Tree hollow densities reduced by frequent late dry-season wildfires in threatened Gouldian finch (*Erythrura gouldiae*) breeding habitat

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Abstract

Context. Tree hollows are a key habitat resource for hollow-nesting species, including the northern Australian Gouldian finch (*Erythrura gouldiae*). Certain fire and disturbance regimes limit tree hollow availability in the northern Australian savannas.

Aims. This study investigated the influence of fire regime and vegetation structure on the density of tree hollows at Gouldian finch breeding sites.

Methods. Fire scars were mapped across breeding sites by using LANDSAT images. Vegetation plots within sites were spatially stratified according to three fire-regime attributes, namely, fire frequency, late dry-season wildfire frequency and time since the last fire. Tree hollow and vegetation structural attributes were measured at each vegetation plot. We modelled the relationship among hollow density, fire and vegetation attributes by using general linear mixed models with site as the random factor.

Key results. We found that the highest tree-hollow density was found at plots with high eucalypt tree density and cover and with the lowest frequency of late dry-season wildfires (<1 wildfire over 5 years). Tree-hollow density declined after >2 years without fire. Hollow density was not directly related to total fire frequency.

Conclusions. This study adds to previous work on grass seed resources in highlighting the importance of fire in Gouldian finch ecology. This study particularly highlighted the importance of reducing the impacts of high-intensity late dry-season wildfires because of their negative impacts on tree-hollow density, which is a key resource for breeding Gouldian finches.

Implications. We recommend the use of a network of interconnected annual patchy early dry-season prescribed burns for protecting Gouldian breeding habitat from threat of high-intensity wildfires. We do NOT recommend fire exclusion from Gouldian finch breeding habitats. This is because fire risks to hollow-bearing trees, and grass seed resources, increase with the long-term accumulation of savanna litter fuels in the absence of fire.

Keywords: fire ecology, savanna, obligate hollow nesting, grass finches, threatened species.

Introduction

North Australian savanna ecosystems are currently undergoing a biodiversity crisis thought to be at least in part attributable to inappropriate fire regimes (Franklin 1999; Franklin *et al.* 2005; McKenzie *et al.* 2007; Woinarski *et al.* 2011; Woinarski and Legge 2013). Fire regimes in much of northern Australia, since the loss of traditional indigenous fire management, have been dominated by high-intensity, frequent, extensive wildfires occurring in the late dry season (Russell-Smith *et al.* 2003*a*). Although fire management has reduced late-season wildfire

extent in some areas in recent decades (Price *et al.* 2012; Murphy *et al.* 2015; Corey *et al.* 2020), inappropriate fire regimes continue where sufficient fire management is not undertaken (Russell-Smith *et al.* 2020). Although much of the savanna biota is thought to be fire resilient (Williams *et al.* 1999; Russell-Smith *et al.* 2003*b*; Clarke *et al.* 2015; Andersen 2020), most threatened elements of the savanna biota appear to be vulnerable to large fires, frequent fires or to high-intensity late dry-season wildfires (Andersen *et al.* 2005; Legge *et al.* 2008, 2015; Lawes *et al.* 2015; Radford *et al.* 2015, 2020; Corey *et al.* 2020). In contrast,

threatened taxa generally respond more favourably to lower-intensity, patchy, early dry-season fires that result from burning conducted when grass fuels are yet to be fully cured and humidity is still high (Andersen *et al.* 2005; Legge *et al.* 2015; Weier *et al.* 2016; Radford *et al.* 2020). Few savanna taxa respond favourably to the long-term absence of fire because this leads to progressive conversion of savanna to closed forest with forest-dominated biota (Woinarski *et al.* 2004; Andersen *et al.* 2014).

Savanna biota considered most at risk under inappropriate fire regimes include obligate-seeder shrubs found in rugged sandstone (tropical heath; Russell-Smith *et al.* 2002), rainforest vegetation elements (Russell-Smith and Bowman 1992), fire-killed species, including *Callitris intratropica* (Bowman *et al.* 2001), fire-sensitive critical weight-range mammals (Burbidge and McKenzie 1989; Andersen *et al.* 2005; Woinarski *et al.* 2011), and also several avian species and groups (Woinarski and Legge 2013). Threatened birds include grass-dwelling species (e.g. fairy wrens; Murphy *et al.* 2010; Skroblin and Legge 2012), granivores, including grass-feeding finches (Franklin *et al.* 2005; Legge *et al.* 2015; Weier *et al.* 2016), pigeons (Fraser *et al.* 2003) and also obligate hollow-nesting species (Tidemann *et al.* 1992; Brazill-Boast *et al.* 2011*b*; Woinarski and Legge 2013). Putative mechanisms underlying fire impacts on plants include fire mortality and differing fire functional responses among different species (e.g. Williams *et al.* 1999; Edwards *et al.* 2003, Clarke *et al.* 2015). Mechanisms underlying fauna fire responses are often more complex and relate to survival and reproductive success in the post-fire environment rather than to immediate fire-related mortality (e.g. Begg *et al.* 1981; Leahy *et al.* 2015; Weier *et al.* 2016). Key factors influencing fauna fire responses include loss or alteration of habitat features, resulting in elevated predation (Johnson 2006; McGregor *et al.* 2014; Leahy *et al.* 2015; Stobo-Wilson *et al.* 2020) and changed food-resource availability (Radford 2012).

