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# Male superb lyrebirds mimic functionally distinct heterospecific vocalizations during different modes of sexual display

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Mimicry has long been a focus of research, but little is known about how and why many species of bird incorporate imitations of heterospecific sounds into their vocal displays. Crucial to understanding mimetic song is determining what sounds are mimicked and in what contexts such mimicry is produced. The superb lyrebird, *Menura novaehollandiae*, is a large oscine passerine with a lek-like mating system. Both sexes are accurate and versatile vocal mimics of the vocalizations of other species, but little is known about how males deploy their repertoire of mimicked sounds across contexts. Using extended focal watches, we recorded adult males displaying during the breeding season. We found that males mimicked heterospecific songs and nonalarm calls during 'recital' displays usually performed while they were perched and visually inconspicuous. In contrast, during visually conspicuous 'dance' displays, commonly performed on display mounds, males only mimicked heterospecific alarm calls. While much rarer than recital displays, dance displays were associated with the final stages of mate choice preceding copulation. These results provide the first evidence of any species varying its repertoire of mimicked sounds with different sexual contexts. Previous work suggests that mimicry in dance displays functions deceptively to manipulate the antipredator responses of females during the final stages of courtship. However, the structure and context of recital mimicry closely resembles the sexual advertisement song performed by nonmimicking songbirds. Given the importance of mimicry in the acoustic ecology of lyrebirds, our results suggest that with recital song males advertise the quality of their mimicry as it likely benefits both male and female offspring. Our finding that male superb lyrebirds mimic functionally distinct heterospecific vocalizations during different modes of courtship suggests that the evolution and maintenance of avian vocal displays are more complex than previously thought.

Many organisms gain adaptive benefits by mimicking other species (Dalziell & Welbergen, 2016b). Mimetic signals can play a crucial role in predator and prey interactions (Ruxton et al., 2018), brood parasitism (Davies, 2015; Feeney et al., 2014) and intrasexual rivalry (Hanlon et al., 2005; Norman et al., 1999; Saetre & Slagsvold, 1996). However, the vast majority of these studies have focused on visual mimetic signals (Ruxton et al., 2005, 2018), neglecting mimetic signals expressed through other sensory modalities (Dalziell & Welbergen, 2016b). Mimetic vocalizations in birds are particularly poorly understood (Dalziell et al., 2015). In some cases, vocal mimicry can deceive heterospecifics, much like many visual signals. Such deceptive vocal mimicry can facilitate interspecific brood parasitism (Langmore et al., 2008), enable the theft of food from heterospecifics (Flower, 2011; Flower et al., 2014) and deter nest predators (Igic et al., 2015; Rowe et al., 1986). In other contexts, vocal mimicry may facilitate interspecific communication about predators, perhaps to the mutual benefit of both mimic and receiver (e.g. Goodale & Kotagama, 2006a; Wheatcroft & Price, 2013; reviewed in Dalziell et al., 2015; Magrath et al., 2015). However, little progress has been made explaining mimetic vocalizations used in the context of sexual displays (Dalziell et al., 2015).

One hypothesis developed exclusively to explain avian vocal mimicry is that it functions to attract mates (Baylis, 1982; Dobkin, 1979; Kelley et al., 2008), but rarely has this hypothesis been tested formally (Dalziell et al., 2015; Kelley et al., 2008). The mate attraction hypothesis attempts to explain why the males of several species of oscine passerine, from disparate families, routinely incorporate imitations of multiple heterospecific sounds into their complex vocal displays (e.g. common starlings, *Sturnus vulgaris*,

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Hindmarsh, 1984; black-browed reed warblers, *Acrocephalus bistrigiceps*, Hamao & Eda-Fujiwara, 2004; northern mockingbirds, *Mimus polyglottos*, Gammon & Altizer, 2011; Albert's lyrebirds, *Menura alberti*, Putland et al., 2006). Such mimetic vocal displays can closely resemble sexual advertisement song (as defined in Catchpole & Slater, 2008), being sexually dimorphic, produced primarily in the breeding season and delivered from a perch in long bouts (e.g. Dowsett-Lemaire, 1979; Howard, 1974). Observations such as these have led to the suggestion that vocal mimicry evolves as a by-product of selection for large repertoires (Baylis, 1982; Hindmarsh, 1986; Howard, 1974; Kelley et al., 2008), as larger vocal repertoires are commonly correlated with male mating success in many nonmimicking species (reviewed in Catchpole & Slater, 2008). In this by-product hypothesis, repertoires of mimetic vocalizations are either functionless mistakes or have the same function as repertories of species-specific song types (Dalziell et al., 2015).

A major conceptual problem with the by-product hypothesis for the production of vocal mimicry during advertisement song is that it does not adequately explain the maintenance of mimetic accuracy (Dalziell & Magrath, 2012; Dalziell et al., 2015; Kelley et al., 2008; Zann & Dunstan, 2008). If females are simply selecting mates that produce the most versatile song, then in theory there is no selection for mimetic accuracy, and mimetic resemblance should erode over time. A study of satin bowerbirds, *Ptilonorhynchus violaceus*, presents a partial solution to this problem. Coleman et al. (2007) found that male mating success was positively correlated with both repertoire size and the accuracy of male vocal mimicry, suggesting that females could be selecting mates with mimicry that most closely resembled model vocalizations. However, there is no explanation for why female satin bowerbirds would select for vocal mimicry in males, rather than choosing males that produce accurate and versatile conspecific song. Fundamentally, hypotheses for the evolution of vocal mimicry in advertisement song are greatly restricted by a dearth of behavioural and ecological data on vocal mimicry in general (Baylis, 1982; Dalziell et al., 2015; Garamszegi et al., 2007; Goller & Shizuka, 2018; Kelley et al., 2008).

Understanding the social, ecological and behavioural contexts in which particular signals are produced is an essential first step to determining how they function (Smith, 1965), and is key to progressing knowledge of avian vocal mimicry in song (Dalziell et al., 2015). Documenting the immediate context in which different types of nonmimetic songs are produced has been highly informative, revealing, for example, that some species use individual song types, or sets of song types, in different contexts, indicating that different song types can have different functions (reviewed in: Byers & Kroodsma, 2009; Catchpole & Slater, 2008; Trillo & Vehrencamp, 2005). Different mimetic song types could similarly have different functions. Contextual information relevant to investigating the function of vocalizations includes the time of day or year, what individuals are present and what other behaviours are performed while vocalizing (Smith, 1965). Context-dependent vocal mimicry has provided valuable insight into the function of vocal mimicry in some species that mimic in nonsong contexts including brown thornbills, *Acanthiza pusilla* (Igic & Magrath, 2014), greater racket-tailed drongos, *Dicrurus paradiseus* (Goodale & Kotagama, 2006a; 2006b) and fork-tailed drongos, *Dicrurus adsimilis* (Flower et al., 2014). It is also useful to determine how mimicry is integrated with species-specific vocalizations (Eens, 1997; Goodale & Kotagama, 2006a; Igic & Magrath, 2014).

A second crucial step in determining the function of mimetic sounds is to identify what species are mimicked and the original function (if any) of the imitated sounds in the model species. Such data can enable researchers to distinguish among different hypotheses for the function of vocal mimicry (Dalziell et al., 2015; Kelley & Healy, 2011), particularly if the ecological relationships among the mimic, model and likely receiver are known. For example, brown thornbills mimic the ‘aerial’ alarm calls that other species produce in response to predatory *Accipiter* hawks in flight (Igic & Magrath, 2014). However, thornbills can mimic these aerial alarm calls in the absence of flying hawks, and specifically when a predator is at their nest. These observations suggest that this mimicry is a deceptive signal used to deter nest predators (Igic & Magrath, 2014), a hypothesis subsequently confirmed by experiments (Igic et al., 2015). In the present study, we examined the mimetic content as well as the acoustic, behavioural and temporal contexts of mimetic vocalizations in the male superb lyrebird, *Menura novaehollandiae*.

Superb lyrebirds are versatile and accurate vocal mimics (Dalziell & Magrath, 2012; Dalziell et al., 2021; Zann & Dunstan, 2008) but despite considerable interest, it has not been clear why male lyrebirds mimic. Superb lyrebirds have a lek-like mating system and are endemic to southeastern Australia (Higgins et al., 2001). During mid-winter when most eggs are laid, adult males perform a spectacular, complex display incorporating a suite of visual and vocal signal components (Dalziell et al., 2013; Higgins et al., 2001). Mature males have elongated, modified tail feathers that they invert over their heads, revealing striking ventral patterns. Males exhibit their feathers in a dance-like display, often performed on one of several circular display arenas (‘display mounds’) that they defend from other males (Dalziell et al., 2013; Higgins et al., 2001). Individuals raised in zoos routinely produce remarkably accurate renditions of anthropogenic sounds, such as chainsaws, car alarms and even crying human infants (Dalziell & Welbergen, 2021), indicating that male lyrebirds have an innate propensity for producing learned, highly accurate vocal mimicry. In the wild, males perform a loud flamboyant song consisting of song types exclusive to lyrebirds and extreme levels of imitations of foreign sounds, most commonly the songs and calls of other species of bird (Higgins et al., 2001; Zann & Dunstan, 2008). Imitated sounds are acoustically diverse and astonishingly accurate (Dalziell & Magrath, 2012; Dalziell et al., 2021; Higgins et al., 2001; Zann & Dunstan, 2008), and make up 70–80% of vocal output (Robinson, 1974; Robinson & Curtis, 1996). While both sexes mimic, only males mimic during intersexual interactions, and females mimic primarily in the contexts of female–female interactions and nest defence (Dalziell & Welbergen, 2016a). This sex-specific context dependence of vocal mimicry suggests that mimetic vocalizations function differently in each sex (Dalziell & Welbergen, 2016a).

