Current Biology

Report

Male lyrebirds create a complex acoustic illusion of a mobbing flock during courtship and copulation

Highlights

- The cacophony produced by avian mobbing flocks is a potent cue of a predator
- Male lyrebirds mimic this complex cue so accurately that other species are fooled
- Males produce it only during copulation or when females ‘break off’ courtship
- Male deception—not female preference—likely drives elaboration of this mimetic song

Authors

Anastasia H. Dalziell, Alex C. Maisey,
Robert D. Magrath,
Justin A. Welbergen

Correspondence

anastasia.dalziell@cornell.edu

In Brief

Dalziell et al. show that male superb lyrebirds create a remarkably accurate acoustic illusion of a flock of mobbing birds. Males give this false signal of danger only during copulation or when females try to leave before copulation, suggesting that male deception rather than females’ “taste for beauty” drives the elaboration of this mimetic song.

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Male lyrebirds create a complex acoustic illusion of a mobbing flock during courtship and copulation

Anastasia H. Dalziell,[1,2,3,4,8,*] Alex C. Maisey,[2,4,5,6] Robert D. Magrath,[2,7] and Justin A. Welbergen[3,7]
[1]Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA
[2]Research School of Biology, Australian National University, Canberra, ACT 2614, Australia
[3]Hawkesbury Institute for the Environment, Western Sydney University, Richmond, NSW 2753, Australia
[4]Centre for Sustainable Ecosystem Solutions, University of Wollongong, Northfields Ave, Wollongong, NSW 2522, Australia
[5]Sherbrooke Lyrebird Survey Group, 30 Moores Road, Monbulk, VIC 3793, Australia
[6]Present address: Department of Zoology, La Trobe University, Bundoora, VIC 3086, Australia
[7]These authors contributed equally
[8]Lead contact
*Correspondence: anastasia.dalziell@cornell.edu
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SUMMARY

Darwin argued that females' "taste for the beautiful" drives the evolution of male extravagance,[1] but sexual selection theory also predicts that extravagant ornaments can arise from sexual conflict and deception.[2,3] The sensory trap hypothesis posits that elaborate sexual signals can evolve via antagonistic coevolution whereby one sex uses deceptive mimicry to manipulate the opposite sex into mating.[3] Here, the success of deceptive mimicry depends on whether it matches the receiver's percept of the model,[4] and so has little in common with concepts of aesthetic judgement and 'beauty.'[1,5–9] We report that during their song and dance displays,[10] male superb lyrebirds (*Menura novaehollandiae*) create an elaborate acoustic illusion of a mixed-species mobbing flock. Acoustic analysis showed that males mimicked the mobbing alarm calls of multiple species calling together, enhancing the illusion by also vocally imitating the wingbeats of small birds. A playback experiment confirmed that this illusion was sufficient to fool avian receivers. Furthermore, males produced this mimicry only (1) when females attempted to exit male display arenas, and (2) during the lyrebirds' unusually long copulation, suggesting that the mimicry aims to prevent females from prematurely terminating these crucial sexual interactions. Such deceptive behavior by males should select for perceptual acuity in females, prompting an inter-sexual co-evolutionary arms race between male mimetic accuracy and discrimination by females. In this way the elaboration of the complex avian vocalizations we call 'song' could be driven by sexual conflict, rather than a female's preference for male extravagance.

RESULTS AND DISCUSSION

In many oscine passerines, song regularly includes vocal imitations of the sounds produced by heterospecifics.[11,12] Such imitations might benefit males by increasing their vocal complexity,[11,13] a trait preferred by females of several non-mimicking songbird species.[13] An alternative is that vocal mimicry could form part of a sensory trap, deployed to increase reproductive success.[12] Such sensory traps involve one sex (typically male) benefiting by mimicking deceptively a model stimulus that the opposite sex is selected to respond to in another context, such as foraging or predator avoidance.[2,3,14] While responding to such mimicry of functionally referential signals or cues is expected to compromise a female's reproductive success, resistance to male trickery may interfere with a female's ability to respond adaptively to the model.[2,3,14] This can lead to a coevolutionary arms race whereby improvements in females to discriminate between mimic and model are countered by increased mimetic resemblance of the male signal to the model stimulus.[2–4] Despite theoretical support for sexually selected sensory traps, empirical examples remain rare across animal taxa.[15]

Here we examine a mimetic signal produced in the sexual display of male superb lyrebirds (*Menura novaehollandiae*), a species of oscine passerine well known for its accurate vocal imitations of heterospecific sounds. During the breeding season, males court females with a series of complex vocal and visual displays, culminating in a stereotyped coordinated song and dance display[10] performed on one of the male's several arenas ('display mounds'; Figure 1A). We test the hypothesis that the final component of this dance display, the 'D-song,'[10] functions as deceptive acoustic mimicry of a mixed-species mobbing flock. Many bird species give acoustically distinct mobbing alarm calls, and mobbing flocks are formed when several individuals of the same or different species harass a predator.[16,17] These mobbing flocks are reliable cues of the presence of a predator, yet would seem impervious to imitation by a single individual. We used detailed acoustic analysis and a field playback experiment to test the prediction that vocal mimicry by male lyrebirds is physically and perceptually similar to real mixed-species

