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PUBLICATION DATE

01-02-2018

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JOURNAL OF AVIAN BIOLOGY

Article

Song parameters of the fuscous honeyeater *Lichenostomus fuscus* correlate with habitat characteristics in fragmented landscapes

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Journal of Avian Biology

2018: e01493

doi: 10.1111/jav.01493

Subject Editor: Simon Griffith

Editor-in-Chief: Thomas Alerstam

Accepted 18 October 2017

Both avian abundance and species richness decline in response to habitat loss and fragmentation. Studying variation in bird song structure across modified landscapes can provide insights into the effects of habitat alterations on coherence of social interactions within populations. Here, we tested whether fragmentation or change of habitat quality within box-ironbark forest of central Victoria impacted cultural connectivity and song characteristics in fuscous honeyeater, a declining common Australian bird. First, we tested whether geographic distance and/or spatially-explicit landscape connectivity models can explain patterns of song similarity across fragmented landscapes. We found no evidence that distance or habitat fragmentation impacts the nature and transmission of fuscous honeyeater song, and concluded that acoustic connectivity at the scale of our study is high. Second, we tested whether variation in habitat quality explains variation in song characteristics. In accordance with acoustic adaptation to habitat structure, birds sang longer songs in sites with more large trees and produced longer common song elements in sites with greater tree height. However, the acoustic adaptation hypothesis cannot explain the finding that in less-disturbed landscapes with higher tree-cover birds sang songs (and song elements) with higher maximum frequency and wider frequency bandwidth. We also found that birds sing longer and more variable songs of wider frequency bandwidth in less disturbed sites with a greater number of large mature trees, which may represent better feeding resources. Our study suggests that changes in song structure with habitat degradation could signal disturbed population processes, such as changes in the acoustic communication among resident birds.

Introduction

Understanding the processes driving population declines is essential for successful conservation management intervention (Ewers and Didham 2006, Lindenmayer et al. 2008). Habitat loss, fragmentation and degradation are known drivers of major



declines in biodiversity worldwide (Foley et al. 2005). These declines may result directly from reduction in available resources, or indirectly through changes in population processes (Amos et al. 2014). For woodland-dependent birds, reduction in the size of patches and an increase in edge ratio of patches in fragmented forests can lead to increased competition and nest predation, decreased habitat condition and reduced food availability (Andren 1992, Yates and Hobbs 1997, Zanette et al. 2000, Huhta et al. 2004, Maron et al. 2011). In some species, fragmentation can inhibit dispersal and result in small fragmented populations, subject to increased probability of extinction due to stochastic loss of genetic variation and inbreeding (Amos et al. 2014). In addition, fragmentation can lead to reduction of vocal interactions across populations and disruption of social networks (McGregor and Dabelsteen 1996, Laiolo and Tella 2005, Pavlova et al. 2012).

Prolonged declines of the avifauna of dry woodlands of south-eastern Australia are attributed to habitat loss compounded by a range of other factors (Robinson and Traill 1996, Ford et al. 2001, Mac Nally et al. 2009, Ford 2011). In box-ironbark forests of south-central Victoria, species richness and incidence of many individual species of woodland birds decline with decrease in native tree cover, and some species disappear from apparently suitable habitat in landscapes with tree-cover below a species-specific threshold (Radford et al. 2005, Radford and Bennett 2007).

Studying variation in bird song structure across modified landscapes can provide insights into the effects of habitat alterations on coherence of social interactions within populations (Briefer et al. 2010, Laiolo 2010, Pavlova et al. 2012). Song elements are likely to be transmitted among individuals in a population through learning from conspecifics (Catchpole and Slater 2008). In addition, neighboring birds can match their songs to those of their neighbors, forming local communication networks (McGregor and Dabelsteen 1996). Ability of birds to exchange song elements with conspecifics constitutes cultural (acoustic) connectivity of a population. Isolation and reduced population sizes can result in decreased acoustic connectivity (i.e. increased acoustic differentiation) though reduced opportunities for learning and retaining acoustic diversity. Thus, decreased similarity in the limited song types across isolated fragments, compared to similarity across more connected habitat patches, can indicate that habitat fragmentation impedes acoustic connectivity, which may contribute to population declines by undermining the important functions for which song is used by birds (Pavlova et al. 2012, Pérez-Granados et al. 2016). On the other hand, birds can adjust the songs to their habitats, and these changes can influence population processes. The acoustic adaptation hypothesis (Morton 1975, Hansen 1979) predicts that acoustic properties of bird songs are adjusted according to the transmission properties of the habitat. In habitats with complex vegetation structure, birds produce songs with lower frequencies, narrower frequency bandwidths, lower frequency modulations (whistles), and longer elements and inter-element intervals. In contrast, in

more open habitats, birds produce songs of higher frequencies, broader bandwidths, higher frequency modulations (trills) and shorter elements and inter-element intervals (Morton 1975). Such intraspecific variation may develop on short timescales, and evidence in support of this hypothesis has been repeatedly reported within and among species (Handford 1988, Parris and Schneider 2009, Nemeth and Brumm 2010, Slabbekoorn et al. 2012).

