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Forest fire reduces dawn singing effort in a passerine bird

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Abstract. Fire is common in ecosystems throughout the world, and is known to have profound effects on animal populations. For species living in fire-prone ecosystems, it has the potential to impact both habitat structure and resource availability, which might influence the health of individuals and reproductive effort, directly or indirectly. Previous studies have shown reduced breeding success immediately after fire, but little is known about behavioural responses that might contribute to this, such as song in birds. In a population of Red-backed Fairy-wrens *Malurus melanocephalus*, we show that dawn singing effort was reduced following a fire. The observed changes might have been driven by reduced physical condition resulting from fire-induced changes in food availability, reduced motivation to perform these behaviours, or both. These results add to our understanding of species' responses to environmental disturbances, such as fire, and might inform investigators of the mechanisms behind the resulting population-scale effects on breeding success and survivorship.

Introduction

Fire is a common and influential process in many ecosystems (Bond & Keeley 2005), affecting population size and community structure (Davis *et al.* 2000; Bradstock *et al.* 2002), although little is known about its effects on the behaviour of individuals (but see Komarek 1969; Brooker & Rowley 1991). As environmental stressors like fire can cause animals to modify typical behaviours, or inhibit their performance, changes in behaviour at the individual level might have important consequences for populations, e.g. if animals alter their reproductive or communicative behaviour in response to fire. In this study, we investigated the effects of a fire early during the breeding season on singing behaviour (which is known to be important in territorial defence and reproduction: Marler & Slabbekoorn 2004) in a population of Red-backed Fairy-wrens *Malurus melanocephalus.*

Song plays an important role in many avian communication systems, and can serve many functions, e.g. mate attraction and assessment (Gentner & Hulse 2000; Gil & Gahr 2002), individual and kin recognition (Christie *et al*. 2004; Akcay *et al*. 2013), territory defence (Slagsvold *et al*. 1994), and mediation of aggressive encounters (Naguib & Mennill 2010; Searcy *et al*. 2006). In addition, it might be influenced by an individual's environment through the acoustic properties of this (Morton 1975; Slabbekoorn 2013) or through its effects on health (e.g. Barnett & Briskie 2006; Grava *et al.* 2009; DeLeon *et al*. 2013; Müller *et al.* 2013).

Environmental influences on health can affect singing behaviour in several ways. Food availability, for instance, can affect both song structure and singing behaviour. Several studies have found that birds given supplementary food increased dawn song output (Cuthill & MacDonald 1990; Thomas 1999; Barnett & Briskie 2006; Grava *et al*. 2009), and might increase song complexity (Barnett & Briskie 2006). Similarly, habitat quality in general might affect energetic state, reducing state-dependent behaviours such as song (Godfrey & Bryant 2000; van Oort *et al*. 2006; Grava *et al*. 2013).

Environmental stressors can also affect song. Birds infected with parasites, for example, may have smaller repertoires (Buchanan *et al*. 1999) or decreased rate of song delivery (Gilman *et al*. 2007), and songs with greater variance in note structure (Gilman *et al*. 2007; Müller *et al*. 2013) or reduced frequency range (Redpath *et al*. 2000). Similarly, birds affected by pollutants also have smaller repertoires and sing fewer songs (Gorissen *et al.* 2005), and their songs show decreased stereotypy (DeLeon *et al*. 2013), lower frequency characteristics, and fewer note types (Hallinger *et al.* 2010). Thus, different stressors can have similar effects on song, particularly in output and repertoire size.

Similar to other environmental stressors, fire might affect the health or condition of exposed individuals, directly through smoke inhalation or heat exposure (e.g. Bradstock *et al.* 2002) or indirectly as a result of decreased food availability or reduced habitat quality (Bradstock *et al*. 2002; Bell *et al*. 2012). It might indirectly reduce the motivation to sing. Several studies have found that lower motivation might explain changes in singing behaviour (Kramer *et al*. 1985; Weary *et al.* 1988). Furthermore, peaks in song output often correlate with the fertile stage of the female reproductive cycle (Cuthill & MacDonald 1990; Welling *et al*. 1995). Thus, if fire reduces breeding opportunities, males might be less motivated to invest in song, regardless of their physical state.