Collectively, previous work on male superb lyrebird song suggests that males have two distinct categories of acoustic performance that differ in mimetic and lyrebird-specific content, but this has not been tested formally. Scientific and natural history accounts of superb lyrebird song report that males regularly mimic multiple songs and other vocalizations of other species of bird (Dalziell & Magrath, 2012; Smith, 1988; Zann & Dunstan, 2008) together with a lyrical, lyrebird-specific song (‘whistle song’: Zann & Dunstan, 2008; previously ‘territorial song’: Powys, 1995; Powys et al., 2019; Robinson & Curtis, 1996; Robinson & Frith, 1981). In contrast, song and dance displays comprise three different lyrebird-specific song types (A–C) coordinated with dance ‘gesture’ types (Dalziell et al., 2013) and concluding with the ‘D song’ comprising mimicry of a limited set of sounds, mostly the mobbing alarm calls of small passerines (Dalziell et al., 2021). Understanding how males deploy these two types of sexual display and in what ways these displays differ in mimetic and nonmimetic content is important for determining the drivers of multicomponent sexual signals in lyrebirds, with implications for our understanding of the evolution and maintenance of mimetic song more generally.

In this study we investigated formally how the different components of the male lyrebird's multimodal sexual display are presented in concert. Specifically, we tested whether male lyrebirds vary their mimetic vocalizations with context. Our preliminary observations suggested that males use vocal mimicry in at least two sexual display modes that are distinct in both acoustic structure and visual display. The first mode appeared predominantly associated with singing from a perch, most notably in treetops before sunrise (dawn chorus), and the other involved elaborate plumage display and appeared mostly confined to a terrestrial display mound. Here we confirmed these observations and tested explicitly whether mimicry differs between these two display modes. Using long focal recordings of individual males singing during the morning, we characterized vocal displays at both large and fine temporal scales. We investigated the relationship between different song structures and several measures of context including time of day, the presence of a female and the male's deployment of visual display components.

## METHODS

### Study Site and Species

We studied the sexual displays of male superb lyrebirds in Sherbrooke Forest (37°53′, 145°21′), part of the Dandenong Ranges National Park, in the traditional Country of the Wurundjeri People, Australia. The Sherbrooke lyrebird population has been studied for more than 60 years by the Sherbrooke Lyrebird Survey Group (e.g. Austin et al., 2019; Kenyon, 1972) and many males are colour-banded (Maisey et al., 2016). Superb lyrebirds are a large (880–1200 g) and mostly ground-dwelling oscine passerine with a slow life history (Higgins et al., 2001). Males play no role in rearing young (Lill, 1979) but females invest substantially in the single offspring they produce each year (Lill, 1986). While breeding, adult males and females defend separate territories from intrasexual competitors (Lill, 1979). Adults are sexually dimorphic, but while subadult males (5–7 years old) are easily identified by plumage, juvenile males (1–5 years old) can appear identical to adult females (Higgins et al., 2001). However, brooding or incubating females can have a characteristic curve in their tails generated from sitting in their domed nest (Dalziell & Welbergen, 2016a). Only adult males with mature plumage defend territories during the breeding season (Higgins et al., 2001). Within their territory, individual males build multiple display mounds comprising circular patches of dirt on the forest floor, 1–2 m in diameter. During the breeding season, males keep their display mounds scrupulously clear of debris. When fertile, a female will leave her territory and visit a male on his territory, and all documented copulations have taken place on display mounds (Campbell, 1941; Dalziell et al., 2021; Dalziell & Welbergen, 2022; Gray, 1942; Smith, 1988; Watson, 1965). Several previous studies have produced summary tables of the species mimicked by males (reviewed in Higgins et al., 2001; Zann & Dunstan, 2008) and showed that males regularly mimic the conspicuous songs of several mid-sized songbird species, the calls of some smaller songbirds and the vocalizations of nonpasserines, most notably laughing kookaburras, *Dacelo novaeguineae*, and several species of parrot and cockatoo.

### Recordings

We recorded the vocalizations of adult male lyrebirds during the breeding seasons of 2007–2009. Morning focal watches were carried out from June to August, which is the key egg-laying period (Higgins et al., 2001). Males were on their territories throughout these focal watches. Recordings were made using a Sennheiser ME66 shotgun microphone and a Marantz PMD670 digital recorder sampling wave files at 44.1 or 48.0 kHz and 16 bits. The microphone was covered by a windshield and secured to a pistol grip handle using a shock mount. We dictated observations into the Marantz during breaks in the males' singing. Lyrebirds in our study population are habituated to humans and appeared largely unaffected by our presence. Nevertheless, to minimize our influence on lyrebird behaviour, we moved slowly, wore clothing that generated limited noise and recorded at a distance that focal birds would tolerate (<20 m, typically 10–15 m). All recordings were visualized in Syrinx (Burt et al., 2001) using the following spectrogram settings: FFT, window type Blackman, transform size 1024.

### Analytical Approach

Our preliminary analysis suggested multiple hierarchal scales of organization within male lyrebirds' vocal displays (Fig. 1). Accordingly, we analysed lyrebird song at two different temporal scales. First, using long focal recordings, we assessed large-scale singing structures and how they vary with behavioural and ecological contexts. Acoustic structures were identified first (song sequence categories), before scoring the accompanying nonsinging behaviours. These analyses of the context of vocalizations differentiated between sounds based on acoustic structure and initially we ignored whether sounds were mimetic or not. We then characterized general patterns of mimetic vocalizations within song sequence categories. Second, we examined the content of mimicry using a sample of short segments of song sequences sung by males in strictly defined contexts (full dance or no dance). Here, the visual display was defined first, and then the acoustic structures were characterized.

All acoustic parameters are illustrated in Fig. 1, except song bouts and pauses between song bouts ('interbout duration'). Visual display postures are illustrated in Fig. 2. The sampling structure is summarized in Table A1.

### Repertoire Deployment Analysis

We investigated how males deployed their repertoires of mimetic and lyrebird specific song. We first described acoustic structures before examining their relationship with nonsinging behaviours and ecological parameters. The singing behaviour of male lyrebirds was quantified from a sample of focal recordings of 18 territorial adult males recorded for 1.4–2.4 continuous hours each (mean = 1.9 h) between 0630 and 1000 hours. Thirteen of these males were colour-banded and three others were distinguishable by plumage. The two remaining males were separated by at least 0.5 km.

A separate set of six recordings of opportunistically recorded male encounters with conspecifics with female-like plumage was analysed separately to the sample of 18 males described above. While juvenile males cannot be distinguished from females, two of these visits resulted in copulations and so all or most of such visitors were likely to be females. These recordings with visitors were analysed separately to the sample of 18 males described above because (1) initial analysis suggested that the presence of females always caused males to sing a dance song sequence, and (2) the rarity of such visits precluded analysis within the main sample.

#### Acoustic analysis

We divided focal recordings into song bouts: periods of continuous singing longer than 10 s. A song bout was considered finished if it was followed by 30 s or more of silence. The 10 s limit