Variations in song may alter bird interactions, especially in social species. Males can change their song characteristics (frequency and duration of song and its elements) in male–male interactions (Osiejuk 2001, Goretzkaia 2004, 2013, Leitão et al. 2006, Naguib 2013, Geberzahn and Aubin 2014). Additionally, bird song is a sexually selected trait, where females select males on the basis of song quality (Weatherhead et al. 1993, Saino and Møller 1994, Gil and Gahr 2002). Thus, changes in song characteristics may affect intrasexual and intersexual interaction and influence population persistence (Naguib 2013).

In this study, we explored whether song variation across fragmented landscapes showed patterns that might hint at processes leading to demographic decline of the fuscous honeyeater *Lichenostomus fuscus*, a highly mobile eastern Australian nectarivorous and insectivorous bird. Fuscous honeyeater populations are inferred to decline in north-central Victoria in response to habitat loss: the probability of the species occurrence in suitable habitat within 10×10 km² landscapes falls dramatically when landscape tree cover falls below 17% (Radford and Bennett 2007, Amos et al. 2012). Analyses of genetic, morphological and haematological variation show that this decline does not result from dispersal limitation (Harrisson et al. 2014) nor impacts of low habitat quality on individual health indices, although sites with higher canopy cover tend to be inhabited by more genetically diverse populations (Amos et al. 2013). Nevertheless, earlier studies did not address whether habitat quality can affect fuscous honeyeater in other ways, which may affect their song and acoustic communication. While nearly all remnant habitat across the study area has been severely disturbed over the past 150 yr (Environment Conservation Council 1997), some sites retain more of the characteristics of undisturbed sites, particularly the number of large old eucalypt trees. Sites with greater numbers of large old eucalypts provide greater floral and nectar resources over longer flowering periods than sites where all such trees have been replaced with regrowth (Wilson and Bennett 1999, Wilson 2003). Because fuscous honeyeaters prefer to feed on eucalypts (Chan 1990), sites with greater proportion of large old trees are expected to provide higher quality food resources for this species.

First, we test whether patterns of acoustic connectivity can be explained by structural connectivity of the habitat. This response would be expected if song exchange is reduced or increased between habitat patches in response to fragmentation. A reduction of song exchange was observed for another bird species in our study system (Pavlova et al. 2012). Because landscape genetic analysis showed no indication of impeded dispersal of fuscous honeyeaters in response

to distance or fragmentation at the study scale (Amos et al. 2014, Harrison et al. 2014), we predict that song similarity is also not influenced by geographic distance or fragmentation (i.e. by landscape resistance to song movement). Second, we test whether differences in habitat structure relate to differences in fuscous honeyeater song structure. In particular, we test 1) whether the significant relationships are consistent with predictions from the acoustic adaptation hypothesis, and 2) whether song characteristics ‘improve’ (as evidenced by increase in song complexity and frequency bandwidth) (Drăgănoiu et al. 2002, Ballentine et al. 2004, Leitão et al. 2006, Naguib 2013, Geberzahn and Aubin 2014) with higher tree cover and greater number of large old trees, i.e. with structural elements relating to vegetation condition closer to undisturbed (Parkes et al. 2003). Changes in song characteristics that are inconsistent with the acoustic adaptation hypothesis and/or consistent with increase in song complexity and frequency bandwidth in less-degraded sites could signal disturbed population processes. If birds sing the same song no matter where no relationship with site or landscape characteristics would be expected. To test our hypotheses, we recorded songs of birds inhabiting landscapes with a range of extent of native tree cover, built spatially-explicit landscape models of acoustic connectivity and tested their ability to explain song similarity across landscapes, and analyzed relationships between landscape and habitat variables and acoustic characteristics.

Material and methods

Study species

The fuscous honeyeater is a medium-small (13.5–17 cm, 12–24 g) honeyeater common in eastern Australia (del Hoyo

et al. 2008). It occupies dry, open sclerophyll eucalypt forests and woodlands and feeds on nectar, insects (and their products including honeydew and lerps) and other invertebrates (Higgins et al. 2001). Fuscous honeyeaters are socially monogamous, but can nest solitarily or semi-colonially, with neighbouring pairs interacting without aggression (del Hoyo et al. 2008). They often forage in small flocks preferring middle and top parts of eucalypt trees. They aggressively defend preferred habitat from conspecifics (Chan 1990). Fuscous honeyeaters were shown to have low recapture rates (mean 1.4%, range 0–8.3% based on sites revisited after six months) and lacked genetic structure across 200 km in our study region, suggesting high mobility (Harrison et al. 2014). Songs of the fuscous honeyeater have not been extensively studied (Baldwin 1972) and, given lack of conspicuous morphological difference between sexes, it is not known whether vocalizations of males and females differ (del Hoyo et al. 2008).