The endangered Gouldian finch (*Erythrura gouldiae*) is vulnerable to fire regimes via its influence both on food resource and on nest-site availability (Woinarski and Legge 2013). Approximately a third of the grass finches in northern Australia have undergone declines under current fire regimes and the Gouldian finch is one of these (Franklin 1999; Franklin *et al.* 2005). In the case of the Gouldian finch, the availability of key grass seed resources as influenced by fire is one mechanism whereby populations may be driven into decline (Dostine *et al.* 2001; Dostine and Franklin 2002; Legge *et al.* 2015; Weier *et al.* 2017, 2018, 2019). However, Gouldian finches are also the only Australian grassfinch that is an obligate tree-hollow nester (Tidemann *et al.* 1992; Brazill-Boast *et al.* 2011*b*) and, there-fore, is also at risk from the impacts of inappropriate fire regimes through effects on trees and tree hollows.

Nest hollows can become an important limiting resource for hollow users generally in savannas (Woolley *et al.* 2018). This is because nest hollows in eucalypt trees may take many decades or longer to be created and only a single disturbance event to be removed. Hollows are mostly formed only once trees attain a certain minimum size (>20 cm diameter at breast height, DBH) through the actions of termites (Woolley *et al.* 2018). Savanna trees are also apparently very slow growing. For instance, eucalypt tree basal area grew in the absence of fire by just 3.5% in 5 years (Williams *et al.* 1999) and by ~30% in

20 years (Russell-Smith *et al.* 2003*b*). When burnt, eucalypt trees in the same areas showed no detectable growth (DBH) over 5 and 20 years respectively. However, it can take just one high-intensity fire (Williams *et al.* 1999), or cyclone (Woolley *et al.* 2018), to remove large hollow-bearing trees because these are structurally vulnerable. It has also recently been found that termite activity not only creates hollows, but can also block them, which can further limit their availability to hollow-using species (Tidemann *et al.* 1999; Penton *et al.* 2020). All of these factors can create a situation of acute shortage of what amounts to a non-renewable resource (in the short term), which may take from decades to more than a century to replenish. Specifically, in relation to Gouldian finches, locations of breeding populations are known to be restricted to areas with high nest-hollow densities (Tidemann *et al.* 1992; Brazill-Boast *et al.* 2011*b*). Gouldian finches have strong selective preferences for particular hollow attributes and dimensions (Tidemann *et al.* 1999; Brazill-Boast *et al.* 2013). Gouldian finches also have to compete for suitable hollows with a more common facultative hollow-using species, the long-tailed finch (*Poephila acuticauda*; Tidemann *et al.* 1999; Brazill-Boast *et al.* 2011*a*). For all these reasons, appropriate fire management of breeding sites for the Gouldian finch is a crucial part of its conservation.

Where potential nesting hollows may be a limiting resource for Gouldian finches, which fire-related factors most strongly influence hollow abundance at breeding sites? Although hollow density was identified as a strong predictor of Gouldian finch habitat use at the broader scale (>60 km^2), Brazill-Boast *et al.* (2011*b*) were unable to identify factors at the fine scale within breeding habitats (~1 km^2) that could explain availability or use of nesting sites. In the present study, we investigated the influence of fire mosaics and vegetation structure on tree-hollow availability. In this way, we hoped to identify fire-related management that could benefit this hollow-reliant species in tropical savanna landscapes.

Materials and methods

Study area and sites

The study area was within 30 km of the town of Wyndham, north-eastern Western Australia (Fig. 1). This area is part of the exten-sive tropical savannas that are continuous across northern Aus-tralia. Rain mostly falls during the monsoonal summer wet season (December–March), with an average annual rainfall of 824 mm (http://www.bom.gov.au/climate/averages/tables/cw_001013.shtml). Very little rain falls during an extended dry season in this region (April–November), leading to high curing and flamma-bility of grasses that dominate the savanna understorey, and frequent fires. The region is hot, with mean annual maximum and minimum temperatures of 35.6°C and 23.1°C respectively.