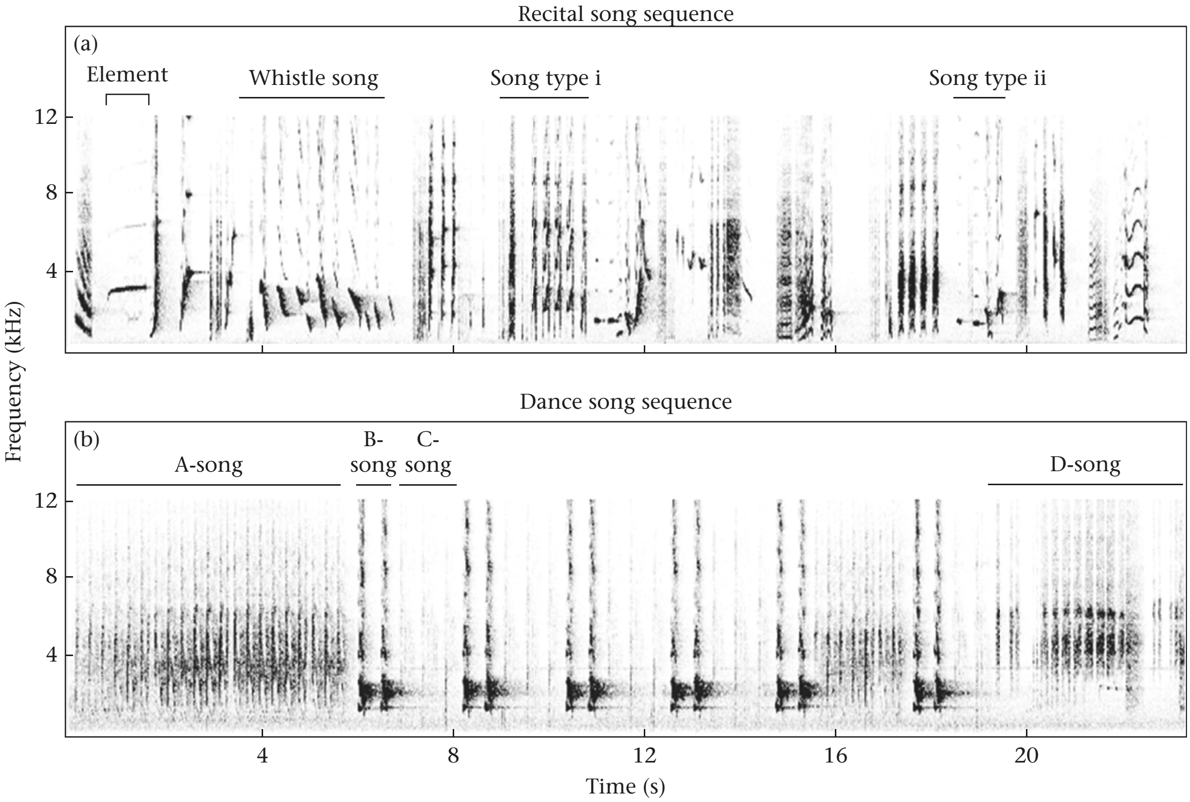

**Figure 1.** Male superb lyrebirds mimicked functionally distinct heterospecific vocalizations during two distinct categories of song sequence: 'recital' and 'dance' (Supplementary Audio S1 and S2). (a) Recital song sequences contain a lyrebird-specific song ('whistle song') and imitations of functionally diverse vocalizations of multiple model species: e.g. song type i is an imitation of a parrot call, *Platycercus elegans*, and song type ii is an imitation of a song sung by the oscine passerine *Colluricincla harmonica*. An 'element' is defined as a single, uninterrupted trace on a spectrogram (Catchpole & Slater, 2008). In this segment, all elements are mimetic except those within the whistle song. (b) Dance song sequences consist of three lyrebird-specific song types (A–C) and one incorporating mimicry (D). D-song almost entirely comprises imitations of mobbing alarm calls from a restricted set of model species. All song types are further divided into elements.

meant that we excluded instances where males performed their species-specific, stereotyped whistle songs (typically 4–10 s) singly, without strings of mimicry (Higgins et al., 2001; Powys, 1995). This appears to constitute a natural performance context for male whistle song (Higgins et al., 2001; Powys, 1995), and is similar to performances of whistle songs by females (Dalziell & Welbergen, 2016a) and male Albert's lyrebirds (Backhouse et al., 2021). Male superb lyrebird whistle songs sometimes include mimetic elements (Higgins et al., 2001; Powys, 1995; Powys et al., 2019; Zann & Dunstan, 2008), so to minimize ambiguity we excluded all bouts of 10 s or less. We measured the duration of song bouts and the duration of pauses between song bouts ('interbout duration').

Song bouts were made up of multiple song types, and we identified song types as discrete, characteristic sequences of elements that recurred (after Catchpole & Slater, 2008). Preliminary field observations suggested that, within a song bout, males clustered certain song types into predictable 'song sequences'. There appeared to be two different categories of song sequence: 'recital song sequence' and 'dance song sequence' (Fig. 1). In this part of the analysis, song sequences were defined by their acoustic characteristics only. However, for consistency and clarity, the descriptive terms 'recital' and 'dance' are used here because subsequent analysis showed a strong relationship between the category of song sequence and the type of display ('recital' or 'dance'; see Results). To determine whether song sequences were a regular feature of lyrebird vocalizations, we characterized the two categories of song sequence using a pilot sample of males opportunistically recorded before the breeding season began. We made no distinction between mimetic and nonmimetic song types when characterizing song sequences. Once we had a definition of each category of song sequence (see Results), we quantified the occurrence of dance and recital song sequences in our formal sample of focal watches of 18 territorial males. Specifically, for each focal watch we quantified the number and duration (s) of each category of song sequence.

In sum, focal recordings were divided into 'song bouts' that were divided into 'song sequences', which were in turn divided into 'song types' made up of 'elements' (Fig. 1).

### *The relationship between acoustic structures and context*

We tested whether recital and dance song sequences occurred in different contexts. Contexts examined included the time of day, as well as a suite of nonsinging behaviours associated with display. Specifically, for each song sequence we scored the location of the male while singing (perch, ground or display mound); whether his tail was in the nondisplay position (Fig. 2a and b) or inverted over his head in the 'display position' (Fig. 2c and d), and whether the male 'danced' (defined below). Since males sometimes changed locations during a song sequence, if the lyrebird occupied a display mound for any part of a song sequence it was scored as a performance on a display mound. In two separate analyses, we also considered whether song sequences were performed at least in part on a perch or on the ground. Males could raise and lower their tail during a song sequence, so the tail was scored as inverted if it was raised for any part of the sequence. Dances were defined as the performance of elaborate leg and wing movements (Dalziell et al., 2013). If any of these movements were performed during the song sequence, then 'dance' was scored as present. These scorings

**Figure 2.** (a, b) Males most commonly sang recital song sequences with their tail folded while perched but (c, d) they sang dance song sequences from terrestrial display mounds with their tail inverted. Males are shown (a, c) from a distance and (b, d) close by. The male in (a) is indicated by the arrow. Photograph credits: (a, b) Anastasia Dalziell, (c) Alexandra Dorland and (d) Alex Maisey.

of the behavioural context of song sequences were performed only on recordings of song sequences for which we had dictated visual observations of the behaviour of the recorded male. In addition, we tested whether males were more likely to dance if they were visited by a female or a bird with female-like plumage, by comparing our sample of six recordings with visits with the sample of 18 males without visits. We also investigated where mimetic vocalizations occurred within song sequences.

### *Mimicry Comparison Analysis*

We tested whether males mimicked different sounds while they were singing without dancing (‘recital display’) or when their mimicry was associated with dance (‘dance display’). Thus, the visual ‘dance’ context was defined before analysing the coinciding vocal signal (and so complementing the Repertoire deployment analysis, where the vocal signal was defined before scoring the context). For the Mimicry comparison analysis, we used recordings of 19 adult males (of which 13 were included in the Repertoire deployment analysis, Table A1) consisting of 12 colour-banded males, two additional males that had distinctive plumage and five that were situated at least 0.5 km apart.

Since recital displays were defined by an absence of dance, we first identified and characterized song sequences that were accompanied by dance before selecting a sample of singing without dances. For each male, we first identified periods of singing where the male was dancing with his tail inverted over his head. The beginning and end of these ‘dance’ periods were determined using spectrograms of songs, and were defined as either when males ceased singing or the transition point between different categories of song sequence (see below). This approach was used because song and dance were intimately related in lyrebirds: males only danced during ‘dance’ song sequences (Dalziell et al., 2013). In this way, we created a sample of dance song sequences that (1) were all accompanied by dances, (2) had clearly defined durations and (3) were defined independently of their mimetic content.

Preliminary examination of the elements within each dance song sequence revealed that mimicry was largely confined to just one dance song type: D-song (see also Dalziell et al., 2021). This was different to mimicry within recital song sequences, where it appeared uniformly distributed throughout. Thus, in our comparison of the type of mimicry sung during dance displays and recital displays, we used only the D-song component of dance displays. For analysis, we chose longer good-quality examples of D-song (19.2 ± 1.91 s). This duration is nevertheless shorter than the likely maximal duration of D-song of male lyrebirds (approximately 45 s: Dalziell et al., 2021). D-song was considered to be finished when males did one of the following: (1) repeated a lyrebird-specific clicking call (defined in Higgins et al., 2001) more than twice ($N = 10$); (2) fell silent ($N = 2$); or (3) began singing a nonmimetic dance song type (defined in Dalziell et al., 2013; $N = 2$). We created a catalogue of elements characterizing D-song using this subsample with unambiguous endings. We then used this catalogue to identify the end of the song type in cases where the male segued from D-song to a recital song sequence ($N = 5$).

The mimicry in dance song sequences (D-song) was compared with an identical duration of ‘recital mimetic song’. Recital mimetic song was conservatively defined here as singing that was produced at least 2 min after dancing and at least 1 min before dancing. Elements within recital mimetic song were then classified as mimetic or lyrebird-specific (see below). Defining both dance and recital mimetic song using the presence or absence of dance allowed us to draw robust conclusions about the relationship between visual display and mimicry. Since D-songs were naturally shorter than recital song sequences, we shortened durations of recital songs to compare meaningfully the mimetic content of each song sequence type. A random number generator was used to select the starting time of sections of recital mimetic song within our focal recordings. We discarded samples with low signal to noise ratios and resampled to replace these data. Since we were interested in differences in the sounds that were mimicked, we also discarded samples that contained more than 4 s of lyrebird-specific ‘whistle song’ (Fig. 1a) and started the sample after this lyrebird-specific song type had finished. Lyrebird whistle songs are noticeably longer than most mimicked sounds and by excluding them we ensured our samples of dance and recital mimetic song were comparable (we had effectively removed all the lyrebird-specific vocalizations from the dance song sequence by limiting our analysis to just D-song). Within each bird, samples of recital mimetic song and of D-song were either recorded on the same day ($N = 16$) or within the same breeding season ($N = 3$).

### *Acoustic analysis: classifying elements*

We examined mimicry produced during recital and dance displays by classifying elements in four ways. First, elements were classified into different types according to their acoustic structure. Second, elements were identified as either mimetic or nonmimetic, and the latter were excluded from these analyses unless otherwise specified. A negligible portion of sounds (9/2368 elements; 0.4%) could not be classified as either mimetic or lyrebird-specific and was excluded from all analysis. We then identified the set of mimetic elements that occurred within D-song and quantified the occurrence of this set of mimetic elements within songs sung during the recital display. Third, all mimetic elements within D-song were classified by model species. Finally, the original function of mimetic elements for the model species was scored as (1) ‘song’, (2) ‘alarm call’ or (3) ‘other’. We defined ‘songs’ broadly as conspicuous ‘advertisement’ vocalizations that mediate inter- and intrasexual interactions, and ‘alarm calls’, including ‘flee’ and ‘mobbing’ alarm calls, as sounds that function in predator defence (Marler, 2004). Our three categories could be applied across model species.

