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RESEARCH ARTICLE

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Depleted cultural richness of an avian vocal mimic in fragmented habitat

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Abstract

Aim: Conservation has recently shifted to include behavioural or cultural diversity, adding substantial value to conservation efforts. Habitat loss and fragmentation can deplete diversity in learnt behaviours such as bird song by reducing the availability of song tutors, yet these impacts are poorly understood. Vocal mimicry may be particularly sensitive to habitat loss and fragmentation through the resulting reduction in both heterospecific models and conspecific tutors. Here we examine the relationship between habitat availability and both mimetic repertoire size and song composition in male Albert's lyrebirds (*Menura alberti*), a near-threatened species renowned for its remarkable mimetic abilities.

Location: Eastern Australia.

Methods: We calculated repertoire size and composition from recordings of male Albert's lyrebirds from throughout the species' range. We estimated patch size and local habitat availability using a species distribution model and remotely sensed vegetation types. We assessed the local model species assemblage through species distribution models and automated acoustic detectors.

Results: Individual males in smaller habitat patches, or in areas with a lower proportion of suitable habitat, mimicked fewer model species and fewer vocalization types. However, they mimicked comparatively more vocalizations from each model species than individuals in larger patches or with more intact habitats. All model species were likely to occur in most study sites, suggesting that repertoires are not driven by the availability of model species.

Main Conclusions: Our results suggest that mimetic repertoire sizes are influenced by habitat availability through the number of lyrebird tutors. Further, individuals in disturbed habitats may partially compensate for mimicking fewer species by mimicking more vocalizations from each species. This study supports the hypothesis that cultural diversity may be impoverished by habitat loss and fragmentation in a similar way to genetic diversity. Variation in song diversity may therefore indicate population health and highlight populations in particular need of conservation action.

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KEYWORDS
animal culture, bird song, cultural conservation, population health, sexual display, vocal learning

1 | INTRODUCTION

Conservation has traditionally focussed on biodiversity, and a recent shift to include behavioural or cultural diversity as additional diversity metrics has the potential to facilitate more comprehensive and efficient conservation efforts (Brakes et al., 2021; Whitehead et al., 2004). Cultural diversity may be reduced through several anthropogenic processes, such as habitat loss and fragmentation, urbanization, and related changes to species assemblages and soundscapes. Cultural diversity is an important consideration in conservation for several reasons. First, socially learnt behaviours are often important for survival (Brakes et al., 2021; Stoinski et al., 2003) or reproduction (Catchpole & Slater, 2008), and changes in or loss of such behaviours due to anthropogenic factors may lead to species declines (Caro & Sherman, 2012). Second, changes in animal cultural diversity may alert us to potential changes in population dynamics and viability, particularly where data on behaviours such as songs are easier to collect than genetic data or traditional assessments of population size (Keighley et al., 2019; Laiolo, 2010; Laiolo et al., 2008; Valderrama et al., 2013). Third, animal cultural diversity has value to humans through its contribution to 'distinctiveness of place' (Carson, 2002; Lomolino et al., 2015). Fundamentally, just as traditional biodiversity is often considered to have important intrinsic value (Sandler, 2012), animal cultural diversity has intrinsic value and is worth conserving for its own sake. To include cultural diversity as an important component of conservation, we must first understand natural patterns and determine the drivers of cultural diversity.

The song of oscine passerines is a cultural trait that often exhibits high phenotypic diversity. Many oscine passerines produce multiple song types (Fayet et al., 2014; Hultsch et al., 2004; Opaev, 2016), and these song types often differ between localities (Catchpole & Slater, 2008; Podos & Warren, 2007). There is therefore substantial song diversity within individual repertoires, populations, and species. The spatiotemporal processes driving change in socially learnt songs are often seen as analogous to genetic evolution (Lynch, 1996), and hence genetics-based conservation theory provides a useful framework for studying cultural behaviours. Like genetic diversity, song diversity can be affected by mutations, random drift, migration rates, and selection (Lynch, 1996). However, additional modes of transmission and mutation in the song mean that vocal diversity can change faster than genetic diversity (Lynch, 1996), and may provide a metric of species viability more sensitive to change than genetic diversity (Laiolo & Tella, 2005).

Two of the greatest threats to biodiversity are habitat loss and fragmentation (Joppa et al., 2016; Tilman et al., 2017), and these threatening processes can also reduce song diversity (Laiolo et al., 2008; Laiolo & Tella, 2007; Sebastián-González & Hart, 2017). Reductions in the size of habitat patches and increases in their geographic isolation reduce genetic variability through processes such as population bottlenecks, founder effects, and more subtle forms of genetic drift (Magurran et al., 1998; Smith & Wayne, 1996). These same processes may also act on song diversity. Smaller habitat patches can influence song diversity through a reduced number of conspecifics tutors from which individuals can learn the song, leading to fewer song variants persisting in the populations (Fayet et al., 2014; Nunn et al., 2009). Increased habitat isolation reduces immigration, which can also reduce song diversity because fewer song variants are introduced locally (Fayet et al., 2014). Low song diversity can indicate low population viability (Laiolo et al., 2008), or lower the reproductive success of individuals (Crates et al., 2021; Hiebert et al., 1989). In small, isolated populations, individuals may be forced to innovate new songs (Parker et al., 2012), or even mistakenly imitate the songs of other species, which could effectively increase song diversity while eroding the species' culture (Crates et al., 2021; Helb et al., 1985). The relationship between cultural diversity and reproductive success can give rise to an Allee effect, where small population sizes erode cultural variation, thereby promoting further population decline and erosion of cultural variation (Crates et al., 2017). While quantifying and preserving song diversity has the potential to be of great importance to species conservation, relatively few studies have investigated song diversity in relation to habitat fragmentation.

The effects of increased habitat loss and fragmentation on the diversity of species-specific songs have been garnering increasing interest (Crates et al., 2021; Laiolo, 2010; Laiolo et al., 2008; Sebastián-González & Hart, 2017), yet the impacts on vocal mimicry are poorly understood. Mimicry of heterospecific vocalizations is widespread across oscine passerines (Dalziell et al., 2015; Goller & Shizuka, 2018) and may be learnt purely from heterospecifics (Kelley & Healy, 2010; Riegert & Jůzlová, 2018) or, in some cases, partially from conspecifics as well (Backhouse et al., 2022; Hindmarsh, 1984; Payne et al., 2000; Putland et al., 2006). Diversity in mimetic repertoires may therefore be depleted through the effects of anthropogenic landscape change on the mimics as well as their models. If mimicry is learnt from heterospecifics, then the diversity of sounds mimicked by an individual or population should correspond with local species richness, which in turn may be impacted by habitat loss or fragmentation (Laiolo et al., 2011). On the other hand, if mimicry is learnt primarily from conspecifics, then the diversity of mimicry may be related to conspecific population dynamics. Examining the size and composition of repertoires of vocal mimicry in relation to habitat loss and fragmentation, and model species assemblages, will aid in both understanding how mimicry is learnt and help establish the nature of the relationship between vocal mimicry and population dynamics of both the vocal mimics and their model species.