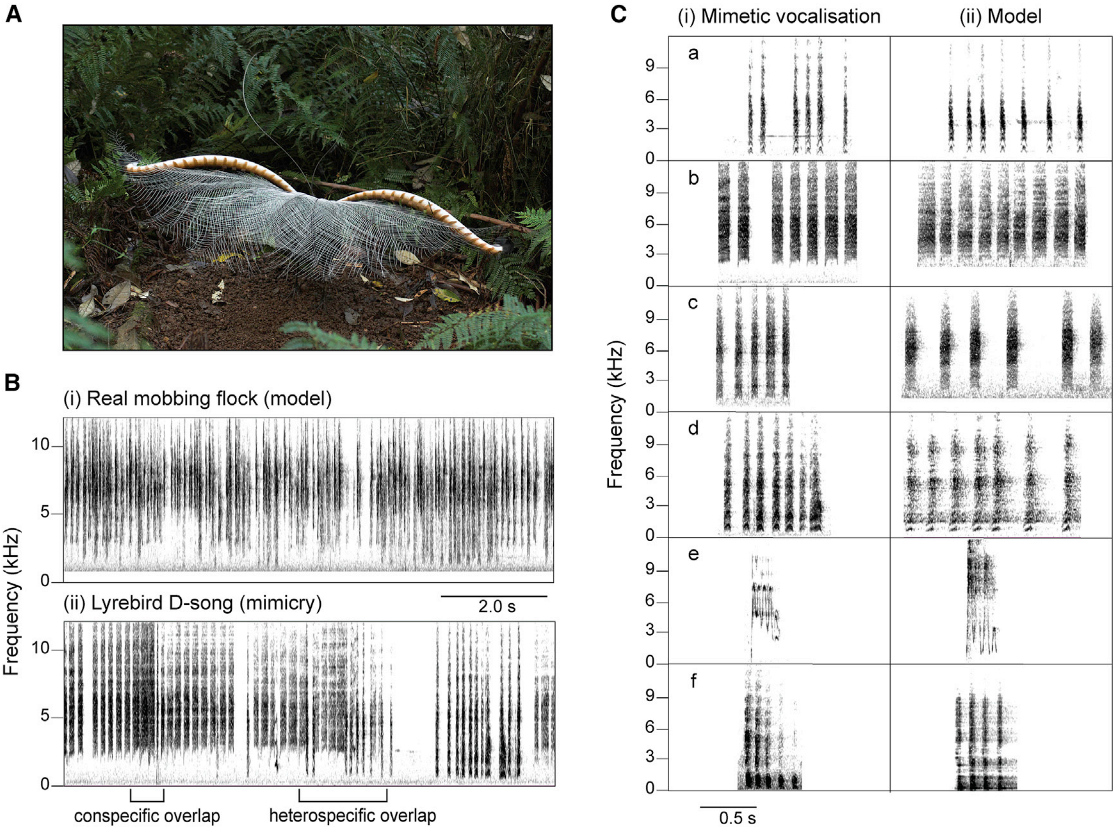

Figure 1. During sexual displays, male superb lyrebirds mimicked multiple acoustic features of real mixed-species mobbing flocks

(A) A male performing on a display mound (photo: A. Maisey).

(B) Segments of (i) a real mixed-species mobbing flock (Audio S1A) and (ii) a male mimicking a mixed-species mobbing flock (D-song; Audio S1B). Indicated are passages where the male creates the illusion of multiple individuals calling simultaneously by mimicking contiguous elements of two conspecifics ('conspecific overlap,' white-browed scrubwren mimicry), and two heterospecific individuals ('heterospecific overlap,' white-browed scrubwren and eastern yellow robin mimicry).

(C) Mimetic and model mobbing alarm calls from four species of oscine passerine: (a) eastern yellow robin (*Eopsaltria australis*), (b) white-browed scrubwren (*Sericornis frontalis*), (c) brown thornbill (*Acanthiza pusilla*), (d) eastern whipbird (*Psophodes olivaceus*), and suspected alarm calls from two marsupials, (e) common ringtail possum (*Pseudocheirus peregrinus*) and (f) bobuck (*Trichosurus cunninghami*). Model credits: d: Anderson, *Xeno-canto* CC XC171916; e and f: McNabb.[18]

See also Figure S1, Tables S1 and S2, and Audio S1A–S1C.

mobbing flocks. We then used audio-visual recordings of sexual interactions in the wild to investigate the context of production and therefore how males could benefit from mimicking mobbing flocks.

There was a striking acoustic similarity between the male lyrebird's D-song and actual mixed-species mobbing flocks (Figure 1; Audio S1A–S1C). Acoustic analysis confirmed that D-song predominantly imitated the alarm call elements of small passerines (Figures 1B, 1C, 2, and S1; Table S1). A hierarchical cluster analysis partitioned model calls into four main groups: eastern yellow robin (*Eopsaltria australis*) calls, brown thornbill (*Acanthiza pusilla*) calls, and two sets of white-browed scrubwren (*Sericornis frontalis*) calls (Figure 2). Most imitations by lyrebirds were randomly clustered within their putative model calls, emphasizing the accuracy of the imitations. Lyrebirds occasionally also included other calls that were associated with alarm. Specifically, males sometimes imitated eastern whipbird (*Psophodes olivaceus*) calls (Figure 1Cd) that are suspected mobbing calls,[19] and a call that red wattlebirds (*Anthochaera carunculata*) produce in alarm contexts (R.D.M. and A.H.D., unpublished data). The calls of the bobuck possum (*Trichosurus cunninghami*) and the ringtail possum (*Pseudocheirus peregrinus*) were imitated by some males (Figures 1Ce and 1Cf) and are suspected to be alarm calls (E. McNabb, personal communication). Males in both of the study populations only mimicked local species (Table S1), so models were sympatric to receivers (female lyrebirds), fulfilling a key functional requirement of mimicry.[12]

In addition to mimicry of heterospecific alarm call elements, D-song had three chorus-level acoustic features of real mobbing flocks. First, males imitated the mobbing alarm calls of several species in quick succession ($\bar{x} = 4.3 \pm 0.33$ SE, range 3–6; Table S1). Second, they patterned elements to emulate a real chorus. Males repeated elements at a similar rate to model species (Table S2) and ran individual mobbing elements together—characteristic of two individuals calling at the same time (Figure 1B; 9/11 recordings, contiguous elements of the same species: $\bar{x} = 4.6 \pm 2.32$ SE, range 0–26; contiguous elements of different

