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Red-backed fairywrens adjust habitat use in response to dry season fires

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Abstract Fire disturbance in tropical savannas is integral to maintaining habitat heterogeneity and biodiversity, but its impact on avian species is highly variable. Savannas in northern Australia have recently been invaded by gamba grass (*Andropogon gayanus*), a perennial tussock grass that fuels late season fires at eight times the intensity of native vegetation. As gamba grass rapidly outcompetes native species and promotes more frequent and intense fires, it greatly decreases landscape heterogeneity and alters the effect of fire in tropical savannas. To investigate how a small passerine, the red-backed fairywren (*Malurus melanocephalus*), responds to fire disturbance and gamba grass cover, we studied their fine-scale habitat use throughout the dry season before and after a high intensity fire. We used two spatially distinct approaches, radio-telemetry and a transect-based population census, to quantify fairywren habitat use at the group and population level, respectively. Radio-telemetry and transect surveys revealed no direct mortality associated with the severe bushfire during the middle of the study season, suggesting fairywrens are resilient in the short-term to fire disturbance. Our results indicate that fairywrens are largely flexible in their habitat use – instead of relocating after fire, they re-centre their home range around the most photosynthetically productive habitats, dominated by saplings. While we found substantial variation in habitat use among social groups, red-backed fairywren groups generally avoided dense habitat areas dominated by mature gamba grass. We conclude that red-backed fairywrens are resilient to fire and flexible in their habitat use in the short-term; however, in the long-term, gamba grass may pose a threat to population viability. The importance of flexible behavioural strategies in tropical passerines will increase as fire regimes are exacerbated by invasive species and climate change.

Key words: fire, gamba grass, habitat use, home range, red-backed fairywren.

INTRODUCTION

Disturbance caused by low-intensity patchy fires increases landscape heterogeneity by removing standing biomass, which can have cascading effects on species habitat occupancy and population demographics (Hobbs & Huenneke 1992; Turner *et al.* 1994; Keeley 2009; Steen *et al.* 2013). Responses to fire disturbance vary in magnitude and direction across taxa, and can often be context-dependent (Hutto 1995; Hobson & Schieck 1999; Woinarski *et al.* 2004). In passerine species, fire disturbance has been correlated with both long-term population growth (Grant *et al.* 2010) and short-term population decline (Nakamura *et al.* 2010; Valentine *et al.* 2012). These potentially conflicting findings emphasize the need for a finer-scale understanding of habitat use and home range movement in association

with fires of varying intensities and frequencies. As the frequency of fires is predicted to increase with anthropogenic climate change (Hughes 2003; Westerling *et al.* 2006), a robust understanding of response to fire is vital in generating projections of population persistence.

Tropical savannas are suitable systems to study the effects of fire on habitat use by passerines because tropical savannas are characterized by frequent and expansive fires due to cyclical wet and dry seasons (Taylor & Tulloch 1985). These cycles create highly combustible vegetation in the late dry season, making savannas naturally fire-prone systems (Russell-Smith *et al.* 1997; Williams *et al.* 1999). Patchy fires have historically increased biodiversity in tropical savannas (Andersen *et al.* 2005) by promoting heterogeneity of landscapes which, in turn, is associated with population increases of many taxa, including passerine prey species (Garcia *et al.* 2011). Hence, fire-driven landscape heterogeneity should support the growth of passerine populations. However, fire disturbance may also render the community susceptible to invasions

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by exotic plant species, which would likely decrease landscape heterogeneity (Hastings *et al.* 2005). One highly invasive grass species, gamba grass (*Andropogon gayanus*), greatly threatens the heterogeneity of many savannas, including those in Northern Territory, Australia.

Gamba grass was introduced to the Northern Territory of Australia in the 1930s for pasture production (Csurhes & Hannan-Jones 2008). While gamba grass itself does not appear to influence passerine prey abundance (Parr 2010), it may affect passerine habitat availability. Gamba grass outcompetes native plant species and senesces more quickly, providing three times the biomass per unit area of native grasses (Rossiter *et al.* 2003). This difference in biomass provides a higher fuel-load for fires in the late dry season (Setterfield *et al.* 2010); fires fuelled by gamba grass are eight times more intense than fires fuelled by other species (Rossiter *et al.* 2003). An increase in intensity and frequency has produced a novel fire regime in Northern Territory savannas, exacerbating the rapid invasion of gamba grass because it outcompetes native species for re-colonization (Brooks & Setterfield 2006; Setterfield *et al.* 2010). Gamba grass may also have a disproportionately large negative impact on wooded habitats because high intensity fires lead to tree mortality and a long-term reduction of canopy cover (Ferdinands *et al.* 2006). Though the influence of gamba grass on fire regimes and plant communities is well studied (Rossiter *et al.* 2003; Ferdinands *et al.* 2006; Setterfield *et al.* 2010), its impacts on avian communities have not yet been described.