Study sites were all within known breeding areas of the Gouldian finch (*Erythrura gouldiae*; Fig. 1). Breeding habitat is confined to areas with relatively high densities of suitable nesting hollows in preferred eucalypt trees (e.g. *Corymbia dichromophloa*, *Eucalyptus miniata*; Brazill-Boast *et al.* 2010, 2011*b*) and co-occurrence of preferred grasses whose seeds make up the diet of finches (e.g. *Sorghum stipoideum*, *Triodia bitextura*, *Alloteropsis semialata*; Dostine *et al.* 2001; Dostine
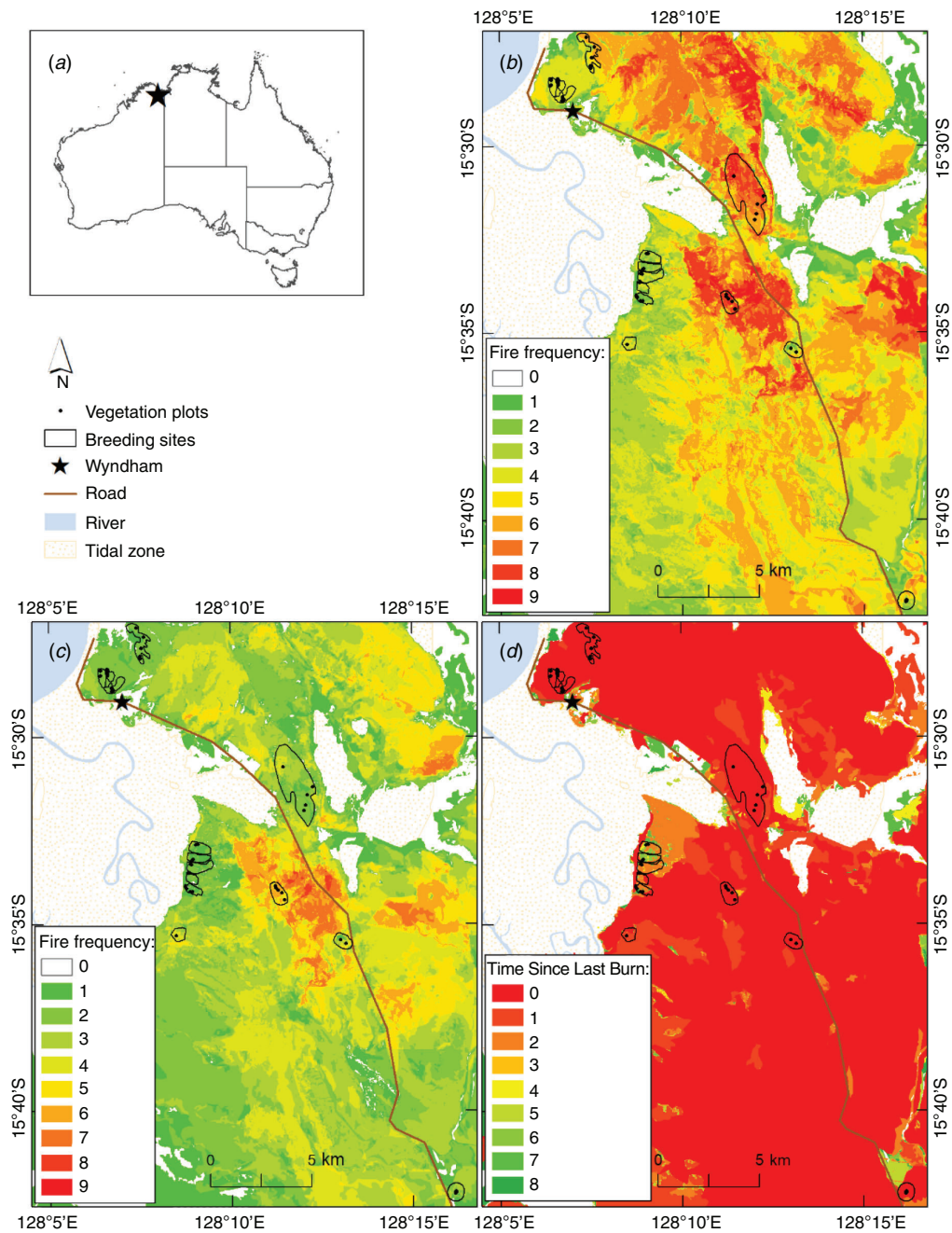
Fig. 1. (*a*) Study region near Wyndham in northern Western Australia, and close-ups of the study region showing fire-regime attributes from 2006 to 2014 including (*b*) total fire frequency, (*c*) late dry-season fire frequency, and (*d*) time since last burn. Different colours represent the areas of the same fire frequency, late dry-season fire and the same time since the last burn. Black dots represent vegetation survey plots and black lines are the boundaries of known Gouldian finch breeding sites in the Wyndham region.

and Franklin 2002; Weier *et al.* 2017, 2018). Most of the suitable breeding habitat in the Wyndham region occurs on low, rocky sandstone hills and ridges with an open eucalypt savanna woodland structure. Discrete breeding sites identified in this context (Brazill-Boast *et al.* 2011*b*; Weier *et al.* 2016) were found on a series of separate ridgelines or hills in the area and so are defined locally by topography and drainage.