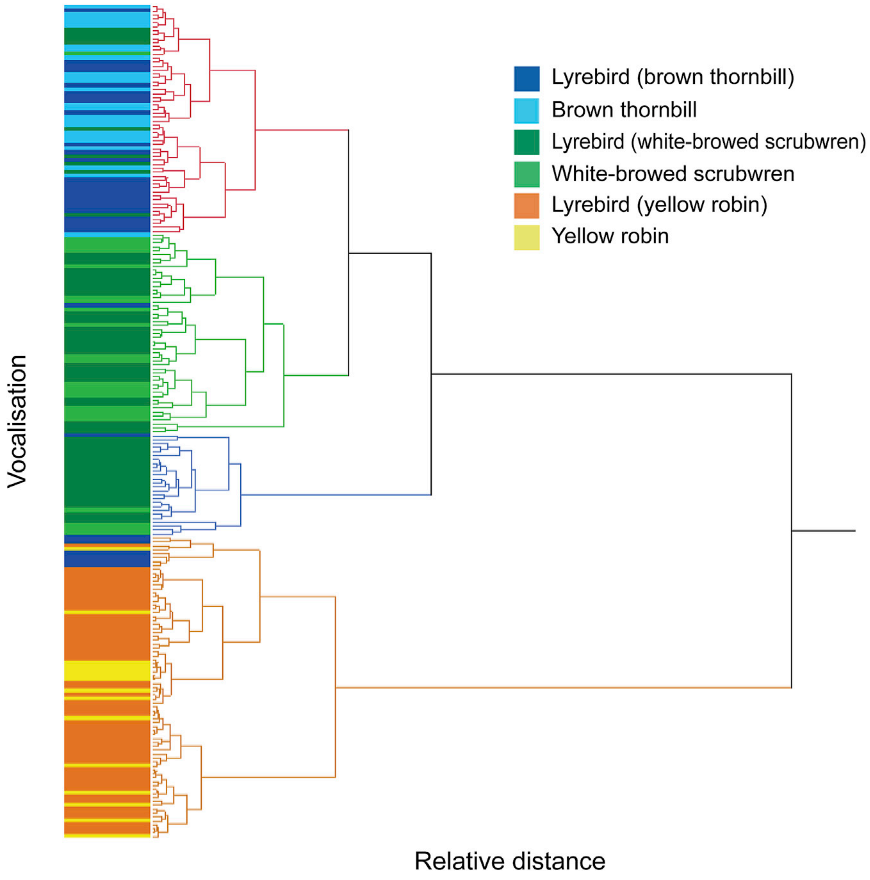

Figure 2. Hierarchical cluster analysis of the acoustic properties of elements produced by males during D-song (mobbing mimicry) and mobbing alarm calls of three sympatric passerines

Acoustic measurements were lowest frequency, peak frequency, duration, and the rate of frequency modulation. The color bar shows the species that produced the element (lyrebird or model) and how the lyrebird element was classified by human observers (classification shown in brackets). Sample sizes, 149 elements from 15 lyrebirds, 15 elements from 4 eastern yellow robins, 24 elements from 8 scrubwrens, and 24 elements from 8 brown thornbills. See also Tables S1 and S4.

species: $\bar{x} = 6.6 \pm 2.15$ SE, range 0–18). Furthermore, lyrebirds overlapped sets of multiple elements to imitate two individuals, of the same or different species, alternating elements with the other (Figure 1B; 9/11 recordings, $\bar{x} = 1.5 \pm 0.39$ SE, range 0–4). Here, on some occasions, one overlapping set was not as loud as the other, creating the illusion of two individuals calling from different distances (Figure 1B). Finally, males often mimicked the wing beats of small birds performing short flights (Figure S1; Table S1; 7/11 recordings) that are common within real flocks. Overall, lyrebird D-song mimicry shared multiple acoustic features with natural mixed-species mobbing flocks.

Our field playback experiment tested the perceptual accuracy of lyrebird mimicry by examining the response of small passerines to D-song. A similar number of individual birds and species approached within 10 m of the speaker broadcasting D-song as an actual mobbing chorus, while birds ignored the control sound of male lyrebirds producing 'recital' mimetic song,[20] a vocal display associated with singing from a perch (Figure 3; Table S3; individuals, GLM: $F_{2,42} = 8.19$, $p < 0.001$; species, GLM: $F_{2,42} = 4.12$, $p = 0.023$). Thus, lyrebird D-song in particular was sufficiently similar to the sound of a real mobbing flock to fool passerines.

Camera trap footage revealed that males produced D-song in two contexts that are key to male mating success: the moment an inspecting female attempts to exit the male's display mound without copulating with the resident, and also during copulation itself. We never observed males producing D-song in the presence of a predator, or during any other phases of the sexual interaction ($n > 1{,}300$ videos and thousands of hours of personal observations of adult male superb lyrebirds by A.H.D., J.A.W., and A.C.M.).

Many visits by females did not end in copulation and instead concluded with the female exiting the display mound (Figure 4A). When the female entered a male's display mound, the male performed his dance display,[10] singing non-mimetic song types A–C, with his tail inverted over his head (26/26 events, N = 12 males). During a single visit, a female could enter and exit a male's display mound multiple times (e.g., Video S1A). All males on all occasions produced D-song immediately after a female left the display mound without copulating (Figure 4B; LMM: $F_{1,23.8} = 896$, $p < 0.0001$; Videos S1A and S1B), with the male switching to D-song about 2 s after a female left the display mound ($\beta = 0.97 \pm 0.033$ s, $p < 0.0001$; y intercept estimate = 2.40 ± 0.772 SEs, $p = 0.007$).