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Here we examine whether the availability of suitable habitat is related to song diversity within individuals in the elaborate mimetic song of male Albert's lyrebirds. Albert's lyrebirds have a highly restricted geographic range on the border of New South Wales and Queensland in eastern Australia, and are listed as Near Threatened under the IUCN Red List (BirdLife International, 2016). Since the European settlement of the area in the 19th century, their habitat has been heavily cleared for timber harvesting and agriculture (Garnett et al., 2011; Higgins et al., 2001), and hence Albert's lyrebirds may be vulnerable to loss of cultural diversity. Previous research suggests that male lyrebirds learn their mimicry from both other lyrebirds and heterospecifics (Backhouse et al., 2022; Putland et al., 2006), and so male mimetic repertoires are expected to be sensitive to processes affecting both lyrebird populations and the diversity and abundance of model species. We first investigate whether mimetic repertoires are driven by the assemblage of heterospecific models at each site. We then test whether mimetic repertoires are reduced in smaller habitat patches or with a lower local availability of suitable habitat and whether repertoire composition is likewise affected by overall habitat availability.

2 | METHODS

2.1 | Study species

Albert's lyrebirds are large (~930 g), sedentary oscine passerines renowned for their exceptional vocal mimicry (Higgins et al., 2001; Robinson & Curtis, 1996). During the breeding season (March–August), adult males defend display territories (Schodde & Manson, 1996) containing display arenas (or 'platforms') upon which they sing or perform elaborate multimodal displays (Backhouse et al., 2021, 2022; Curtis, 1972; Higgins et al., 2001). Territories occupy about 5–15 ha and are thought to be loosely aggregated to form groups of displaying males known as 'dispersed' or 'exploded' leks (Higgins et al., 2001, Robinson & Curtis, 1996). During the breeding season, male lyrebirds are largely solitary except during sexual interactions or territorial encounters (Higgins et al., 2001). Territory boundaries break down outside the breeding season when multiple individuals can forage together (Higgins et al., 2001). Males can be distinguished from females and juveniles by their longer, more extravagant tails (Higgins et al., 2001).

2.2 | Study songs

Male Albert's lyrebirds have a varied but structured repertoire including both their own, species-specific vocalizations as well as mimicry of heterospecific vocalizations and environmental sounds (Backhouse et al., 2021, 2022; Putland et al., 2006). Here we focus on the 'recital mimicry' (Backhouse et al., 2022, sensu Dalziell et al., 2022), which is both the predominant form of vocal mimicry and the largest component of the vocal display (Backhouse et al., 2022), and is composed of stereotyped sequences of imitations of complete vocalizations and non-vocal sounds – such as wingbeats – of other species (Backhouse et al., 2022). Both the species-specific 'whistle song' and the recital mimicry vary geographically (Backhouse et al., 2021, 2022), with audible differences between leks as little as 1.5 km apart (F. Backhouse personal observation).

2.3 | Study sites

We studied Albert's lyrebirds throughout the species' range in montane subtropical and temperate rainforest and wet sclerophyll forest in Bundjalung Country, eastern Australia (as defined in AIATSIS, 1996). Previous habitat clearing has largely restricted Albert's lyrebirds to the higher ranges between 28.89° and 27.89°S and 152.36° and 153.40°E (Backhouse et al., 2021; Higgins et al., 2001). We collected data for this study from seven different populations that encompass the species range and have varying levels of habitat availability (Figure 1a). Study populations were distinguished by geographic distance and differences in both species-specific and mimetic song repertoires. Three study populations contained highly acoustically similar subpopulations separated by 2.5–8 km.

2.4 | Field methods

We recorded 35 adult male Albert's lyrebirds from May–July in 2016, 2018 and 2019, with two to eight birds from each of the seven populations (one to five per subpopulation), using both handheld and autonomous sound recorders. A small field team took handheld recordings using a Sennheiser ME 66/K6 shotgun microphone and a Marantz PMD 661 set to record at a 96 kHz sample rate and 24-bit depth, typically 15–30 m from the focal individual. We used recordings from autonomous sound recorders for six of the 35 individuals, and to collect environmental recordings from an additional four territories to help determine the heterospecifics present. We placed the autonomous sound recorders ('Swifts': Terrestrial Passive Acoustic Recording Unit, developed by the Cornell Lab of Ornithology) at 7–10 m from two display platforms in five core populations, set to record at 48 kHz sample rate, 16-bit depth, and 33 dB gain from 1 h before sunrise to 3 h after sunrise. Adult male lyrebirds are long-lived (possibly at least 22 years: H.S. Curtis, cited in Higgins et al., 2001), occupy the same territory each year (Higgins et al., 2001), and often sing from the same display platform (F. Backhouse, personal observation), and so we identified individuals by location. We confirmed sex and adult status by plumage from personal observations or through camera traps paired with autonomous sound recorders (Backhouse et al., 2021).