Study region

The study was conducted within 170×50 km region in box-ironbark forest in central Victoria, Australia, which was a subject of previous ecological (Radford et al. 2005, Radford and Bennett 2007), morphological (Amos et al. 2013), genetic (Harrison et al. 2012, 2013, 2014, Amos et al. 2014) and acoustic (Pavlova et al. 2012) studies of woodland birds, including the fuscous honeyeater. Acoustic recordings of fuscous honeyeaters were performed in six 10×10 km landscapes with a range of extent of native tree-cover varying from 11 to 72%, embedded in agricultural matrix (Fig. 1). Birds’ songs were recorded in 12 sites within six landscapes (from 1 to 3 sites per landscape; Fig. 1) and in one additional site (G11_2; Supplementary material Appendix 1). Sites were chosen opportunistically

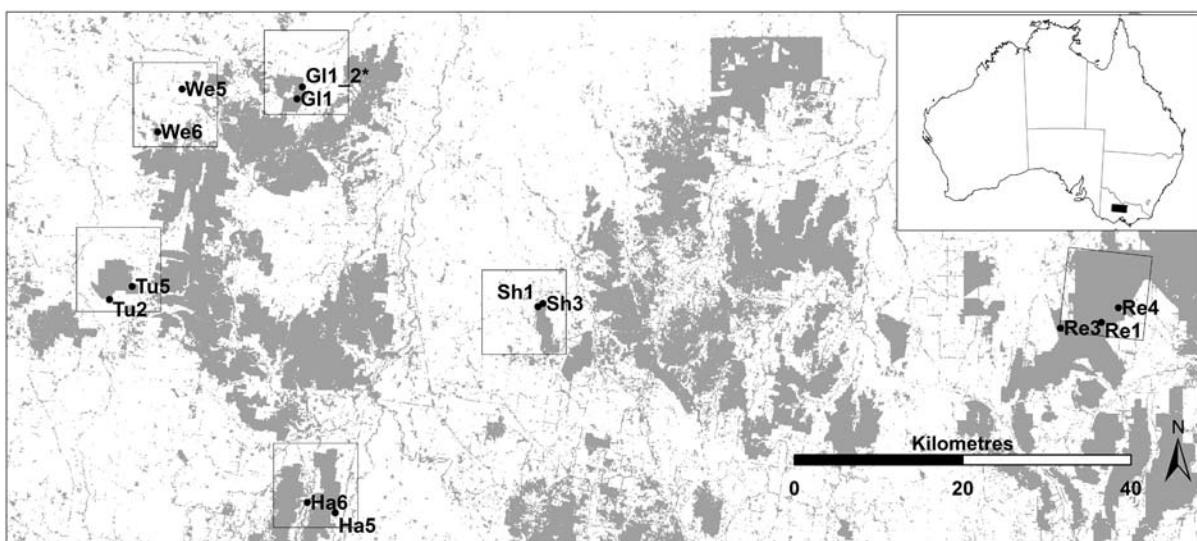


Figure 1. Study landscapes (squares, 10×10 km each) and sites (black circles) where acoustic data were collected; tree-cover is shown in grey color. The site marked with asterisk was not located within the borders of the sites scored for vegetation attributes by Amos et al. (2012).

where small flocks of 5–20 singing fuscous honeyeaters were observed.

Acoustic recordings and data analyses

Recordings were made from 16 September to 9 November 2009, during the breeding season of the fuscous honeyeater. Sequences of songs (of 5–15 min in length) were recorded from each singing bird using Marantz PMD 660 recorders, with Sennheiser and ATR55 microphones. A total of 196 songs were recorded (from 13 to 84 per landscape). Because individuals were unmarked (and sex unknown), recordings were made along several routes from the center of the site (~1 km radius) in different directions to avoid recording the same individual more than once.

Songs were digitized at a sampling rate of 22.5 kHz and resolution of 16-bit and analyzed with Avisoft SasLab Pro software (R. Specht, Berlin, Germany); only good-quality signals were chosen for analyses. The following definitions were used: a song is a long and variable signal transferred for a long distance, and consisted from a sequence of elements and phrases; an element is a non-interrupted fragment of a song, or a group of fragments isolated from other such groups by gaps greater than those between fragments; a phrase is a sequence of similar elements (those having similar shape of frequency modulation) or a sequence of different elements that were sung together (Fig. 2) (Catchpole and Slater 2008).

