

Title: Performative manipulation of the environment by displaying Albert's lyrebirds

Fiona Backhouse^{1,2}, Justin A. Welbergen², Bryce W. Robinson¹, Anastasia H. Dalziell^{1,2}

¹ Cornell Lab of Ornithology, Cornell University, Ithaca, New York, USA

² Hawkesbury Institute for the Environment, Western Sydney University, Richmond, Australia

Corresponding author: Fiona Backhouse, frb27@cornell.edu

ORCID:

Fiona Backhouse - 0000-0001-9308-620X

Justin A. Welbergen - 0000-0002-8085-5759

Bryce W. Robinson - 0000-0003-1422-8842

Anastasia H. Dalziell - 000-0003-3602-0495

Keywords: Dance, extended phenotype, music, sexual selection, theatrical prop, vocal mimicry

MS type: Natural History Miscellany note

Abstract

Where dramatic sexual displays are involved in attracting a mate, individuals can enhance their performances by manipulating their physical environment. Typically, individuals alter their environment either in preparation for a performance by creating a ‘stage’, or during the display itself by using discrete objects as ‘props’. We examined an unusual case of performative manipulation of an entire ‘stage’ by male Albert’s lyrebirds (*Menura alberti*) during their complex song and dance displays. We found that males from throughout the species’ range shake the entangled forest vegetation of their display platforms, creating a highly conspicuous and stereotypical movement external to their bodies. This ‘stage shaking’ is performed in two different rhythms, with the second rhythm an isochronous beat that matches the beat of the coinciding vocalizations. Our results provide evidence that stage shaking is an integral, and thus likely functional, component of male Albert’s lyrebird sexual displays, and so highlight an intriguing but poorly understood facet of complex communication.

Introduction

Individuals of many species perform elaborate sexual displays where the quality of the performance may directly influence their mating success. Animal performers can enhance their display by actively manipulating their performance environment, either before the performance or during the performance itself. One common way in which performers enhance their display is by using a display court or ‘stage’. Stages can be modified features of the environment, such as the grass tufts used as ‘dance rings’ by Jackson’s widowbird (*Euplectes jacksoni*, Andersson 1991), the sand craters built by cichlids (*e.g.*, *Cyathopharynx furcifer*, Schaedelin and Taborsky

2006), or the built and decorated bowers of bowerbirds (e.g., satin bowerbird, *Ptilonorhynchus violaceus*, Borgia 1985). A well-constructed stage can showcase a performer's cognitive abilities or physical condition (Schaedelin and Taborsky 2009) and can increase the conspicuousness of the performer's plumage (Uy and Endler 2004), and so help the performer attract a mate.

Animal performers may enhance their displays with 'props'; discrete objects manipulated by the performer during a performance (after Madden 2003). 'Props' in animal displays are analogous to 'hand props' in human theatre, which are objects carried by a performer to fulfil a theatrical function (Kennedy 2003, Strawn 2012). Examples of props in animal performances include male Australian humpback dolphins (*Sousa sahalensis*) carrying marine sponges when females are present (Allen et al. 2017), and male splendid fairy-wrens (*Malurus splendens*) presenting flower petals while performing a face-fan display (Rowley 1991).

Animal performers may also actively manipulate features of their stage during display; a behavior that combines features of pre-performance staging and during-performance prop use that we call "performative manipulation of the environment". This display behavior can involve constructed stages, like the webs that are used to create vibrational signals during courtships in spiders (Sivalinghem et al. 2010, Girard et al. 2011), or carefully chosen perches, such as in the King of Saxony bird of paradise (*Pteridopha alberti*), where males bounce on a vine or sapling that the female is also perched on (Frith and Frith 1997). A performer's manipulation of the stage environment during sexual display can create sound, tactile vibrations, or movement, and so form an integral component of a multicomponent or multimodal sexual signal (sensu Hebets and Papaj 2005, Partan and Marler 2005, Heinsohn et al. 2017, Ota and Soma 2022). When combined with song, performative manipulation of the environment may further constitute a

musical performance, with inclusion of musical components such as song, dance, and percussion (Fitch 2015, Heinsohn et al. 2017, Ota and Soma 2022).

In this study, we investigate a suspected novel example of performative environmental manipulation in the display of male Albert's lyrebirds (*Menura alberti*), a sexually dimorphic, lekking oscine passerine restricted to the montane rainforest and wet sclerophyll forests of Bundjalung country, in eastern Australia. Albert's lyrebirds are poor fliers and largely ground-dwelling birds that spend most of their time foraging for invertebrates in and below the abundant leaf litter (Higgins et al. 2001, see Talbot 2016, ML201731881 for video). During the Austral winter, male Albert's lyrebirds perform complex audio-visual sexual displays comprising both mimetic and non-mimetic song (Backhouse et al. 2021, Backhouse et al. 2022) and dance movements performed on a stage known as a 'display platform' comprised of vines, fallen branches, or other vegetation on or close to the ground (Curtis 1972). These display platforms appear to contain more vines or sticks than the surrounding areas in their territory (Backhouse et al. in prep); while woody lianas and vines are typical of their rainforest habitat, these have been shown to contribute only a small amount to the overall ground cover (e.g., 2.2%: Hegarty 1991), the majority of which is leaf litter (Riordan et al. 2020). Therefore, Albert's lyrebirds appear selective in the location of their display platforms (Backhouse et al. in prep). Male Albert's lyrebirds were first suggested to use their feet to 'tap' or shake vegetation during their sexual display (henceforth 'stage shaking') by Curtis (1972), who observed that the vines on display platforms had a worn appearance as if repeatedly grasped in the same spot. Prior to this study, accounts of such stage shaking were based on in-person observations and two videos of the display that were largely of one now-deceased individual male named 'George', who was

habituated to human presence (Robinson and Curtis 1996, Curtis 1998, Trelfo 2004, Curtis 2009, Taylor 2018).

Here, we analyze a dataset of 15 audiovisual recordings of 10 displaying male Albert's lyrebirds from five populations covering the species range to investigate stage shaking within male multimodal sexual displays. Specifically, we systematically describe stage shaking, examine how it is integrated with vocal display components, determine if stage shaking is a species-wide trait, investigate whether stage shaking is an integral component of male multimodal displays, and discuss whether the behavior can be usefully described as a form of performative environmental manipulation.

Methods

We studied five geographically dispersed populations of lyrebirds that encompass the species' range and contain a variety of habitat types (Table 1; Supplementary Material, Figure S1). All populations except Goomburra contain the spiny vine-like palm *Calamus muelleri*, commonly known as 'wait-a-while' or 'lawyer cane', because it hooks onto and entangles other plants with its backward-facing spines. Thus, when a single cane of wait-a-while is moved, much of the adjoining vegetation moves in tandem, amplifying the original movement.

We investigated stage shaking during a discrete phase of the male Albert lyrebird's song and dance display termed the 'gronking display' (Robinson and Curtis 1996). Stage shaking may occur during multiple display components (F. Backhouse, pers. obs.), but the gronking display is a very discrete and distinctive performance that can easily be compared among males. The gronking display comprises two acoustically distinct song types: first, a rhythmically irregular

song type composed of loud ‘gronk’ elements and quieter ‘crack’ and ‘crackle’ elements; and a second song type composed of 1-2 low-frequency, alternating and repeated ‘rhythmic’ elements that to a human listener follow a regular beat (terms from Robinson and Curtis 1996). We here call these two song types ‘loud gronking’ and ‘rhythmic gronking’. Males have been qualitatively described shaking their stage “in perfect time” with their gronking song (Robinson and Curtis 1996, Curtis 2009, page 6). Here, we test formally for regularity, or isochrony, in the beat of the stage shaking, and for coincidence in timing, or synchrony, between the stage shaking and the vocalizations. Here, an isochronous beat is defined as stage shaking with a consistent time-interval between each shake, and synchrony is defined as each stage shake occurring at the same time as a vocalization.