Accordingly, the goal of the current study was to investigate finer-scale effects of fire on habitat use and movements of a tropical passerine, the red-backed fairywren (*Malurus melanocephalus*), specifically focusing on their use of habitats dominated by gamba grass. The red-backed fairywren is a well-studied resident passerine species of tropical savannas in northern Australia with distinct breeding and non-breeding seasons that coincide with seasonal wet and dry seasons, respectively (Rowley & Russel 1997; Noske & Franklin 1999). As grass-dwelling insectivores (Murphy *et al.* 2009), red-backed fairywren survival and reproductive success is dependent on dry season fires that maintain biodiversity, resource abundance, and habitat for foraging and nesting (Bradstock *et al.* 2002; Parr & Andersen 2006). Red-backed fairywrens may serve as an indicator for other sympatric grass-dependent species in tropical savannas. Passerines are generally considered good indicators because they occupy a mid-trophic position and are usually habitat specialists. Red-backed fairywrens also satisfy prerequisites for indicator species as their populations are easily quantified and their ecology is well understood (Ormerod & Tyler 1993).

Despite red-backed fairywren dependence on fires to maintain the abundance of invertebrate-prey and grassland habitat in the longer-term, they appear to exhibit variable responses to fire in the shorter-term (Murphy *et al.* 2010; Nakamura *et al.* 2010). In the period immediately following fire, important resources for the red-backed fairywren such as grasses and invertebrate prey are often depleted, reducing habitat quality within their home range (Rose *et al.* 2014). Previous studies suggest that, immediately following fires, red-backed fairywrens form unstable flocks and remain within their original home ranges (Nakamura *et al.* 2010) or engage in short-distance relocation away from burned areas when there is adjacent unburned habitat (Murphy *et al.* 2010). This implies that fairywrens will adjust their habitat use as long as there are small patches of potential refuge remaining after the fire. However, with the invasion of gamba grass reducing habitat heterogeneity, there is a need to understand finer-scale habitat use and social group-level responses. Habitat use and home range locations in the non-breeding season may ultimately influence breeding season territory establishment by social pairs and later reproductive success (Brooker & Rowley 1991; Brooker & Brooker 1996). For this reason, knowledge of how finer-scale habitat association is influenced by fire regimes can help direct avian conservation and land management practices (Skroblin & Murphy 2013).

A high-intensity bush fire during the dry season allowed us to opportunistically examine how fire influenced finer-scale red-backed fairywren habitat use and movements, with a focus on the following questions: (i) How does the presence of gamba grass relate to habitat composition? (ii) What habitats do red-backed fairywrens use before and after fire? (iii) How does fire impact red-backed fairywren home ranges?

We surveyed vegetation across our study site and in known areas of red-backed fairywren presence, both before and after fire. This allowed us to describe the vegetative community assemblage on a study site undergoing an active, albeit patchy, invasion of gamba grass. To study the impact of fire on red-backed fairywrens and their habitat use, we used two spatially distinct approaches: line transect population surveys and radio telemetry of social groups. Lines transect surveys allowed us to quantify the effects of a large, gamba grass-fuelled bush fire on habitat occupancy of red-backed fairywrens, at a population level. Radio telemetry allowed us to examine the home ranges of fairywren groups and habitat occupancy, at a social-group level. Additionally, radio telemetry allowed us to quantify individual survival of red-backed fairywrens during fire events.