In addition, fire can affect song through changes to the acoustic environment. For example, the acoustic adaptation hypothesis predicts that long-distance vocalisations of animals differ between those inhabiting open and closed habitats (Morton 1975). Though this hypothesis typically refers to long-term evolutionary effects, birds might also modify song structure in response to recent changes in the acoustic environment (such as urban noise, e.g. Slabbekoorn 2013). Some birds even adjust their songs in real time to playback of noise (Halfwerk & Slabbekoorn 2009; Bermudez-Cuamatzin *et al*. 2011). Birds might also adjust songs in real time in response to changes in habitat structure. The acoustic adaptation hypothesis predicts that songs of birds in more open habitats with less vegetation have wider and higher frequency ranges and more/longer notes per phrase, whereas in closed habitats songs are selectively constrained to have the opposite characteristics because of the more restrictive transmission properties of the environment (Morton 1975; Hunter & Krebs 1979; Nemeth *et al.* 2001; Boncoraglio & Saino 2007). It is possible that, by changing the habitat structure, fire can relax environmental constraints on song transmission, allowing individuals in closed habitats to produce songs with characteristics approaching those of species occupying more open habitats, even over short time periods.

We investigated the potential effects of fire on song and singing behaviour in the Red-backed Fairy-wren, a small, insectivorous Australian passerine. Following a bushfire during the breeding season at the study site, we compared individuals' songs and dawn song bouts across 5 years to gauge the effect of fire on singing behaviour. We predicted that if fire lowered the health of the birds or reduced their motivation to sing, then song complexity, repertoire size, and/or measures of dawn song output (e.g. dawn bout length) might decrease. If birds responded to a more open transmission environment because of the fire, we expected songs and notes to show increased frequency, bandwidth, note rate, and/or complexity.

Study area and methods

We studied a population of colour-banded Red-backed Fairy-wrens near the town of Herberton in north-eastern Queensland (17°23′S, 145°25′E). This species provided an ideal system for our questions because it is found in dry schlerophyll forests that are prone to seasonal bushfires (Webster *et al.* 2010). The study site consisted of open forest dominated by *Eucalyptus* spp., with a canopy height of 20–30 m, sparse understorey of eucalypt saplings, and ground-cover of mostly grasses and *Lantana* shrubs. Fairy-wrens are insectivorous, and forage and nest in grass, low brush, and understorey plants, which are regularly burnt in bushfires (Brooker *et al*. 1990; Rowley & Russell 1997; Murphy *et al.* 2010). Additionally, males regularly give an extended song bout starting just before, and ending just after, sunrise (Dowling & Webster 2013), providing both a convenient sampling time and a concentrated period of display activity that might be sensitive to disturbance. Song is used to mediate territorial encounters in this species (Dowling & Webster 2013; Greig & Webster 2013), and is likely involved in female mate choice within the genus *Malurus* (Dalziell & Cockburn 2008).

A bushfire burned through our long-term study site in mid October 2012, after Red-backed Fairy-wren territories had been established and breeding groups formed, but before any nests had been built or copulatory behaviour observed. The fire consumed all grass and defoliated or consumed all shrubs, saplings, and fallen trees, with estimated flame heights of 0.5–2.0 m. We used Byram's equation for calculating fireline intensity, which provides a quantitative measure to evaluate the impact of fire on forest ecosystems (Byram 1959; Alexander 1982). From our estimates of low and high flame heights, we calculated a fire intensity score (I) of 57.6–1172.6 kW/m, which is characteristic of slow spreading surface fires with primarily low flames that consume forest-floor fuels such as grasses, much of the understorey vegetation, and can consume ladder fuels, such as bark and lichens (Byram 1959; Hirsch 1996).