To investigate whether and how male Albert’s lyrebirds incorporate stage shaking into their multimodal sexual displays, we placed motion sensing cameras (Bushnell Aggressor No Glow HD Trophy Cam and Stealth Cam DS4K) at display platforms over the 2018 and 2019 breeding seasons (May – August). We selected 15 videos of gronking song from 10 males to form three samples: five videos from one male from different days (‘within male’), one video each from five males from one population (‘within population’), and one video each from five different populations (‘across populations’). No videos were repeated across samples, but a different video from one male (Goomburra population) was used in each of the ‘within population’ and ‘across populations’ samples. We used videos where the male was for at least part of the video in ‘maximal display’, defined as the male inverting his tail over his back (e.g., Figure 1a; *sensu* Dalziell et al. 2013), in order to keep all display components consistent across males. Visits from birds with female-like plumage were rare, so we restricted our samples to

videos where the displaying male was alone in the camera's field of view to avoid potential variations in behavior when another bird was present.

To describe stage shaking behavior, we first used the 'within male' sample comprising five videos of one male from Lamington as a display 'holotype', as this population is the closest to where stage shaking was observed and filmed for the habituated male 'George'. We viewed these videos without sound to describe the behavior independently of the vocalizations, and to devise a list of criteria to define and characterize the display.

Next, to determine the extent to which stage shaking is a species-wide trait, we viewed the remaining ten videos from the 'within population' and 'across population' samples (Table 1) and defined similarities and differences between the videos based on the display criteria. We hypothesized that if the behavior is a species-wide trait, the behavior could be classified in the same way as the holotype across all populations. We further classified the direction of leg movement in each male, recorded the timing of any apparent changes in rhythm, noted the characteristics of the vegetation on the display platform (e.g., wait-a-while, woody lianas, tree fern fronds, bogruses, or part of a shrub; Table 1), and measured within the camera frame how far from the male the adjoining vegetation moved (in meters). In addition, we visually estimated from the videos the percentage of bare ground or leaf litter on the display platform on a 10 percent increment scale of 0-100 percent. We used these data to document any potential geographical variation in these patterns.

Finally, we investigated whether stage shaking by Albert's lyrebirds could be an integral, and thus functional, component of the male's sexual display or incidental to other dance movements. We hypothesized that if stage shaking is an integral component of the sexual display, then while displaying males will (i) consistently have a foot on one moveable structure

(e.g., vine or stick), regardless of display platform architecture, (ii) mostly be stationary on the display platform while shaking these structures, and (iii) move these structures in a stereotypical manner that is consistently synchronized with at least part of the gronking song. In contrast, if stage shaking is an incidental by-product of the birds' dance movements, these three criteria will not be met simultaneously, and movement of the display platform structures will only be a result of males moving around during the display.

To analyze the beat of the stage shaking display and its synchrony with the loud gronking and the rhythmic gronking, we used the video analysis software BORIS (Friard and Gamba 2016) to view the videos frame-by-frame and scored when the lyrebirds pressed the display platform structures with their legs (a single 'shake'). We then viewed the audio spectrogram in Raven Pro 1.6 (Bioacoustics 2023) and measured the timing of each 'gronk' or 'rhythmic' song element from the 'loud gronking' and 'rhythmic gronking' song types respectively. To measure shaking rate, isochrony, and synchrony with the vocalizations, we used R v4.1.2 (R Core Team 2021) to calculate (a) the inter-onset-interval (IOI) between each shake, (b) the unbiased coefficient of variation (CV) of the IOI and (c) the normalized pairwise variability index (nPVI) of the stage shaking (isochrony), and (d) the Root Mean Square Deviation (RMSD) in time between the shakes and their closest vocalizations (synchrony; Ravignani and Norton 2017, Burchardt and Knörnschild 2020). To compare these measures with a null model, we then created randomized sequences of stage shakes based on the lengths and shaking rates of real sequences, and recalculated the same variables. We then ran linear mixed models using the package 'lme4' (Bates et al. 2015) to compare the duration of each gronking song type, variables (a) – (d) between stage shaking during the two gronking types, and variables (b) – (d) between the real and the randomized stage shaking separately for the two gronking song types, with

population and individual male included as random effects (Kuznetsova et al. 2017; further details in Supplementary Material, Text S1). To test for individual or geographic variation in the rhythm of stage shaking during each song type, we also compared the IOI between shakes for each male using an ANOVA.

Results

Initial description of stage shaking using a 'holotype'

The primary male from Lamington (the display 'holotype' in our study) performed on a platform composed of wait-a-while canes that extended across the display platform into the surrounding vegetation (Figure 1). The male stayed in one single location on the display platform in 4/5 videos, and only changed his location once during one 30 s video. While displaying, the male gripped a vine on the platform with at least one leg and repeatedly pressed it by extending each leg below his body, one leg at a time. Often there was no clear underlying pattern governing which leg shook the vines. However, for 1-3 periods in 3/5 videos he moved his right leg twice and left leg once in a repeated sequence of movement with a regular beat. Prior to the analysis on stage shaking rhythm, we observed across all videos a regular beat in the movement of the male's legs for 51% of the time. When the male moved the vines there was visible movement in the vegetation across the entire camera view (approximately 1.1 m to either side of the male).

Based on these visual observations, we devised the following criteria to test for the behavior in other populations and across display platform structures, and independent of sound. To qualify as stage shaking, the male should exhibit the following three behaviors: (1) have at least one foot on a moveable structure (e.g., vine or stick, rather than bare ground), (2) raise or lower the foot

and so depressing or lifting the moveable structures, and (3) move with a regular beat during part of the display.

Extent of stage shaking across populations and display platform structures

Four out of five videos from the Goomburra ‘within population’ sample, and all five videos from the ‘across population’ sample satisfied the criteria for the stage shaking behavior. Despite differences in the vegetative characteristics of display platforms (Table 1), all males had at least one foot on a vine or other moveable structure during the display, and in 6/10 videos across both the ‘within population’ and ‘between population’ samples the males had both feet on moveable structures. In 9/10 videos the males raised or lowered their feet, in turn moving the display platform structures. The remaining male (Goomburra population) did not satisfy criteria 2 of raising and lowering his feet, but he had both legs splayed to the side and swayed vigorously from side to side while pulling the vines in towards his body. An additional six males (7/10 videos) also swayed the body or shifted the weight from left to right while raising and lowering their feet.

Prior to the quantitative analysis on stage shaking rhythm, all nine males (10/10 videos) were observed moving the display platform structures with a regular beat for at least part of the display (mean $42 \pm 14\%$ of display). Males within and across populations differed in the pattern of leg movement during this part of the display: some alternated legs with each movement, some moved one leg more than the other, and some moved both legs at the same time (details in Supplementary Material, Table S1). In all cases (10/10), the stage shaking resulted in movement

of the surrounding vegetation, observed across the entire camera view (approximately 0.5 - 1.2 m from the male).

Do males deliberately shake their stage?

Stage shaking did not appear to be incidental to other movements, as all males had at least one foot on a moveable structure, despite 6/10 platforms containing 20-80% bare ground or leaf litter (e.g. Figure 1b), and were stationary while shaking these structures. In half the videos (5/10, five males) the male displayed in one spot for the entire video and in the remaining videos males changed location up to three times during a video (with the birds' relocation taking up 0.8% to 14.5% of the video duration), and so movement of the display platform structures was not from simply walking around the display platform.