To identify imitated model species, we listened to recordings and inspected spectrograms of recordings of both lyrebirds and model species. For this process we used our own field recordings of lyrebirds and of model species, and we also referred to two commercial compilations of Australian animal vocalizations (McNabb, 2005; Plowright et al., 2007). To identify the original function of imitated sounds we consulted the literature (e.g. Higgins et al., 1990–2006) and drew on our personal expertise developed studying, watching and listening to birds in southeast Australia. We also consulted colleagues with similar skills. Nevertheless, some sounds posed particular problems. Flee alarm calls of white-browed scrubwrens, *Sericornis frontalis*, and brown thornbills are similar in acoustic structure, so it was not always possible to distinguish which was being mimicked. However, both were counted as ‘alarm calls’. Imitations of wingbeats could not be assigned to a species or easily partitioned into elements using spectrogram traces, and so were excluded from detailed analyses. However, imitations of mandible snaps were assigned into elements, and classified as ‘other mimicry’ for the analysis of function.

### *Statistical Analysis*

For features of focal recordings (Repertoire deployment analysis), we constructed linear models and used residual and quantile–quantile plots to check that residuals were normally distributed. Models of structures within focal recordings (e.g. parameters of song bouts and characteristics of mimicry; see sections Repertoire deployment analysis and Mimicry comparison analysis, respectively) included multiple measurements from individual males, so we constructed linear mixed models with the identity of the singing male modelled as a random term, and estimated effects using the restricted maximum likelihood method. We constructed a generalized linear mixed model (GLMM) with a binomial error distribution of the odds a male sang at least one dance song sequence in a focal watch. Where practicable, we report predicted means from models and the standard error of differences (SED). Elsewhere, descriptive statistics report grand means and associated errors (rather than means of individual means) along with sample sizes.

In the Repertoire deployment analysis, we investigated temporal patterns in singing behaviour (sensu Smith, 1965) by regressing acoustic parameters on the time of year (Julian days) and time since sunrise, determined from tables at Geoscience Australia (http://www.ga.gov.au/geodesy/astro/sunrise.jsp). The variables ‘bout duration’ and ‘interbout duration’ were log transformed to normalize the distribution of error.

To examine whether mimetic sounds produced during recital and dance displays differed (Mimicry comparison analysis) we performed nonparametric tests (Wilcoxon signed-ranks and Fisher's exact tests) and a one-way ANOVA on the proportion of mimetic song and alarm elements and the number of different element types. The ANOVA was performed in JMP Pro 14 2018 (SAS Institute Inc., Cary, NC, U.S.A.) and all other analyses were performed in Genstat 13th edition 2010 (VSN International, Hemel Hempstead, U.K.).

### *Ethical Note*

This research was conducted under permits from the Animal Experimentation Ethics Committee of the Australian National University (#F.BTZ.09.07) and the Victorian Department of Sustainability and Environment (1004124). The research was purely observational, involving the recording and observation of natural behaviour of wild animals moderately habituated to humans. As such, this research had a very low impact on superb lyrebirds and other fauna in the study site.

## RESULTS

### *Repertoire Deployment Analysis*

#### *Patterns of singing*

Male lyrebirds started producing bouts of song as early as 30 min before sunrise from roosts up to 30 m high in the canopy. From there, males glided to the ground, or lower perches, and subsequent bouts of singing were interspersed with feeding or maintenance of their display mounds. After vacating their high, night-roosting perches, males sang from perches ranging in height from locations within the mid-storey (10–20 m high) to logs or tree roots that were scarcely above the ground. They also sang from display mounds, or while standing or walking on the forest floor. Males often sang from several sites during the same bout of song.

The peak of singing effort occurred at the beginning of the season, close to sunrise. The total time males spent singing during focal watches declined as the season progressed (linear model of the sum of song bouts: $F_{1,15} = 13.3$, $P = 0.002$, $\beta = -51.6$, after controlling for the duration of the recording, $F_{1,15} = 16.1$, $P = 0.001$, $\beta = 0.61$). As the morning progressed, bouts of singing became shorter (linear mixed model: $F_{1,226.9} = 19.4$, $P < 0.001$, $N = 231$, $\beta = -0.000085$) and pauses between song bouts became longer (linear mixed model: $F_{1,190.3} = 20.0$, $P < 0.001$, $N = 213$, $\beta = 0.000065$).

#### *Two categories of song sequence*

Our analysis confirmed that male lyrebirds sang two acoustically distinct categories of song sequence (Fig. 1; Supplementary Audio S1 and S2). The first category was highly varied, consisting of multiple mimetic song types as well as lyrebird-specific song types (‘recital song sequence’: Fig. 1a; Supplementary Audio S1). In contrast, the second category of song sequence consisted only of four distinctive and highly stereotyped song types: A–D (‘dance song sequence’: Fig. 1b; Supplementary Audio S2) as has been defined previously (Dalziell et al., 2013). Each of the song types A, B and C involved the production or repetition of a syllable, the structure of which was unique to each song type (Fig. A1; Dalziell et al., 2013). D-song contained repetitions of one or more single-element syllables from a set of approximately seven syllables (Dalziell et al., 2021). The small number of song types that made up the dance song sequence made it easy to classify song sequences into categories, despite the large number of song types that were sung during recital song sequences. Accordingly, we classified song sequences as ‘dance’ if they contained two or more of the set of song types A–D, and as ‘recital’ if not. We then investigated whether these two categories of song sequence were sung by our test sample of 18 territorial males singing during the breeding season.

Both dance and recital song sequences were sung during 10 of 18 focal watches of different male lyrebirds with the remaining eight males producing only recital song sequences. Recital and dance song sequences were easily distinguished by visual inspection of spectrograms or by ear and were easily recognizable across males (Figs. 1, A2, Supplementary Audio S1 and S2). Dance song sequences were sung less often than recital song sequences (Table 1; GLMM: $F_{1,35.0} = 159.8$, $P < 0.001$; after controlling for the total number of song sequences: $F_{1,\ 35.0} = 56.8$, $P < 0.001$) and were considerably shorter (Table 1; GLMM: $F_{1,268.2} = 17.3$, $P < 0.001$; after controlling for Julian day: $F_{1,13.9} = 6.00$, $P = 0.028$). All dance song sequences began with A-song and ended with either D-song (30/31) or C-song (1/31), while recital song sequences had more diverse beginnings and endings (see below). Males switched between recital and dance song sequences within a single bout of song, typically without a clear pause in singing (Fig. 3). In our sample, dance song sequences never started a bout of song.

#### *Behavioural and temporal context of each song sequence category*

The most striking contextual difference between the two categories of song sequence was that one was usually accompanied by a particular set of dance-like movements and the other never was. For this reason, we called the two categories of song sequence ‘dance’ and ‘recital’, respectively. Dance movements performed by males included a distinctive step movement to the side, two-legged jumps or bobs and flapping both wings (Dalziell et al., 2013). The majority of dance song sequences were accompanied by at least some of these dance-like movements (19/24 stereotyped song sequences, from 10 males). On the other hand, males did not perform any of these dance movements while singing recital song sequences ($N = 216$ sequences from 18 males). This difference remained significant even after restricting the analysis to the subset of 10 males that performed both dance and recital song sequences (Wilcoxon signed-ranks test: $W = 45$, $N = 10$, $P = 0.004$). Males were also more likely to invert their tail into the display position

**Table 1**
The structure of adult male superb lyrebird song

| | Mean ± SD | Minimum | Maximum | $N$ (components) |
|---|---|---|---|---|
| Proportion of time singing[a] | 0.564 ± 0.147 | 0.335 | 0.795 | 18 |
| Song bout duration (s) | 293 ± 422 | NA[c] | 3437 | 229 |
| Interbout duration (s) | 192 ± 270 | NA[d] | 1944 | 213 |
| Dance song sequence proportion[b] | 0.0249 ± 0.0316 | 0 | 0.116 | 18 |
| Recital song sequence duration (s) | 269 ± 409 | NA[c] | 3437 | 250 |
| Dance song sequence duration (s) | 43.9 ± 25.7 | NA[c] | 101 | 32 |
| No. of recital song sequences/h | 7.61 ± 2.83 | 3.21 | 13.01 | 250 |
| No. of dance song sequences/h | 0.979 ± 1.20 | 0 | 3.21 | 32 |

Singing in 18 adult male superb lyrebirds, each recorded for 1.4–2.4 continuous hours (mean: 1.87 ± 0.274 h) during which they sang 1.94 ± 0.51 dance song sequences and 13.9 ± 1.02 recital song sequences. Grand means are shown.

[a] Sum of song bout durations divided by the duration of the recording.

[b] Proportion of total singing effort comprising dance song sequence (the remainin are recital).

[c] The minimum duration was set to 10 s.

[d] Pauses had to be at least 30 s long.