Immediately following the fire, the study population of Red-backed Fairy-wrens relocated to adjacent unburnt areas and formed large foraging groups of 10–50 birds (Murphy *et al*. 2010; Nakamura *et al.* 2010). After *c*. 2 weeks, the birds returned to their territories within the burnt area and again began producing dawn song. Despite this, there was very little indication of breeding; only one of 23 groups in the study population built a nest, and only one of the 29 males captured after the fire had developed a cloacal protuberance, a sperm-storage organ associated with breeding status in male birds (Wolfson 1952). Some sparse grass regenerated during the study and, though Fairy-wrens were frequently observed on the ground early in the day, all foraging within the burnt area took place in the canopy.

We recorded a total of 476 songs (400 songs from 22 males; 76 songs from 10 females) between November and mid January after the fire during the 2012–2013 breeding season, from Red-backed Fairy-wrens occupying territories within the burnt area. For comparison, we used recordings from the same population from three previous breeding seasons, October–January 2009–2010 (28 songs from 10 males; 19 songs from 10 females), 2010–2011 (49 songs from 17 males; 50 songs from 11 females), 2011–2012 (177 songs from 24 males; 40 songs from 15 females), and also from the season following the year of the fire, 2013–2014 (100 songs from 14 males; no songs from females present). We sampled 34 individuals in ≥2 years. We recorded songs during the dawn chorus and opportunistically throughout the day. Red-backed Fairy-wren songs do not differ in song type or qualitative structure between dawn and daylight (unpubl. data). We also recorded full male dawn song bouts in 2010–2011 (12 bouts from 8 birds), 2011–2012 (27 bouts from 18 birds), 2012–2013 (8 bouts from 8 birds), and 2013–2014 (20 bouts from 14 birds). We measured dawn song bout length for an additional 51 bouts from 12 birds in 2010–2011. Including these, we measured a total of 118 dawn song bouts from 36 individuals, with 12 individuals sampled in ≥2 years. We refer to each field season by the year it ended. Our sampling methods were non-invasive, and seemed to have little effect on the birds' behaviour. For all recordings, we used Marantz PMD 661 solid-state digital recorders (Marantz America, Itasca, Illinois, USA) and highly directional Sennheiser ME 67 shotgun microphones with Rycote softie windshields and shock-mounts (Sennheiser Corp., Old Lyme, Connecticut, USA). We collected songs as uncompressed WAV files at a sampling rate of 96 kHz and with 24-bit depth.

We analysed songs using RavenPro 1.4 (Cornell Laboratory of Ornithology, Ithaca, New York, USA) and Luscinia (Lachlan 2007). We applied a high-pass filter set to 2.3 kHz and a low-pass filter set to 35 kHz, except where songs contained energy below 2.3 kHz, in which case we adjusted our high-pass filter accordingly. For most songs from the 2010 season, we used a low-pass filter set to 24 kHz. We also spot-filtered songs to eliminate excess background noise. We did not use recordings where background noise interfered substantially with the target song and could not be satisfactorily removed by filtering, though this did not substantially impact the sample size for any individual in any year.

We measured song and singing behaviour of individual birds at the level of (1) individual notes, (2) whole songs, and (3) full dawn song bouts (see Table 1 for summary of measurements). For analyses of whole-song and dawn song bout characteristics, we drew selection boxes around each song in RavenPro to obtain song counts and measurements of highest frequency (the frequency at which 95% of the energy in the song is lower), lowest frequency (the frequency at which 95% of the energy is higher), bandwidth (highest frequency minus lowest frequency), and aggregate entropy (a measure of the spread of energy across the frequency range of the selection). We created spectrograms in RavenPro using default settings [16-bit sample transform; discrete Fourier transform (DFT) = 512 samples; frequency resolution = 124 Hz; time resolution = 11.6 seconds; frame overlap = 50%]. For analyses of full dawn song bouts, we calculated song length (end time of each selection minus start time), dawn song bout length (clock time of last song end minus start time of first song, dictated on recordings), dawn song output (total number of songs sung in dawn song bout), and average song rate (dawn song output divided by bout length). Red-backed Fairy-wrens sing at fairly consistent song rates throughout the dawn chorus, so we designated the end of a chorus as the last song after which songs are no longer given at a consistent rate. Song length was calculated only in years 2012–2014, so 2011 was not included in this analysis.