Fire-regime attributes

Known breeding sites were stratified according to fire regime, so as to test for its effect on the density of suitable Gouldian finch nesting hollows. A fire atlas containing the annual burnt areas between 2006 and 2014 was compiled for the study area, with information about area burnt (ha) and the year and season of fires. Mapping of the annual burnt areas was derived from

Landsat 5 Thematic Mapper (2006), Landsat 7 Enhanced Thematic Mapper Plus (2007–2012) and Landsat 8 Operational Land Imager (2013–2014) imagery, downloaded from the Geographical Survey Global Visualisation Viewer (glovis.usgs. gov). These maps have a spatial resolution of 30 m.

At least one satellite image per month was selected between April and December. Late dry-season fires were classified as those occurring from July to December. No fires were recorded in the months of January to March. However, not all images were suitable because of incomplete coverage caused by clouds, especially in the latter part of the dry season, and more than one image was investigated to ensure full coverage. Pre-processing of the Landsat images was performed with the software ENVI version 5.2 (Exelis Visual Information Solutions, Boulder, Colorado USA) and involved radiometric calibration, converting digital numbers to reflectance, and atmospheric correction, by using dark pixel subtraction.

Burnt-area classification was performed using object-based image analysis (OBIA) with the software eCognition Developer 8.7 (Trimble 2011). OBIA has two steps, namely, segmentation and classification. Segmentation splits the image into unclassified objects on the basis of a measure of spectral properties (e.g. colour), shape, size, texture and context, controlled by parameters set by the user. The best settings for segmentation parameters vary widely, and were determined through a combination of trial and error. After an image was segmented into appropriate image objects, the image was classified by assigning each object to one of two classes, namely, 'Burnt' and 'Unburnt', on the basis of predetermined features and criteria. Classification results were complemented by thorough manual on-screen editing. The output was nine annual and late dry-season burnt-area maps (2006–2014). This information was used to create separate maps spatially stratifying breeding areas according to time (years) since the last burn (TSLB), fire frequency (number of fires between 2006 and 2014; FF) and frequency of late dry-season fires (number of fires from July to December between 2006 and 2014; freq_LDS).

Vegetation plots

Fifty-five vegetation plots at 14 known Gouldian finch breeding sites were measured for tree-hollow and vegetation variables.

Plot locations were initially selected remotely on the basis of stratified maps constructed of fire-history attributes (i.e. TSLB, FF and freq_LDS; see Fig. 1). Vegetation plots were visited in the field in the wet–dry transition (March–May) during 2015, so as to assess vegetation structural attributes before the fire season in that year. Once at each plot location, plots were assessed as suitable or unsuitable Gouldian finch breeding habitat on the basis of the presence of suitable nesting eucalypt trees, such as, for example, *C. dichromophloa* and *E. miniata*, and the presence of *S. stipoideum* grass, which is the main source of grass seeds for Gouldian finches during the breeding season (Weier *et al.* 2016). Only plots in suitable breeding habitat were recorded. On-ground site assessments of TSLB were made by experienced field savanna ecologists (BB and IJR) to validate the accuracy of fire-regime designation. This assessment was based on the presence of recent fire-killed stems, recent basal and epicormic resprouting among shrubs and trees, post-fire *Triodia* spp. hummock grass regrowth and the presence of senescent grass and leaf litter at the plot location. Owing to the fine-scale spatial intricacy of both recent (visible) and historic (invisible) fire mosaics, different plot fire attributes were often found within only a few metres of one another. However, plot locations were set a minimum of 50 m apart to ensure independence of both fire regime attributes and vegetation/hollow measurements among vegetation plots.

Each plot was assessed for nest-hollow availability and vegetation structural characteristics (Table 1). From each GPS plot point, all trees (all plants >4 m height) were identified to species and projected tree species canopy cover was estimated using a 1% Bitterlich gauge (Lindsey *et al.* 1958). Tree basal area (m^2 ha^{-1} timber) was estimated using a Factor 1 glass prism. Eucalypt tree density (*Eucalyptus* and *Corymbia* spp.) and total tree density were recorded within a 0.25 ha plot area (50 × 50 m) centred on the plot point. Tree hollows suitable for Gouldian finches (e.g. entrance diameter >30 mm) were counted within the 0.25 ha plot area. Although there is some inherent inaccuracy in using ground-based tree-hollow counts (Penton *et al.* 2020), low stature (mean canopy height <10 m) and open canopy structure at the study sites relative to many savanna woodlands/forests in northern Australia, are likely to increase detectability and visibility of hollow entrances in this context. The three nearest trees to the plot point were assessed

Table 1.   Explanatory variables measured at survey sites, their definitions and summary statistics