In addition, males always produced D-song during their long copulation (Figure 4C; Table S1; Videos S1C–S1E; Audio S1D and S1E; N = 8 copulations). In all cases the onset of D-song coincided with the start of copulation, to within 1 s. While mounted on the female, the vocalizations of 7/8 males comprised D-song only, while one male switched from D-song to a lyrebird-specific clicking call during the later stages of copulation (after 23.9 s of 43.6 s copulation). Males never performed D-song before or after copulations when the female was on the display mound. All copulations immediately followed the male's performance of the song types A–C that were coordinated with stereotyped dance.[10] In all six filmed copulations, after mounting the female the male lowered his tail in the non-display position (so that it was just above the female's tail, with the dark 'cryptic' side facing upward; Figure S2; Videos S1C–S1E). Lyrebird copulations lasted on average 45 ± 0.73 SEs (range: 42–49 s). Cloacal contact appeared to occur immediately before the male dismounted (STAR methods), implying that the unusually long duration of mounting[21] was not due to the mechanical requirements of sperm transfer (e.g., Winterbottom et al.[22]). During

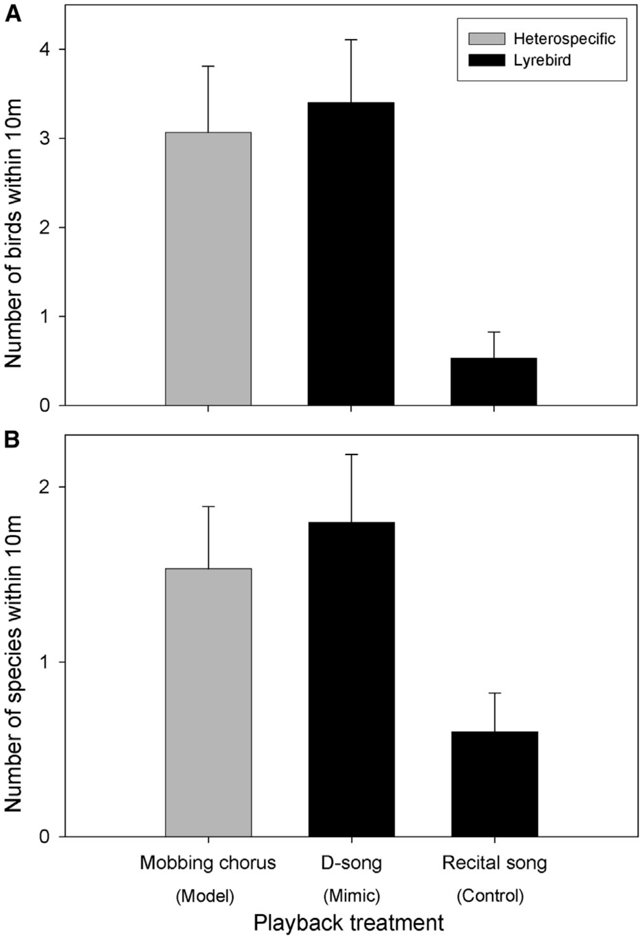

Figure 3. Passerines were more likely to approach playback of lyrebird D-song (mobbing flock mimicry) and real mobbing chorus (model) than lyrebird recital song (non-mobbing flock mimicry)

The average number (+SE) of (A) individual birds and (B) species that approached within 10 m of a speaker broadcasting a playback of an actual mobbing flock, mimicry of a mobbing flock by a male ('D-song'), or non-mobbing flock mimicry by a male ('Recital song') (n = 15 per treatment). See also Table S3.

copulation, the male beat his wings in front of him, which obscured the view of the female's head (Figure S2; Videos S1C–S1E).

During moments crucial to male reproductive success, including copulation, male superb lyrebirds create an extraordinary acoustic illusion of a mixed-species mobbing flock. Most calls imitated by males were heterospecific mobbing alarm calls, which signal a hidden or stationary predator.[16,23] However, lyrebird males only gave the mimicry deceptively in a sexual context, when no predators were present. The acoustic illusion of a mobbing flock was enhanced by imitations of the wingbeats of small birds and the temporal juxtaposition of mimetic elements to create the impression of multiple individuals calling simultaneously. This striking acoustic similarity between mimetic and model sounds, together with the similar responses from heterospecifics to acoustic playback of the lyrebirds' mimicry and true mobbing flocks, confirm that male lyrebirds vocally imitate a mixed-species mobbing flock, creating a compelling cue of a predator.

The complexity of lyrebird D-song broadens our understanding of functional mimicry,[4] and does not conform to standard models of vocal learning. While most definitions of mimicry assume that the model is a single taxon (reviewed in Quicke[24]), the percept[4] mimicked by males during D-song is an auditory representation of an ecological event: a mixed-species mobbing flock triggered by the presence of a predator. Real mobbing flocks differ in fine-scale acoustic structures, due to variation in the species composition and temporal arrangements of calls of mobbing individuals, but receivers might identify them using higher-order cognitive processes, such as Gestalt grouping principles (*sensu* Dent and Bee[25]), to integrate general acoustic features common to these flocks. A mimic, therefore, needs to mimic these perceptually salient features in order to fool receivers, and our playback experiment indicates that lyrebird D-song can deceive avian observers into responding to it like to an actual mobbing chorus. In producing this complex vocalization male lyrebirds copy a *polyphonic* model sound, comprising two or more independent 'vocal lines' (also known as 'voices' or 'melodic lines' *sensu* Frobenius et al.[26]). This feat seemingly constitutes a degree of cognitive and physical complexity beyond the traditional, general model of imitative vocal learning, which involves the imitation by a tutee of a discrete vocalization as produced in solo singing by a tutor of a particular class (e.g., social father or adult conspecific:[27–29] in essence the vocal reproduction of a *monophonic* model sound (*sensu Grove Music Online*[30]).