To compare finer-scale aspects of songs, we used Luscinia (Lachlan 2007) to take measurements of individual notes. We measured individual notes from each song, for a total of 38 000 notes. For each note, we measured duration (in milliseconds), maximum peak frequency (the highest frequency with the greatest energy across all spectral slices in the note), minimum peak frequency (the lowest frequency with the greatest energy in the note), overall instantaneous peak frequency (the frequency within the note with greatest energy), bandwidth (maximum peak frequency minus minimum peak frequency) and slope (bandwidth divided by duration, an approximation of the overall contour of the note). For each song, these measurements allowed us to quantify the number of notes, number of different note types, note rate (number of notes per second) and complexity (defined here as the proportion of unique note types within each song, calculated as number of distinct note types divided by the total number of notes per song).

Note types were classified as in Schwabl *et al.* (2015). We used JMP® 11.0 (SAS Institute Inc., Cary, North Carolina, USA) to classify notes into groups of note types using normal mixtures clustering. From this, we identified an optimal number of clusters (i.e. note types) using values derived from Aikake Information Criterion corrected for small sample size AICc (Burnham & Anderson 2013) as the fit statistic to determine the optimal number of clusters (i.e. we set up a new classification for the current sample rather than using note type classification from a previous study of this species: Schwabl *et al*. 2015). This yielded 39 note types, which were then visually inspected to confirm that they were classified appropriately.

To assess differences in dawn singing behaviour, whole-song characteristics, and note-based song measures between the years sampled in this study, we used linear mixed-effect models (LMMs) with individual identity as a random effect, using the lme4 package in R version 3.3.0 (R Core Team 2016). Because essentially no breeding occurred in the year of the fire, we could not control for breeding stage in the comparisons with previous years. As a proxy, we created a model with date as a fixed effect for each response variable that we wished to test. We conducted an Analysis of Variance (ANOVA) on each model to determine if there were significant effects of date or an interaction between date and year. If the effect of date was significant in explaining any of the variation (*P* <0.05), we left it in the model, but if it did not explain any of the variation on its own, we removed it and added an interaction between date and year as a fixed effect. If the interaction was statistically significant in explaining any of the variation, we left it in the model; if not, it was

Table 1. Acoustical measurements for Red-backed Fairy-wrens, Herberton, Queensland, 2011–2014.

Measurement group	*Measurement*	*Definition*
Dawn singing behaviour	Song length	End minus start time of song
	Dawn song bout length	Clock time of last song end minus first song start
	Song output	Total number of songs in dawn song bout
	Song rate	Song output divided by length
Whole-song	Highest frequency	Frequency at which 95% of energy in song is lower
	Lowest frequency	Frequency at which 95% of energy in song is higher
	Bandwidth	Highest frequency minus lowest frequency
	Aggregate entropy	Spread of energy across bandwidth of song
Note-based	Length	End minus start time of note
	Maximum peak frequency	Highest frequency with greatest energy in note
	Minimum peak frequency	Lowest frequency with greatest energy in note
	Overall instantaneous peak frequency	Frequency within note with greatest energy
	Bandwidth	Maximum peak frequency minus minimum peak frequency
	Slope	Bandwidth divided by length

removed. We assessed assumptions of equal variances and normality, and mostly our data met these criteria. In the few cases where data were not normally distributed, we performed square-root transformations, which produced normal distributions. All reported *P* values are two-tailed.