METHODS

Site description

We studied a colour-banded population of red-backed fairywrens on Coomalie Farm (9.2 km², 13°02' S, 131°02' E), approximately 90 km south of Darwin in Northern Territory, Australia during the dry season from June to August, 2014 (see Lantz & Karubian 2016 for additional information on the study population). The site is a tropical eucalypt-dominated grassland savanna, with a monsoonal wet season from October to April and a fire-prone dry season from May to September (Bowman *et al.* 2010). Gamba grass began invading the area more than 5 years prior to this study (Csurhes & Hannan-Jones 2008); however, its invasion is not ubiquitous on the site, which in conjunction with bush fires, created highly variable habitat across the site (Fig. 1). Standard controlled burns (each approximately 150 m² in area) were conducted throughout the study period by the landowner as one hypothesized method to control the gamba invasion and create fire-breaks (Csurhes & Hannan-Jones 2008). A small, low intensity bush fire occurred in early June 2014, and a large, high intensity bush fire occurred in mid-July 2014. The early June fire was typical of dry season fires and occurred in an area without dense understory biomass. Since the June fire was a low intensity burn (maximum scorch height 0.7 m; Sommer, unpublished data, 2014) and did not qualitatively change the available substrate composition and configuration, we focused on understanding changes following the high intensity July fire (maximum scorch height 18 m; Sommer, unpublished data, 2014). Approximately 65% of the study area was burned during the July fire (Fig. 2).

Vegetation surveys and remote-sensed data

To quantify the effect of fire on vegetation, we measured vegetation community composition in 10 m² plots

($n = 273$) using multiple parameters of percent cover, count measurements, and spatial imagery (Table 1). While the study site has been invaded by other non-native short grasses including *Urochloa mutica*, *Hymenachne amplexicaulis*, and *Pennisetum polystachion*, these grasses have biomass similar to that of native grasses (Commonwealth of Australia 2012) and support similar invertebrate communities (Parr 2010). Thus, we distinguished only between gamba grass and other grasses based on ecological function (Lavorel & Garnier 2002). In addition to field measurements, we used remote sensing techniques to calculate normalized difference vegetation index (hereafter NDVI) for each plot (Landsat 8 OLI satellite, glovis.usgs.gov). NDVI is commonly used as a proxy for photosynthetic productivity of living vegetation (Rhew *et al.* 2011). Spatial resolution for NDVI Landsat is 30 m and was appropriate for our fine-scale vegetation analyses. All remote sensing and analyses were performed in ArcGIS 10.0 (ESRI, Redland, California, USA).

To quantify habitat use of red-backed fairywrens pre- and post-fire, we categorized all vegetation surveys by fairywren observations and fire occurrence (Fig. 2). We categorized plots as occupied if we observed birds at that location during transect surveys or radio tracking sessions (see below). We generated random points for additional vegetation surveys within the study area using ArcGIS, and categorized them as sites of absence, or unoccupied, if we did not observe birds at that location. We recognize that some of the unoccupied sites may be used by fairywrens even though we did not observe them at those locations during our surveys. However, occupancy modelling returned very high detection probabilities for this species (see statistical analyses) and as passerine detection probabilities are normally quite low, we considered the classifications to be sound (Diefenbach *et al.* 2003; Thomas *et al.* 2010). We further categorized plots as burned or unburned based on field observations and spatial overlap (visualized in ArcGIS 10.0) with data from the Northern Australia Fire Imagery (NAFI, 250 m resolution).

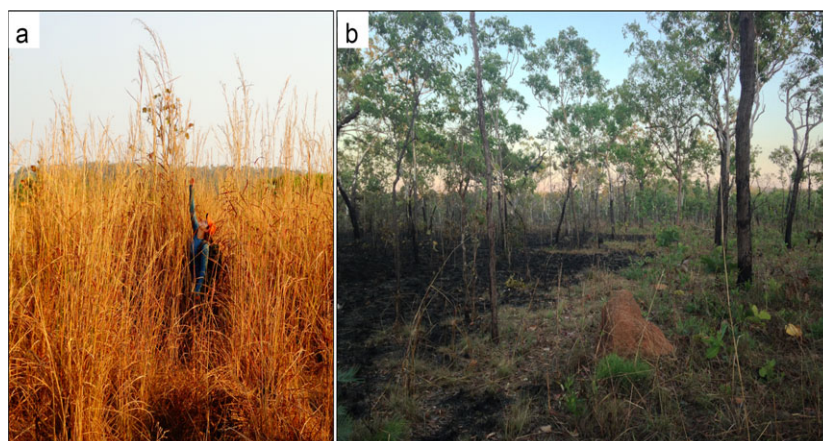


Fig. 1. Extremes of habitat structures across our study site. (a) Tall, dense stands of mature gamba grass and (b) a heterogeneously burned area with some short non-gamba grasses, shrubs and eucalypt trees. Note that images are not scaled to each other. Image a shows a surveyor of 1.8 m height with arm stretched overhead. Image b shows eucalypt trees around 5 m in height. Photos by S. Lantz (a) and N. Sommer (b).