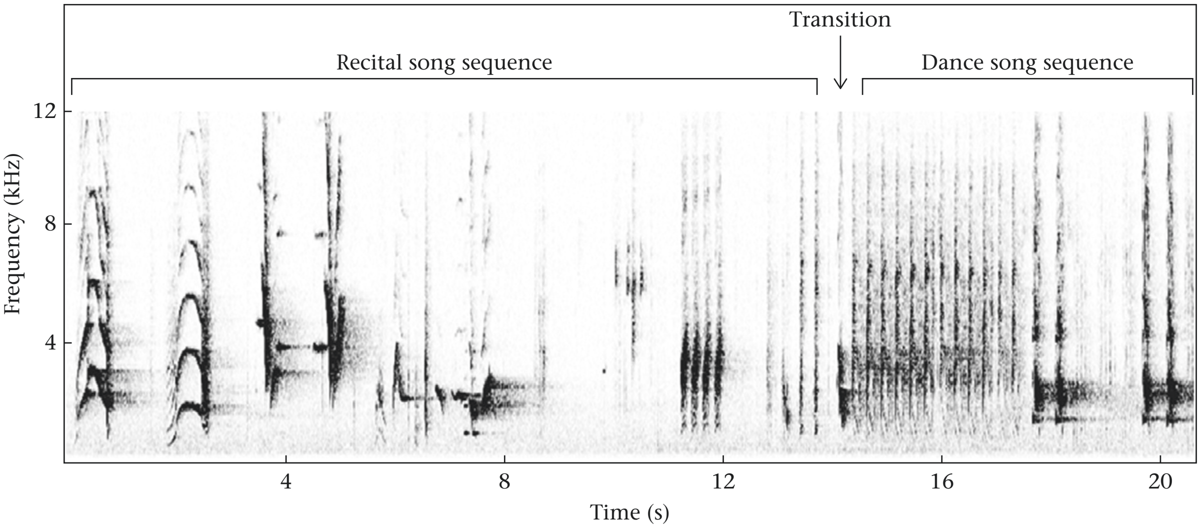

**Figure 3.** A segment of a song bout showing a transition from a recital song sequence to a dance song sequence. The dance song sequence is preceded by an imitation of an element from a yellow-faced honeyeater, *Lichenostomus chrysops*, marked in the spectrogram with an arrow.

(Fig. 2c and d) while singing dance song sequences than while singing recital song sequences (71% versus 13%; Table 2).

Dance song sequences were more likely to be performed on display mounds than recital song sequences (Table A2, e.g. Fig. 2c and d). Of the 10 birds that performed both categories of song sequences during focal recordings, 44% of dance song sequences, but only 14% of recital song sequences, were sung while on display mounds (back-transformed means, Table A2). The other dance song sequences were performed on the ground (7/29) or on the trunk of a fallen tree or a branch (8/29). Just over half of all recital song sequences were performed at least in part on a perch (109/215, $N = 18$ males; e.g. Fig. 2a and b), and it was also common for recital song sequences to be delivered entirely on the ground (82/215, $N = 18$ males). Dance song sequences tended to occur towards the end of a morning focal watch (Table A2) but the odds that a male would sing at least one dance song sequence within a focal watch did not change over the course of the season (binomial GLM: $\chi = 2.10$, $P = 0.10$). The duration of the recording also did not affect whether the male sang at least one dance song sequence ($\chi = 0.19$, $P = 0.66$).

**Table 2**
The attributes of recital and dance displays performed by male lyrebirds

| | Recital | Dance |
|---|---|---|
| **Visual components** | | |
| Dance movements (legs and wings) | Never | Common |
| Tail displayed | Rare | Common |
| Most common location | Perch | Display mound |
| **Acoustic components** | | |
| Mimicry (model function) | Song, alarm, others | Alarm[a] |
| Mimicry (no. of species) | ≥ 22 birds[b,c] | 5 birds, 2 possums[a] |
| Mimicry (no. of different sounds) | ≥ 90[b] | 7 |
| Species-specific vocalizations | Whistle song and others[d] | Song types A–C[e] |

The two display types (‘recital’ and ‘dance’) are defined by the category of song sequence. Data are from this study unless stated otherwise.

[a] See also Dalziell et al. (2021).
[b] Zann & Dunstan (2008).
[c] Higgins et al. (2001).
[d] Dalziell (2007–2009).
[e] Dalziell et al. (2013).

Both dance and recital song sequences were associated with visits by females and mating. Three focal watches included a visit by a bird known to be a female (either identified by colour bands or because she mated with the male). In addition, a bird with female-like plumage visited during focal watches of three other males. In all six cases, the male sang a dance song sequence, while simultaneously dancing on a display mound, when the visiting bird was present. In contrast, males only sang dance song sequences in 10 of 18 focal watches without visits, and there was a trend for this difference to be significant (Fisher's exact test: $P = 0.066$). Twice, visits led to mating. In each case, the male ran to a display mound and inverted his tail. The female followed and the male first sang one recital song sequence followed by one dance song sequence with accompanying dance movements. For much of the dance the female was on the display mound with the male, and at the end of the dance copulation took place on the display mound. In three other focal watches the sequence of behaviours was similar except that the dance ended upon the visitor leaving the area.

### *Patterns of mimicry within recital and dance song sequences*

Mimicry could occur anywhere within recital song sequences but was almost entirely restricted to ‘D-song’; the final song type within dance song sequences. Recital song sequences usually started with an imitation of a yellow-tailed black cockatoo, *Zanda funerea* (52%, of 217 sequences from 18 males). A further 11% began with the lyrebird-specific whistle song and an additional 11% began with imitation of a call from the eastern whipbird, *Psophodes olivaceus*. There were no sounds that predictably concluded recital song sequences, although before switching to dance song sequences males produced particular ‘transitional’ elements. An imitation of an element of a yellow-faced honeyeater, *Caligavis chrysops*, immediately preceded 90% of dance song sequences ($N = 31$ sequences, from 10 males). Furthermore, 61% of dance song sequences were preceded by imitations of the contact calls of the white-browed scrubwren less than 5 s before the start of the dance song sequence. Of the four song types that made up dance song sequences, mimicry never occurred in B-song or C-song but A-song sometimes contained an imitation of a syllable from the intersexual duet of the eastern whipbird (see Zann & Dunstan, 2008). In our sample of 97 exemplars of song type A (from 32 dance song sequences from 10 males) an imitation of one male ‘whip element’ occurred in nine sequences, two whip elements were imitated in one sequence, and an imitation of a female whipbird (Rogers, 2005) occurred in two sequences. Thus, 12% of renditions of A-song contained one to three mimetic elements but since the average A-song comprised 10 elements in total, the contribution of mimetic elements to A-song was small overall. (Dalziell et al., 2013). In contrast, D-song always contained mimetic elements and nearly all elements within D-song were mimetic (97.8%, $N = 1415$ elements from 19 males). Hence, for the following analyses of mimicry in the two categories of song sequences (recital and dance), we only focus on the D-song component of the dance song sequence.

### *Mimicry Comparison Analysis*

Sounds mimicked in recital displays differed substantially from those sung while dancing in (1) the original function of the mimicked sound in the model species (song versus alarm call versus other) and (2) the diversity of the mimetic sounds (per unit time or across renditions). These patterns were more compelling given that many of the model species were common to both displays.

Heterospecific songs were regularly imitated during recital displays, but never during dances (Fig. 4: $W = 0$, $N = 19$, $P < 0.001$). Instead, mimicry during dances comprised almost entirely imitations of heterospecific alarm calls that were rarely produced when not dancing (Fig. 4: $W = 0$, $N = 19$, $P < 0.001$). The majority of elements mimicked during D-song in dance displays were classified as one of just seven element types from seven different species (96.4%, $N = 1415$ elements from 19 males). These were imitations of the mobbing alarm calls of five species of passerine (white-browed scrubwren, brown thornbill, eastern whipbird, eastern yellow robin, *Eopsaltria australis*, and red wattlebird, *Anthochaera carunculata*) and imitation of suspected alarm calls (McNabb, 1994) from the bobuck possum, *Trichosurus cunninghami*, and common ringtail possum, *Pseudocheirus peregrinus*. However, recital displays rarely included imitation of any of these calls and never of brown thornbill mobbing alarm calls (Fig. 5). Furthermore, while lyrebirds regularly imitated the songs of eastern yellow robins, eastern whipbirds and red wattlebirds in recital displays (Figs. 6 and 7), and sometimes the alarm calls of these species, males never imitated the songs of these species in dance displays. Finally, D-song contained one-third as many element types as equivalent durations of recital mimetic song (D-song: mean = 7.2, recital song: mean = 23.9; ANOVA: $F_{1,18} = 43.2$, $P < 0.001$).

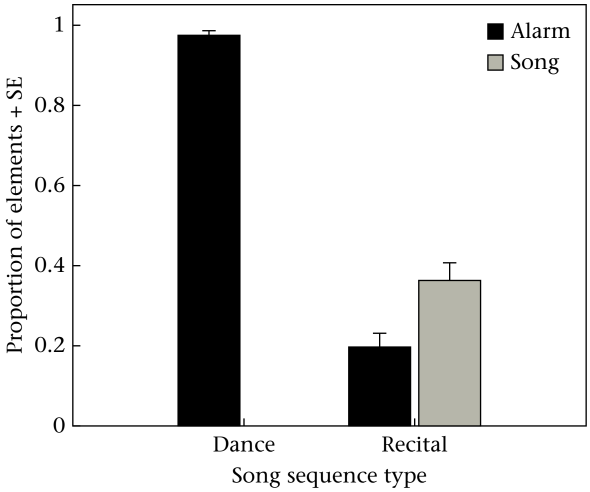

**Figure 4.** The mean proportion of mimetic elements produced during dance and recital displays, according to the function in model species: alarm and song. Elements that were imitations of other vocalizations (e.g. begging calls, contact calls, flight calls, etc.) are not shown. The mean proportions + SE of one segment of dance and recital mimetic song each from 19 males are shown.