Three groups of response variables were created, reflecting repertoire, song characteristics and characteristics of a common song element. Repertoire reflected presence–absence of each element at each site. Song characteristics were: song length (s), number of elements per song, number of different elements per song (dif. element per song), peak frequency, minimum frequency, maximum frequency and frequency bandwidth (maximum frequency minus minimum frequency; Hz). Characteristics of the common element ‘O’ ($n = 130$), one of the two elements that all birds sang across all sites (Fig. 2) were: duration (s), peak frequency, minimum frequency, maximum frequency, frequency bandwidth and number of ‘O’ elements per phrase.

Landscape acoustic models of vocal connectivity

Electrical circuit theory-based models of gene flow through land-uses with different ‘resistances’ (isolation-by-resistance; McRae 2006, McRae and Beier 2007) have been successfully used to model ‘song-flow’ (song similarity across space) and test for reduction or increase of vocal (acoustic) connectivity of birds across fragmented landscapes (Pavlova et al. 2012). As in Amos et al. (2012), we used Circuitscape 3.5.1 (McRae et al. 2008) to classify each 25 by 25 m grid cell in our study region as either treeless or treed, and to generate resistance surfaces for 1) the null model of isolation-by-distance (IBD), which assumes that geographic distance is the sole factor limiting song flow (modelled via uniform resistances across the grid: resistance of treed habitat = 1,

treeless = 1), 2) a model of reduced song-flow through treeless areas (RSF, modelled via doubled resistance of treeless cells: treed 1, treeless 2), and 3) a model of increased song-flow through treeless areas (ISF, modelled via halved resistance of treeless cells: treed 1, treeless 0.5). From these three surfaces, pairwise geographic distances and pairwise landscape resistances for RSF and ISF were calculated for each pair of sampling sites. Song elements are likely to be transmitted among individuals through learning and, thus, will reflect cultural connectivity. Thus we tested whether habitat-clearing has impacts on song transmission across landscapes using pairwise per-site repertoire dissimilarities, calculated as Bray–Curtis dissimilarities (appropriate for presence–absence data) from data on presence or absence of each song element in each site.

First, song dissimilarities were tested for correlation with pairwise resistances from all three landscape models using Mantel tests. Second, partial Mantel tests were used to separate the effects of distance from the effect of fragmentation: RSF or ISF models were considered to fit the data better than IBD if partial Mantel test conditioned on geographic distance resulted in a significant r . If habitat fragmentation impedes cultural connectivity, then dissimilarities in acoustic repertoire are expected to fit the model of reduced song-flow (RSF) better than they do IBD. In contrast, if fragmentation facilitates connectivity, then song dissimilarities are expected to fit the model of increased song-flow (ISF) better than they do IBD. Distances were calculated and Mantel and partial Mantel tests performed using package ‘ecodist_1.2.9’ (Goslee and Urban 2007) in R 3.1.0 (R Development Core Team). Landscape acoustic analyses were run only on sites that were included in the landscape design of Amos et al. (2012) (Supplementary material Appendix 1). Because none of the landscape models were supported by the data, we also tested whether straight geographic distances [IBD (GEOG)] or log geographic distances [IBD (logGEOG)] explained song dissimilarities using Mantel tests; geographic distances were calculated using R package ‘fields’ (Furrer et al. 2010).

Landscape- and site-scale habitat quality variables

Five landscape- and site-scale habitat quality variables were used to test for relationships between habitat and song characteristics. The landscape-scale variable was Tree cover, percent of native tree cover (Dept of Sustainability and Environment 1990–1999) calculated in ARCGIS (Environmental Systems Research Inst. 1999–2008) (Amos et al. 2013). This variable was found to be the strongest predictor of the presence of the fuscous honeyeater at a site (Radford and Bennett 2007) with values below the threshold of 17% corresponding to very low probability of species occurrence (Amos et al. 2012). Four site-scale vegetation condition scores, assessed for Amos et al. (2013) using the ‘habitat hectares’ methodology (Parkes et al. 2003) and believed to best represent habitat parameters relevant to breeding, feeding and vocalization of fuscous honeyeaters (Chan 1990), were included in the analysis. These were Large trees, number of large trees (with diameter