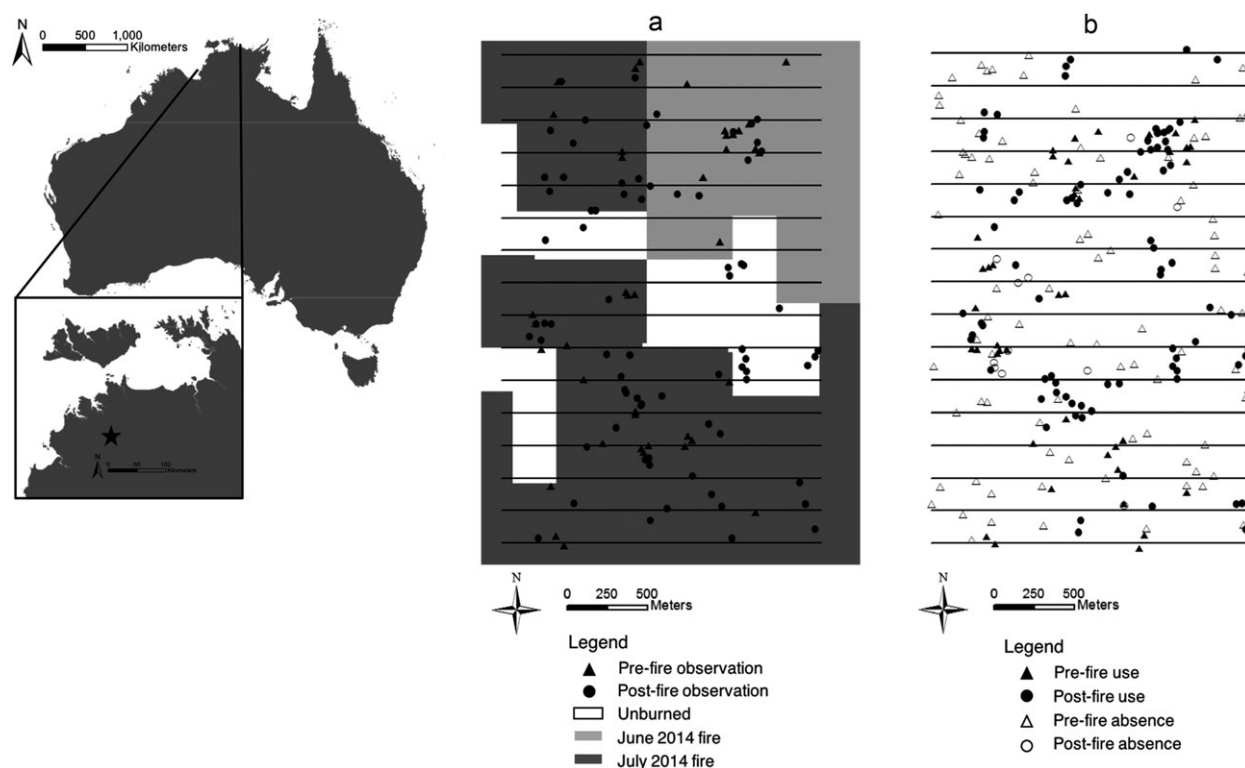


Fig. 2. Our study site was located on Coomalie Farm, south of Darwin, NT. Lines running horizontal along the panels indicate the survey route for the sixteen line transects, each 200 m apart and 2000 m long. Panel (a) shows fire-scars during the 2014 dry season and red-backed fairywren observations. Panel (b) displays classifications and locations of vegetation surveys. Fire scar data were retrieved from NAFI, with a spatial resolution of 250 m². This image does not capture the heterogeneity of the fire scar, but it gives a representation of the spatial extent of the fire scar.