Stage shaking rhythm is correlated with song structure

All 15 videos from the within male, within population and across population samples contained both gronking song types. Each sequence of loud gronking was on average $4.68 \pm \text{SD } 3.67$ s long, and each sequence of rhythmic gronking was on average $4.34 \pm \text{SD } 0.77$ s long, with no statistical difference in duration between the two gronking song types (Supplementary Material Table S2). The males shook their stages at an average rate of $2.26 \pm \text{SD } 0.78$ shakes/s during loud gronking, and $3.06 \pm \text{SD } 0.16$ shakes/s during rhythmic gronking. The rate and regularity of stage shaking differed between gronking song type (Figure 2, Figure 3, Supplementary Material Table S2): the IOI between shakes was significantly shorter ($p < 0.001$) and less variable (CV of IOI: $p < 0.001$, nPVI: $p < 0.001$) during rhythmic gronking than during loud gronking. The beat

of stage shaking during the rhythmic gronking was more isochronous than expected from the random sequences (CV of IOI: $p < 0.001$, nPVI: $p < 0.001$), whereas the beat of stage shaking during the loud gronking was no different from the random sequences in the CV of IOI ($p = 0.486$), though the nPVI was smaller than expected from the random sequences ($p < 0.001$). The stage shaking was more closely aligned with the vocal syllables during rhythmic gronking than during loud gronking (RMSD: $p < 0.001$, Figure 2, Figure 3, Figure 4), and was more closely aligned than expected from the random sequences during the rhythmic gronking ($p < 0.001$), but not during the loud gronking ($p = 0.896$). There was no significant difference between males in the IOI between shakes during rhythmic gronking ($p = 0.267$) or loud gronking ($p = 0.075$)

Discussion

During their sexual display, male Albert's lyrebirds shook vines or other vegetation on their display platform 'stage'. Stage shaking was visually arresting, resulting from the movement of vegetation surrounding the display platform, which appeared to amplify the movement of the male. Several lines of evidence point to stage shaking being an integral, and thus functional, component of male Albert's lyrebird sexual displays. First, stage shaking occurred across all populations and in five different display platform architectures. Second, all males in our study shook their stage with two distinct rhythms that varied with the song type the male sang. Indeed, during the 'rhythmic gronking', males synchronized the beat of song elements with the beat of their stage shaking, thus confirming previous observations (Robinson and Curtis 1996, Curtis 2009). Finally, the movements generating the stage shaking were stereotyped and distinct from prosaic movements such as walking or foraging. We suggest that the stage shaking by Albert's lyrebirds is likely an unusual form of performative environmental manipulation, where

performers increase their reproductive success by manipulating features of their environment during sexual displays. Further, such a performance, combining learnt song and dance with distinct rhythms, could be considered a convincing example of music in a non-human animal (Fitch 2015, Heinsohn et al. 2017), and indeed the ‘tapping’ of vines in Albert’s lyrebirds have been likened to the use of a musical instrument (Robinson and Curtis 1996).

Variation in the technique males used to shake their stage suggests that the movement of vegetation itself is under selection, rather than the specific body movements of the males. All males stood on and shook the vegetation of their display platform, but while most males lifted and pressed the display platform structures, one male tugged from the side. Nonetheless, this technique generated movement in the surrounding vegetation comparable to movement generated by the other males. Furthermore, the pattern in which males moved their legs also differed among some males but did not differ consistently among populations, suggesting that differences in patterns of leg movements may be incidental to the architecture of the particular stage, or the male’s position on the stage, rather than distinct cultural traditions, although further sampling across populations may detect geographic variation in stage shaking. Overall, such variation in leg movements in the performance of what is otherwise a highly stereotyped sexual display suggests that the signal receiver is more sensitive to the stage shaking itself than the specific leg movement patterns that generate the stage shaking. Whether the stage shaking functions as a visual, acoustic (e.g., through the sound of rustling vegetation; pers. obs.), vibrational or multimodal signal remains to be determined.

How might stage shaking enhance a male Albert’s lyrebird’s mating success? By shaking the vegetation surrounding his display platform, a male may create the illusion that he is bigger or more vigorous. Females of many species prefer to mate with large males (Price 1984,

Andersson and Iwasa 1996, Hunt et al. 2009, Auld et al. 2019) and males can use techniques to appear larger, such as male green frogs (*Rana clamitans*) that reduce the frequency of their calls as a dishonest indicator of body size (Bee et al. 2000), and greater bowerbirds (*Chlamydera nuchalis*) that construct bowers that may create a visual illusion of largeness (Endler et al. 2010). Similarly, females can prefer the most vigorous males (Ward and McLennan 2009, Dunning et al. 2020) and so in theory males could benefit by enhancing female's perception of their vigor. Alternatively, females may prefer males who best synchronize their stage shaking and rhythmic gronking song, perhaps because it demonstrates his cognitive and physical abilities (Dalziell et al. 2013), or enhances the female's perception of some other male signal component (Partan and Marler 2005, Halfwerk et al. 2019). It is also possible that stage shaking may function deceptively. During courtship and copulation, male superb lyrebirds (*Menura novaehollandiae*) create the acoustic illusion of a mixed-species mobbing flock – a potent cue of a predator – in an apparent attempt to prolong sexual interactions on the male's 'stage' (Dalziell et al. 2021). Similarly, by moving the surrounding vegetation while the female is on the display platform, male Albert's lyrebirds may create a visual and perhaps an acoustic illusion that there is a dangerous predator beyond his display platform, and that the female is safer to stay put. However, such a deceptive illusion may also drive females away, and the synchrony between the stage shaking and the male's quiet gronking song is instead more consistent with a signal demonstrating male quality. Further studies assessing female responses to variation in male displays and display platform architecture are required to test these hypotheses.

Albert's lyrebirds are not the only species to incorporate performative environmental manipulation into their sexual displays (e.g., Frith and Frith 1997, Heinsohn et al. 2017, Ota and Soma 2022), but the phenomenon is not well understood. Along with stage choice or

construction and the use of discrete props, performative environmental manipulation is an example of an extended phenotype (Dawkins 1982), providing these signal components enhance the reproductive success of the performer. Displays that rely on manipulating the environment may be particularly sensitive to the availability of suitable display environments (either created or naturally available) and to the cognitive or physical abilities required to manipulate the environment while displaying. Such interactions between the signaler and the environment may not be obvious or even present in lab-based studies as the signal components themselves rely on natural environmental conditions, and so further valuable research into performative environmental manipulation or other similar behaviors requires thorough natural history observations.

Acknowledgements

We acknowledge the Traditional Owners of the land on which this work was conducted, the Yugambeh and Bundjalung Nations. This research was supported by an Australian Government Research Training Program scholarship through Western Sydney University (F.B.), Birdlife Northern NSW (F.B.), the Cornell Lab of Ornithology Rose Postdoctoral Fellowship Program (A.H.D.), a University of Wollongong VC Postdoctoral Fellowship (A.H.D.), the Hawkesbury Institute for the Environment (J.A.W.) and an NSF grant no. 1730791 (A.H.D. and J.A.W.). We are grateful to NSW and QLD Parks and Wildlife Service for access to and advice about field sites. We thank local landowners for access to private property, and Hannah Miranda and Tristan Herwood for data collection. Special thanks to previous naturalists for first observing and writing about this display.

All work for this study was approved by the Western Sydney University Animal Care and Ethics Committee (#A12077) and data collected under Scientific Research Permits from the NSW Parks and Wildlife Service (#SL101351) and the QLD Parks and Wildlife Service (#WITK18768218).

Statement of authorship

Conceptualization – F.B., J.A.W. and A.H.D.; Funding acquisition – F.B., J.A.W. and A.H.D.; Methods development – F.B., J.A.W. and A.H.D.; Data collection and analysis – F.B.; Data visualization – F.B. and B.W.R.; Writing (original draft) – F.B.; Writing (review and editing) – J.A.W., B.W.R. and A.H.D..