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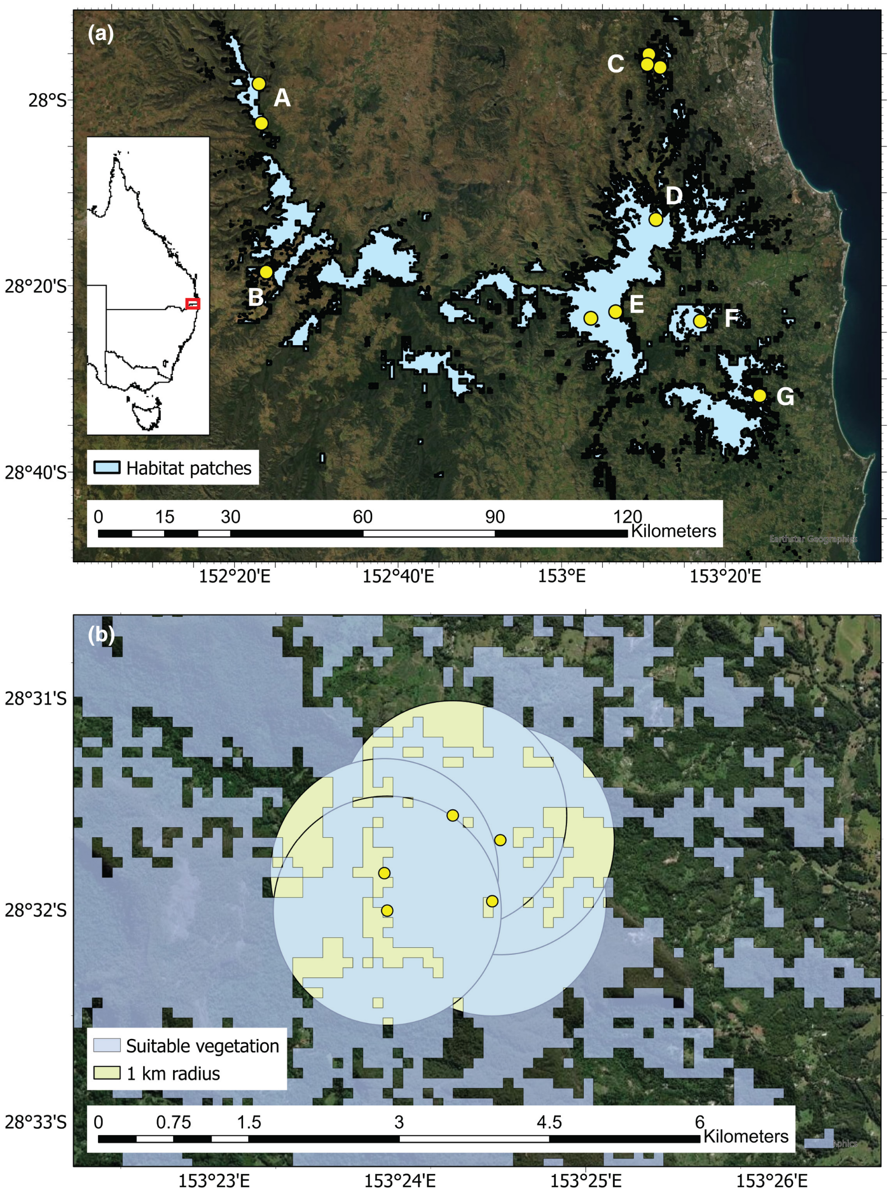

FIGURE 1 (a) The suitable habitat patches (blue) based on both climate and vegetation in which Albert's lyrebirds are likely to be found (see Section 2.7 for details). The locations of the seven study populations are in yellow: A, Goomburra; B, Killarney; C, Tamborine; D, Lamington; E, Border Ranges; F, Wollumbin; G, Mt Jerusalem. Goomburra (A), Tamborine (C) and Border Ranges (E) contain subpopulations. (b) Habitat availability based on vegetation type within 2 km of individual lyrebirds illustrated in the Mt Jerusalem population (G in Figure 1a). Blue denotes suitable vegetation; light green shows unsuitable vegetation within the 2 km radius (outlined in black) used to calculate the proportion of suitable vegetation; yellow points are the locations of individual lyrebirds.

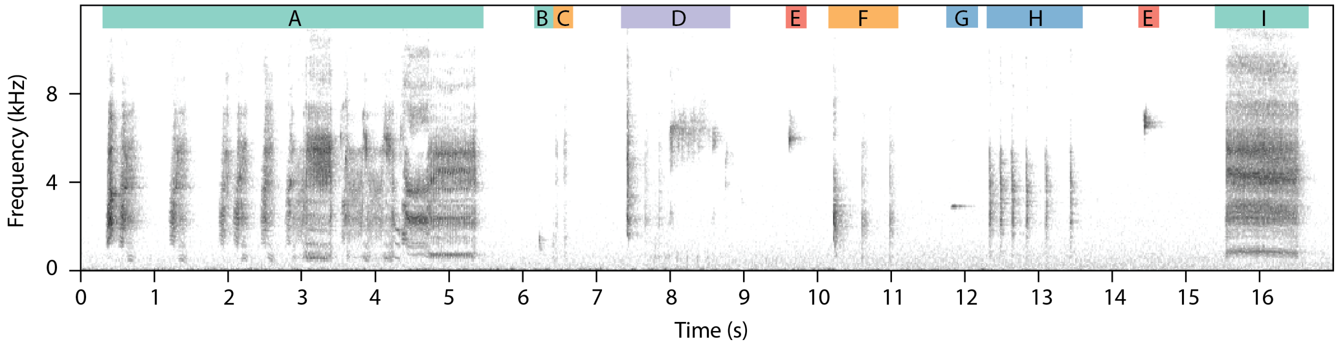

FIGURE 2 An extract of recital mimicry from an individual lyrebird from the Border Ranges population showing the classification of vocal and non-vocal mimetic units and species. Colour indicates species or non-vocal mimetic units; letters indicate unit type. A, B, I: satin bowerbird; C, F: non-vocal units (mimicry of two types of taps); D: white-browed scrubwren and wingbeats (counted as a vocal mimetic unit in this analysis); E: green catbird; G, H: eastern yellow-robin. For an example recording see Audio S1.

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2.5 | Song metrics

To investigate the relationship between habitat availability and mimetic song diversity we quantified both the size and the composition of mimetic repertoires of 35 individual male Albert's lyrebirds. We selected up to 15 minutes of recital mimicry from the recordings of each of the males, resulting in a sample size of 108–429 (mean 301) temporally and acoustically discrete vocalizations ('mimetic units': Backhouse et al., 2022; Figure 2) per male (see Appendix S1, Table S1.1 for sampling information; further details in Backhouse et al., 2022). Where possible, this sample comprised continuous mimicry from one recording. For seven males, we analysed mimicry recorded over two different days from the same year. We recorded mimicry from just one male over 2 days from two different years.

We manually identified the mimetic units from the spectrogram and by ear, visualizing sound recordings in Raven Pro 64 bit 1.5 (Bioacoustics Research Program 2017). For mimicry of vocal sounds, we defined and identified individual units by model species and vocalization type (Figure 2). We defined mimicry of non-vocal sounds qualitatively based on sound (see Appendix S1, Text S1.1).

Albert's lyrebirds mimic both multi-element vocalizations and non-vocal sounds of multiple species, often with several vocalization types from each model species (Figure 2, Audio S1), and so may vary in several measures of repertoire size and composition. To investigate the relationship between habitat availability and repertoire size, we defined repertoire size in three different ways: (a) 'total mimetic unit repertoire size', as the number of both vocalizations and non-vocal units mimicked; (b) 'vocal unit repertoire size', as the number of vocalizations mimicked; and (c) 'model species repertoire size', as the number of model species mimicked.

These three measures of repertoire size have the potential to vary independently, resulting in quantitative differences in the composition of mimetic repertoires that may not be revealed by simple measures of repertoire size. Accordingly, to investigate the relationship between habitat availability and mimetic repertoire composition, we calculated three ratios of mimetic units: (a) total number of mimetic unit types compared with the number of species mimicked; (b) number of vocal units mimicked compared with the number of species mimicked; and (c) number of non-vocal units mimicked compared with the number of species mimicked.