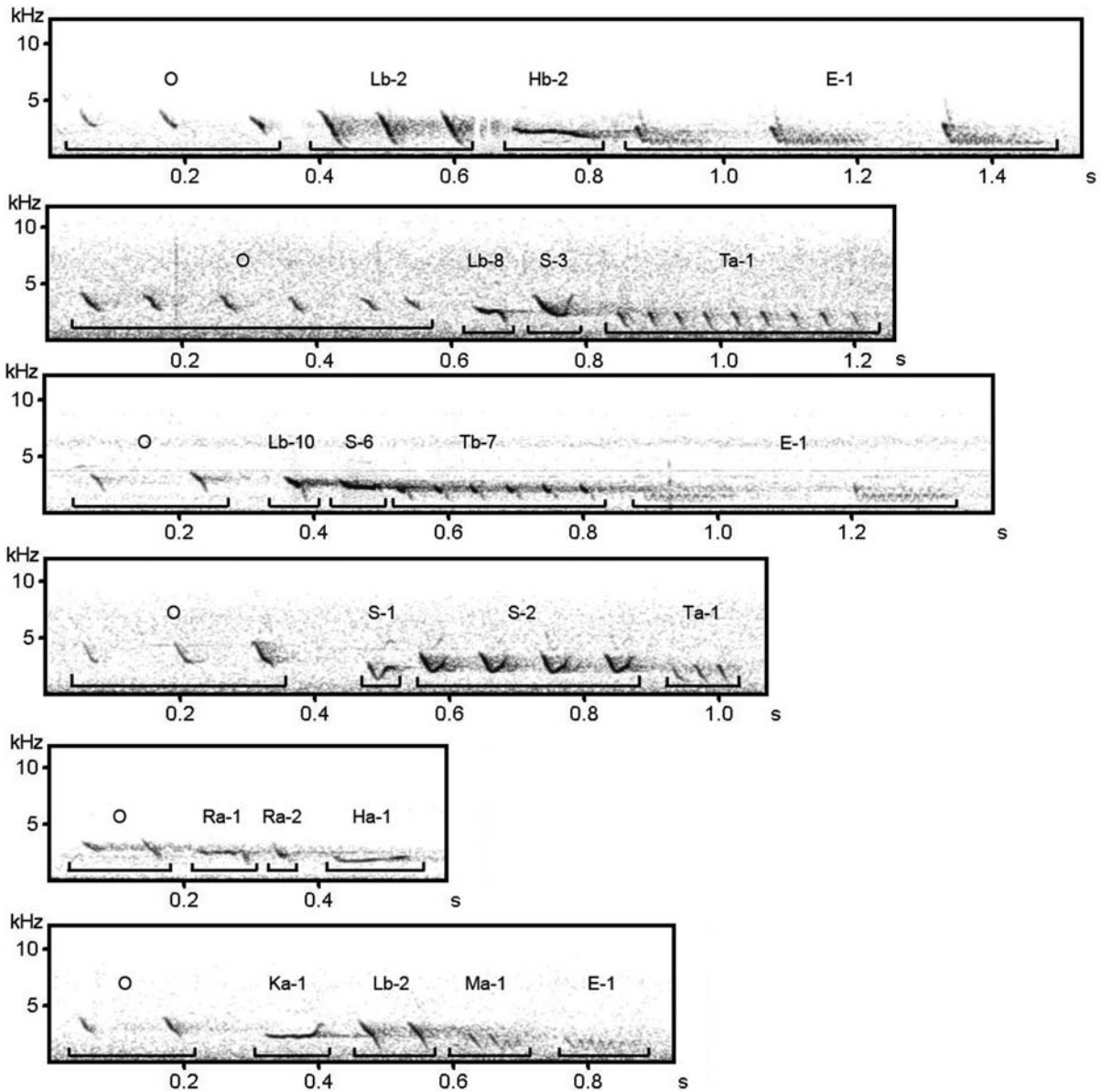


Figure 2. Examples of the sonograms of various fuscous honeyeater songs (x-axis is frequency in kHz, y-axis is time in seconds); different elements are indicated by letters (some with numbers to indicate variants). Elements 'O' (often used at the start of the song) and 'E' commonly occurred in songs of birds across all landscapes and sites.

at breast height greater than 0.7 m) per hectare (range 0–7, mean 2.4, SD 1.8), Tree height, average height (in meters) of all trees at a site (range 12–25.6, mean 13.7, SD 11.3), Canopy, projected percent of canopy cover by individual trees that are > 80% of their mature height (range 15–30, mean 21, SD 4.0) and Shrubs, the sum of projected cover of small (< 1 m), medium (1–5 m) and large (> 5 m) shrubs (range 0–40, mean 13.7, SD 11.3; Supplementary material Appendix 1) (Parkes et al. 2003, Amos et al. 2013). Because Tree cover and Shrubs were positively correlated with Tree height Spearman $r=0.37$ and 0.69 , respectively; $p<0.05$), and Large trees tends to be related to Shrubs ($r=0.5$; $p<0.1$) and Tree height ($r=0.56$; $p=0.056$), habitats with a greater

number of Large trees and higher Tree cover appear to have denser vegetation (Supplementary material Appendix 6).

Habitat models

The one landscape-scale variable (Tree cover) and four site-scale variables reflecting vegetation complexity of each sampling site (Large trees, Tree height, Canopy and Shrubs) explained above were used as predictors of characteristics of each song (number of elements per song, number of different elements per song, peak frequency, minimum frequency, maximum frequency and frequency bandwidth) in linear mixed models (LMM), implemented in function

Table 1. Song characteristics of the fuscous honeyeater.