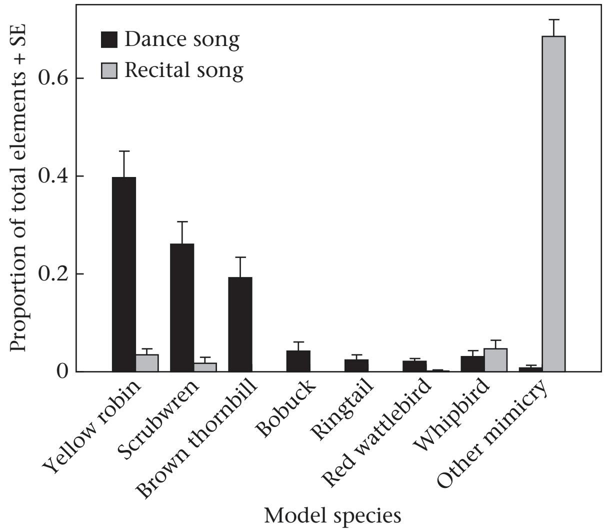

**Figure 5.** The distribution of different types of mimetic elements (labelled by model species) between songs sung during dance and recital displays. Distributions are shown for the seven elements most commonly imitated during dance displays and all other mimetic elements (‘other mimicry’). For clarity, elements are identified by species names, but each bar represents just one element type for each species. The mean proportions + SE of one segment of dance and recital mimetic song each from 19 males are shown.

## DISCUSSION

Male superb lyrebirds mimicked different sets of sounds in two structurally and contextually distinct multicomponent sexual displays (Table 2). Males mimicked a large set of bird songs and calls during ‘recital displays’, and this set of mimicry differed

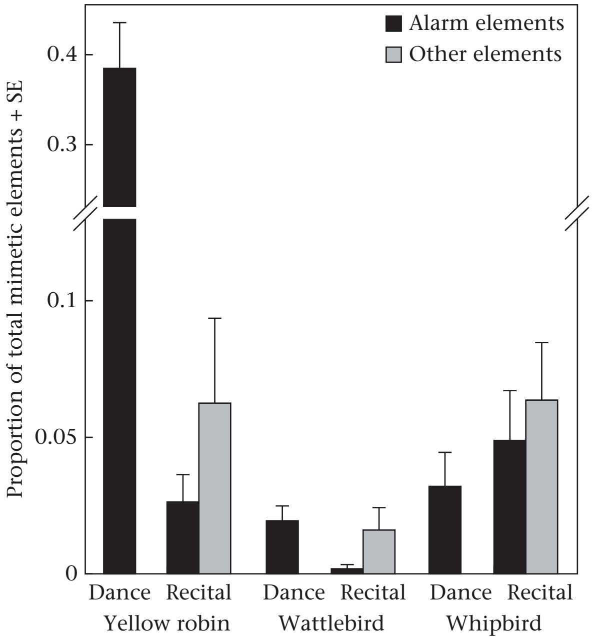

**Figure 6.** The distribution of mimetic elements from three different species, broken down by the function of the call in the model, between mimicry produced during dance and recital displays. The mean proportions + SE of one segment of dance and recital mimetic song each from 19 males are shown.

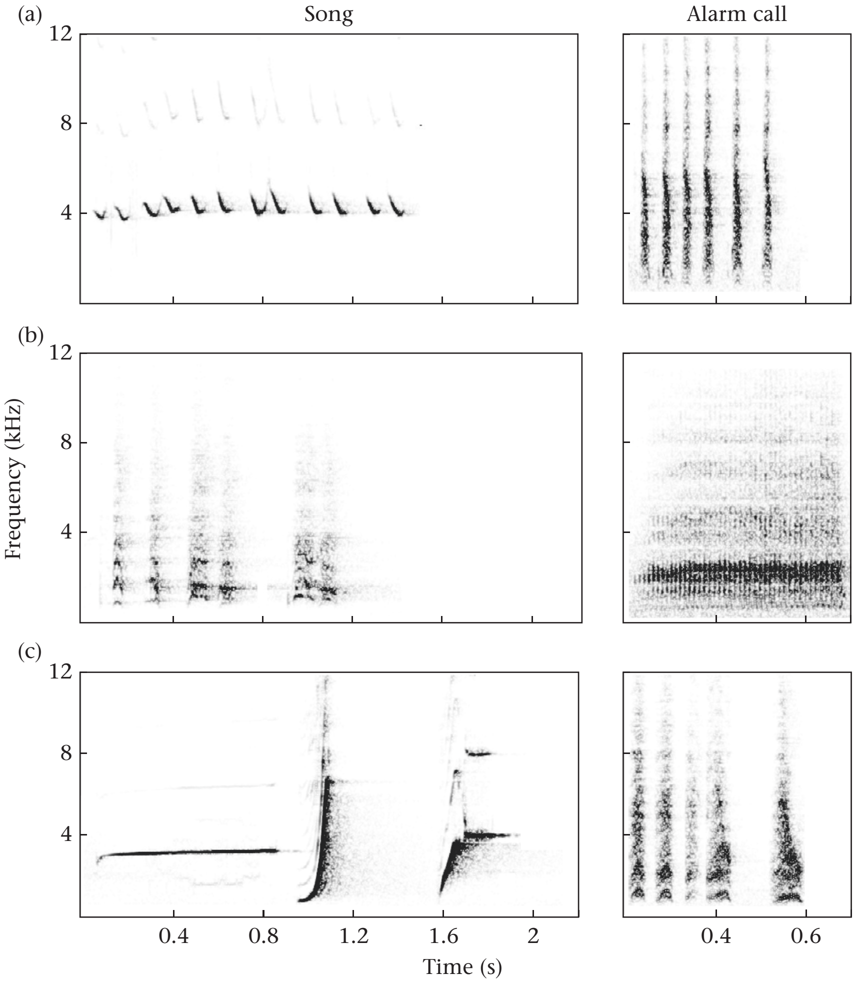

**Figure 7.** Examples of lyrebird mimicry of a song and an alarm call from three different species: (a) eastern yellow robin, (b) red wattlebird and (c) eastern whipbird. Song examples come from lyrebird recital displays and alarm call examples from dance displays.

dramatically from the small, discrete set of avian and mammalian alarm calls sung during 'dance displays' (see also Dalziell et al., 2021). Unlike dance displays, recital displays were typically performed while perched, and were never coordinated with stereotyped dance movements (sensu Dalziell et al., 2013). Previous analyses have treated the male lyrebird's mimetic repertoire as a homogeneous set (Higgins et al., 2001; Robinson & Curtis, 1996; Zann & Dunstan, 2008), and given the relative rarity of dance displays compared with recital displays, we conclude that earlier descriptions are based solely on recital displays (Robinson & Curtis, 1996; Robinson & Frith, 1981; Zann & Dunstan, 2008). Together with previous work focusing on dance displays (Dalziell et al., 2013, 2021), this study provides evidence that the male superb lyrebird's two sets of mimicry are driven by different selective processes. These results argue against the longstanding explanation that vocal mimicry in the song of oscine passerines is a by-product of selection for large song type repertoires (Hindmarsh, 1986; e.g. see Byers & Kroodsma, 2016). Instead, this study highlights the importance of considering functional explanations for vocal mimicry in oscine song (sensu Dalziell & Welbergen, 2016b; Dalziell et al., 2015).

Our finding that male lyrebirds partition their large repertories of mimetic sounds between two distinct multicomponent displays has parallels with studies of nonmimicking oscine passerines. In nonmimicking oscines, song repertoires are often partitioned, with different song variants performing different functions (reviewed in Byers & Kroodsma, 2009). In several species, repertoires of song types are used in graded, intrasexual song 'duels' where the degree of aggression signalled by a particular song type may be intrinsic (Templeton et al., 2012) or depends on the song type (or song types) previously sung by the opponent (e.g. banded wrens, *Thryophilus pleurostictus*: Vehrencamp et al., 2007; song sparrows, *Melospiza melodia*: Searcy et al., 2014). In other species, different components of song repertoires have different receivers, typically with some songs directed at potential mates and others at rivals (reviewed in Byers & Kroodsma, 2009). Discrete sets of vocalizations can also operate at different stages of mate choice. The males of several lek-breeding oscines and nonoscines use discrete sets of vocalizations to attract females to display sites before switching to a separate set of vocalizations when females have entered male display sites (e.g. sage grouse, *Centrocercus urophasianus*, Gibson, 1996; toothbilled bowerbirds, *Scenopoeetes dentirostris*, Frith & Frith, 1993; long-tailed manakins, *Chiroxiphia linearis*, McDonald, 1989). In lyrebirds, it seems likely that the differing signal requirements of different stages of mate choice (sensu Candolin, 2003) is one driver for the partitioning of mimetic repertoires, and the two displays could form components of a graded series. However, these general explanations do not explain the particular patterns of mimetic repertoire partitioning reported here.