To assess the nature of differences revealed by the model, we conducted *post hoc* tests of all pair-wise comparisons between least-squares means generated by each model using the lsmeans package in R. Because dawn song data were not collected in 2010, our dawn song analyses were limited to the years 2011–2014. Additionally, no whole-song data from 2014 were analysed. All data were analysed by year to assess baseline variation between normal years, with which measurements from the year of the fire could be compared. Only males were included in dawn song analyses, as females do not give typical dawn song bouts. Both males and females were included in note-based analyses. To control for potential confounding effects of sex, we added sex as a fixed effect in each model, but sex had no effect, and thus was removed from all models (see also Schwabl *et al*. 2015). As changes in population density can affect dawn singing (Stehelin & Lein 2014), we performed a Chi-square goodness-of-fit test on the number of territories established at the site across the years of this study, with expected counts equal across years.

Results

Dawn song bout length was shorter in 2013 (the year of the fire), but changes in other dawn singing behaviour and note-based song measures were more ambiguous in relation to fire. Whole-song characteristics showed no response to fire. We found no significant differences in the number of territories established between years ($\chi^2 = 2.74$, $P = 0.60$), suggesting that changes in population size did not influence our results.

Dawn song bout length was significantly shorter in 2013 than in other years (Table 2, Figure 1a). Bout length also varied as a function of date (Table 2). We found a similar trend in total dawn song output and average song rate, though not all year comparisons were significant for these variables. Total dawn song output (number of songs) was lower in the year of the fire (2013), but the difference was significant only between 2013 and 2014 (Figure 1b, Table 2). Year explained the variation in dawn song output, with no effect of date and no interaction between date and year. Average song rate was slightly lower in the year of the fire, but again this difference was significant only between years 2013 and 2014 (Figure 1c, Table 2). Year was the only significant predictor of song rate, with no effect of date and no significant interaction between date and year. Song length did not differ between 2012 and 2013, but songs from 2014 were significantly longer than those of both previous years (Figure 1d, Table 2). Year was again the only significant predictor of song length, with no effect of date and no significant interaction between date and year.

Whole-song analyses showed some significant differences between years (Table 3), but none of these could be explained by fire. Similarly, note-based analyses showed no significant differences between 2013 and other years. In 2014, overall instantaneous peak frequency was significantly lower than in any previous year (Figure 2a, Table 4), and this effect was influenced by date (Table 4).

Table 2. Results from Linear Mixed-effect Models (LMMs) for each dawn song measure for Red-backed Fairy-wrens, Herberton, Queensland. DF = degrees of freedom, *P* = probability

Parameter	*Effect*	*χ^2*	*DF*	*P*
Dawn song bout length	Year	28.2	3	<0.0001
	Date	36.05	1	<0.0001
Total dawn output	Year	20.5	3	<0.001
Dawn song rate	Year	16.77	3	<0.001
Average song length	Year	19.28	2	<0.0001

Table 3. Results from Linear Mixed-effect Models (LMMs) for each whole-song measure for Red-backed Fairy-wrens, Herberton, Queensland. Interaction is indicated by × between interacting variables; DF = degrees of freedom, *P* = probability.

Parameter	*Effect*	*χ^2*	*DF*	*P*
Lowest frequency	Year	6.51	3	0.09
Highest frequency	Year	31.36	3	<0.0001
Bandwidth	Year	21.44	3	<0.0001
Aggregate entropy	Year	108.27	3	<0.0001
	Date	0.22	1	0.64
	Year×Date	21.89	3	<0.0001

Table 4. Results from Linear Mixed-effect Models (LMMs) for each individual note measure for Red-backed Fairy-wrens, Herberton, Queensland. All frequency parameters refer to peak frequencies. Interaction is indicated by x between interacting variables; DF = degrees of freedom, *P* = probability.

