.83 | 0.005 |
| | Pair*Species | 14 | 0.85 | 0.615 |
| | Context | 1 | 2.66 | 0.103 |
| | Context*Species† | 1 | 9.11 | 0.003 |
| Approach within 15 m of the speaker | Whole model | 31 | 2.54 | <0.001 |
| | Pair | 14 | 2.12 | 0.008 |
| | Species | 1 | 7.99 | 0.005 |
| | Pair*Species | 14 | 1.75 | 0.039 |
| | Context | 1 | ~ 0.00 | <1 |
| | Context*Species† | 1 | 7.76 | 0.005 |

The dependent variable was dichotomous and the experiment had a split-plot design.
† Model predictions are shown in Fig. 5.

**Table 4**
Experiment 2, song context: final generalized linear models of the number of songs grey shrike-thrushes sang in response to playback of shrike-thrush song sung by either a superb lyrebird or a shrike-thrush ('species'), embedded in either a period of silence or a sequence of lyrebird song ('context')

| Dependent variable | Effects | *df* | Approximate *F* | *P* |
|---|---|---|---|---|
| Songs during 5 min playback | Whole model | 16, 43 | 2.75 | 0.004 |
| | Pair | 14, 43 | 1.97 | 0.045 |
| | Species* | 1, 43 | 5.59 | 0.023 |
| | Number of birds singing | 1, 43 | 11.19 | 0.002 |
| Songs 5 min after playback | Whole model | 17, 42 | 2.54 | 0.007 |
| | Pair | 14, 42 | 1.64 | 0.106 |
| | Initial distance from speaker | 1, 42 | 7.47 | 0.011 |
| | Species* | 1, 42 | 6.01 | 0.021 |
| | Number of birds singing | 1, 42 | 7.33 | 0.010 |

* Model predictions are reported in the text.

$N = 19$, $P = 0.75$) showing that lyrebirds maintained the same song structure as models but sang fewer repetitions of each element type (Fig. 1).

## DISCUSSION

Our playback experiments and sound analyses show that superb lyrebirds are accurate mimics of grey shrike-thrush songs. Indeed, their mimetic songs were accurate enough to prompt grey shrike-thrushes to approach the playback speaker in most circumstances. However, there were subtle differences between the mimetic and model songs that models responded to, particularly once alerted to the presence of a lyrebird.

### *Accuracy, Signal Context and Model Response*

Shrike-thrush pairs responded strongly towards both mimetic and model songs when both songs were presented in isolation (experiment 1: mimic versus model). We detected no differences between the behaviour of shrike-thrushes towards mimetic lyrebird songs and those sung by real shrike-thrushes in any measure of speaker approach behaviour or in singing effort. Most strikingly, measures of approach within 15 m of broadcasts of mimic and conspecific song were identical, and birds sang an almost identical number of songs. The response to mimetic song was not a response to lyrebird mimicry in general, because shrike-thrushes rarely approached during control playbacks of lyrebird mimicry of another species, and in that situation their song rate was half that to lyrebird mimicry of shrike-thrushes.

Experiments using a similar bioassay to test the accuracy of mimicry of northern mockingbirds found differences in response according to model sex and species. Male red-winged blackbirds, *Agelaius phoeniceus* (Brenowitz 1982), but not females (Searcy & Brenowitz 1988), reacted equally strongly to model and mimetic songs. However, these two studies measured different responses by each sex and played back songs from only one mockingbird, making it difficult to draw general conclusions. A third, well-replicated study found that Florida scrub-jays, *Aphelocoma coerulescens*, responded less strongly to mockingbird imitations of their territorial 'weep' calls than towards conspecific weep calls (Owen-Ashley et al. 2002). These studies suggest that either mimetic accuracy varies with the model or that discriminatory ability differs between models.

Our second experiment showed that shrike-thrushes were more likely to approach a speaker broadcasting mimetic songs when they were presented alone, than together with lyrebird song containing

**Table 5**
Differences between the acoustic structures of model and mimetic songs

| Effects | Estimate | SED | LSD | *df* | *F* | *P* |
|---|---|---|---|---|---|---|
| **Songs** | | | | | | |
| Number of elements* | −1.2105 | 0.3613 | 0.7326 | 1, 36.0 | 11.23 | 0.002 |
| Song length* | −0.3374 | 0.1072 | 0.2173 | 1, 36.0 | 9.91 | 0.003 |
| Sound duration | −0.14184 | 0.04958 | 0.1042 | 1, 18.0 | 8.19 | 0.010 |
| Average element length | 0.004723 | 0.005139 | 0.01080 | 1, 18.0 | 0.84 | 0.37 |
| Peak frequency† | −0.005280 | 0.008055 | 0.01692 | 1, 18.0 | 0.43 | 0.52 |
| Element rate* | 0.05544 | 0.1660 | 0.3367 | 1, 36.0 | 0.11 | 0.74 |
| **Elements** | | | | | | |
| Frequency range | −119 | 76.4 | 150.7 | 1, 176.6 | 2.43 | 0.121 |
| Peak frequency†,‡ | −1.975 | 58.49 | 0.05412 | 1, 179.0 | ~0 | 0.973 |
| Maximum frequency | −55.7 | 99.06 | 195.5 | 1,177.3 | 0.32 | 0.575 |
| RMS amplitude§ | 501.6 | 444.9 | 877.8 | 1,181.9 | 1.27 | 0.261 |
| Duration | 0.00267 | 0.006125 | 0.01209 | 1, 178.5 | 0.19 | 0.663 |