Bird censuses and radio tracking

Line transect surveys

We performed line transect surveys for red-backed fairywrens before and after the large, high-intensity bush fire in mid-July. The transect survey area was a 2 × 3 km subpart of the site, divided into 16, 2 km line transects (running East-West) spaced 200 m apart (North-South) (Fig. 2). We randomized the transect order and walking direction (i.e. from East to West, or from West to East) to reduce sampling bias. To account for increased fairywren activity in the early morning, surveyors began between 0620 and 0650 and finished between 0930 and 1015. As surveyors walked, they stopped every 200 m and conducted 5 min point-counts. After each transect was walked once, surveyors repeated the transects in the same randomized order but in the opposite direction. If fairywrens were seen or heard at any point within 100 m of the transect, their location was georeferenced (Garmin eTrex) and flagged for a vegetation survey. If fairywrens were detected off the transect line, which was common, the surveyor left the transect line, flagged the location of the bird, and returned to the point of deviation to continue the survey. Surveyors took care not to push the birds along the transect line to avoid resampling. Within 9 days, researchers returned to each flagged location and conducted an “occupied” vegetation survey, as

described above. One full round of transects (two visits along each line) was completed before the July fire and another full round was completed post-fire, 18 days after the fire event.

Radio tracking

We captured colour-banded individuals in mist nets and attached radio transmitters (LB-2X, Holohil Systems Ltd. Carp, Ontario, Canada, 0.31 g) to 19 individuals (15 males, 4 females; average mass = 6.63 g, SD = 0.29) using elastic figure eight harnesses (Rappole & Tipton 1991). The mass of the transmitter and harness was no greater than six percent of each individual’s mass. We monitored all tagged birds closely upon release to verify that the transmitter did not impair normal flight and movement. We tracked all radio-tagged individuals using an AOR 8200 MkIII wide-range receiver (Authority on Radio, California, USA) and either a Yagi 3-element antenna or Telonics H-antenna (Wildlife Materials, Murphysboro, Illinois, USA). Tracking sessions occurred in the morning (0630–1130) and in the later afternoon (1430–1800). Sessions lasted approximately 60 min, during which we obtained an average of 10 (SD = 2) locations of the focal bird, where every location measurement was separated by a 5 min interval. The first location of each session was flagged for a vegetation survey. We took locations when we were able to

Table 1. Vegetation parameters and descriptions

Parameter	Metric	Description
Density	Percent	Percentage of visible squares on a checkerboard; held 50 cm above the ground in the centre of the plot, while an observer recorded percentage from the four cardinal corners of the plot; values were averaged across the plot, with a lower percentage indicating denser vegetation
Canopy cover	Percent cover	Percentage of visible sky occluded by canopy cover; an observer stood at the four cardinal corners of the plot and used a cylindrical densiometer (4 cm diameter) held vertically 30 cm above the eye to estimate percentage; estimates were averaged across plots (Stumpf 1993)
Eucalyptus	Count	Genera <i>Eucalyptus</i> , <i>Melaleuca</i> , <i>Erythrophleum</i> ; measured in height classes: canopy (>5 m), subcanopy (2 m to 5 m) and understory (<2 m)
Cycads	Count	Genera <i>Livistona</i> and <i>Pandanales</i> ; measured in height classes: canopy (>5 m), subcanopy (2 m to 5 m) and understory (<2 m)
Eucalypt saplings	Percent cover	Sapling growth <1 m; genera <i>Eucalyptus</i> , <i>Melaleuca</i> , <i>Erythrophleum</i>
Cycad saplings	Percent cover	Sapling growth <1 m; genera <i>Livistona</i> and <i>Pandanales</i>
Gamba	Percent cover	Gamba grass; measured in height classes: high (>2 m), mid (1 to 2 m) and low (<1 m)
Non-gamba	Percent cover	Non-gamba grasses; includes invasive species with biomass similarity to native grass; measured in height classes: mid (1 to 2 m) and low (<1 m). No grasses >2 m were measured
Bare	Percent cover	Includes bare ground, rocky surfaces, dirt roads
Logs and Shrubs	Percent cover	Woody ground cover; shrubs species indiscriminate, logs include fallen trees and branches
Creek	Percent cover	Dense bamboo and adjacent empty stream bed
NDVI	Raster value	Landsat Imagery; greenness index

Eighteen vegetation parameters were used in ordination analyses and modelling. The parameters were condensed from vegetation surveys into categories of ecological function (Lavorel & Garnier 20002). All parameters, excluding trees and spatial imagery, are quantified as percent or percent cover. See descriptions for the breakdown of grass height classes.

determine the bird's location visually, vocally, or with a strongly localized radio signal. If we were unable to determine the bird's location, we skipped the time point and waited another 5 min to record the next location. During radio-tracking sessions we took care not to push the birds and waited to obtain georeferenced locations (Garmin eTrex) until the birds had moved on their own. We performed radio tracking sessions on each group at varying times of day to reduce temporal sampling bias.