### Vocal Mimicry and Recital Displays

The majority (ca. 98%) of the lyrebird's large output of mimetic and species-specific song was performed as part of a ‘recital’ rather than a ‘dance’ display. The acoustic component of recital displays was highly varied, containing a higher diversity of element types than dance displays and incorporating imitations of multielement songs as well as imitations of alarm calls and other sounds (Figs. 1a and 4). A previous study of the lyrebird's entire mimetic repertoire suggested that lyrebirds imitated more than 90 structurally distinct vocalizations from approximately 23 species (Zann & Dunstan, 2008), and our analyses indicate that almost all of these occur within ‘recital’ displays. Unlike dance displays, recital displays were characterised by an absence of conspicuous dance components and were never accompanied by dance movements. Males sang recital song sequences most commonly on perches or on the ground, and 87% of song sequences were performed with the tail folded in a resting position, with the dark, dorsal side facing upwards, making the male visually inconspicuous. A distinctive, multielement song (‘whistle song’) that was largely made up of lyrebird-specific elements was exclusively associated with recital display. While the acoustic structure of lyrebird song was highly distinctive, overall temporal patterns in lyrebird song output were similar to those of many other passerines (Catchpole & Slater, 2008), declining both as the morning and the season progressed. Robinson and Frith (1981) also reported a decline in lyrebird song over the course of the breeding season, and an analysis of the song produced by one male in 1 day, showed that the male sang most intensely just after dawn (Robinson & Curtis, 1996), although the predawn song production was not quantified in that study. We found that dance song sequences were more likely to occur as the morning progressed, perhaps because better light levels increased the visual impact of the dance display.

### Vocal Mimicry and Dance Displays

Only a small, distinct set of mimetic sounds was produced during the spectacular dance display performed by male lyrebirds and these were associated with ‘D-song’, the final of the four song types that comprised sequences of dance song (Fig. 1b; Dalziell et al., 2013). The majority (70%) of dance song sequences was accompanied by a stereotyped set of dance-like movements, often performed on a display mound. As was also reported in a previous study with a smaller sample size (Dalziell et al., 2021), D-song was almost entirely made up of imitations of the alarm calls of five passerines and, less often, the calls of two species of possum. The original function of model calls, rather than the species, was strongly associated with their inclusion in dance mimicry; while lyrebirds imitated the songs of yellow robins, whipbirds and wattlebirds in recital displays (Figs. 6 and 7), they imitated only alarm calls of these species in dance displays. The only possible exception to this rule was the finding that while 12/19 recordings of D-song contained an imitation of one of two species of herbivorous possum (the bobuck or the common ringtail) no possum calls of any species were imitated in our sample of recital mimetic song. However, it is difficult to draw any conclusions about the mimicry of possums given little is known about their vocal behaviour, and nothing about their interactions with lyrebirds.

### Function of Vocal Mimicry in Song

This report of context-dependent, functionally distinct mimetic vocalizations implies that vocal mimicry can have more than one function within species. In superb lyrebirds, a previous study showed that with the D-song mimicry of dance displays, males create an acoustic illusion of a mixed-species avian mobbing flock, a potent cue of a hidden predator (Dalziell et al., 2021). That study found that males only and always used D-song in two specific contexts, during copulation or when a female attempted to leave a male's display mound before copulating, which provides strong evidence that D-song is crucial for male reproductive success (Dalziell et al., 2021). In D-song, vocal mimicry likely functions as a deceptive mimetic signal of a dangerous predator (a sensory trap sensu Arnqvist, 2006; Christy, 1995; West-Eberhard, 1984), probably benefiting male lyrebirds by deterring females from prematurely terminating sexual encounters (Dalziell et al., 2021). Importantly, D-song is a relatively quiet, short-range signal and can only function in the final stages of mate choice in lyrebirds, and males must first attract a female to the display mound before they can perform their dance display and deploy deceptive mimicry (Dalziell et al., 2021).

The features of recital mimicry imply selection for long-range signalling, most likely to attract females to a male's territory. Unlike D-song, recital song sequences include mimicry of an eclectic set of model species spanning numerous families and diverse ecological niches. Furthermore, the functions of the heterospecific vocalizations range broadly from territorial multielement songs (e.g. grey shrike-thrush, *Colluricincla harmonica*; Dalziell & Magrath, 2012) to flight calls (e.g. yellow-tailed black cockatoo) and begging calls (e.g. pied currawong, *Strepera graculina*). Neither our results nor those of previous authors (e.g. Smith, 1988; Zann & Dunstan, 2008 Robinson & Curtis, 1996) point to an underlying ecological feature driving the mimetic content of recital displays. Recital mimetic song does, however, have multiple features in common with the species-specific song of songbirds under sexual selection for structurally complex vocalizations (Catchpole & Slater, 2008). Just like many nonmimicking songbird species, male lyrebirds perform recital song sequences loudly from perches, often without visual displays, and mainly during the breeding season. Furthermore, male superb lyrebirds (like male Albert's lyrebirds: Backhouse et al., 2022) appear to order their songs such that each new song type is different from the previous one (‘singing with immediate variety’: Catchpole & Slater, 2008), suggesting that recital displays function to demonstrate the diversity of male vocal (in this case mimetic) repertoires. Collectively, these features are characteristic of long-range sexual signalling suitable for dense habitats, like the lyrebird's forest, or for performance in the predawn darkness. But why use mimicry, and how is mimetic accuracy maintained (Dalziell & Magrath, 2012; Zann & Dunstan, 2008)?

Accurate vocal mimicry in lyrebird recital song may persist if male mimetic accuracy is an honest signal of male quality to potential mates (Coleman et al., 2007; Zann & Dunstan, 2008) or rivals (Dalziell et al., 2015). Mimetic accuracy could, for example, be an honest signal of rearing conditions (Coleman et al., 2007) or general cognitive ability (Boogert et al., 2011). Mimetic accuracy might be more informative than the accuracy of imitated species-specific vocalizations, if mimicking other species is more physically or cognitively demanding than copying species-specific vocalizations (Dalziell et al., 2015). We suggest an even simpler idea: that accurate mimicry is itself under selection. Females select for mimetic accuracy in recital song because the ability to mimic accurately benefits both male and female offspring (indirect benefits model of sexual selection sensu Bradbury & Vehrencamp, 2011). For sons, the ability to mimic the sound of a mobbing flock appears necessary for mating (Dalziell et al., 2021) making sophisticated, locally relevant vocal mimicry essential to male mating success. Adult males can also mimic when confronted by foxes (Dalziell, 2007–2009), known predators of adult lyrebirds (Higgins et al., 2001), suggesting that vocal mimicry could also have antipredator functions for males. With recital mimetic song, a male can vocally advertise his mimetic ability while reserving deceptive mimicry to the few sexual encounters that progress to later stages of courtship, thus keeping deceptive signals rare (Bradbury & Vehrencamp, 2011; Mokkonen & Lindstedt, 2016). For daughters, skillful vocal mimicry may deter nest predators (Dalziell & Welbergen, 2016a) and reduce the threat to nests posed by rival females (Austin et al., 2019; Dalziell & Welbergen, 2016a). While speculative, we suggest that the hypothesis that mimetic song signals mimetic ability to prospective mates provides a parsimonious explanation for mimetic song that could apply to other avian vocal mimics. There is already good evidence among species that vocal mimicry has multiple functions (Dalziell et al., 2015; Goller & Shizuka, 2018). To test whether a broad ecological utility of vocal mimicry within species explains the evolution of mimetic song requires detailed, species level empirical data on vocal mimicry, in both sexes and across multiple ecological contexts, but at present such data are limited (Austin et al., 2021).

### *Conclusion*

Mimetic song is one of the most highly conspicuous forms of mimicry (Dalziell et al., 2015), but while it is widespread among oscine passerines, it continues to be understudied. Our finding that male superb lyrebirds mimic functionally distinct heterospecific vocalizations during different modes of sexual display shows that traditional hypotheses for complex song in oscine passerines (Byers & Kroodsma, 2016; Catchpole & Slater, 2008) inadequately explain the structural and functional diversity of oscine song. Hence, this work highlights the importance of further empirical research on vocal mimicry and emphasizes the need for the formulation and testing of new hypotheses for the evolution and maintenance of complex vocalizations in birds.

## Author Contributions

**Anastasia Dalziell**: Conceptualization (lead), Methodology (lead), Formal analysis (lead), Investigation (lead), Funding acquisition (equal), Writing–Original Draft (lead), Writing–Reviewing and Editing (lead). **Justin Welbergen**: Conceptualization (supporting), Funding acquisition (supporting), Writing–Reviewing and Editing (supporting). **Robert Magrath**: Conceptualization (supporting), Formal analysis (supporting), Funding acquisition (equal), Investigation (supporting), Methodology (supporting), Resources (lead), Supervision (lead), Writing–Reviewing and Editing (equal).

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## Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2022.04.002.

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# Appendix

**Table A1**
The individual adult male lyrebirds sampled for each of the three sample groups

| Male ID no. | Focal watches<br>(repertoire deployment analysis) | Recital vs Dance<br>(mimicry comparison analysis) | Female visits<br>(repertoire deployment analysis) |
|---|---|---|---|
| 1 | * | * | * |
| 2 | * | * | |
| 3 | * | * | |
| 4 | * | * | * |
| 5 | * | * | |
| 6 | * | * | * |
| 7 | * | * | |
| 8 | * | * | |
| 9 | * | * | |
| 10 | * | * | |
| 11 | * | * | |
| 12 | * | * | |
| 13 | * | * | |
| 14 | * | | |
| 15 | * | | |
| 16 | * | | * |
| 17 | * | | |
| 18 | * | | |
| 19 | | * | |
| 20 | | * | |
| 21 | | * | * |
| 22 | | * | |
| 23 | | * | |
| 24 | | * | |
| 25 | | | * |

An asterisk indicates that male was included in that sample group. Not all males performed dance in addition to recital displays during focal watches (Table 1) and so we supplemented our set of focal recordings with high-quality but shorter recordings of other males for the comparison of dance and recital mimicry. Males behaved very differently during the rare focal watches with visits by females (or suspected females) compared with those without, so focal watches with visits were analysed separately.