Preliminary analysis showed that the total mimetic unit and the vocal unit repertoire sizes were correlated with the number of units sampled across individuals (Appendix S1, Table S1.2), so for the analyses of repertoire sizes we used the same number of units from each individual. For each measure of repertoire size, we maximized the total possible repertoire of each individual, while minimizing the number of individuals excluded due to the small sample size. This resulted in 149 units from 32 males used to calculate total the mimetic unit repertoire size and vocal unit repertoire size, and 108 units from 35 males to calculate the model species repertoire size (Figure 3; see Appendix S1, Table S1.3 for details of calculations). For analyses of repertoire composition (ratios), we used the full sample of each bird, as the three ratios of unit types to species mimicked are not highly correlated with sample size when compared across individuals (Appendix S1, Table S1.2).

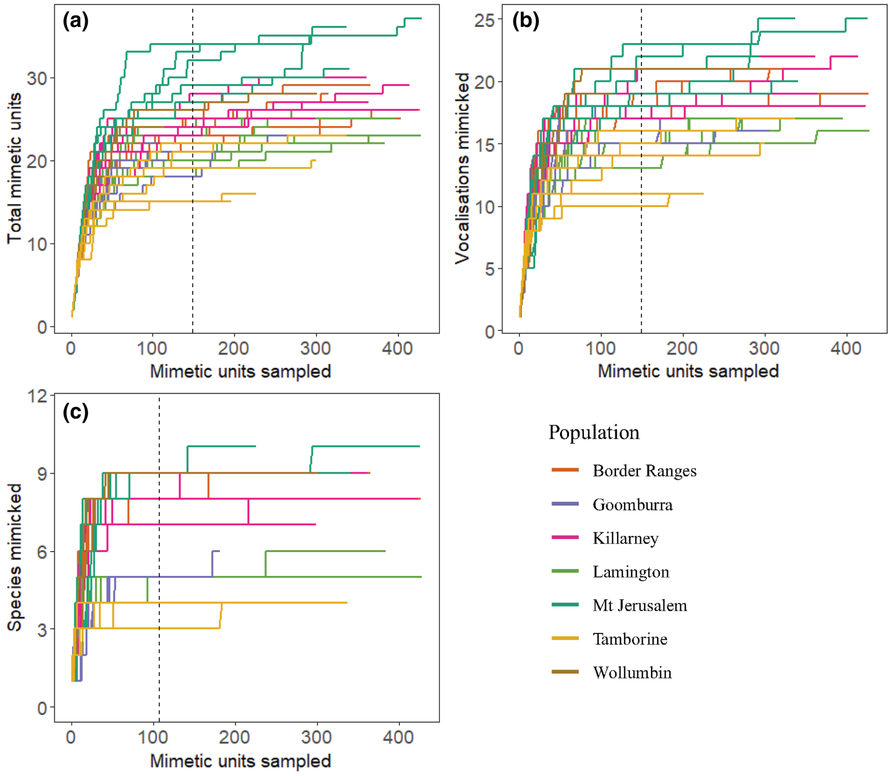

FIGURE 3 Individual lyrebird repertoire accumulation curves for (a) total mimetic units, (b) vocalizations mimicked, (c) species mimicked. Population is indicated by colour. The selected sample size for each analysis is indicated by the dashed line; for (a) and (b) this is 149 units, and for (c) this is 108 units.

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2.6 | Model species occurrences

To determine if differences in species assemblage explain differences in repertoire size or composition, we estimated the likelihood of the avian species mimicked by male Albert's lyrebirds occurring in all study locations, and ground-truthed estimates of a sub-set of three species using recordings of the environment obtained using handheld and autonomous recorders. We chose these broad-scale estimates of species occurrences over other methods (such as standardized bird surveys) because the spatiotemporal dimensions of our chosen methods are probably closer to the scale of the acoustic environment experienced by male Albert's lyrebirds, given that males are long-lived (up to 22 years) and, outside the breeding season, likely traverse an area well beyond their display territories.

We estimated the occurrence of the avian species mimicked by male Albert's lyrebirds using publicly available Species Distribution Models (SDMs) from Research Data Australia (Garnett et al., 2013; VanDerWal, 2012). These SDMs were developed using records from the Atlas of Living Australia (ALA, 2019) filtered by expert opinion and bioclimatic data at a 0.05° (~5 km) grid scale (variables listed in Appendix S1, Table S1.4), and were run using the presence-only modelling program Maxent (Phillips et al., 2006; VanDerWal, 2012). We imported the current SDMs of the species mimicked more than once by more than one individual (listed in Appendix S1, Table S1.5) into ArcGIS v10.6.1 (ESRI®). As the distance between individual male lyrebirds within some populations was greater than the resolution of the SDMs, we calculated the likelihood of each model species occurring in each population or subpopulation by predicting the result of the relevant SDM at the central coordinate of each population or subpopulation. Species were deemed likely to occur if the likelihood was greater than a threshold at which model sensitivity (true positive rate) is equal to model specificity (true negative rate, Liu et al., 2005). We chose this value over the threshold of maximum sensitivity and specificity as the values were higher for all species and would thereby reduce false positives (threshold values in Appendix S1, Table S1.9).

We used automated acoustic detectors to confirm the presence of eastern yellow robins (*Eopsaltria australis*), Australian logrunners (*Orthonyx temminckii*), and Lewin's honeyeaters (*Meliphaga lewinii*) in acoustic recordings from May–September from each site. These model species were mimicked at only half of the sites, and (unlike the other model species) are easily detected due to the high amplitude and simple and distinct acoustic structure of their common vocalizations, and their usual ground or midstory foraging position, which is where we placed our sound recorders. We used Kaleidoscope Pro (Version 5.4.2; Wildlife Acoustics Inc.) to build an automated detector for the three chosen model species using a separate set of parameters to detect each species (Appendix S1, Table S1.6). We first ran an advanced cluster analysis using example recordings, then scanned test recordings from each population or subpopulation to detect the presence of each of the model species (see Appendix S1, Text S1.2 for details). We manually checked spectrograms of potential detections of the model species until we identified the species of interest with high confidence (subsequently ignoring the remaining detections) or until there were no more detections. Where a species was not detected in a location, we manually checked full recordings to eliminate false negatives. Mimicry by lyrebirds of these model species is clearly identifiable by its incorporation into a sequence of mimicry and so mimicry could not be mistaken for models during manual checks.

2.7 | Habitat metrics

To investigate the effects of habitat availability on individual male Albert's lyrebird song diversity we estimated the size of habitat patches and local habitat availability within and surrounding each individual's territory. We defined a habitat patch as a discrete, continuous area of habitat expected to be occupied by Albert's lyrebirds. By this definition, every habitat patch was surrounded by habitat expected to be unsuitable for Albert's lyrebirds. A patch could contain multiple populations or subpopulations. We defined local habitat availability as the proportion of suitable versus unsuitable vegetation in the area surrounding each individual male's territory. As the relationship between habitat availability and song diversity may vary with geographic scale, we calculated local habitat availability for each individual within different radii at multiple scales: (a) 500 m, representing a single territory and immediate neighbour, (b) 1 km, representing a single lek (often four to six individuals, F. Backhouse, personal observation), (c) 2 km, representing neighbouring leks, (d) 5 km, representing multiple, more distant leks, and (e) 10 km, representing a broader population (see Appendix S1, Figure S1.1 for examples).