Our study period coincided with the non-breeding season for red-backed fairywrens, during which they flock in flexible social groups (Webster *et al.* 2010). The 19 radio-tagged individuals represented 15 different social groups. We defined groups as two or more individuals that were consistently observed with the focal bird during at least 50% of the radio tracking sessions. However, we were unable to accurately measure group size over multiple tracking sessions because not all individuals were colour banded and group composition in the dry season can be variable (Webster *et al.* 2010). Table 2 presents summary data on the social groups. We conducted all home range analyses at the level of the group. As only two social groups were tracked both pre- and post-fire within the main study area, we randomly assigned those groups to either pre- or post- fire models, to maintain independent sampling.

Home range estimations

From the radio-tracked locations we estimated habitat utilization distributions for each social group to relate habitat

attributes to relative space use (Worton 1989; Marzluff *et al.* 2004; Barg *et al.* 2005). Habitat utilization distributions delineate the probability of social group space use on the basis of radio telemetry locations. We used inverse utilization isopleths where the 5%-contour delineated the outer boundary of the home range and the 50%-contour delineated the inner home range core. We created the isopleths using 95% Gaussian kernels with a resolution of 10 m and a likelihood cross-validation (CVh) bandwidth. The CVh bandwidth is recommended for small sample sizes and when there is lack of independence among locations (Horne & Garton 2006). We chose the CVh bandwidth over the commonly used least-squares cross-validation (LSCV) bandwidth (Gitzen *et al.* 2006) because the LSCV has been shown to produce estimates that are imprecise and of poor fit when locations are highly clumped (Horne & Garton 2006), which is often the case for red-backed fairywrens due to their relatively small ranges and repeated visits to core areas. All analyses were performed in Geospatial Modeling Environment (GME 0.7.2.0, Spatial Ecology, 2012).

Statistical analyses

Vegetation community composition

We performed two ordination analyses to assess vegetation community composition: nonmetric multidimensional

Table 2. Summary telemetry data for all groups during June and July, 2014

Group identity	Affected by fire?	Tracked pre/post July fire?	Tracked birds (#)	Total banded birds (#)	Total locations	Tracking duration (days)	50% isopleth area (ha)	95% isopleth area (ha)
BAF(WEY)	Yes	Post	1	2	67	7	1.6	7.4
BWY	Yes	Both	1	1	51	8	1.9	10
CHAP	Yes	Post	1	2	79	17	2.1	9.8
FYA	Yes	Post	1	1	86	6	1.5	6.0
GYW	Yes	Pre	1	1	89	17	1.7	7.7
KATH	Yes	Both	2	3	127	12	2.5	13
LILDAM	Yes	Post	1	2	78	11	1.5	9.8
MAIN1	Yes	Post	1	1	125	10	1.3	5.8
MAIN2	Yes	Post	1	2	99	9	0.7	3.3
MORDOR	No	NA	1	3	109	12	1.0	3.9
SEAIR1	Yes	Pre	2	2	134	18	1.0	5.4
SEAIR2	Yes	Pre	1	2	81	6	2.4	9.3
TIP	Yes	Post	3	5	194	29	1.5	10
WBW	Yes	Post	1	1	90	13	0.7	4.2
YFE	Yes	Both	1	1	130	25	1.9	11
		Mean	1	2	103	13	1.6	7.8
		SD	0.6	1	35.3	6.8	0.56	2.9

Isopleths and area were calculated in ArcGIS. Group YFE was tracked outside of the main study site and was thus excluded from modelling.

scaling (NMDS, R package *vegan* v2.3-1) and a principle components analysis (PCA, R package *FactoMineR* v3.2.3). NMDS was used in conjunction with PCA as it requires fewer assumptions (Kendall 1971) but has less explanatory power than PCA (Sibson 1972). We applied power transformations to vegetation categories (Table 1) to meet PCA assumptions of Euclidean distance (Dale & Webb 1975; Legendre & Gallagher 2001). NMDS and PCA together allowed us to assess multidimensional vegetative community composition, relative to our categorization of survey plots as burned and unburned. We used NMDS first to examine dissimilarity in community composition across the study site pre- and post-fire, then PCA to describe correlations between individual vegetation types. We did not use the resultant scores from either ordination analysis in modelling.