Parameter	*Effect*	*χ^2*	*DF*	*P*
Instantaneous frequency	Year	48.92	4	<0.0001
	Date	1.43	1	0.23
	Year×Date	9.97	4	0.04
Minimum frequency	Year	39.66	4	<0.0001
	Date	1.92	1	0.17
	Year×Date	13.16	4	0.01
Maximum frequency	Year	34.38	4	<0.0001
	Date	0.8	1	0.37
	Year×Date	12.61	4	0.0133
Note slope	Year	41.49	4	<0.0001
	Date	0.53	1	0.47
	Year×Date	24.82	4	<0.0001

Three other frequency measures (minimum peak frequency, maximum peak frequency, and note slope) showed a similar, non-significant trend toward lower values in 2014 (see Figures 2b–d, Table 4) and a significant interaction between year and date. Note rate, number of notes per song, and song complexity did not differ between years. There were differences between years in note bandwidth

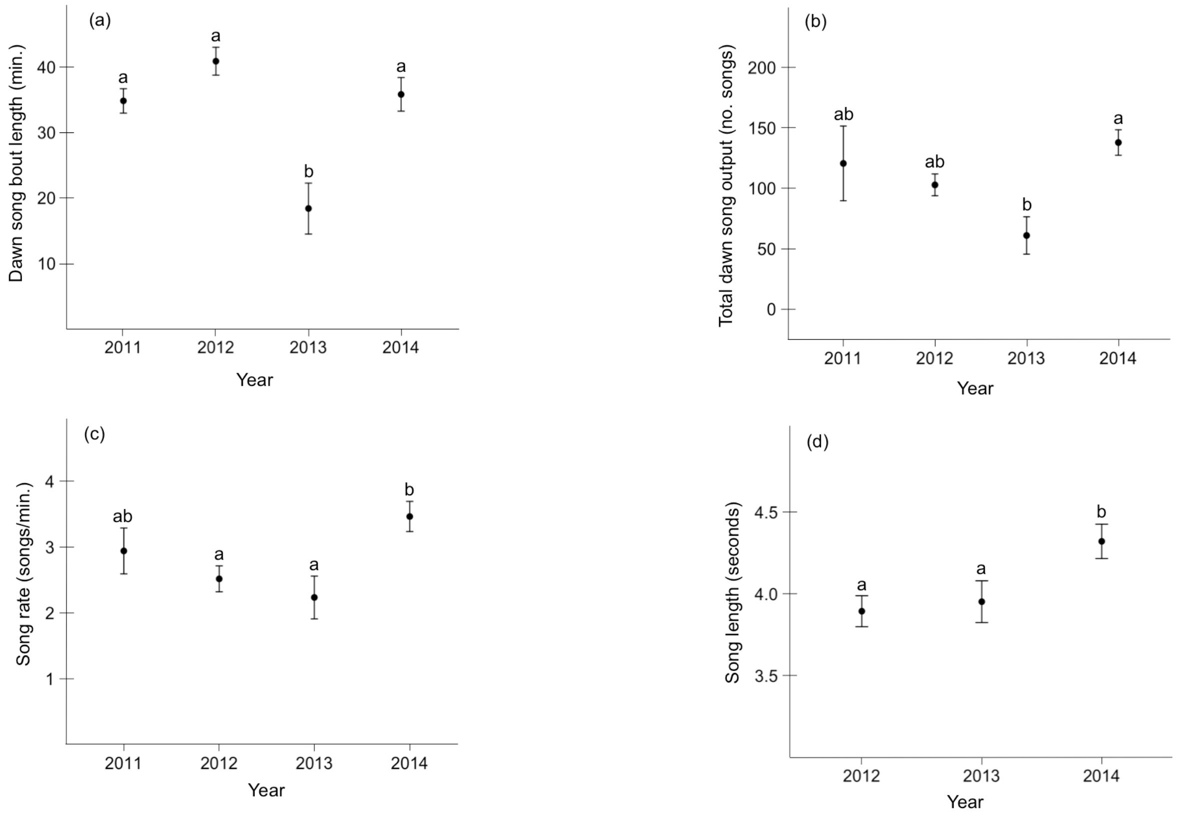

Figure 1. Variation by year in songs of Red-backed Fairy-wrens, Herberton, Queensland, 2011–2014: (a) dawn song bout length, (b) total dawn song output, (c) average dawn song delivery rate, and (d) average dawn song length (not calculated for 2011). Year of fire was 2013. Points show mean ± one standard error. Letter groups above means indicate statistical significance at $P < 0.05$.