Data and code accessibility

Data and code are publicly available on figshare: doi.org/10.6084/m9.figshare.25230503.v1. The videos used for the analysis are archived in Macaulay Library at the Cornell Lab of Ornithology (ML615390191, ML615390192, ML615390194, ML615390195, ML615390196, ML615390198, ML615390199, ML615390200, ML615390201, ML615390202, ML615390207, ML615390208, ML615390209, ML615390211, ML615390212).

Literature Cited

- Allen, S. J., S. L. King, M. Krützen, and A. M. Brown. 2017. Multi-modal sexual displays in Australian humpback dolphins. *Scientific Reports* 7:1-8.
- Andersson, M., and Y. Iwasa. 1996. Sexual selection. *Trends in Ecology & Evolution* 11:53-58.

- Andersson, S. 1991. Bowers on the savanna: display courts and mate choice in a lekking widowbird. *Behavioral Ecology* 2:210-218.
- Auld, H. L., D. L. G. Noakes, and M. A. Banks. 2019. Advancing mate choice studies in salmonids. *Reviews in Fish Biology and Fisheries* 29:249-276.
- Backhouse, F., A. H. Dalziell, R. D. Magrath, A. N. Rice, T. L. Crisologo, and J. A. Welbergen. 2021. Differential geographic patterns in song components of male Albert's lyrebirds. *Ecology and Evolution* 11:2701-2716.
- Backhouse, F., A. H. Dalziell, R. D. Magrath, and J. A. Welbergen. 2022. Higher-order sequences of vocal mimicry performed by male Albert's lyrebirds are socially transmitted and enhance acoustic contrast. *Proceedings of the Royal Society B* 289:20212498.
- Backhouse, F., J. A. Welbergen, B. W. Robinson, and A. H. Dalziell. 2024. Data from: Performative manipulation of the environment by displaying Albert's lyrebirds. *American Naturalist*, Figshare, <https://doi.org/10.6084/m9.figshare.25230503.v1>.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1-48.
- Bee, M. A., S. A. Perrill, and P. C. Owen. 2000. Male green frogs lower the pitch of acoustic signals in defense of territories: a possible dishonest signal of size? *Behavioral Ecology* 11:169-177.
- Bioacoustics, K. L. Y. C. f. C. 2023. Raven Pro: Interactive Sound Analysis Software (Version 1.6.4). The Cornell Lab of Ornithology, Ithaca, NY.
- Borgia, G. 1985. Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Animal Behaviour* 33:266-271.
- Burchardt, L. S., and M. Knörnschild. 2020. Comparison of methods for rhythm analysis of complex animals' acoustic signals. *PLOS Computational Biology* 16:e1007755.
- Curtis, H. 2009. Messiaen Meets Menura—Part 2. *AudioWings* 12:5-6.
- Curtis, H. S. 1972. The Albert lyrebird in display. *Emu* 72:81-84.
- Curtis, S. 1998. Lyrebirds: veiled in secrecy. Pages 32-41 *Nature Australia*. Australian Museum.

- Dalziell, A. H., A. C. Maisey, R. D. Magrath, and J. A. Welbergen. 2021. Male lyrebirds create a complex acoustic illusion of a mobbing flock during courtship and copulation. *Current Biology* 31:1970-1976. e1974.
- Dalziell, A. H., R. A. Peters, A. Cockburn, A. D. Dorland, A. C. Maisey, and R. D. Magrath. 2013. Dance choreography is coordinated with song repertoire in a complex avian display. *Current Biology* 23:1132-1135.
- Dawkins, R. 1982. *The extended phenotype: The long reach of the gene*. Oxford University Press, Oxford.
- Dunning, J. L., S. Pant, K. Murphy, and J. F. Prather. 2020. Female finches prefer courtship signals indicating male vigor and neuromuscular ability. *PLoS One* 15:e0226580.
- Endler, J. A., L. C. Endler, and N. R. Doerr. 2010. Great bowerbirds create theaters with forced perspective when seen by their audience. *Current Biology* 20:1679-1684.
- Fitch, W. T. 2015. Four principles of bio-musicology. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370:20140091.
- Friard, O., and M. Gamba. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution* 7:1325-1330.
- Frith, C. B., and D. W. Frith. 1997. Courtship and mating of the King of Saxony bird of paradise *Pteridopha alberti* in New Guinea with comment on their taxonomic significance. *Emu* 97:185-193.
- Girard, M. B., M. M. Kasumovic, and D. O. Elias. 2011. Multi-modal courtship in the peacock spider, *Maratus volans* (O.P.-Cambridge, 1874). *PLoS One* 6:e25390.
- Halfwerk, W., M. Blaas, L. Kramer, N. Hijner, P. A. Trillo, X. E. Bernal, R. A. Page, S. Goutte, M. J. Ryan, and J. Ellers. 2019. Adaptive changes in sexual signalling in response to urbanization. *Nature Ecology & Evolution* 3:374-380.
- Hebets, E. A., and D. R. Papaj. 2005. Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology* 57:197-214.

- Hegarty, E. E. 1991. Leaf litter production by lianes and trees in a sub-tropical Australian rain forest. *Journal of Tropical Ecology* 7:201-214.
- Heinsohn, R., C. N. Zdenek, R. B. Cunningham, J. A. Endler, and N. E. Langmore. 2017. Tool-assisted rhythmic drumming in palm cockatoos shares key elements of human instrumental music. *Science Advances* 3.
- Higgins, P. J., J. M. Peter, and W. K. Steele. 2001. *The Handbook of Australia, New Zealand and Antarctic Birds*. Oxford University Press, Melbourne, Victoria.
- Hunt, J., C. J. Breuker, J. A. Sadowski, and A. J. Moore. 2009. Male–male competition, female mate choice and their interaction: determining total sexual selection. *Journal of Evolutionary Biology* 22:13-26.
- Kennedy, D. 2003. *The Oxford Encyclopedia of Theatre and Performance*. Oxford University Press.
- Kuznetsova, A., P. B. Brockhoff, and R. H. Christensen. 2017. lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* 82:1-26.
- Madden, J. R. 2003. Male spotted bowerbirds preferentially choose, arrange and proffer objects that are good predictors of mating success. *Behavioral Ecology and Sociobiology* 53:263-268.
- Ota, N., and M. Soma. 2022. Vibrational Signals in Multimodal Courtship Displays of Birds. Pages 237-259 in P. S. M. Hill, V. Mazzoni, N. Stritih-Peljhan, M. Virant-Doberlet, and A. Wessel, editors. *Biotremology: Physiology, Ecology, and Evolution*. Springer International Publishing, Cham.
- Partan, S. R., and P. Marler. 2005. Issues in the classification of multimodal communication signals. *American Naturalist* 166:231-245.
- Price, T. D. 1984. Sexual Selection on Body Size, Territory and Plumage Variables in a Population of Darwin's Finches. *Evolution* 38:327-341.
- R Core Team. 2021. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Ravignani, A., and P. Norton. 2017. Measuring rhythmic complexity: A primer to quantify and compare temporal structure in speech, movement, and animal vocalizations. *Journal of Language Evolution* 2:4-19.
- Riordan, C. E., C. Pearce, B. J. F. McDonald, I. Gynther, and A. M. Baker. 2020. Vegetation structure and ground cover attributes describe the occurrence of a newly discovered carnivorous marsupial on the Tweed Shield Volcano caldera, the endangered black-tailed dusky antechinus (*Antechinus arktos*). *Ecology and Evolution* 10:2104-2121.
- Robinson, F. N., and H. S. Curtis. 1996. The vocal displays of the lyrebirds (Menuridae). *Emu* 96:258-275.
- Rowley, I. 1991. Petal-carrying by fairy-wrens of the Genus "*Malurus*". *Australian Bird Watcher* 14:75-81.
- Schaedelin, F. C., and M. Taborsky. 2006. Mating craters of *Cyathopharynx furcifer* (Cichlidae) are individually specific, extended phenotypes. *Animal Behaviour* 72:753-761.
- Schaedelin, F. C., and M. Taborsky. 2009. Extended phenotypes as signals. *Biological Reviews* 84:293-313.
- Sivalinghem, S., M. M. Kasumovic, A. C. Mason, M. C. B. Andrade, and D. O. Eliasd. 2010. Vibratory communication in the jumping spider *Phidippus clarus*: polyandry, male courtship signals, and mating success. *Behavioral Ecology* 21:1308-1314.
- Strawn, S. 2012. *The Properties Director's Handbook: Managing a Prop Shop for Theatre*. Routledge.
- Talbot, N. 2016. Albert's lyrebird (ML201731881). Macaulay Library.
- Taylor, H. 2018. Can George dance? Biosemiotics and human exceptionalism with a lyrebird in the viewfinder. *Social Semiotics* 28:60-76.
- Trelfo, G. 2004. *Albert lyrebird: Prince of the Rainforest*. O'Reilly's Rainforest Guesthouse, Australia.
- Uy, J. A. C., and J. A. Endler. 2004. Modification of the visual background increases the conspicuousness of golden-collared manakin displays. *Behavioral Ecology* 15:1003-1010.