Population-level habitat use model

More than 80% of the fairywren transect counts did not occur during the point-count stops, but instead occurred as surveyors were walking between stops. Detection probability between point-counts and walking transects was not significantly different. Therefore, we treated all observations along the transect as a linear survey. To ensure adequate modelling of the patchy habitat post-fire, we subdivided the 2 km transects into smaller transect segments of 500 m. We calculated a sum count of red-backed fairywren observations for each subdivided transect and characterized habitat by assigning and averaging plots. Due to the nested hierarchy of subdividing transects and repeated site visits, the transects were treated as a random effect in later modelling. Using program Distance 7.0 (Thomas *et al.* 2010), we first calculated detection probability for pre-fire and post-fire rounds of surveys. The average bird was found within 38 m of a transect (SD = 27.9). Pre-fire detection probability was 0.70 (model

half-normal cosine, SE = 0.32) and post-fire detection probability was 0.87 (model hazard-rate cosine, SE = 0.14). High detection probability indicates the transect surveys were effective in sampling red-backed fairywren activity, given that the bird was in the survey area. As these detection probabilities are high, we did not incorporate detection probability in our analyses (Diefenbach *et al.* 2003; Thomas *et al.* 2010). Other variables typically included in distance modelling to account for heterogeneity in detection probability are cluster size, Julian date, observer, and the observation distance from transect. None of these variables produced results different from the null occupancy model (i.e., the model containing no covariates) and were not incorporated into our main analyses.

We used linear mixed-effects models (GLMER, R package *lme4*, Bates *et al.* 2015) to estimate the effects of fire on habitat use by red-backed fairywrens. We included fire treatment (pre-fire = 0, post-fire = 1), vegetation, and interaction terms between fire and vegetation as factors. We verified the assumption of non-collinearity among vegetation types using Spearman rank correlation and retained variables with correlations less than |0.7|. Vegetation with structural similarity and high correlation ($\geq |0.7|$, Spearman rank) were collapsed into functional groups (Table 1). As the model had a count-based response variable, we used a Poisson distribution and logarithmic link function (Bolker *et al.* 2008). We included a nested random effect structure because the subdivided transects were embedded within the main transects (Zuur *et al.* 2009). In all models, we included random intercepts but not random slopes because the transect surveys were conducted within the same study site. To identify a candidate set of variables for multivariate models, we first ran all possible univariate vegetation models with fire treatment, vegetation, and interaction term included as factors. Candidate variables were retained if their AIC (Akaike's Information Criterion) value was lower than that of the null model (Burnham &

Anderson 2002). We then created a candidate set of multivariable models containing either one or two interaction terms. We refrained from using models with more than two interaction terms to avoid overfitting of models and improve model convergence. We selected variables to include in the multivariable models by their AIC values, and retained models with the greatest ΔAIC from the null model (sum of AIC weights = 0.95).

Social group-level habitat-use model

We did not track the same social groups before and after fire, and thus we created two different models of habitat use: social groups pre-fire and social groups post-fire. We first extracted proportional isopleth values from the habitat utilization distribution to vegetation survey plots and multiplied values by 100 to convert proportion into values ranging from 1 to 99. Following methods similar to the population-level model, we used standardized vegetation data collapsed into functional groups (Table 1). As both social group models had a count-based response variable, we again used a Poisson distribution and logarithmic link function with optimizer bobyqa engaged in R (Bolker *et al.* 2008). We included social-group identification code as a categorical random effect. As with the population-level models, we first selected a candidate set of variables whose AIC values were below the null model. We then constructed multivariate models on the basis of AIC and confidence intervals (Zuur *et al.* 2009).