The association between mobbing-flock mimicry and sexual interactions implies that this mimicry confers reproductive benefits on males. While such mimicry might function as a signal of male quality—attracting females via either handicap or Fisherian processes—this hypothesis does not explain why males produce mimicry rather than species-specific vocalizations or why mobbing-flock mimicry is not performed during other important stages of courtship, including pre-copulation dance displays and the dawn chorus.[10,20] Alternatively, creating a false cue of a predator might reduce the risk that a real predator preys upon the vulnerable mating lyrebirds. However, it is unclear why an anti-predator vocalization would benefit males when females are departing, or why mobbing-flock mimicry is not then used by females, who are themselves adept vocal mimics.[31]

Instead, mobbing-flock mimicry has important features of a sensory trap: it is produced only by the competing sex (males), sung only during key stages of the mating sequence, and comprises deceptive mimicry of an informative acoustic cue.[2,3] The sensory trap hypothesis further predicts that male lyrebirds benefit by exploiting anti-predator behavior in females, and females are indeed vulnerable to several terrestrial predators that prompt mixed species-mobbing flocks (STAR methods). Ideally, playback experiments to females could test their responses to mobbing flocks, particularly in non-sexual contexts, and confirm whether females respond similarly to male mimicry and real mobbing flocks. Work on species more amenable to experimentation point to possible mechanisms in lyrebirds in both contexts of female departure and copulation. For example, male topi antelopes (*Damaliscus lunatus*) use false species-specific alarm calls when females attempt to depart from male display arenas, delaying female departure, which ultimately results in additional copulations by

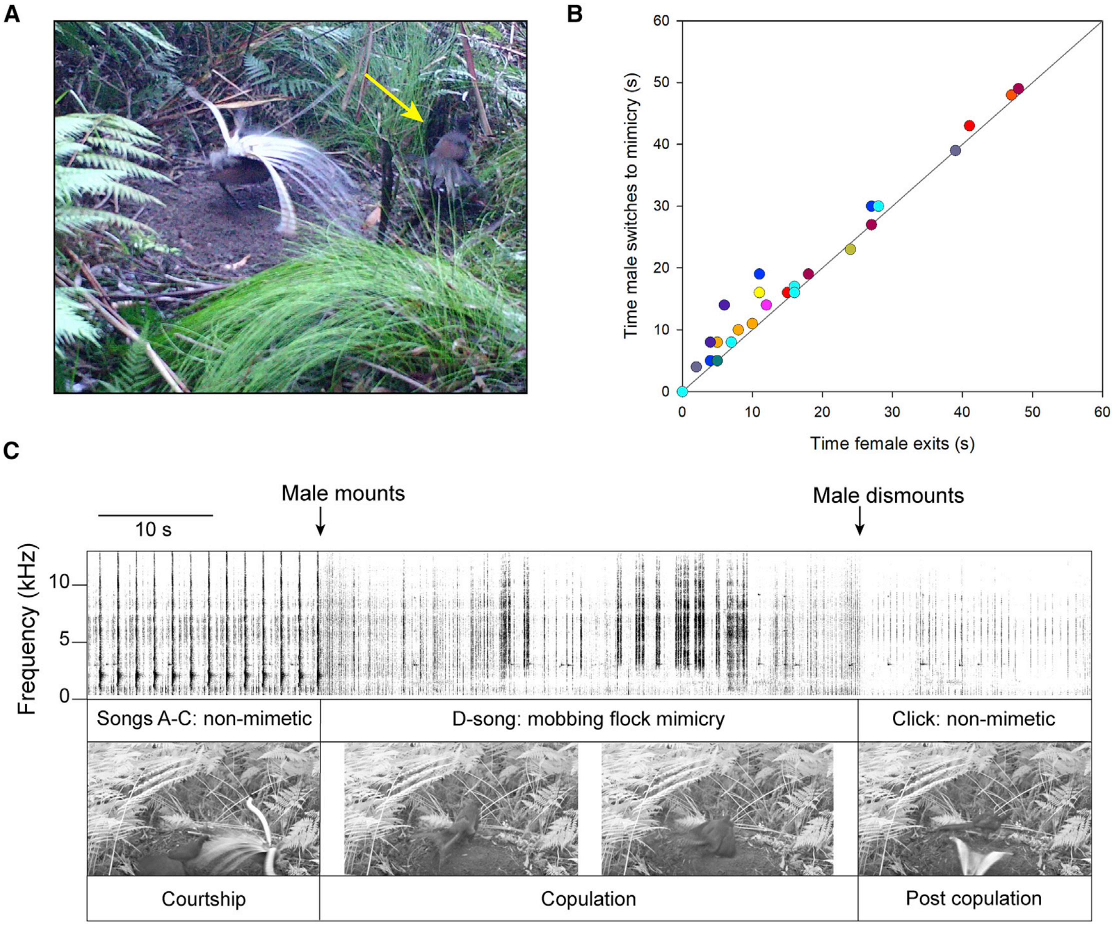

Figure 4. Males produced mobbing flock mimicry in two distinct sexual contexts: when a female attempts to leave a displaying male without copulating, and during the prolonged copulation

(A) A female (arrow) leaving the mound of a displaying male without copulating (Video S1B).

(B) The onset of D-song by male regressed on the time (since the start of the 60 s video) a visiting female departed from the display mound without copulating (N = 26 departure events; N = 12 males, indicated by colors). The reference line is the predicted association if males switch to D-song and females exit simultaneously (y = x).

(C) Audio (Audio S1E) and visual (Video S1E) data from a single copulation event (Table S1, event B^2) with spectrogram of the copulation, preceded by final moments of the dance display[10] ('Courtship'), and the display performed by the male after dismounting the female ('Post copulation').

See also Figure S2, Table S1, Audio S1D and S1E, and Videos S1A–S1E.

males.[32] Furthermore, male Asian corn borer moths (*Ostrinia furnacalis*) can mimic the echolocation calls of predatory bats, causing females to freeze and enabling mating.[33–35] Like topi antelopes, male lyrebirds may exploit female antipredator behavior during mate inspection in an attempt to prevent females from prematurely ending sexual interactions, perhaps because like some other species of lekking bird[36,37] copulations occur only after a female has spent a minimum period of time inspecting the male. Indeed, females that had recently left a male sometimes lingered within hearing range while the male mimicked (e.g., Video S1B), and some females returned (e.g., Video S1A). Like the mimicking moths, during copulation male lyrebirds could use mimicry to prevent females from moving away and ending the copulation, perhaps because sperm transfer occurs approximately 40 s after mounting in this species. Copulations longer than 2 s are very rare among songbirds and may benefit males by deterring females from subsequently re-mating with other males[21,38–40] (also Løvlie et al.,[41] Ekstrom et al.,[42] and Arnqvist and Rowe[43]).