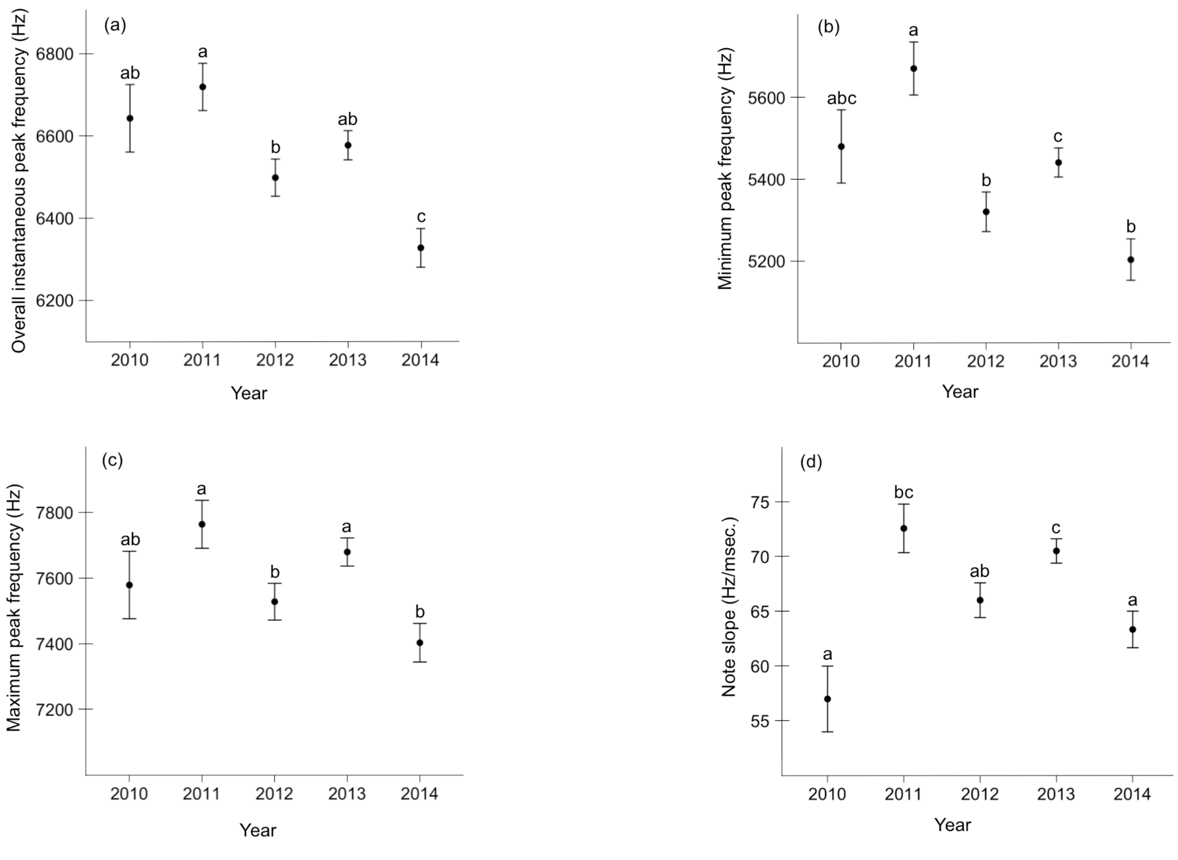

Figure 2. Variation by year in songs of Red-backed Fairy-wrens, Herberton, Queensland: (a) overall instantaneous peak frequency, (b) minimum peak frequency, (c) maximum peak frequency, and (d) slope of individual notes. Year of fire was 2013. Points show mean ± one standard error. Letter groups above means indicate statistical significance at $P < 0.05$.

and note duration, but no variable that we measured explained this variation.