Name	Abbrev.	Description	Range	Mean
Site	Site	Site-specific variation as a random effect	–	–
Tree-hollow density (hollows ha^{-1})	Hollows	Number of nest hollows in trees within the 0.25 ha plot (expressed per hectare)	0–124	25
Eucalypt tree canopy cover (%)	Euc Cov	Projected *Corymbia* and *Eucalyptus* spp. tree (>4 m height) canopy cover as a percentage	0–18	6.5
Eucalypt tree density (trees ha^{-1})	Euc Dens	Density of all *Corymbia* and *Eucalyptus* spp. trees (>4 m height) in 0.25 ha plot (expressed per hectare)	0–108	32
Fire frequency (fire $year^{-1}$)	FF	Number of fires at plot between 2006 and 2014 expressed as number of fires per year	0.22–1.0	0.54
Time since last burn (years)	TSLB	Number of years since the last fire occurred at the plot	Four categories 0, 1, 2, 6	0
Frequency of late-season fire (fire $year^{-1}$)	LDS	Number of late dry-season fires (from July to December) at the plot between 2006 and 2014 expressed as number of fires per year	0.11–0.67	0.28

for number of hollows and tree DBH, i.e. 1.3 m from the ground, was recorded.

Statistical analyses

To model the relationship between hollow density and fire-regime attributes, while controlling for vegetation attributes on a site, we used a generalised linear mixed model (GLMM) with Poisson distribution and log-link, and site was included as a random effect. The response variable was hollow density (number of hollows per hectare). Five covariates were included in the global model (eucalypt cover, eucalypt density, fire frequency, frequency of late dry-season fires, time since last burn; Table 1). There was no collinearity evident among variables. Continuous covariates were centred and standardised for comparison on a similar scale. Pair-plots showing Pearson correlations between covariates showed no inter-correlations (i.e. >0.7). Where Poisson models were over-dispersed, we used a negative binomial distribution. Models were ranked from best to worst on the basis of the second-order Akaike information criterion (AICc). We calculated AICc weights (*wi*), i.e. conditional probabilities that each model is the best model, and used these to select the top model. Data analyses were run in the R statistical package version 3.6.3 (R Core Team 2020) and the contributed *MuMIn* (Barton 2019) and lme4 (Bates *et al.* 2015) packages. Optimal model assumptions were evaluated by plotting residuals versus fitted values, as well as variables included and not included in the model. To test for a significant relationship between the number of hollows and DBH of individual trees, we used a GLMM with site as a random factor.

Results

In the period from 2006 to 2014, fire frequency within Gouldian finch breeding habitat ranged from burnt two to burnt nine times (Fig. 1), frequency of late dry-season fires ranged from burnt one to burnt six times, and time since the most recent fire ranged from 0 to 6 years. None of the Gouldian finch breeding habitat had remained unburnt during the 9-year study period (2006–2014; Fig. 1).

When controlling for eucalypt density and cover, the explanatory fire-attribute variables included in the top-ranked (optimal) model as predictors of site-level tree-hollow density were the frequency of late dry-season fires (2006–2014) and time since the most recent fire (Table 2, Fig. 2). Total fire frequency was not included in the optimal model (Table 2). Tree-hollow density increased with an increasing eucalypt

density and cover, and decreased with an increasing frequency of late dry-season fires (Fig. 3). Greatest hollow density was found at intermediate time since the last fire (~2 years post-fire) and declined to the lowest density at sites after longer periods post-fire (~6 years; Fig. 3). Hollow number among individual trees was strongly (Fig. 4) and significantly (*z*-value = 9.179; $Pr < 2e^{-16}$) influenced by tree DBH.

Discussion

Frequency of late dry-season fires, but not overall fire frequency, had the greatest predictive value for occurrence of suitable nesting hollows for Gouldian finch in the study area, with more frequent high-intensity fires resulting in fewer suitable hollows. Late dry-season fires are known to have a disproportionately large impact on larger hollow-bearing trees (Williams *et al.* 1999; Radford *et al.* 2008; Woolley *et al.* 2018) because hollows are more common in large trees and because larger, older hollow-bearing trees are more vulnerable to fire impacts. Wildfire-related loss of hollows is likely to lead to their
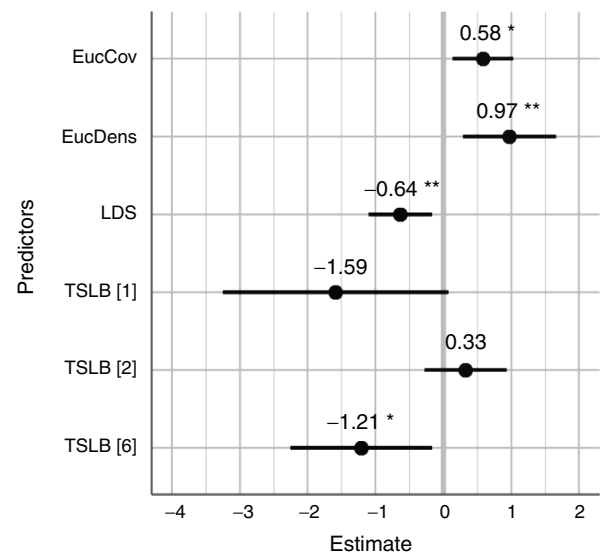
Fig. 2. Standardised coefficient estimates (filled circle with numerical label) and standard errors (error bars) for optimal GLMM predictors. EucCov, eucalypt canopy cover; EucDens, eucalypt density; LDS, frequency of late dry-season fire; TSLB, time since last burn (Levels 1, 2 and 6). Asterisks indicate significance: *$P < 0.05$, **$P < 0.01$.