Ward, J. L., and D. A. McLennan. 2009. Mate choice based on complex visual signals in the brook stickleback, *Culaea inconstans*. Behavioral Ecology 20:1323-1333.

References Cited Only in the Online Enhancements

Backhouse, F., J. A. Welbergen, R. D. Magrath, and A. H. Dalziell. 2023. Depleted cultural richness of an avian vocal mimic in fragmented habitat. Diversity and Distributions 29:109-122.

Burchardt, L. S., P. Norton, O. Behr, C. Scharff, and M. Knörnschild. 2019. General isochronous rhythm in echolocation calls and social vocalizations of the bat *Saccopteryx bilineata*. Royal Society Open Science 6:181076.

Norton, P., and C. Scharff. 2016. "Bird Song Metronomics": Isochronous Organization of Zebra Finch Song Rhythm. Frontiers in Neuroscience 10.

Peterson, R. A. 2021. Finding optimal normalizing transformations via bestNormalize. R Journal 13.

Tables

Table 1. The location, sampling details and description of each sampled population of Albert's lyrebirds. Display platform composition is the type of vegetation comprising the display platform.

Population	Location	No. videos (no. males)	Habitat type	Display platform composition
Lamington (Binna Burra)	28.21° S, 153.19° E	6(2) ^{a,c}	Temperate rainforest	Stems of wait-a-while (<i>Calamus muelleri</i>)
Goomburra	27.97° S, 152.39° E	6(5) ^{b,c}	Temperate rainforest	Tangles of woody vines (n = 4), pile of dead tree fern fronds (n = 1)
Border Ranges	28.38° S, 153.08° E	1(1) ^c	Temperate rainforest	Stems of wait-a-while (<i>C. muelleri</i>)
Mt Jerusalem	28.53° S, 153.40° E	1(1) ^c	Wet sclerophyll forest	Thicket of bogrushes (genus: <i>Shoenus</i>)
Tamborine	27.93° S, 153.19° E	1(1) ^c	Subtropical rainforest	Depressed base of invasive scrambling shrub <i>Lantana camara</i>

^a Used in 'within male' sample.

^b Used in 'within population' sample.

^c Used in 'across populations' sample.

Figure legends

Figure 1. (a) The focal male from Lamington in ‘maximal’ display, and (b) the structure of his display platform. The yellow circles indicate where the male grips a vine on the platform during the display. The corresponding video is archived in Macaulay Library (ML615390211).

Figure 2. The differences in four rhythm measures between the two gronking song types, ‘loud gronking’ and ‘rhythmic gronking’: (a) the Inter Onset Interval (IOI) between shakes (seconds), (b) the unbiased Coefficient of Variation (CV) of the IOI between shakes, (c) the normalised Pairwise Variability Index (nPVI) of the stage shaking, (d) the Root Mean Square Deviation (RMSD; seconds) between the shakes and associated vocalizations. All variables were significantly different between the two gronking song types.

Figure 3. A – the leg movements of the male on his display platform and in the surrounding vegetation. B – the timing of (a) gronking song, and (b) stage shaking taken from one video of the holotype male from Lamington. G = ‘Gronk’ elements, C = ‘Crack’/‘Crackle’ elements, R = ‘Rhythmic’ elements (Robinson and Curtis 1996). Loud gronking was on average $4.68 \pm \text{SD } 3.67$ s long with $9.93 \pm \text{SD } 7.24$ stage shakes, and rhythmic gronking was on average $4.34 \pm \text{SD } 0.765$ s long with 13.0 ± 2.45 shakes. Artwork: Bryce W. Robinson.

Figure 4. Circular histograms showing the time difference between stage shakes and their closest ‘gronk’ vocalization in relation to the IOI between gronks during (a) the rhythmic gronking, and (b) the loud gronking. 0/360 represents the vocalizations, and the bars represent a histogram of the timing of stage shakes. The time of the stage shaking between its two closest vocalizations was converted to a scale of 0-360°, with 0 – 180° meaning the stage shake fell after its closest vocalization, and 180 – 360° meaning the stage shake fell before its closest vocalization.

Figure 1

A This is the author's accepted manuscript without copyediting, formatting, or final corrections. It will be published in its final form in an upcoming issue of *The American Naturalist*, published by The University of Chicago Press. Include the DOI when citing or quoting: <https://doi.org/10.1086/730523>. Copyright 2024 The University of Chicago.



Figure 2

This is the author's accepted manuscript without copyediting, formatting, or final corrections. It will be published in its final form in an upcoming issue of *The American Naturalist*, published by The University of Chicago Press. Include the DOI when citing or quoting: <https://doi.org/10.1086/730523>. Copyright 2024 The University of Chicago.