To estimate habitat patches, we first built an SDM for Albert's lyrebirds in R v4.0.3 using occurrence records from ALA and bioclimatic variables from WorldClim at a resolution of 0.5 min of a degree (Fick & Hijmans, 2017). Building our own SDM for the Albert's lyrebird allowed us to control the explanatory variables and use a higher spatial resolution. After filtering the occurrence records from ALA to remove points outside the known distribution for Albert's lyrebirds, we used 5433 presence points and 10,000 background points, and built the SDM using maximum entropy modelling (Maxent; see Appendix S1, Text S1.3, Table S1.7 for details on SDM construction, and Appendix S2 for the ODMAP protocol). We clipped the resulting model to only include values over the threshold of maximum sensitivity and specificity (0.477; Liu et al., 2016), representing climatically suitable areas.

To refine estimates of habitat patches and determine local habitat availability, we also estimated the extent of suitable vegetation types. We achieved this using a bootstrap method in R adapted from Fournier et al. (2017) to compare the number of lyrebirds found in each vegetation type with the expected number, using the filtered ALA occurrence records and a map of Major Vegetation Subgroups from the National Vegetation Information System (NVIS v6.0; see Appendix S1, Text S1.3 for details). If the real number of lyrebird occurrences was significantly smaller than expected, then that

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vegetation subgroup was classed as unsuitable. If the real number was the same or significantly larger than expected, the vegetation subgroup was classed as suitable.

The SDM predicted a high climatic suitability in some areas that have been and remain cleared since European settlement. In addition, some vegetation subgroups that were calculated as suitable fell outside the climatically suitable areas. Accordingly, we clipped the climatically suitable area from the SDM by the suitable vegetation subgroups, such that the remaining area was suitable in both climate and vegetation type. This resulted in the expected habitat patches occupied by Albert's lyrebirds, based on both climatic data and vegetation type (Figure 1a). As the resolution of the SDM was low (approximately 925 × 925 m), we used only the extent of suitable vegetation, with a resolution of 100 × 100 m, to calculate local habitat availability.

To obtain habitat metrics for each individual male we determined the spatial location of individuals by calculating the centroid of any GPS points at which an individual was recorded. We determined the size of habitat patches by calculating the area of continuous patches of habitat (as defined above). To determine the local habitat availability we calculated the proportion of suitable vegetation subgroups by area within the radii surrounding each individual defined above (Figure 1b).

2.8 | Statistical analysis

We constructed linear models of the relationship between patch size and local habitat availability and repertoire size and composition using the package 'lme4' (Bates et al., 2015) in R. We transformed distributions of the six habitat variables with an Order Norm transformation using the package 'bestNormalize' (Peterson, 2021). We ran models of the three repertoire size response variables using Generalized Linear Mixed Models (GLMMs) with a family specified as Poisson and a log link, and models of repertoire composition using Linear Mixed Models (LMMs).

Individual habitat availability at each scale is nested because habitat availability within smaller radii influences the habitat availability within larger radii, so we investigated the effects of habitat availability at each scale separately. The transformed patch size was highly correlated with the transformed habitat availability within 500 m, 1 km, and 2 km (correlation coefficients of 0.80, 0.94, 0.90 respectively), and moderately correlated with the transformed habitat availability within 5 km or 10 km (correlation coefficients of 0.65 and 0.64 respectively). We therefore focus on models containing single fixed effects only and report results from models containing both patch size and habitat availability within either 5 km or 10 km in the Supporting Information (Appendix S1, Text S1.4, Tables S1.16 and S1.18). Repertoire sizes of birds from the same population are assumed to be non-independent given that individuals within populations could be learning from similar or the same lyrebird tutors or heterospecific models, and so we included population identity defined by the study site as a random effect in all GLMMs and LMMs.

We tested model significance using the package 'lmerTest' (Kuznetsova et al., 2017). Some of the models were singular, due to a random effect variance of near zero. When this occurs, the problem may be fixed by simplifying the model by dropping fixed or random effects (Bolker et al., 2009). Patch size and local habitat availability were correlated with population identity (Appendix S1, Table S1.8) and so any variance related to population identity was already explained by the variation in habitat metrics. We, therefore, dropped the random effect from five of the final models and report results from Generalized Linear Models (GLMs) or Linear Models (LMs) for those instead.

3 | RESULTS

3.1 | Albert's lyrebird mimetic repertoires

We identified 68 mimetic unit types in the recital mimicry of Albert's lyrebirds across their range. Of these units, we identified mimicry of 44 unique vocalization types from 15 model heterospecifics, 20 types of non-vocal sounds (e.g., wingbeats, beak taps), and four vocal sounds that could not be classified by model species. Populations differed in both the species mimicked and the proportions with which each species occurred in the repertoires (Table 1). Within populations we found mimicry of 18–31 (mean 22.9 ± 4.34 SD) vocalization types from 5–11 (mean 7.86 ± 2.19 SD) species, and 7–15 (mean 9.71 ± 3.04 SD) types of non-vocal sounds. Individual repertoire sizes ranged from 15 total mimetic unit types in the Tamborine population to 37 in the Mt Jerusalem population (mean 25.3 ± 5.16 SD). Individual repertoires contained 11–25 (mean 18.3 ± 3.20 SD) vocalizations of 4–10 (mean 6.60 ± 2.09 SD) model species and 3–12 (mean 6.71 ± 2.30 SD) non-vocal sounds.

3.2 | Model species

Male lyrebirds mimicked native bird species that varied in taxa, ecology, and size, with occasional mimicry of avian predators (grey goshawk, *Accipiter novaehollandiae*, and wedge-tailed eagle, *Aquila audax*) and a marsupial species (short-eared brushtail possum, *Trichosurus caninus*). All species except grey goshawks and wedge-tailed eagles were commonly encountered at most field sites (F. Backhouse, personal observation). Satin bowerbirds (*Ptilonorhynchus violaceus*), Australian king-parrots (*Alisterus scapularis*), crimson rosellas (*Platycercus elegans*), and green catbirds (*Ailuroedus crassirostris*) were commonly mimicked in all or most populations (Table 1). The remaining 11 species were mimicked in four or fewer populations (Table 1).