Parameters were modelled in univariate linear mixed models or linear models with species as a fixed effect. Song-level analyses contained 'Song type' modelled as a random term unless the variance of this component approximated zero, in which case Song type was dropped from the model (Payne et al. 2010). For element-level analyses, the phrase within the song, nested in song type, was modelled as a random term. Estimates of the differences between the means (lyrebird−shrike-thrush), the standard error of difference between the means (SED) and the approximate least significant differences (LSD) at the 5% level are shown.

* These models were run without the variable 'song type' as a random effect.

† This variable was log transformed to normalize the residuals.

‡ Frequency with maximum power.

§ Root-mean square of the amplitude across the duration of the element.

imitations of other species. Discrimination was not simply based on the presence of lyrebird song: shrike-thrushes more often approached model than mimetic songs when both were presented with lyrebird song. However, even when mimetic songs were presented with lyrebird song, shrike-thrushes still approached 50% of the time, suggesting that discriminating between mimic and model continued to be difficult.

Two further results from our experiments suggest that while shrike-thrushes responded strongly towards their songs sung by both conspecifics and lyrebirds, their reaction was more intense towards their own song. First, in the context experiment (experiment 2) shrike-thrushes sang fewer songs in response to playbacks of imitations than to model songs. This effect was not present in the first experiment, possibly because many pairs had started incubating by the time the second experiment was conducted, forcing birds to respond strongly only to the greatest threats. Second, shrike-thrushes were more likely to song type-match a playback of a song sung by a conspecific than an imitation, although this effect was only present in experiment 1. Song type matching can be a more aggressive signal than singing a nonmatching song type (Molles & Vehrencamp 2001; Beecher & Campbell 2005), again suggesting that shrike-thrushes responded marginally more strongly towards playback of models. Importantly, these effects were subtle and the presence of lyrebird song was the only factor influencing whether or not a shrike-thrush approached a playback of an imitation.

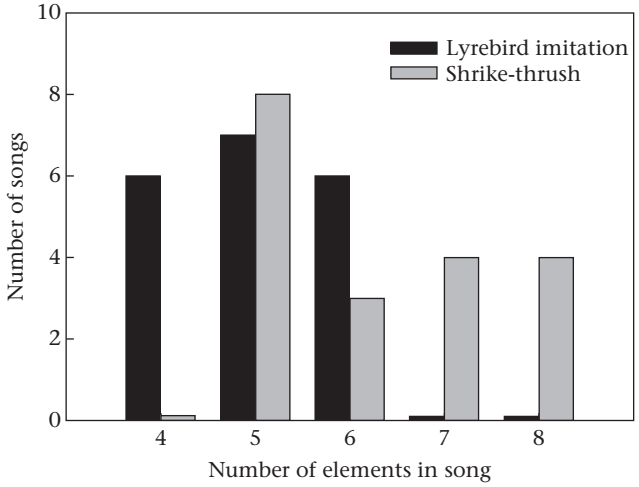


**Figure 6.** The number of songs with different numbers of elements sung by both grey shrike-thrushes and superb lyrebirds. The sample contained one song sung by a lyrebird and one by a shrike-thrush for 19 different song types. Statistics are shown in Table 5.

That shrike-thrushes are more discriminating when mimicry was presented with a sequence of lyrebird song shows that shrike-thrushes have a flexible acceptance threshold and that they integrate cues to distinguish model from mimetic songs. Traditional theory argues that it is impossible to reduce the risk of responding to a false signal, such as an imitation, without simultaneously increasing the risk of failing to respond to a real signal, and vice versa (Wiley 1994). However, animals can mitigate the costs of mistakenly responding to a mimic by varying their threshold criteria for signal identification (acceptance) depending on other cues ('flexible acceptance thresholds': Reeve 1989). For example, several host species of brood parasites are more likely to reject unusual eggs if they have recently been exposed to a cuckoo (Davies & Brooke 1988; Moksnes & Røskaft 1989; Davies et al. 1996; Bártol et al. 2002), or had additional evidence that cuckoos were present (Hauber et al. 2006; Stokke et al. 2008; Langmore et al. 2009). In our study, shrike-thrushes appeared to use the context of the signal to decide whether or not to approach playback of a mimetic song. Contrary to the predictions of signal detection theory, raising their acceptance threshold did not simultaneously reduce the chance they would fail to respond to their own song, although further experiments are required to explore this hypothesis. To our knowledge, only one other study has formally tested the use of context by model species in a vocal mimicry system (Owen-Ashley et al. 2002). However, this study found that models responded weakly to mimetic calls regardless of context. In contrast, our study adds to the growing literature showing that signal acceptance thresholds are plastic and context dependent.