Table 2. Results of AICc-based model selection for number of tree hollows per site hectare

Only the most supported models with AICc difference (delta) of <3 are presented. Number of model parameters (d.f.), maximised log-likelihood values (logLik), AICc values (AICc), AICc differences (delta), Akaike weights (weight) and percentage of deviance explained (marginal and conditional R^2) are shown for each of the models. See Table 1 for abbreviations of habitat and fire attributes

| Model	d.f.	logLik	AICc	Delta	Weight	Marginal R^2	Conditional R^2
~Euc Cov + Euc Dens + LDS + TSLB	9	−220.85	463.70	0.00	0.38	0.21	0.44
~ Euc Cov + Euc Dens + LDS	6	−225.06	463.86	0.16	0.35	0.20	0.38
~ Euc Cov + Euc Dens + LDS + FF	7	−225.04	466.47	2.77	0.09	0.19	0.33
~ Euc Cov + Euc Dens + TSLB	8	−223.67	466.48	2.78	0.09	0.19	0.34
~ Euc Cov + Euc Dens	5	−227.70	466.63	2.93	0.09	0.18	0.27
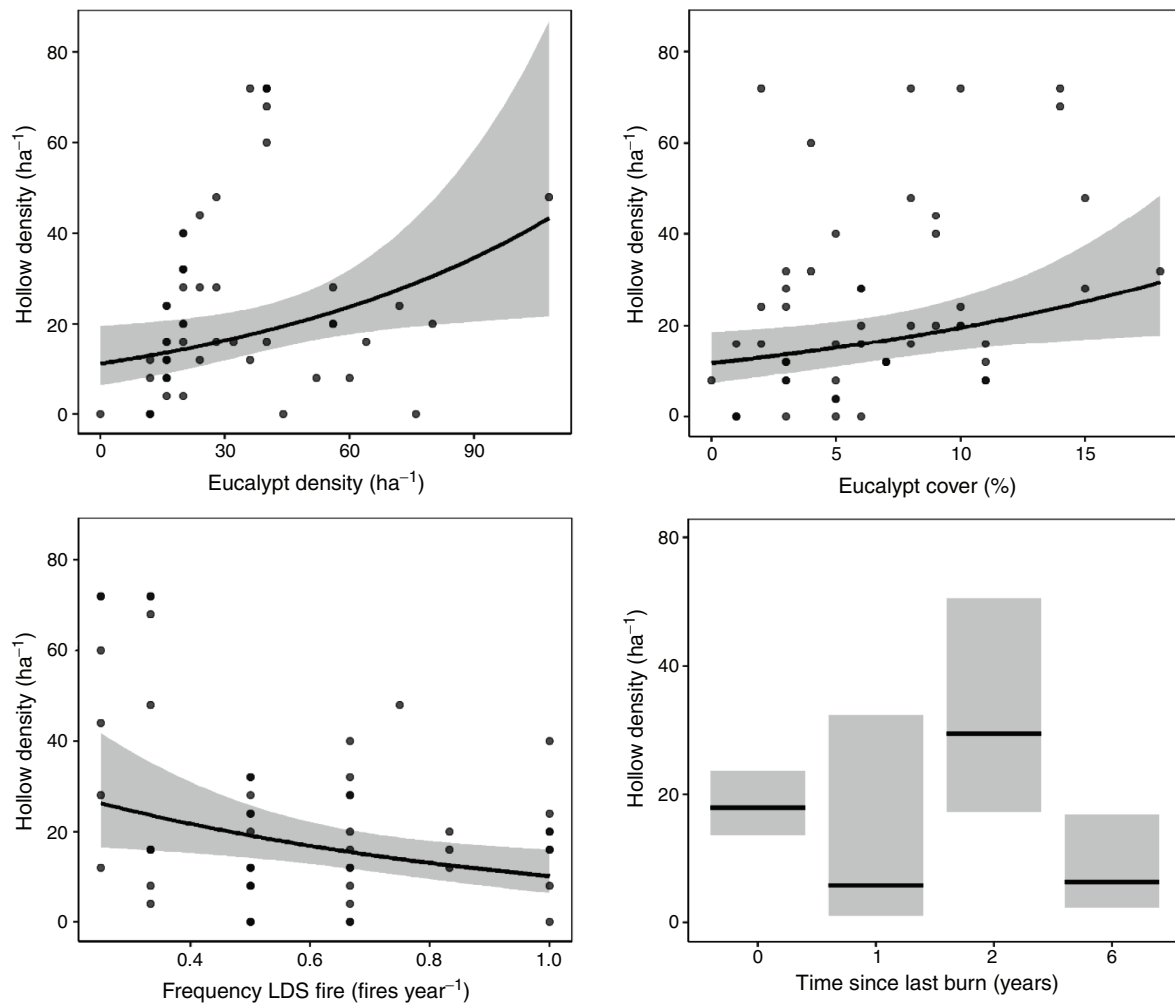
Fig. 3. Relationship between hollow density (hollow count per hectare) and each optimal model predictor variable, while holding all other variables fixed at their median level (continuous variables) and most common category (categorical variable). Model fit is shown by a black line and 95% confidence interval is represented by a grey band. Grey circles indicate observed data values and are darker when repeated observations occur at the same point. LDS, late dry season.