Discussion

In this study, we found that male Red-backed Fairy-wrens sang shorter dawn song bouts during a breeding season in which fire interrupted normal breeding and territorial activities (2013), compared with seasons in years without fire (2010–2012 and 2014). They also tended to sing fewer songs at dawn and to reduce singing rate. These results are consistent with our prediction that birds might lower dawn singing effort if fire indirectly reduced their condition or motivation to sing. Several song measures showed no clear response to fire, and differences likely resulted from baseline variation across years from unmeasured variables. We found no support for the acoustic adaptation hypothesis, indicating that, if fire changed the transmission environment, birds did not respond by changing their songs.

Birds might reduce dawn singing effort because of physiological costs resulting from fire. We did not measure the condition of the Red-backed Fairy-wrens whose songs we recorded, but Murphy *et al.* (2010) found that in recently burnt areas this species had lower physiological condition than in areas outside the burn. By eliminating the understorey, fire might reduce food availability (Brooker & Rowley 1991), especially for this species, which forages primarily on or near the ground (Brooker *et al.* 1990; Rowley & Russell 1997). In other species, decreased health or condition negatively affects song characteristics and dawn singing behaviour (e.g. Gorissen *et al.* 2005; Gilman *et al*. 2007), and birds with more available food and higher fat reserves show higher dawn singing performance (Barnett & Briskie 2006; Grava *et al*. 2009).

Alternatively, birds might be less motivated to sing because fire reduces the likelihood of successful breeding. Dawn song appears to be an important aspect of breeding in many species (Gentner & Hulse 2000; Gil & Gahr 2002). Male song performance peaks during the female's fertile period (Slagsvold *et al*. 1994; Welling *et al*. 1995; Ballentine *et al*. 2003), and might have a role in extra-pair mate choice by females of several species (Poesel *et al*. 2006; Suter *et al*. 2009), including a congener, the Superb Fairy-wren *Malurus cyaneus* (Dalziell & Cockburn 2008). As dawn song likely serves a sexual function, an almost complete absence of breeding opportunities following the fire might have reduced motivation to perform. In a separate project at our study site, only one of the 29 males captured had a cloacal protuberance during the year of the fire, whereas all breeding males developed these in non-fire years (Lindsay *et al.* 2011). If dawn song bouts contain signals to fertile females, there would seem to be little use in investing when there are few or no receivers for those signals.

We predicted that if fire changed the acoustic transmission properties of the environment, birds might respond by changing their songs to take advantage of relaxed constraints. However, in this study, Red-backed Fairy-wrens sang notes with lower frequency characteristics after the fire, opposite to what the acoustic adaptation hypothesis predicts. We did not determine whether the transmission environment was changed after the fire, but concluded that the birds did not adjust their songs to a more open understorey environment. Although rapid changes to the acoustic environment might cause birds to modify their songs (Slabbekoorn 2013), changes to the transmission environment in particular might not have the same effect over shorter time periods.

It is unclear why Red-backed Fairy-wrens sang notes with lower frequencies in the year following the fire. This might have been unrelated to the fire, but could reflect a lingering negative effect on physiology or health, which can affect frequency characteristics of song (Barnett & Briskie 2006; Hallinger *et al*. 2010). We also noted an unusually high proportion of adult male Fairy-wrens that did not moult into colourful breeding plumage (unpubl. data; see also Dowling & Webster 2017), which is hypothesised to indicate male quality (Karubian *et al.* 2008). This also suggests lingering negative effects on physical condition.

In conclusion, we found that fire affects dawn singing behaviour in a population of Red-backed Fairy-wrens. Changes in dawn singing behaviour might have been because of reduced physical condition, reduced motivation to engage in breeding behaviours, or both. These results provide new information on the effects of fire on bird populations in the wild. Song is an important breeding behaviour in many species and, at the individual level, changes to singing behaviour can affect breeding decisions made by females, or an individual's ability to successfully defend or acquire a resource. In fire-prone ecosystems, it is important to consider the effects of fire on species' behaviour in order to better understand their responses and capacity for recovery.

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