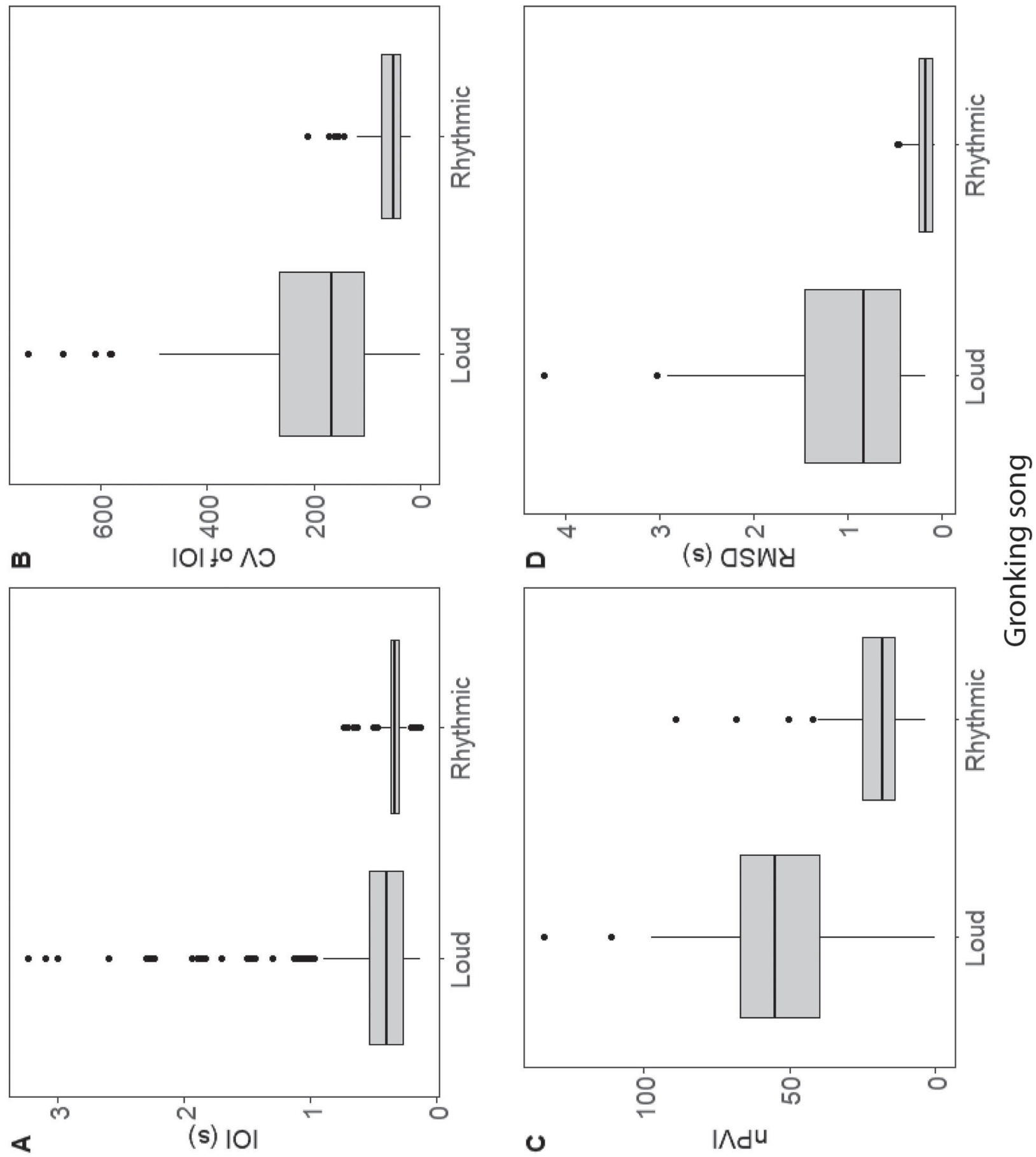


Figure 3

This is the author's accepted manuscript without copyediting, formatting, or final corrections. It will be published in its final form in an upcoming issue of The American Naturalist, published by The University of Chicago Press. Include the DOI when citing or quoting: <https://doi.org/10.1086/730523>. Copyright 2024 The University of Chicago.



(a) Gronking song

Loud gronking

Rhythmic gronking

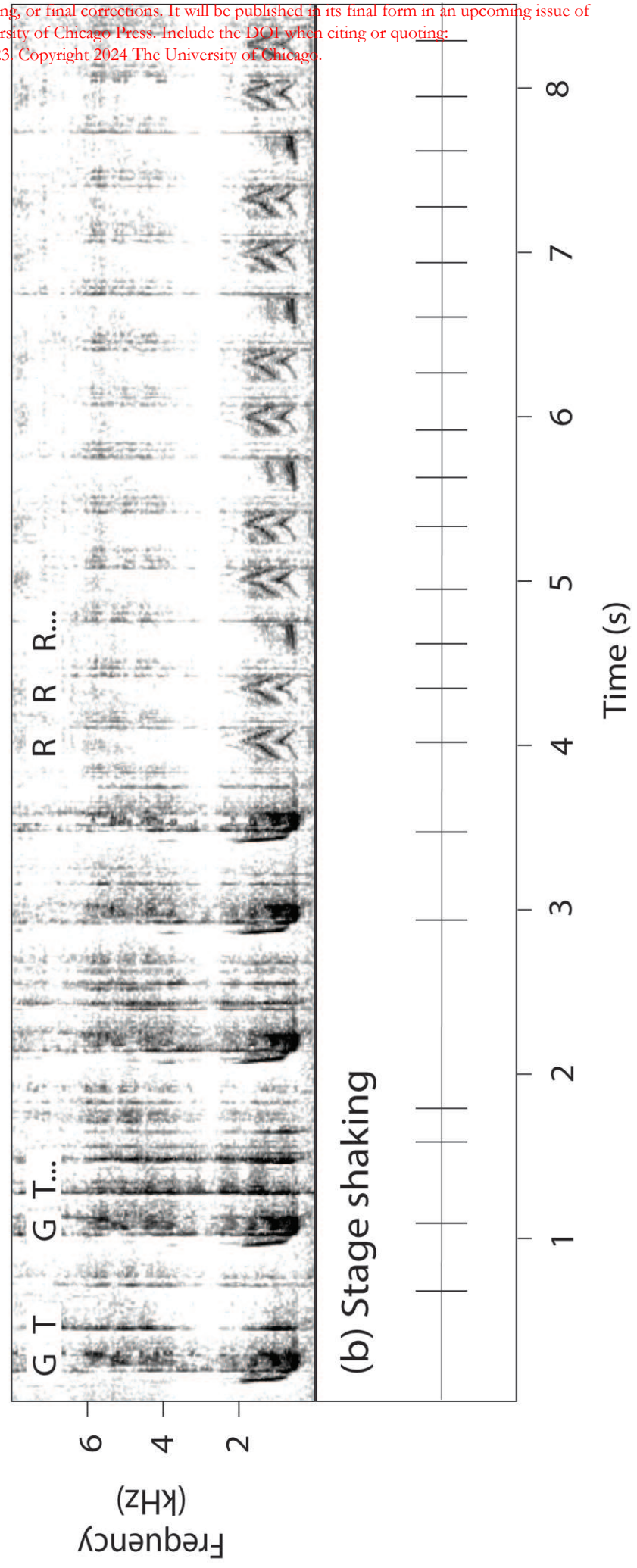
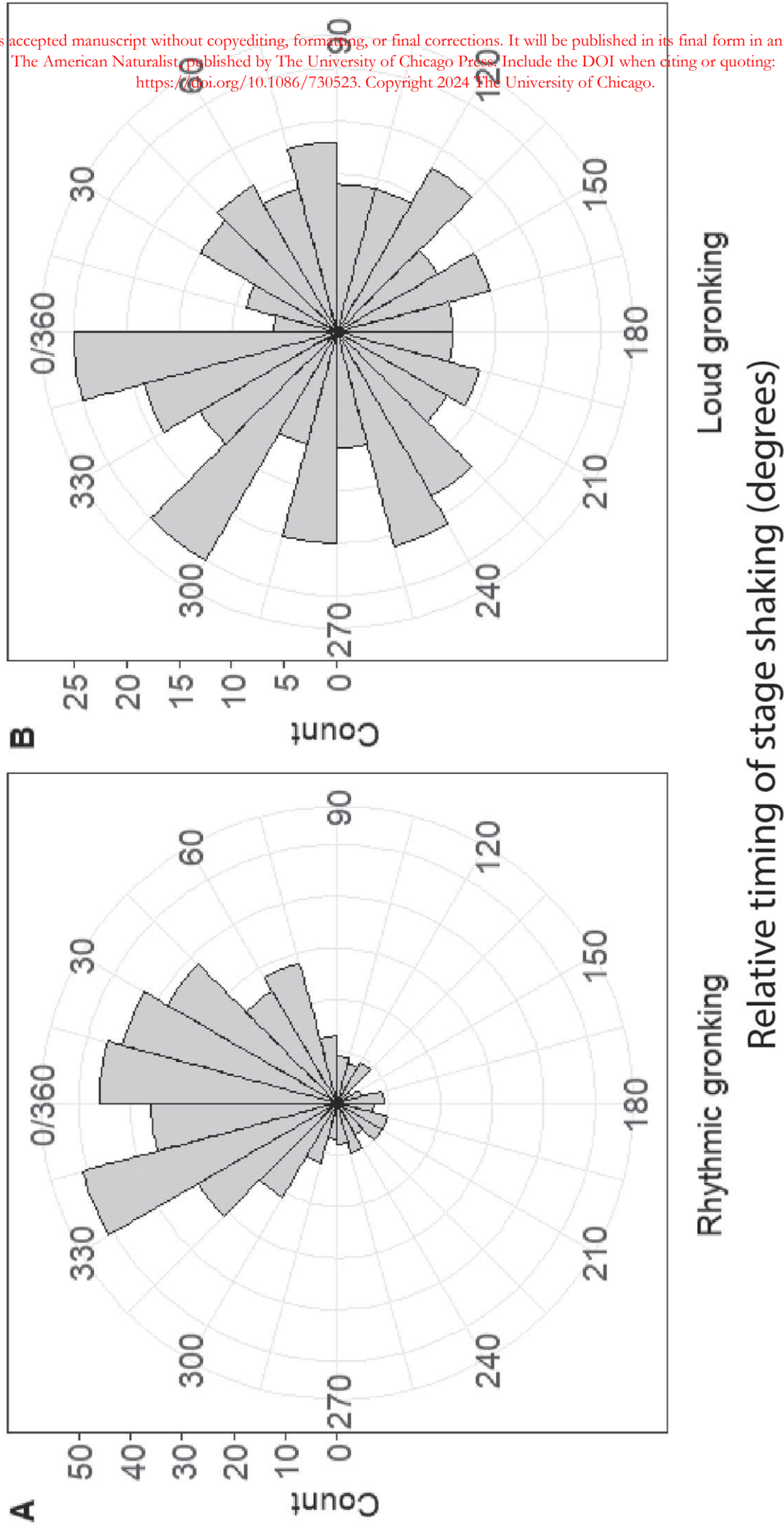