long-term absence from a site because of the extended period (decades to over a century) that may be necessary for sufficient tree growth, disturbance and termite activity to replace those lost (Williams *et al.* 1999; Russell-Smith *et al.* 2003*b*; Woolley *et al.* 2018; Penton *et al.* 2020). It is, therefore, crucial to maintain this non-renewable breeding resource (in the short-term) in known finch breeding habitats.

Fire frequency has often been identified as an important influence on biodiversity in northern Australia (Yates *et al.* 2008; Griffiths *et al.* 2015) and has also been shown to significantly influence savanna hollow densities generally (Woolley *et al.* 2018). Failure of total fire frequency to influence hollow availability here may be related to the rocky substrates and low fuel biomass found in known Gouldian finch habitat. Gouldian finches breed in rocky, low, infertile sandstone hills in the Wyndham area and across much of northern Australia (Dostine *et al.* 2001; Brazill-Boast *et al.* 2011*b*; Legge *et al.* 2015; Weier *et al.* 2016). Fires occurring in these rocky, infertile hills early in the dry season may be patchy and of low intensity at

the micro-scale because of sparse and patchy grass fuels, leaving many of the eucalypt trees in this environment unscathed (Russell-Smith and Yates 2007; Oliveira *et al.* 2015). In contrast, late-season wildfires occurring when grass fuels are fully cured and humidity is very low may be sufficiently intense and pervasive to enter and ignite tree hollows in larger hollow-bearing trees, leading to mortality and consumption of above-ground stem biomass (Williams *et al.* 1999; Woolley *et al.* 2018). Clearly, conservation managers trying to optimise fire regimes for obligate hollow-nesting species, including the threatened Gouldian finch, need to minimise incursions of these late dry-season wildfire to retain high tree-hollow densities associated with known successful breeding habitats (Brazill-Boast *et al.* 2011*b*).

As might be expected, high tree-hollow density occurred at sites where there was high eucalypt density and canopy cover. Trees with larger canopies are also likely to be trees with a large DBH, and large DBH trees were found to have the highest hollow density in the present and other studies (Woolley *et al.*
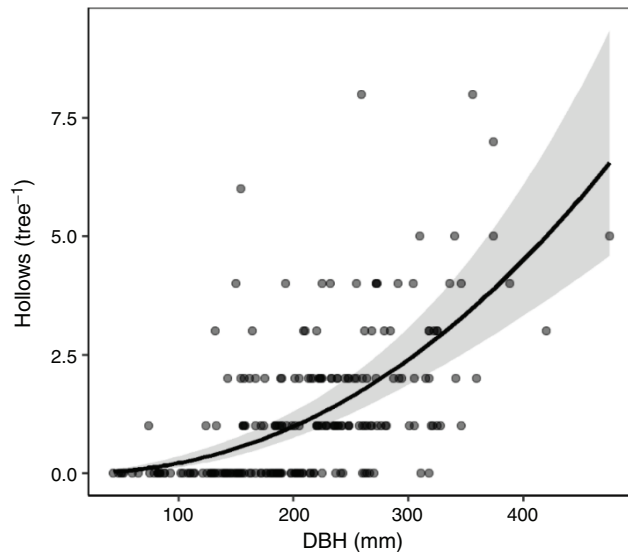
Fig. 4. Relationship between hollows per tree and tree diameter at breast height (DBH), derived from negative binomial GLMM with site as the random effect. Model fit is shown by a black line and 95% confidence interval is represented by a grey band. Grey circles indicate observed data values and are darker when repeated observations occur at the same point.

2018). However, the steepness of the increasing relationship between hollow number and eucalypt tree density declined as eucalypt density increased in the study area. This could be related to density-dependent competition among trees leading to a reduced mean tree DBH at very high densities. Under this hypothesis, very dense stands of trees would preclude many trees reaching the size where they can support multiple hollows. In northern Australia (Woolley *et al.* 2018) and in the study area (Fig. 4), tree hollow numbers at the individual tree level were positively related to tree DBH, with larger trees having greater hollow-bearing capacity than do smaller trees.