The elaborate displays by male lyrebirds incorporating mobbing flock mimicry suggest that sexually antagonistic co-evolution can give rise to multicomponent and multimodal ('complex'[44]) mimetic signals. To create a sensory trap, lyrebird males could simply produce false, conspecific alarm calls (like Topi[32]) or mimic the sound of a predator (like *O. furnacalis* moths[35]). Instead, lyrebirds mimic the cacophony provoked by a predator to produce an illusion of an ecological scene. This remarkable complexity is consistent with a protracted inter-sexual coevolutionary arms race,[3,45,46] whereby female lyrebirds evolve more acute perception of the males' mimicry, and males counter with more elaborate trickery, and vice versa. Selection to increase the efficacy of deceptive mimicry could further result in male lyrebirds evolving non-mimetic signal components that thwart female facilities to distinguish between mimic and model.[4] Indeed, male lyrebirds appear to attempt to prevent the female from detecting the deception. For instance, a copulating male covers the female's head with his flapping wings, perhaps blindfolding her (Figure S2; Videos S1C and S1D) and so depriving her of visual information about the putative threat. Display mounds may similarly function as an obscurant: males construct mounds in dense, tall undergrowth, so while on a mound a visiting female is enclosed within a wall of vegetation, further limiting her view of her surroundings (Videos S1A–S1E; Figures 1, 4, and S2). Regardless of whether these non-vocal male behaviors function to enhance the efficacy of the acoustic illusion, the male lyrebird's mimicry of a mobbing flock provides a dramatic example of complex mimicry.

Finally, our results conflict with widely accepted theories about the drivers of complex learned vocalizations in birds, including avian vocal mimicry. The evolution of vocal learning in oscine passerines is typically attributed to sexual selection leading to elaborate conspecific song,[27] whereby complexity in song honestly signals singer or territory quality.[27,47] In contrast, our findings provide evidence that complex learned vocalizations can function as deceptive mimicry, most likely a sensory trap, promoting the evolution of elaborate avian vocalizations via sexually antagonistic co-evolution. Our study thus provides evidence for a new functional hypothesis for the avian vocal signals we call 'song' that does not rely solely on the usual explanations of male-male competition or female choice.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2021.02.003.

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AUTHOR CONTRIBUTIONS

A.H.D. conceived the study with subsequent input from R.D.M. and J.A.W.; A.H.D., R.D.M., and J.A.W. designed the data collection and analysis; A.H.D., A.C.M., and J.A.W. collected the data; A.H.D. wrote the manuscript with help from J.A.W. and R.D.M.; and all authors discussed results and contributed to the final manuscript.

DECLARATION OF INTERESTS

Authors declare no competing interests.

INCLUSION AND DIVERSITY

While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list. The author list of this paper includes contributors from the location where the research was conducted who participated in the data collection, design, analysis, and/or interpretation of the work

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological Samples		
Copulation video files	This paper	Videos S1C–S1E; Macaulay Library
Copulation audio files	This paper	Audio S1D and S1E; Macaulay Library
Sexual interactions video files	This paper	Videos S1A and S1B; Macaulay Library
Male lyrebird mimicry (D-song) audio files	This paper	Audio S1B and S1C; Macaulay Library
Model species audio files	This paper, unless otherwise specified	Figure 1; Audio S1A
Eastern whipbird (*Psophodes olivaceus*) call	https://www.xeno-canto.org	*Xeno Canto* XC171916
Bobuck possum (*Trichosurus cunninghami*) and Common ringtail possum (*Pseudocheirus peregrinus*) audio files	[18]	Tracks 39 and 46
Deposited Data		
Species mimicked during D-song	This paper	Table S1
Species mimicked during copulation	This paper	Table S1
Similarity between mimicry and model	This paper	Table S4
Results of playback experiment	This paper	Table S3
Software and Algorithms		
Raven	https://ravensoundsoftware.com	N/A
Syrinx	[18]	N/A
Genstat	https://www.vsni.co.uk/software/genstat	N/A
JMP	https://www.jmp.com/en_au/home.html	N/A
VLC	https://www.videolan.org/vlc/index.html	N/A
Adobe illustrator	https://www.adobe.com/au/products/illustrator.html	N/A

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Anastasia Dalziell (anastasia.dalziell@cornell.edu).

Materials Availability

This study did not generate new unique reagents.

Data and Code Availability

The audiovisual data generated during this study are available at the Macaulay Library (https://www.macaulaylibrary.org).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We studied a mimicry complex involving superb lyrebirds. Data were obtained from two lyrebird populations in south-eastern Australia approximately 700 km apart: Sherbrooke Forest within the Dandenong Ranges National Park (37°53'S, 145°21'E) and Jamison Valley, located in the Blue Mountains National Park (33°45'S, 150°21'E).

Study subjects

The mimic – male superb lyrebird

Male superb lyrebirds routinely incorporate vocal imitations of heterospecifics into their vocal displays,[48,49] but while these mimetic vocalizations are implicated in mate attraction, the selective mechanisms are unclear.[20,50] During the winter when females lay their single clutch of one egg, individual males defend territories in which they construct several circular 'display mounds' (1 – 2 m in diameter) on the forest floor, and these male territories tend to be clustered. Males play no role in the raising of young[51] and once all females are incubating, males moult their elaborate tail feathers and cease displaying. Thus, lyrebirds broadly align with the definition of an exploded lek mating system: extravagant male display, no male parental care, aggregation of male territories, 'free' female choice of mates, and females gaining no resources from males other than sperm.[52,53]

Males court females with a multicomponent display that falls into two distinct display types, both including vocal mimicry. The more common 'recital display' comprises flamboyant song, and involves song-types exclusive to lyrebirds, as well as a large repertoire of accurate imitations of the songs and calls of other species of bird[20] (archived audio-visual recording: ML475993, https://macaulaylibrary.org/asset/475993). Recital displays are never accompanied by dances.[10] Dance displays, on the other hand, are typically performed on display mounds,[20] and involve a male inverting his tail over his head while coordinating dance movements with four distinct song-types delivered in a predictable sequence[10] (Figure 1A; archived audio-visual recording: ML 475994, http://macaulaylibrary.org/video/475994). However, only the quiet, final song type of the dance display, D-song, is mimetic. Here, we examine the structure and function of this display component.