Figure 4

This is the author's accepted manuscript without copyediting, formatting, or final corrections. It will be published in its final form in an upcoming issue of *The American Naturalist*, published by The University of Chicago Press. Include the DOI when citing or quoting: <https://doi.org/10.1086/730523>. Copyright 2024 The University of Chicago.



Supplementary material for: Performative manipulation of the environment by displaying Albert's lyrebirds

Fiona Backhouse^{1,2}, Justin A. Welbergen², Bryce W. Robinson¹, Anastasia H. Dalziell^{1,2}

¹ Cornell Lab of Ornithology, Cornell University, Ithaca, New York, USA

² Hawkesbury Institute for the Environment, Western Sydney University, Richmond, Australia

Corresponding author: Fiona Backhouse, frb27@cornell.edu

Article published in *The American Naturalist*.

Complex displays of Albert's lyrebirds

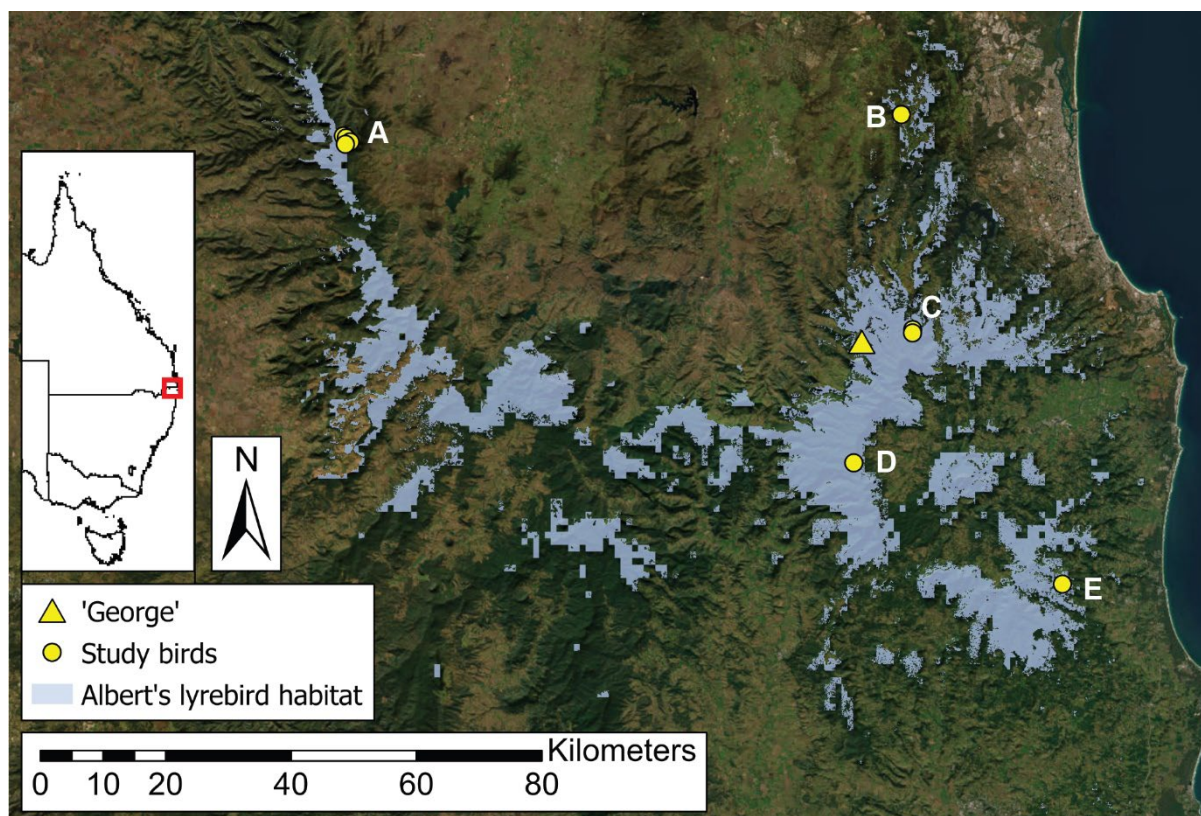


Figure S1. The locations of all study individuals (circles) and, the now deceased, 'George' (triangle), the male on whom earlier descriptions of the dance display were based (Curtis 2009). Present study populations are (A) Goomburra, (B) Tamborine, (C) Lamington, (D), Border Ranges, and (E) Mt Jerusalem. Modeled suitable Albert's lyrebird habitat is in blue (from Backhouse et al. 2023).

Text S1. Methods for measuring the timing of stage shaking and gronking

To compare the rhythm of the stage shaking across the two gronking song types we first measured the timing of both the stage shaking and the accompanying vocalisations. To measure the timing of stage shaking, we viewed the videos in BORIS using the frame-by-frame function. All videos had a frame rate of 30 frames/s. We counted each time the male both lifted and pressed his leg onto a stage structure (e.g., vine or stick), noting the time his foot first reached the lowest point of the movement (constituting a single 'shake'). We did not

count movements from walking or shifting on the display platform, but if one foot was pulling a vine or other platform structure, and the other foot was only stepping up and down onto one spot, we counted the movements of both feet as shakes. We then viewed the spectrogram in BORIS and noted when the male shifted between the 'loud gronking' song type and 'rhythmic gronking' song type, and manually assigned the relevant song type to each shake.