**Table A2**
Model estimates of the relationship between the category of song sequence (recital or dance) and the behavioural and temporal context in which the song is performed

| Dependent variable[a] | Independent variable | Effect | SE/SED[b] | *df* | *F*[c] | *P* | *N*[d] |
|---|---|---|---|---|---|---|---|
| **Behavioural context of sequences** | | | | | | | |
| Tail inverted | | | | | | | |
| Random effects | Bird | 0.191 | 0.356 | | | | 10 |
| Fixed effects | Constant | 0.901 | 0.476 | | | | |
| | Sequence category[e] | | 0.528 | 1139.3 | 28.7 | < 0.001 | |
| | Recital | −1.93 | | | | | 119 |
| | Dance | 0.901 | | | | | 23 |
| Performed on a display mound | | | | | | | |
| Random effects | Bird | 1.51 | 0.961 | | | | 10 |
| Fixed effects | Constant | −0.222 | 0.573 | | | | |
| | Sequence category[e] | | 0.486 | 1155.6 | 11.3 | <0.001 | |
| | Recital | −1.86 | | | | | 133 |
| | Dance | −0.222 | | | | | 29 |
| **Temporal context of sequences** | | | | | | | |
| Sequence category (Recital = 1) | | | | | | | |
| Random effects | Bird | 0.787 | 0.520 | | | | 18 |
| Fixed effects | Constant | 2.22 | 0.289 | | | | |
| | Time after sunrise | −0.000298 | 0.0000965 | 1248.4 | 9.53 | 0.002 | 282 |

[a] Mixed models were estimated using the restricted maximum likelihood method.
[b] Standard errors are shown for random effects and continuous dance effects while SED is reported for sequence category.
[c] Satterthwaite's *F* associated with deletion of dance effects from the model is shown.
[d] Models of behaviour come from a subsample of 10 males that sang both dance and recital song sequences. The model of time was based on the full sample of 18 males.
[e] Back-transformed means are reported in the text.

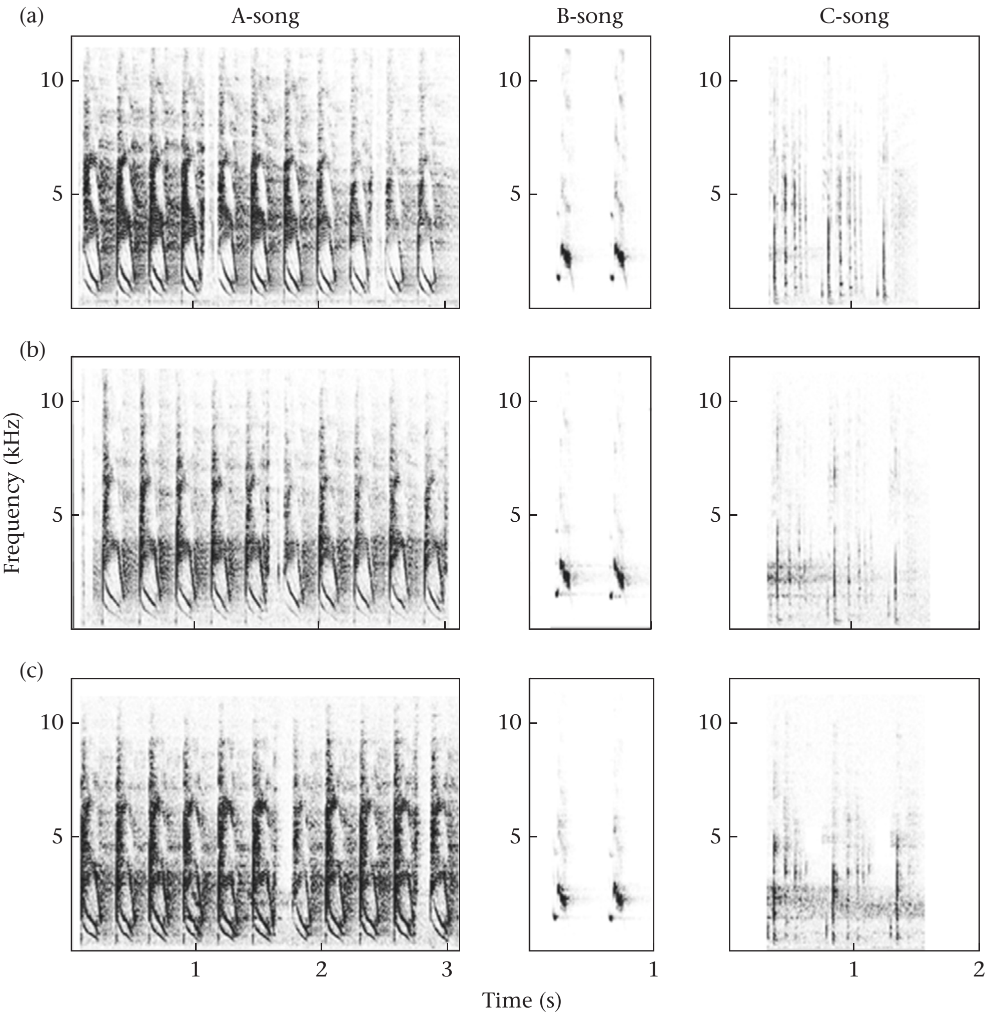

**Figure A1.** Examples of the three lyrebird-specific song types (A-song, B-song and C-song) sung during sequences of dance song, from (a–c) three adult male lyrebirds.

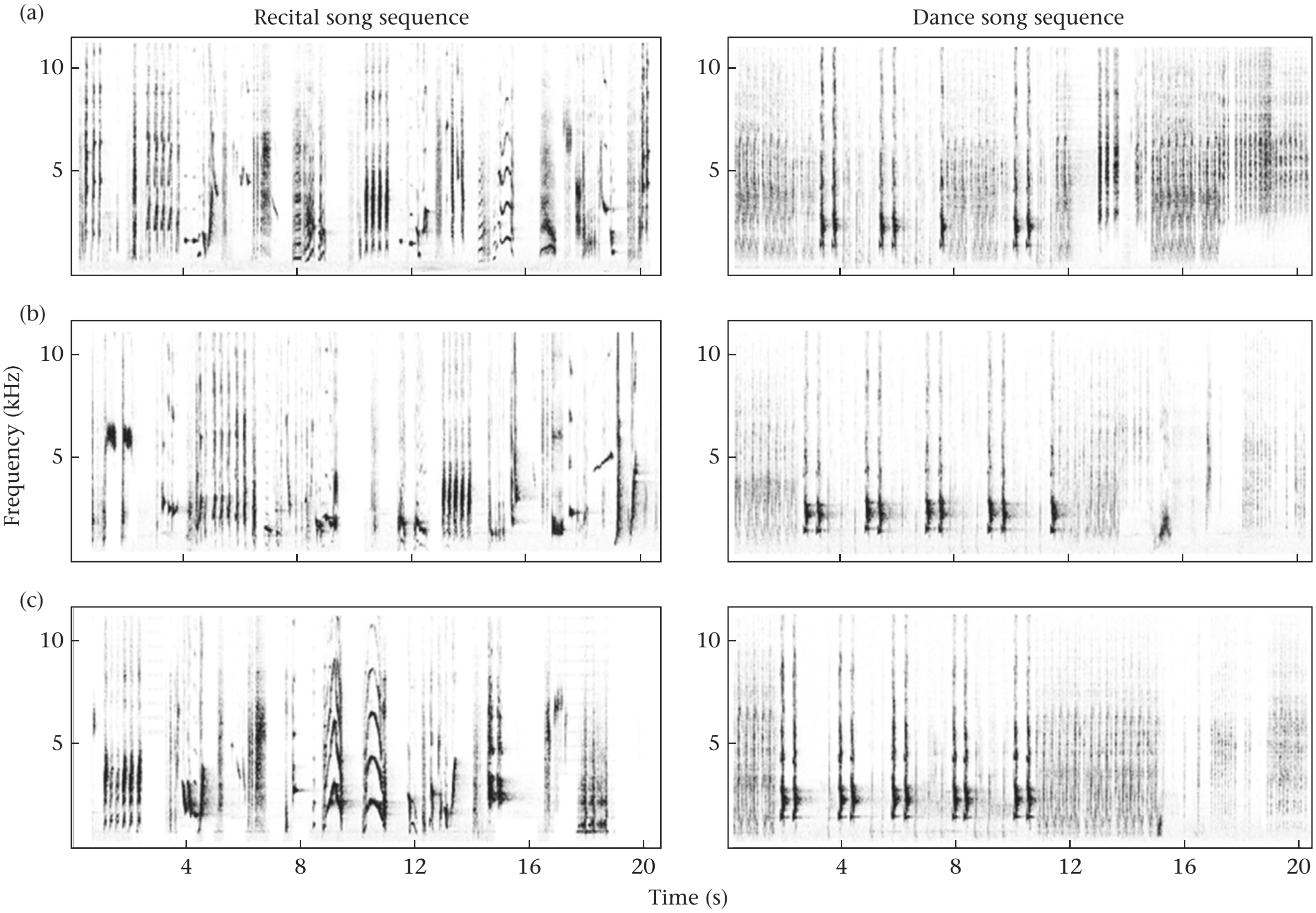

**Figure A2.** Examples of recital and dance song sequences from (a–c) three adult male lyrebirds.