The model – mixed-species mobbing flock?

Mobbing is an anti-predator behavior common among diverse birds, usually involving a group of individuals of the same or different species harassing a predator.[16,17,54] Typically, birds mob a predator that is not posing an immediate threat to them, such as an ambush predator attempting to hide or a hawk that is perched. Participant species of mobbing flocks are not always recognized prey of the targeted predator. Mobbing flocks are often initiated after calls from one individual in response to the presence of a predator attract other individuals of the same or another species, and many bird species use mobbing alarm calls that are acoustically distinct from other vocalisations.[16,17,55] In the forests of SE. Australia, mobbing flocks can form around snakes, large lizards, cats, foxes, roosting owls, and perched hawks (unpublished data), all of which are threats to adult lyrebirds or their young.[49] Mobbing flocks are acoustically conspicuous and are reliable cues of the presence of a concealed predator.[17]

The receiver – female superb lyrebird

Female superb lyrebirds are smaller than males and cryptic in appearance and behavior.[49] While they are accurate and versatile vocal mimics, females are silent during intersexual interactions.[31] When fertile, females visit male display mounds and some visits culminate in copulation. Copulation is thought to take place only on male display mounds,[49] but information has been restricted to anecdotal reports[49] and a documentary film showing edited video footage (without the original audio).[56]

Ethical note

The work was approved by the Western Sydney University Animal Care and Ethics Committee (A10699 and A12077), the Cornell University Animal Care and Use Committee (2009-0105), and the Animal Experimentation Ethics Committee of the Australian National University (F.BTZ.09.07). All procedures were designed to minimize the number of individuals used, while limiting disturbance and stress.

METHOD DETAILS

Recording mimicry (D-song)

We recorded the D-songs of 11 different males (duration: $\bar{x} = 21.8 \pm 2.49$ SE s, range 9.9-37.1 s) during focal observations (06:30 – 09:30 h) conducted during the breeding season (May–July, 2007-2009) in Sherbrooke Forest. Of these males, seven were color-banded by the Sherbrooke Lyrebird Survey Group,[57] two were identifiable by physical anomalies, and the remaining two males occupied distinct, non-adjacent territories. In order to obtain recordings made under comparable ecological conditions, we included examples only where the focal male accompanied his song with dance-like movements to form a multimodal display,[10] and we did not include rare recordings of displays that concluded in copulations, which were analyzed separately. We analyzed only one dance display from each of the 11 males, to avoid pseudoreplication.

Recording models (mobbing calls and mobbing flocks)

We prompted mobbing calls by presenting a physical model of a predator placed on the ground, accompanied by playback of mobbing alarm calls recorded from white-browed scrubwrens (*Sericornis frontalis*) or previously recorded mixed-species mobbing flocks. While the presentation of a physical model alone was sometimes sufficient, in most cases small passerines did not respond unless initially alerted by playback of alarm calls. Predator models were either a rubber red-bellied black snake (*Pseudechis porphyriacus*; Australian Geographic Shop) or a taxidermic mount of a boobook owl (*Ninox novaeseelandiae*). Both these predators occur in the study site. The combination of physical model and playback attracted up to approximately 40 passerines in a single event, many of which vocalized. We supplemented our sample with recordings of eastern yellow robins made in Canberra, ACT, since we were seldom able to induce yellow robins to produce mobbing calls. All other recordings of model species were made within the Dandenong Ranges National Park between May and September 2009. Recordings were made using a handheld Sennheiser ME66 shotgun microphone and a Marantz PMD670 digital recorder sampling wave files at 16 bit and 44.1 or 48.0 kHz (converted to 44.1 kHz for analysis and playback).

Acoustic analysis

Sound recordings were visualized using Syrinx spectrogram settings: FFT window type Blackman, transform size 1024 (J. Burt, e.g., Burt et al.[58]). Fine scale analysis was performed in Raven Pro 1.3 (Cornell Laboratory of Ornithology 2008, Ithaca, NY, U.S.A.) using the waveform and spectrogram (‘Blackman’, 582 samples, time grid 2.08ms, frequency grid 23.4Hz). Sounds were maximized before analysis and spectrograms were kept at a constant scaling (16 kHz, 0.47 s per line).

Playback experiment

We broadcast sounds from a ‘Peerless’ 4-inch, midrange speaker, attached via an amplifier to a Roland Edirol R-09 HR solid-state digital player. We flagged a 10 m radius around the speaker to facilitate measurements, and for 3 min before and after the start of the playback two observers recorded the number of each species of bird that approached within 10 m of the speaker . We did not count birds that were more than 20 m above the speaker. Trials were not started until the 10 m speaker radius was empty of birds, although occasionally 1 – 3 individuals came within the radius toward the end of the initial 3 min silent observation period. To control for this variation, we initially fitted as a covariate the number of birds within 10 m of the speaker before the playback commenced. We also fitted the date of the playback. However, both covariates were dropped after a backward stepwise regression indicated that neither significantly affect the model ($p > 0.05$).