To measure the timing of the vocalisations, we used VLC media player to extract the audio from the videos in MP3 format, with a sampling rate of 44.1 kHz. We then viewed these videos in Raven with a "Hann" display type and the window set at Fast Fourier Transform 1,050. We drew selection boxes around the 'gronk' elements in the loud gronking and the 'rhythmic' elements in the rhythmic gronking (Main text, Figure 3) and noted the type of gronking song. We only measured the 'gronk' elements in the loud gronking as the 'crack' and 'crackle' elements are much quieter and less reliably measured. Preliminary analysis suggested that the timing of stage shaking was not associated with 'crack' elements, and 'crackles' were almost continuous between 'gronks'. We then extracted the 'begin time' of each selected element, measured as the beginning of the signal on the waveform.

To compare the timing of stage shaking between the two gronking song types, we measured the Inter Onset Interval (IOI) between each shake. We then used this to calculate the unbiased coefficient of variation (CV) of the IOI for each song type in each video. The unbiased coefficient of variation ensures that the variation is not underestimated for small sample sizes (Burchardt and Knörnschild 2020). If the gronking song types were repeated within a video, we measured the CV of the IOI for each occurrence of the song separately. We further measured the normalized pairwise variability index (nPVI) of the stage shaking for each occurrence of the song types within each video, providing a measure of how

isochronous (or regular) the beat of the stage shaking is (Ravignani and Norton 2017, Burchardt and Knörnschild 2020).

To assess the synchrony between the stage shaking and the vocalisations, we found the time of the closest vocalisation to each shake and calculated the absolute difference in time between the shake and the vocalisation. We then used this to calculate the Root Mean Square Deviation (RMSD) for each sequence of each song type. This follows a similar method to Norton and Scharff (2016) and Burchardt et al. (2019) where the RMSD is used to calculate the similarity to a simulated isochronous pulse. In these examples, the RMSD is further standardised by the frequency of the pulse to account for differences in the intervals between pulses of different speeds. However, as we were more interested in how closely the stage shaking was aligned with the vocalisations than in how similar the rhythms of the stage shaking and the vocalisations are, we did not standardise the RMSD, and kept it as a measure of how closely aligned the two signals were.

To compare the above measurements with what would be expected if the stage shaking was performed with a random rhythm, we created random sequences of stage shaking timings. Random sequences were created using each real sequence of loud or regular gronking and the associated stage shaking, with one sequence ending and a new sequence beginning every time the male switched gronking song type. We used the 'sample' function in R to assign each stage shake a random time within the start and end time of the sequence, and then re-ordered the stage shakes based on these new random times to create a new sequence. To account for possible biological restrictions on the speed of stage shaking, we restricted the timing of the randomized stage shaking such that no two shakes could be closer than the smallest IOI found between real shakes (0.133 s). For each sequence of real stage shaking within each gronking song type, we thus created a paired sequence of stage shaking

Complex displays of Albert's lyrebirds

with the same length and average shaking rate as the real sequence, but with a randomized rhythm.

We then compared the above four measures – the IOI between shakes, the CV of the IOI, the nPVI, and the RMSD from the vocalisations – as well as the length of each song type between the two gronking stages using linear mixed models in R v4.1.2. We compared each of the five variables between stage shaking during the rhythmic gronking and the loud gronking, and compared the CV of the IOI, the nPVI, and the RMSD from the vocalisations between real stage shaking and randomised stage shaking during the rhythmic gronking, and between real stage shaking and randomised stage shaking during the loud gronking. All variables except song duration were positively skewed, and so were transformed using the package ‘bestNormalize’ (Peterson 2021). We used the transformed variables where required to produce normal model residuals (indicated in Table S2). We ran the models using the package ‘lme4’ (Bates et al. 2015) and estimated the significance of the variables with the package ‘lmerTest’ (Kuznetsova et al. 2017).

Complex displays of Albert's lyrebirds

Table S1. The identified patterns of leg movement within the sampled videos. All listed patterns were observed at least 3 time sequentially within a video. Some videos contained multiple patterns of movement.

Pattern	Number Males	Male ID(s)	Number videos	Population(s)
Alternating feet	6	BRVP3, LBBC2, GBLR2, GBLR4, GBSL1	6	Border Ranges, Lamington, Goomburra
All left foot	4	LBBC1, LBBC2, GBLR3, GBSL5	4	Lamington, Goomburra
Both-left-both-left	3	LBBC2, GBLR3, GBSL5	3	Goomburra
Both feet together	2	MJKR1, TMWFSB	2	Mt Jerusalem, Tamborine
Right-right-left	1	LBBC1	3	Lamington
Right-both-left	1	LBBC1	1	Lamington
All right foot	1	LBBC1	1	Lamington

Complex displays of Albert's Lyrebirds

Table S2. Results from Linear Mixed Models comparing measures on the timing of shakes and vocalisations between the two gronking song types and between real and randomised sequences of stage shaking. Models tested for an effect of gronking song type or permutation on the response variables.

Model	Response variable	Comparison	Estimate (\pm standard error)	t value	p value
1 ¹	Inter Onset Interval	Regular vs loud gronking (real sequences)	-0.413 (\pm 0.0711)	-5.81	< 0.001
2 ¹	Coefficient of Variation of IOI	Regular vs loud gronking (real sequences)	-0.955 (\pm 0.210)	-4.54	< 0.001
3 ¹		Real vs random sequences (regular gronking)	-1.51 (\pm 0.152)	-9.95	< 0.001
4 ¹		Real vs random sequences (loud gronking)	-0.262 (\pm 0.207)	-1.27	0.211
5 ¹	Normalised Pairwise Variability Index of IOI	Regular vs loud gronking (real sequences)	-1.10 (\pm 0.200)	-5.51	< 0.001
6		Real vs random sequences (regular gronking)	-50.13 (\pm 4.59)	-10.9	< 0.001
7		Real vs random sequences (loud gronking)	-26.6 (\pm 5.59)	-4.76	< 0.001
8 ¹	Root Mean Square Deviation	Regular vs loud gronking (real sequences)	-1.49 (\pm 0.150)	-9.98	< 0.001
9 ¹		Real vs random sequences (regular gronking)	-1.15 (\pm 0.177)	-6.50	< 0.001
10 ¹		Real vs random sequences (loud gronking)	-0.0243 (\pm 0.185)	-0.131	0.896
11	Song duration	Regular vs loud gronking (real sequences)	0.0881 (\pm 0.242)	0.365	0.717

¹Dependent variable was transformed with an Ordered Quantile (ORQ) normalization transformation prior to analysis.

References

- Backhouse, F., J. A. Welbergen, R. D. Magrath, and A. H. Dalziell. 2023. Depleted cultural richness of an avian vocal mimic in fragmented habitat. *Diversity and Distributions* **29**:109-122.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**:1-48.
- Burchardt, L. S., and M. Knörnschild. 2020. Comparison of methods for rhythm analysis of complex animals' acoustic signals. *PLOS Computational Biology* **16**:e1007755.
- Burchardt, L. S., P. Norton, O. Behr, C. Scharff, and M. Knörnschild. 2019. General isochronous rhythm in echolocation calls and social vocalizations of the bat *Saccopteryx bilineata*. *Royal Society Open Science* **6**:181076.
- Curtis, H. 2009. Messiaen Meets Menura—Part 2. *AudioWings* **12**:5-6.
- Kuznetsova, A., P. B. Brockhoff, and R. H. Christensen. 2017. lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* **82**:1-26.
- Norton, P., and C. Scharff. 2016. “Bird Song Metronomics”: Isochronous Organization of Zebra Finch Song Rhythm. *Frontiers in Neuroscience* **10**.
- Peterson, R. A. 2021. Finding optimal normalizing transformations via bestNormalize. *R Journal* **13**.
- Ravignani, A., and P. Norton. 2017. Measuring rhythmic complexity: A primer to quantify and compare temporal structure in speech, movement, and animal vocalizations. *Journal of Language Evolution* **2**:4-19.