	Mean	SD	Minimum	Maximum
Song lengths, seconds	0.98	0.58	0.03	5.44
Number of elements per song	12.8	7.72	3	57
Number of phrases per song	4.43	1.96	1	20
Maximum frequency, kHz	4016	436	2620	5120
Minimum frequency, kHz	1076	180	680	1760
Frequency bandwidth, kHz	2912	432	1760	3970
Peak frequency, kHz	2284	240	860	3270

lme in 'nlme' package (Pinheiro and Bates 2000) in R 3.1.0 (R Development Core Team). Song length was not analyzed, as it strongly correlated with the number of elements per song (Spearman $r=0.72$, $p < 0.001$, $n=180$, Supplementary material Appendix 5). All models included landscape and site identities as random nested variables. Variables were excluded from the model design according to a backward model simplification protocol (Zuur et al. 2009), and normality of residuals was checked at each step.

Results

Fuscous honeyeater song and repertoire of elements

A typical song of the fuscous honeyeater consists of 2–5 (maximum 20) phrases composed of 5–12 (maximum 57) elements (Table 1; Supplementary material Appendix 3, 7). The majority of songs begin with the element 'O' common to different sites and landscapes (Fig. 2) (Supplementary material Appendix 4, 8). Songs have frequencies from 680 to 5120 Hz and are up to 5.44 s long (Table 1).

In total, 60 different elements were found in the repertoire of the fuscous honeyeater. Of these, only two were shared by birds across all sites and landscapes. The number of different elements detected per landscape varied from 8 in Havelock to 28 in Redcastle (Table 2). Both rare and common (frequently sung) elements were present in all landscapes, and the number of common elements was similar across landscapes (3–5; Table 2).

Habitat models

The number of large trees per hectare (Large trees) was a significant ($p < 0.05$) predictor of three fuscous honeyeater song characteristics: in sites with more mature trees, birds sang songs with a greater number of elements per song,

higher maximum frequency and larger frequency bandwidth (Table 3).

In denser sites with a higher proportion of shrubs (Shrubs), the number of elements per song was significantly lower ($p=0.04$); song maximum frequency and frequency bandwidth also tended to be lower, albeit not significantly so ($p < 0.1$). The number of different elements per song was higher in landscapes with higher tree cover (Tree cover; $p=0.01$) and in sites with higher projected canopy cover (Canopy; $p=0.01$). In addition, in landscapes with higher tree cover songs were more variable (e.g. had more different elements per song; $p=0.01$; Table 3). None of the other landscape- or site-scale variables were significant predictors of song characteristics.

The landscape-level tree cover (Tree cover) was a significant predictor of three characteristics of the most common song element 'O', shared by the birds in all sites: in landscapes with higher tree cover, 'O' was of longer duration, higher maximum frequency, and larger frequency bandwidth (Table 4). The number of times 'O' was repeated per phrase also tended to increase, albeit not significantly so, with landscape-level tree cover ($p=0.058$; Table 4). Four additional significant relationships were detected: 'O' duration was longer in habitats with a larger number of tall trees (Tree height), and shorter in denser habitat with a higher proportion of shrubs (Shrubs). The number of large trees per hectare (Large trees) was a significant predictor of two characteristics of element 'O': in sites with a greater proportion of mature trees, birds sang 'O' of higher maximum frequency and larger frequency bandwidth. The frequency bandwidth of 'O' was narrower in sites with a larger number of tall trees (Tree height; $p=0.058$) (Table 4).

Landscape acoustic models

In line with our first prediction, we did not find any significant effects of habitat fragmentation on acoustic connectivity (measured by song similarity). Dissimilarities of song elements were weakly structured according to isolation-by-distance (IBD (GEOG) Mantel $r=0.39$, $p=0.01$; Supplementary material Appendix 2), but this relationship was not significant when an additional site (GL1-2, which lies outside predefined landscapes) was added to the analysis (Partial Mantel $r=0.20$, $p=0.07$). Although the model of decreased song flow due to fragmentation was also supported by a marginal Mantel test ($r=0.47$, $p=0.006$).

Table 2. Number of song elements (repertoire) per landscape.

Landscapes	Number of different elements	Number of frequently-used elements	Total number of analyzed elements	Number of songs
Glenalbyn	9	4	61	14
Havelock	8	5	129	28
Redcastle	28	3	409	84
Shelbourne	11	4	63	13
Tunstalls	18	3	210	35
Wehla	14	3	96	20
Total	mean = 14.7 SD = 7.5	mean = 3.7 SD = 0.8	968	194

Table 3. Significance of factors obtained by ANOVA comparisons of GLMM models testing relationships between habitat conditions and songs; LRT – likelihood ratio test, df – degree of freedom in the model. Only song variables that demonstrated significant response to changes of habitats and landscape parameters are listed in the table. p-values for significant differences are in bold font, those near significance are in italic font.