The analyses on species occurrences predicted most species to occur at all sites. SDMs for the model species predicted that most species had a greater chance of occurrence than the threshold of equal sensitivity and specificity at all sites (Appendix S1, Table S1.9). The only exception was crimson rosellas, which had lower likelihood

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TABLE 1 The percentage of mimetic repertoires occupied by each model species, unknown sounds, or non-vocal sounds for each population of Albert's lyrebirds.

	Albert's lyrebird population						
Model species	Border Ranges	Lamington	Mt Jerusalem	Wollumbin	Goomburra	Tamborine	Killarney
Satin bowerbird (*Ptilonorhyncus violaceus*)	32.12	32.58	31.37	25.24	33.03	45.50	45.76
Crimson rosella (*Platycercus elegans*)		13.63	2.70	10.34	17.35	15.06	14.40
Australian king-parrot (*Alisterus scapularis*)	8.00	6.60	10.62	4.81	15.82	3.57	0.12[a]
Green catbird (*Ailuroedus crassirostris*)	5.87	6.23		5.77	6.83	12.50	3.14
Eastern yellow robin (*Eopsaltria australis*)	8.75	10.14	9.39		0.18		
White-browed scrubwren (*Sericornis frontalis*)	11.46	4.56	4.79	5.77			
Australian logrunner (*Orthonyx temminckii*)	4.26		5.59	8.17			6.62
Laughing kookaburra (*Dacelo novaeguineae*)	3.45	3.76	3.25	5.29			
Lewin's honeyeater (*Meliphaga lewinii*)			3.68	9.86	3.62		
Yellow-throated scrubwren (*Sericornis citreogularis*)	4.43	1.88	2.70				
Paradise riflebird (*Ptiloris paradiseus*)		0.11		1.92			
Grey shrike-thrush (*Colluricincla harmonica*)							0.70
Short-eared brushtail possum (*Trichosurus caninus*)			0.12			0.23	
Grey goshawk (*Accipiter novaehollandiae*)			0.06[a]				
Wedge-tailed eagle (*Aquila audax*)	0.06[a]						
Unknown			0.61		0.73	0.62	0.58
Non-vocal	21.59	20.50	25.11	22.84	22.43	22.52	28.69

Note: Populations are ordered by average patch size and local habitat availability.

[a] Only occurred once in the local population.

of occurring in all three subpopulations of the Tamborine population, though they were mimicked by all individuals in this population. The automatic detector found three focal species in the recordings from almost all sites. Logrunners and Lewin's honeyeaters (*Meliphaga lewinii*) were detected at all sites except Mt Jerusalem, although these species were both mimicked in that population. Further manual checking of recordings from Mt Jerusalem confirmed a single Lewin's honeyeater vocalization. Eastern yellow robins (*Eopsaltria australis*) were detected at all sites except two sites where they were also not mimicked: Wollumbin, and the northern subpopulation of Tamborine.

3.3 | Albert's lyrebird habitat metrics

From the ALA records, Albert's lyrebirds occurred in 21 of the 98 vegetation types included in the NVIS Major Vegetation Subgroups map. Lyrebird occurrences were higher than expected in 12 vegetation subgroups that were subsequently classified as suitable habitats (Appendix S1, Table S1.10). The highest occurrences of lyrebirds were in 'warm temperate rainforest' (45.8% of records), 'wet sclerophyll' (18.6%) and 'tropical or sub-tropical rainforest' (13.7%).

The Border Ranges and Lamington populations both occupied the largest habitat patch and had the highest local habitat availability (Table 2). The remaining populations differed in patch size, with Tamborine occupying a cluster of very small habitat patches, fragmented by urbanization. The Killarney population occupied the smallest habitat patch and often had the lowest local habitat availabilities.

3.4 | Mimetic repertoire and habitat availability

The number of species males mimicked increased with both patch size and habitat availability within all radii except 500 m (model results in Table 3; Figure 4). Vocal unit repertoire size increased with both patch size and habitat availability within 10 km, and had a non-significant positive trend with habitat availability within 1 and 5 km (Table 3; Figure 4). The total mimetic unit repertoire size (vocal and non-vocal units) was not significantly related to patch size or local habitat availability.

Despite the increase in repertoire size with increasing habitat availability, the ratio of units mimicked per model species decreased with increasing habitat availability. Specifically, individuals mimicked both fewer total units and fewer vocal units per model species mimicked in larger habitat patches and with greater habitat availability within all radii except 500 m (Table 3; Figure 4). Individuals mimicked fewer non-vocal units per model species mimicked with a greater habitat availability within 500 m, 1 km and 10 km (Table 3; full model results in Appendix S1, Tables S1.11–S1.18).

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TABLE 2 The patch size and proportion of suitable habitat (local habitat availability) within different radii surrounding each lyrebird, averaged within the eight study locations.

		Proportion of suitable habitat within radius				
Population	**Patch size (km^2)**	**500 m**	**1 km**	**2 km**	**5 km**	**10 km**
Border Ranges	523	1.00	0.996	0.969	0.895	0.706
Lamington	523	1.00	0.992	0.957	0.785	0.648
Mt Jerusalem	286	0.869	0.806	0.678	0.519	0.510
Wollumbin	72.1	0.911	0.937	0.926	0.715	0.459
Goomburra	62.6	0.892	0.744	0.542	0.331	0.191
Tamborine	8.15	0.626	0.418	0.408	0.402	0.288
Killarney	6.16	0.691	0.345	0.281	0.413	0.320

TABLE 3 Model estimates (SE), *p*-values, and *z* or *t* values from the GLMMs comparing repertoire size and LMMs comparing repertoire composition with patch size and the amount of suitable habitat surrounding Albert's lyrebirds at different scales.

		Local habitat availability				
Model	**Patch size**	**500 m**	**1 km**	**2 km**	**5 km**	**10 km**
Repertoire sizes						
Vocal unit repertoire[a]	*0.112 (0.0503)* *$p = .027$* *$z = 2.22$*					*0.0902 (0.0420)* *$p = .032$* *$z = 2.15$*
Model species repertoire[b]	*0.283 (0.0794)* *$p < .001$* *$z = 3.56$*		0.229 (0.0858) $p = .008$ $z = 2.66$	0.228 (0.0758) $p = .003$ $z = 3.01$	0.203 (0.0838) $p = .015$ $z = 2.42$	0.209 (0.0846) $p = .014$ $z = 2.47$
Ratios						
All units/species[c]	−0.683 (0.173) $p = .008$ $t = -3.95$		−0.545 (0.148) $p = .004$ $t = -3.67$	−0.492 (0.160) $p = .012$ $t = -3.32$	−0.523 (0.142) $p = .013$ $t = -3.80$	−0.480 (0.174) $p = .041$ $t = -2.76$
Vocal units/species[d]	−0.553 (0.110) $p = .003$ $t = -5.83$		−0.369 (0.110) $p = .008$ $t = -3.35$	−0.411 (0.0981) $p = .003$ $t = -4.19$	−0.363 (0.115) $p = .007$ $t = -3.15$	−0.336 (0.142) $p = .039$ $t = -2.37$
Non-vocal units/species[e]		−0.194 (0.0662) $p = .008$ $t = -2.93$	−0.168 (0.0691) $p = .040$ $t = -2.43$			*−0.115 (0.0508)* *$p = .030$* *$t = -2.26$*

Note: Only significant results from models containing a single fixed effect are shown. Results in italics are from models excluding random effects (GLMs). Full model outputs are included in Appendix S1, Tables S1.11–S1.18. Repertoire sizes and ratio measurements are: [a]the number of vocalization types mimicked, [b]the number of species mimicked, [c]the ratio of total units mimicked to species mimicked, [d]the ratio of vocal units mimicked to species mimicked, and [e]the ratio of non-vocal units mimicked to species mimicked.