Time since the most recent fire also unexpectedly had an influence on hollow abundance in the present study. Plots with low (1 year) and intermediate times since the most recent fire (2 years) had greater hollow densities than did the plots with longer periods post-fire (6 years). It should be noted here that only three plots in two adjacent breeding sites had 6 years since the most recent fire. However, it is not immediately clear why hollow densities would decline after longer periods without fire. Possibly eucalypts benefit from frequent low-intensity fires through flushes of nutrients in the soil and also because of stimulation of epicormic growth following fire (Burrows 2013). In contrast, absence of fire in savanna trees can lead to increases in termite abundance (Dawes-Gromadzki 2007), possibly leading to increased termite activity and increased mortality among hollow-bearing trees. Another possibility is that sites where fire occurs only infrequently may experience periodic very high intensity fires due to local plant growth and litter fuel accumulation. Such sites may experience high mortality among hollow trees equivalent to that after multiple lower-intensity fires (Williams *et al.* 1999). Trees with extensive hollow formation would be particularly vulnerable to such high-intensity fires (Williams *et al.* 1999; Woolley *et al.* 2018).

Previous studies have identified that, at the broader scale ($\sim$60 km^2), the strongest predictor of nesting density of Gouldian finches was abundance or density of suitable nesting hollows (Brazill-Boast *et al.* 2010, 2011*b*). Brazill-Boast *et al.* (2011*b*) reported the no single factor explained the locations of nesting sites at the finer intra-breeding site scale ($\sim$1 km^2). In the present study, we have shown that fine-grain fire-mosaic attributes affect the density of suitable nesting hollows. In particular, hollow density is related to the frequency of occurrence of late dry-season fires, and also to time since fire. Given this information, it appears that focus on reducing total fire frequency, or keeping fire out of Gouldian finch breeding habitats for long periods, may be ineffective or even counterproductive (see Fig. 2) in facilitating retention of nesting hollows for Gouldian's at these sites. In contrast, it is clear that late dry-season fires are detrimental in Gouldian finch breeding habitat because they reduce the density of nest hollows as they become more frequent. The present study joins several recent studies calling for the modification of fire regimes for Gouldian finch conservation to an early season patchy fire mosaic rather than fire exclusion (Legge *et al.* 2015; Weier *et al.* 2016, 2017, 2018, 2019). Weier *et al.* (2016) showed that Gouldian finches bred more successfully at sites that had been recently burnt and Weier *et al.* (2017) went on to show that there were nutritional benefits of recent fires in *Sorghum stipoideum* seeds, which make up the dominant food resource for breeding finches from those burnt areas. In addition, it was shown that high-intensity late-season fires resulted in a reduction of *S. stipoideum* seed availability the year following the fire, owing to high seed mortality at the soil surface. Multiple small, patchy early dry-season fires were associated with higher breeding success of Gouldians (Weier *et al.* 2016), possibly owing to protection of longer unburnt *Triodia* spp. hummock grasses that take 2–3 years without fire to produce wet-season seeds for Gouldian finches (Dostine *et al.* 2001; Dostine and Franklin 2002). These data, plus the observation that late-season fire frequency also reduces the density of suitable nesting hollows for Gouldian finches, whereas total fire frequency does not, support the use of patchy early dry-season fires within Gouldian finch habitats. This will simultaneously increase suitability of Gouldian feeding resources and also protect their key breeding resource (nesting hollows and large trees with more of these) from high-intensity late dry-season wildfires.

Conclusions

After identifying Gouldian finch breeding habitat, we recommend the use of a network of annually prescribed patchy early dry-season burns. The aim of early dry-season burning networks is to achieve fire-break protection for Gouldian breeding sites to protect from external fires, but also to reduce the intensity of fire behaviour if late dry-season wildfires do penetrate breeding areas. Reduction of wildfire incursion and reduction in high-intensity fire behaviour will prevent or reduce the loss of large trees and tree hollows. A mosaic of early dry-season burning will also reduce within-site mean fire frequencies, ideally down to one fire every 3–4 years, to maintain both recently burnt (<1 year) and longer unburnt (>3 years) vegetation. This regime will maximise the food value (nutritional content) of

annual sorghum grass seeds, increase perennial grass seed availability by allowing slow growing species, including *Triodia* spp., to mature, as well as maximising nest-hollow densities within breeding habitat. We do NOT recommend fire exclusion from Gouldian finch breeding habitat. However, as much as possible, high-intensity, extensive, late dry-season wildfires should be reduced in frequency, or excluded from, known finch breeding habitat so that nesting hollows and feeding resources can be retained.

Conflicts of interest

The authors declare no conflicts of interest.

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