Song characteristics	Factor	LRT	df	p	t (for significant model)
Number of elements per song	Tree cover	0.14	7	0.7	
	Large trees	4.08	4	0.04	2.91
	Tree height	3.24	5	<i>0.07</i>	1.83
	Canopy	0.15	8	0.96	
	Shrubs	4.26	6	0.04	-2.04
Maximum frequency	Tree cover	0.005	7	0.82	
	Large trees	5.72	4	0.017	2.56
	Tree height	0.45	6	0.55	
	Canopy	0.0004	8	0.94	
	Shrubs	3.11	5	<i>0.08</i>	-2.21
Frequency bandwidth	Tree cover	0.005	8	0.94	
	Large trees	7.34	4	0.007	3.38
	Tree height	0.92	6	0.33	
	Canopy	0.14	7	0.7	
	Shrubs	2.77	5	<i>0.095</i>	-1.72
Number of different elements per song	Tree cover	6.6	5	0.01	3.26
	Large trees	1.54	6	0.21	
	Tree height	0.19	7	0.65	
	Canopy	6.51	5	0.01	2.70
	Shrubs	0.25	8	0.61	

Discussion

We tested whether geographic distance, habitat fragmentation and variation in habitat quality could explain variation in the song of the fuscous honeyeater, potentially linked to disruption of vocal communication that could contribute to population declines. Our results of landscape acoustic analyses suggested that acoustic connectivity among populations of fuscous honeyeater is not impacted by habitat

fragmentation. Nevertheless, a possibility of song deterioration in more disturbed sites was suggested by significant relationships unexpected under acoustic adaptation hypothesis, such as increased frequency bandwidth and maximum frequency with increase in number of mature trees. More detailed studies of marked birds are required to understand significance of these finding for future population persistence. Below we discuss possible explanations for our results.

Table 4. Significance of factors obtained by ANOVA comparisons of GLMM models testing relationships between landscape and habitat attributes and characteristics of the most common song element 'O' (shared by the birds in all sites). LRT – likelihood ratio test, df – degree of freedom in the model. Only 'O' characteristics that demonstrated significant changes in response to changes of habitats and landscape parameters are listed in the table. p-values for significant differences are in bold font, those near significance are in italic font.

Song characteristics	Factor	LRT	df	p	t (for significant model)
'O' duration	Tree cover	3.84	5	0.049	2.36
	Large trees	1.34	7	0.23	
	Tree height	7.67	5	0.006	2.96
	Canopy	0.18	8	0.67	
	Shrubs	7.04	5	0.008	-2.84
'O' maximum frequency	Tree cover	6.95	5	0.008	2.64
	Large trees	5.43	5	0.02	2.72
	Tree height	2.59	6	0.11	-1.59
	Canopy	0.46	7	0.5	
	Shrubs	0.0035	8	0.95	
'O' frequency bandwidth	Tree cover	8.99	6	0.003	4.19
	Large trees	8.41	6	0.004	3.18
	Tree height	5.82	6	0.015	-2.4
	Canopy	0.08	8	0.78	
	Shrubs	0.96	7	0.33	
Number of times 'O' repeated per phrase	Tree cover	3.58	4	<i>0.058</i>	2.18
	Large trees	2.08	6	0.15	
	Tree height	0.79	7	0.37	
	Canopy	0.13	8	0.72	
	Shrubs	3.68	5	<i>0.055</i>	-1.91

We tested whether geographic distance, habitat fragmentation and variation in habitat quality could explain variation in the song of the fuscous honeyeater, potentially linked to disruption of vocal communication that could contribute to population declines. We found no effect of geographic distance on similarity of the repertoire of elements, which suggests high acoustic connectivity of fuscous honeyeaters at the scale of our study (200 by 50 km). Lack of acoustic structure across the study area is consistent with high mobility of the fuscous honeyeater, which was previously inferred from lack of genetic structure within the same study region (Amos et al. 2014, Harrison et al. 2014). This result contrasts with finding for a more sedentary species, the grey shrike-thrush, whose acoustic connectivity in our study area was found to be compromised by fragmentation (Pavlova et al. 2012).