### *Acoustic Differences Between Model and Mimetic Songs*

Our comparison between the acoustic parameters of mimicked and model songs revealed few differences. Lyrebirds accurately reproduced the temporal patterning of elements that characterize shrike-thrush songs. This is an unusual characteristic in birds that

imitate many different sounds (versatile avian mimics), which more commonly imitate fragments of song or short vocalizations (Hindmarsh 1984; Ferguson et al. 2002). In addition, lyrebird reproductions of individual elements within the model song were indistinguishable from model elements. However, lyrebirds may not be able to imitate all model elements as accurately as shrike-thrush songs, as lyrebirds are less accurate mimics of the 'whip' element in the eastern whipbird song, perhaps because of the large and rapid frequency change (Zann & Dunstan 2008).

In our study, mimetic and model songs differed only in the number of elements (Table 5), causing mimetic songs to be on average the shorter of the two. Lyrebirds abridged model songs by reducing the number of repetitions of particular element types while conserving the order and number of different element types and thus the structural complexity of the model song (Fig. 1). This suggests that differences between mimic and model were unlikely to be caused by limitations of the lyrebird's auditory system. Instead, our results support previous speculation that lyrebirds are not passive imitators of common sounds (Higgins et al. 2001; Zann & Dunstan 2008). Rather, lyrebirds appear either to imitate selectively shorter examples of model songs or to abridge the songs they hear. In our study, shrike-thrushes might have used the differences in element number to distinguish between model and mimetic songs, but confirmation requires further experiments.

Imitations of shrike-thrush songs are not the only imitations that lyrebirds appear to shorten. Zann & Dunstan (2008) showed that lyrebird imitations of male whipbird song had a shorter introductory 'tone' element than model songs, and lyrebirds appear to truncate imitations of the vocalizations of other species such as the 'laugh' calls of laughing kookaburras, *Dacelo novaeguineae* (Smith 1988, A. H. Dalziell, personal observation). Such shortening of mimicked sounds may be a feature common to versatile avian mimics. For example, imitations by northern mockingbirds of the 'weep' calls produced by Florida scrub-jays were shorter in element duration than the model species itself (Owen-Ashley et al. 2002).

### *Why are Lyrebird Imitations Shorter Than Model Songs?*

Lyrebirds might sing shorter versions of model songs as a result of selection pressures imposed by a conspecific receiver. Short imitations may arise if male lyrebirds need to balance two requirements: to sing highly accurate imitations, but also to demonstrate their versatility to a conspecific receiver who may listen for only a short time. This is a modification of the 'Jack of all trades' hypothesis, which predicts that mimetic accuracy is traded off against mimetic versatility (Edmunds 2000; Zollinger & Suthers 2004). However, rather than being the result of limitations of the vocal apparatus of the mimic (Zollinger & Suthers 2004), differences in the length of model and mimetic sounds may reflect conflicting signal requirements. Alternatively, male lyrebirds may sing shorter songs to facilitate discrimination by conspecifics between lyrebirds and model species, although it seems plausible that visual cues or other acoustic cues, such as song context, should be sufficient for discrimination. Further research is required to determine why lyrebirds abridge model songs and whether it is a widespread strategy among versatile mimics.

### *Mimetic Accuracy in Nondeceptive Mimicry Systems*

Our bioassays combined with acoustic analysis revealed remarkably accurate mimicry of a complex auditory signal by a nondeceptive mimic. Given the motor challenges of producing song in birds (Gil & Gahr 2002; Catchpole & Slater 2008; Podos et al. 2009), our results are consistent with selection for accurate mimicry in male lyrebirds and suggest that there is selection for discrimination in receivers. Future studies will need to conduct playback experiments to other lyrebirds to confirm whether conspecifics are the receivers selecting for accurate mimicry. In nondeceptive mimicry systems the conspecific receiver conceivably has a more complex cognitive task than a heterospecific receiver. This is because the conspecific receiver not only has to discriminate between model and mimetic vocalizations, but it also has to discriminate between mimics on the basis of their mimetic ability. Overall, our results highlight the complexity of adaptations evolved by mimics and the value of examining the similarities and differences between model and mimetic signals.

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