4 | DISCUSSION

While conservation has often overlooked animal culture as an important component of biodiversity, behaviours such as the vocalizations involved in communication are important to species' persistence and can be uniquely informative about conservation needs. Here we examined the relationship between the mimetic repertoires of male Albert's lyrebirds and habitat loss and fragmentation. We showed that the number of species and vocalizations mimicked by males increased with patch size and local habitat availability. The mimetic diversity of a male's repertoire could thus reflect the effects of total habitat availability on the number of heterospecific models or conspecific tutors. Mimetic repertoires in each population were not fully explained by estimated differences in model species assemblage, suggesting that mimetic repertoires are at least partially learnt from other male lyrebirds. Surprisingly, individuals in smaller patches or areas with a lower proportion of suitable habitat mimicked more vocalizations from each heterospecific model. Male lyrebirds are commonly assumed to be under sexual selection for large repertoires (e.g., Zann & Dunstan, 2008), and our results suggest that males in fragmented habitat partially compensate for the smaller number of species imitated by increasing the number of vocalizations mimicked from the locally available or 'suitable' model species. The results of this study suggest that habitat availability plays an important role in the mimetic repertoires of Albert's lyrebirds through the impacts on the availability of conspecific tutors or models.

4.1 | Repertoire size

The number of species mimicked by male Albert's lyrebirds increased significantly with patch size and local habitat availability,

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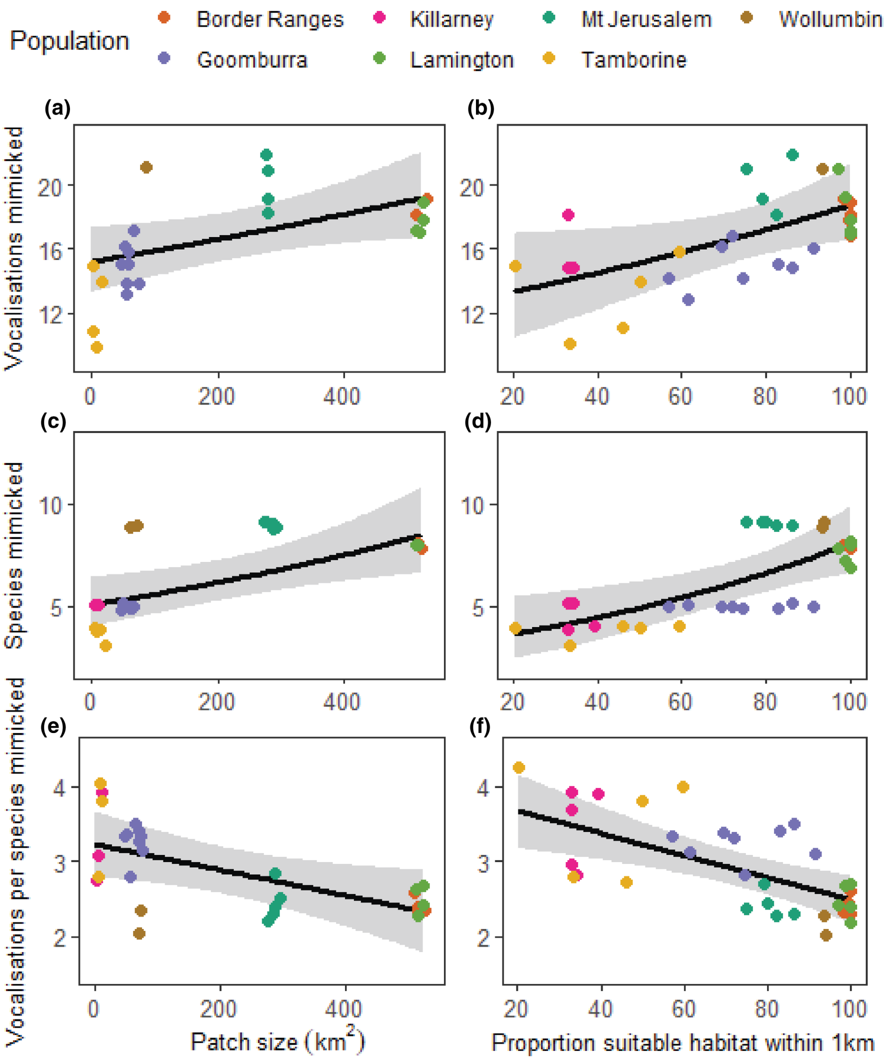

FIGURE 4 The number of vocalizations mimicked (a–b), the number of species mimicked (c–d), and the ratio of vocalizations to species mimicked (e–f) in relation to patch size (a, c, d) and the amount of available habitat within 1 km (b, d, f). Each point represents the repertoire size of an individual lyrebird. Trend lines are taken from a GLMM (a–d) or LMM (e–f) using untransformed fixed effects, plotted using jtools and ggplot2. Shaded areas are 95% confidence intervals. All relationships shown were significant in the models, excepting the relationship in (b), which had a positive trend approaching significance ($p = .0952$).

and the number of heterospecific vocalizations mimicked significantly increased with patch size, consistent with overall habitat availability affecting the opportunity to learn. In some songbird species, repertoire sizes of the species-specific songs are affected by the number of available tutors (Paxton et al., 2019; Sebastián-González & Hart, 2017; Williams & Slater, 1990), or the number of immigrants introducing new song variants into the population (Fayet et al., 2014). In theory, vocal mimics can learn from both heterospecifics and conspecifics (Hindmarsh, 1984; Laiolo et al., 2011; Putland et al., 2006). In *Galerida* larks, mimetic diversity increases with heterospecific diversity, suggesting that mimetic repertoires are affected by the opportunity to learn from a diverse range of heterospecific tutors (Laiolo et al., 2011). Our estimates of model species occurrence predicted most model species mimicked by Albert's lyrebirds to occur at all sites, suggesting that all lyrebirds had the opportunity to learn directly from most, if not all, of the model species. Variations in repertoire size are therefore unlikely due to variations in the presence of available model species, and instead may be driven by variation in the abundance of model species or in the presence of conspecific tutors. This last explanation would be consistent with previous work that has found that both the acoustic structure and the temporal organization of Albert's lyrebird mimicry are at least partially learnt from other lyrebirds (Backhouse et al., 2022; Putland et al., 2006). As population sizes and levels of immigration are often affected by habitat fragmentation, correlations between repertoire size and habitat availability may indicate population size and isolation.