Two significant relationships detected by habitat models were consistent with expectations from the acoustic adaptation hypothesis: birds sang longer songs (e.g. songs with more elements) in sites with greater number of large old trees and produced longer element 'O' in sites with greater average height of all trees. Other results appeared to contradict the predictions of the acoustic adaptation hypothesis. For example, contrary to expectations of lower frequency and narrower bandwidth in habitats with complex vegetation, frequency bandwidth and maximum frequency were higher in the sites with more mature trees for complete songs and element 'O'. Because fuscous honeyeaters are flocking birds, they may use 'ranging', employing degradation in the signal to estimate distance to conspecifics, and they may choose to use a broad bandwidth signal, which partially degrades. Thus, if we assume that broad frequency bandwidth is a specific characteristic that birds are forced to reduce in habitats where mature trees are lacking, these changes in song characteristics may disrupt patterns of female choice and/or male–male interaction. It was shown for other songbirds that males and females can recognise small variations in song type and react to them (Lietão et al. 2006). Consequently, these acoustic changes may prevent natural communication between mates and lead to decrease in the population density in habitats lacking mature trees.

Another explanation of our results may be related to acoustic characteristics of fuscous honeyeaters reflecting male quality. Because song length and frequency bandwidth can reflect birds' individual wellbeing (quality) and age (Podos 1997, Christie et al. 2004), it is possible that older and/or more competitive birds, which have longer and higher frequency bandwidth songs, displace younger/less competitive birds from larger habitat blocks and/or better quality sites. Non-random settlement of migratory birds according to genetic variation with respect to habitat quality has been observed in tree swallows *Tachycineta bicolor* (Porlier et al. 2009). Longer songs and songs with higher frequency bandwidths have been shown to reflect individual bird quality (Lambrechts and Dhondt 1986, Lampe and Espmark 1994, Goretskaia 2004, Linhart et al. 2012). Increased song frequency was correlated with increased nesting success and was considered to better advertise territory quality in

male blackcap *Sylvia atricapilla* (Hoi-Leitner et al. 1993). Whereas no relationships between individual body condition, hematological measures and habitat were previously found for fuscous honeyeaters in our study area, a positive relationship between individual heterozygosity and canopy cover provides an indication that a link might exist between habitat quality and individual fitness (Chapman et al. 2009, Porlier et al. 2009, Amos et al. 2013). This is in agreement with our finding of positive correlation between the number of large trees, and landscape tree-cover, with longer song and higher song frequency.

In the dry woodlands of south-eastern Australia, the majority of habitat remnants occur in areas of low primary productivity with greatly reduced food resources for insectivorous birds (Watson 2011). Large mature trees represent an important food resource and a depleted habitat element for nectar feeding birds in box-ironbark forest (Wilson and Bennett 1999). Consequently, habitats with large mature trees may be occupied by older fuscous honeyeaters. Age has been shown to be related to several song characteristics and song repertoire (Gil et al. 2001, Kiefer et al. 2006, Nicholson et al. 2007). Songs were longer in older great reed warblers *Acrocephalus arundinaceus*, barn swallows *Hirunda rustica*, collared flycatchers *Ficedula albicollis* and pied flycatchers *F. hypoleuca* (Galeotti et al. 2001, Forstmeier et al. 2006, Garamszegi et al. 2007, Popova et al. 2012). Older pied flycatchers also have wider frequency bandwidth (Popova et al. 2012) as do older great tits *Parus major* (Bueno-Enciso et al. 2016). A study of offspring survival and age structure of fuscous honeyeaters across sites ranging in landscape tree-cover and habitat quality is warranted to test this hypothesis.

Overall, our data show that current levels of habitat loss and degradation within box-ironbark forest of central Victoria resulted in significant changes in characteristics of fuscous honeyeater song. These changes could reflect birds' acoustic adaptation to habitat differences, or differences in age structure across populations settling in different habitat areas. Whether the identified disruption to vocalizations is linked to observed population declines in low tree-cover landscapes requires an investigation of the impact of the song variation on male–male interactions and female choice, and of the relationships among habitat quality and birds' ages and fitness. The amount of tree cover and presence of large trees appear to be important for fuscous honeyeaters, hence maximizing these parameters should be important for species management. However it is the unidentified variables could be responsible for the patterns we observe and we now acknowledge this. Our finding is a first step in studying acoustic behaviour of the fuscous honeyeater in different habitats. Further experiments on marked populations would allow determination of whether song structure variations are important in population-level interactions.

Funding – Acoustic analysis was supported by of the Russian Science Foundation (project 14-50-00029 'Scientific basis of the national biobank – depository of the living systems'). The study

was supported by the Russian Foundation for Basic Research, grants 15-29-02771. Field component was supported by grant FT140100131 from the Australian Research Council and by the Australian Research Council Linkage Grant (LP0776322), the Victorian Dept of Sustainability and Environment, Museum of Victoria, Victorian Dept of Primary Industries, Parks Victoria, North Central Catchment Management Authority and Gouldburn Broken Catchment Management Authority.

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Supplementary material (Appendix JAV-01493 at <www.avianbiology.org/appendix/jav-01493>). Appendix 1–8.