The playback experiment was conducted between 4th and 14th September 2009 in Sherbrooke Forest, and used 15 unique replicates each of the three treatments. Recordings from 15 adult male lyrebirds were used to make up the two different lyrebird treatments with one sample of D-song (mimic) and one sample of recital mimetic song from each individual. Each mobbing flock treatment (model) consisted of six renditions of a 20 s exemplar, followed by 10 s of silence. Recordings of D-song were edited so that all recordings consisted of 20 s (close to the mean length of recorded D-songs 21.8 s, STAR Methods) and were also broadcast six times. We selected exemplars with the highest signal to noise ratio. All sounds were filtered under 400 Hz, normalized to 90%, and broadcast at 51 dB at 8 m, which is the mean natural amplitude of imitations of white-browed scrubwrens and brown thornbills by lyrebirds at that distance (as determined using a D 1405E Sound Level Meter, Dawe Instruments England). To ensure that mobbing elements in the mobbing flock and mimetic playbacks were equivalent in amplitude, we excluded from the D-song tracks any imitations of the red wattlebird call – a much louder call that male lyrebirds occasionally mimic (Figure S1). Each trial was conducted in a different location, and the order of presentation of treatments was balanced. In order to minimize the risk of multiple testing of individual birds, playback sites were at least 300 m apart and neighboring positions were tested on different days. To help ensure that playbacks were heard by species that join mobbing groups, we placed the playback speaker near at least two brown thornbills or white-browed scrubwrens, both species which commonly attend mixed-species mobbing. We conducted playback trials only on days when there was no rain, little or no wind, and with minimal or no cicada calls.

Audio and video recordings

Camera trap footage of natural sexual interactions was obtained from a population of lyrebirds in the Jamison Valley during winter 2014-2018. The cameras (Bushnell NatureView Cam HD, model #119439) recorded for 60 s after triggering, the maximum possible, and at the highest available resolution (1080p HD 16:9: 20-30 fps in color, 15-20 fps infrared; settings automatically determined using an inbuilt light sensor). Cameras were set to trigger at any time of day. Male-female interactions often lasted longer than 60 s, so that there were often gaps in footage of variable duration while the camera re-triggered. Videos were inspected using VLC media player 3.03 and the audio components were visualized using Raven Pro 1.5 (Cornell Laboratory of Ornithology 2017, Ithaca, NY, U.S.A.). To avoid observer bias, we first viewed each 60 s video with the sound switched off and logged female behavior to the nearest second. We then measured to the nearest second the start of the D-song from the audio track, with the video switched off.

Females exiting male display mounds

We investigated whether males produced D-song in response to a female leaving his mound by examining the relationship between the onset of D-song by the male and the timing of the female’s departure from the mound. If the female’s departure triggers the male’s D-song, then the D-song should begin shortly after the female exits the mound. From our database of 1,020 60 s videos of lyrebirds on display mounds, we identified 26 events involving 12 different males where a single female exited the mound without copulating, after observing a male perform all or part of his dance display (songs A – C). Our hypothesis predicted a male response to a female leaving his mound. Accordingly, we did not analyze events where (i) the female only exited the mound at the end of the 60 s camera-trap video because this left < 1 s for the male to respond (N = 3), or (ii) it was ambiguous whether the female had in fact left the mound (N = 3) because she lingered to within one body length from the edge of the mound.

Copulations

Six copulations were filmed using camera traps in the Blue Mountains and two were observed and sound-recorded in person in Sherbrooke Forest. In Sherbrooke Forest, the two copulations took place at 08:15 and 08:30. In the Blue Mountains, six copulations were filmed using camera traps (set to record audio), with five occurring between 06:50-08:40, and one at 13:25. In three of the filmed copulations, the mating sequence was also sound-recorded in its entirety using an autonomous sound recording device (*Wildlife Acoustics*: SM2 or SM4 recording uncompressed, unfiltered sound at 44.01 kHz, 16 bit). For the remaining three filmed copulations (without an additional sound recording) there was an unrecorded 5 s, 7 s and a 13 s delay between motion-triggered videos; however, the beginning and end of these copulations were captured on film. While mounted on the female, the male flapped his wings audibly, allowing the duration of mounting to be measured from recordings including the audio recordings for events where a video was not available or incomplete. This paper uses the formal definition of copulation duration for birds;[21] that is, the duration of mounting, not just the cloacal contact required for sperm transfer. Cloacal contact appeared to occur immediately before the male dismounted. Whereas footage of the first ~40 s of copulations shows the male's tail on top of the female's tail, in the final seconds of the copulation the male shifts closer to the female's posterior, and his tail is seen adjacent to or underneath the female's tail, consistent with cloacal contact (observable in 4 filmed events, involving three different males). This change in position was accompanied by an audible increase in the pace of wingbeats (e.g., Video S1C).

QUANTIFICATION AND STATISTICAL ANALYSIS

Linear mixed models, hierarchical cluster analysis, and t tests were performed using JMP 9.0 2010 or 11.0 2013 (SAS Institute, Cary, North Carolina), and generalized linear models were constructed in Genstat 13th ed. 2010 (VSN International, Hemel Hempstead). All statistical details of analyses and experiments are specified in the Results, the Figures or Figure legends. Statistical significance was defined as $p < 0.05$. To assess the similarity between lyrebird mimicry and suspected model sounds, we used Ward's method to conduct a hierarchical cluster analysis on the standardized acoustic measurements of call elements produced by both lyrebirds and three model species (eastern yellow robin, white-browed scrubwren and brown thornbill). The final number of appropriate clusters accounted for the distance bridged by combining clusters and how model species' calls were separated. We then compared the rate of element production between model and mimetic sounds using paired t tests.

To analyze the playback experiment, we constructed generalized linear models using a log link function and assuming a Poisson distribution of the number of birds and the number of species within 10 m of the speaker. Dispersion parameters for the models were estimated. The playback treatment was fitted as the explanatory term preceded by two control variables: the date of the playback (Julian days) followed by the number of birds or species within a 10 m of the speaker during the three minutes preceding the playback.

To test whether males produced D-song in response to a female leaving his display mound, we constructed a linear mixed model with time of onset of D-song as the dependent variable, time females left a mound as the explanatory variable, and male ID as a random factor. Regression diagnostic plots of residuals were used to assess whether the data met the assumptions of the model. We predicted that males should switch to D-song very shortly after visiting females had left the mound, but that males should not sing D-song while the female was on the mound, and so the y-intercept of the linear model should be positive and the slope ~1. Alternatively, if D-song caused female departure, then female departure should occur after males sang D-song and the y-intercept should be negative. If D-song was unrelated to female departure, then we would be unlikely to find a relationship between the two variables.