Alternatively, repertoire sizes may increase with age or body condition (Dabelsteen et al., 2012; Hesler et al., 2012), which in turn may be associated with territory quality. However, we found population-level differences in repertoire size, and it seems unlikely that the populations differ substantially in age structure or body condition. In addition, while life-span or body condition could be linked to fragmentation, our finding that the number of vocalizations mimicked per model species increased with habitat fragmentation suggests that repertoire sizes, particularly in the species mimicked, are impacted by a reduced opportunity to learn from conspecifics, rather than a reduced ability to learn. Our findings, therefore, support learning opportunities as the most likely explanation for the differences in repertoire size, though further work comparing repertoire sizes and habitat fragmentation with lek size or population density of Albert's lyrebirds is needed to help exclude alternative hypotheses.

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The relationship between repertoire size, habitat availability, and tutor availability in Albert's lyrebirds may help to explain differences in repertoire sizes between the two extant lyrebird species. Individual males of the southern species, the superb lyrebird (*Menura novaehollandiae*), can include vocalizations from at least 21 model species in their recital mimicry (Zann & Dunstan, 2008), whereas we found mimicry of no more than 10 model species in the recital mimicry of Albert's lyrebirds. This is surprising given species richness is expected to be higher in the subtropics, where Albert's lyrebirds are found, than in the temperate range of superb lyrebirds (Filloy et al., 2015; Hawkins et al., 2003), and may indicate a greater loss of biodiversity or cultural diversity throughout the range of Albert's lyrebirds. In addition, superb lyrebirds have a much broader and possibly less patchy distribution than Albert's lyrebirds, and this may facilitate the greater social transmission of mimetic repertoires from a more varied pool of conspecific tutors. Further, superb lyrebirds occupy a wider variety of habitat types (Higgins et al., 2001), and as a species may be exposed to a greater diversity of heterospecific models and vocalizations, that are then shared among individual lyrebirds across habitat types.

4.2 | Repertoire composition and innovation

Males in smaller patches and areas with lower local habitat availability mimicked fewer heterospecific model species but relatively more vocal and non-vocal units from each heterospecific model, thus partially compensating for a reduced repertoire size in model species mimicked. If mimetic repertoire sizes are indeed affected by the availability of lyrebird tutors, model species could be randomly lost from the mimetic repertoire through cultural drift, while directional selection for large total mimetic repertoires partially counteracts the reduction in overall repertoire size by favouring an increase in the number of vocalizations mimicked from the remaining model species. While males within a population often mimic the same vocalization types from each model species (F. Backhouse, personal observation), observations of Albert's lyrebirds mimicking species during subsong that are not included in the recital mimicry (such as pied currawongs, *Strepera graculina*, and sulphur crested cockatoos, *Cacatua galerita*: F. Backhouse, personal observation), indicate that individuals are capable of mimicking a much wider range of sounds than they sing during recital mimicry. However, rather than increasing mimetic repertoires by mimicking heterospecifics that are not mimicked by other males, it may be more advantageous for individuals to follow social cues on model choice and instead innovate by copying additional vocalizations from this set of 'culturally acceptable' model species.

If male Albert's lyrebirds rely on social cues for model choice but still have the ability to innovate and learn directly from the models, what happens in the absence of conspecific tutors? Mimicry in captive superb lyrebirds suggests that lyrebirds retain the ability to mimic but may have unusual models, such as chainsaws, sirens, and even the crying of a human baby (Dalziell & Welbergen, 2021). Studies on repertoires of naturally isolated individuals in mimicking species should be highly informative about the relative roles of innovation and social conformity in the development of mimetic repertoires.

4.3 | Cultural conservation of Albert's lyrebirds

The results of this study suggest that cultural diversity in Albert's lyrebirds is sensitive to the loss and fragmentation of suitable habitat; processes identified as historical threats to the species (Garnett & Crowley, 2000; Higgins et al., 2001). While much of the habitat is within protected areas such as national parks, the spread of invasive species such as *Lantana camara*, and changes to vegetation through climate change and altered fire regimes, may further threaten the habitat of Albert's lyrebirds (Garnett et al., 2011; Sullivan, 2020), which could in turn lead to a decrease in their cultural diversity.

As yet, it is unclear whether smaller mimetic repertoires would reduce the fitness of individuals and the viability of populations of Albert's lyrebirds. Reduced or unusual vocal repertoires in smaller populations may prevent females from making accurate assessments of male quality or may impede a male's ability to attract a mate (Laiolo, 2010), and so further reduce population size through Allee effects (Crates et al., 2017, 2021). It is therefore of concern that over time, smaller mimetic repertoires could lead to a further decline in population numbers.

There is now good evidence that the recital mimicry of Albert's lyrebirds is a cultural construct (Backhouse et al., 2022), in contrast to some traditional views of avian vocal mimicry as simply a passive sampling of the environment (Hindmarsh, 1984; Kelley et al., 2008). Specifically, there is evidence that individual Albert's lyrebirds are influenced by other lyrebirds in both what to mimic (this study) and how to organize their mimicry (Backhouse et al., 2022). The dynamics of cultural diversity in the mimicry of Albert's lyrebirds may therefore be comparable to human communication that, in some languages, shows a pattern of higher innovation in larger populations and greater cultural loss in smaller populations, with population size related to available area (Bromham et al., 2015). Such locality-specific cultures, particularly when driven by environmental influences such as habitat loss and fragmentation, can indicate target groups for conservation (Brakes et al., 2021). Culturally impoverished populations may also indicate a need for cultural rescue through the translocation of lyrebirds or their song, just as genetic rescue may be implemented to maintain genetic diversity in small or isolated populations (Tallmon et al., 2004; Whiteley et al., 2015). Given the relationship between habitat availability and mimetic repertoire size and composition, and the increasing evidence that mimetic repertoires are learnt in part from other male lyrebirds, we suggest that the diversity in mimetic repertoires may provide a useful indicator of population health in Albert's lyrebirds or of local avian biodiversity. Furthermore, this study reinforces recent findings that cultural diversity can become impoverished through anthropogenic habitat change (Crates et al., 2021; Laiolo & Tella, 2007; Sebastián-González & Hart, 2017), and therefore should play a more important role in wildlife conservation.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

All data and code used in the analyses are available on Dryad (https://doi.org/10.5061/dryad.7pvmcvdw3).

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BIOSKETCH

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