Effects of fire on home range size

We applied a basic linear regression to compare fairywren home range size to the number of locations and tracking duration, in order to determine if differences in home range size were an artefact of length of tracking. To test the effect of fire on space use by red-backed fairywrens, we compared average home range sizes for social groups tracked pre-fire and groups tracked post-fire using an independent samples *t*-test. We also used a one-way ANOVA to compare NDVI of “core” home range (within the 50% isopleth) and “outer” (beyond the 5% isopleth) locations both pre-fire and post-fire. All analyses were conducted in R (v 3.3.1, R Core Team 2016).

RESULTS

Vegetation community composition

Even with small fires occurring throughout the season, habitat availability for red-backed fairywrens was strongly affected by the high-intensity July fire. The composition of the vegetative community differed from pre-fire to post-fire (NMDS, $k = 3$, stress = 0.142, $R^2 = 0.98$), which provided validation for the pre- and post-fire categorization around the high-intensity July fire. Irrespective of the occurrence of fire, there were three main patterns in the vegetative community (Table 3). All grasses, regardless of

species or height, correlated with increased density of vegetation (PC1, 24.6% variation). Gamba grass was negatively associated with non-gamba grasses (PC2, 17.1% variation), and there was a positive yet weak correlation between short gamba grass and saplings (PC3, 15.5% variation). From our field observations, habitat with short gamba grass and saplings had recently (<2 years) experienced a low intensity burn. Interpreted together, the first three principle components indicate that gamba grass is negatively correlated with other grass species and trees, and the occurrence of gamba grass is associated with increased density of vegetation (cumulative variation, 57.3%).

Effects of fire on habitat use

Fire did not have an effect on fairywren transect counts (Table 4), and all radio-tagged birds survived the fire, suggesting that the fairywren population size is not immediately affected by fire. For both analyses of levels of habitat use (population and social group), fairywrens displayed a consistent change in their use of habitat after fire, in that they were more likely to be in areas with saplings and less likely to be in areas with non-gamba grasses.

Population-level habitat-use

The top five models for population-level habitat use ranged from 18 to 23 ΔAIC from the null model

Table 3. Principle components analysis (PCA) of vegetation communities

	PC 1	PC 2	PC 3
Eigenvalue	2.711	1.882	1.709
Percent	24.643	17.112	15.536
Cumulative percent	24.643	41.755	57.291
Correlations with original variables			
Density	−0.786 [†]	0.166	0.035
Eucalypt canopy trees	−0.348	0.138	0.370 [†]
Cycad canopy trees	−0.095	−0.094	−0.147
Eucalypt saplings	−0.103	−0.082	0.822 [†]
Bare	−0.897 [†]	−0.017	−0.184
Logs and shrubs	0.179	0.659 [†]	0.039
Gamba grass: high	0.622 [†]	−0.452 [†]	−0.162
Gamba grass: mid	0.582 [†]	−0.634 [†]	0.029
Gamba grass: low	−0.041	−0.674	0.334 [†]
Non-gamba grass: mid	0.572 [†]	0.550 [†]	0.121
Non-gamba grass: low	0.625 [†]	0.536 [†]	0.133

Components summarize vegetation community composition, irrespective of fire. Loadings of each parameter for the first three components are given. Parameters with loadings approaching zero for all components were excluded from this table.

[†]Denotes strong correlations.

Table 4. Population-level mixed effects model

	Null Model		Model 1		Model 2		Model 3		Model 4		Model 5	
AIC	544.82		521.61		522.48		523.61		524.49		526.17	
Δ AIC	0.00		23.22		22.34		21.21		20.33		18.65	
Weight	0.00		0.40		0.26		0.15		0.10		0.04	
	Estimate	Std. Error	Estimate	Std. Error	Estimate	Std. Error	Estimate	Std. Error	Estimate	Std. Error	Estimate	Std. Error
Fixed effects												
Intercept	0.32	0.14	0.47	0.17	0.33	0.16	0.17	0.17	0.25	0.16	0.34	0.18
Fire			−0.29	0.20	0.11	0.16	0.07	0.16	0.06	0.15	−0.01	0.15
Non-gamba, mid-height							0.19	0.11				
Gamba, low-height									0.08	0.12	0.18	0.13
Eucalypt saplings					−0.13	0.13					0.01	0.14
Bare ground			−0.37	0.13	−0.34	0.13	−0.17	0.16	−0.33	0.13		
NDVI			−0.49	0.20								
Interaction terms												
Non-gamba × Fire							−0.70	0.25				
Gamba × Fire									0.26	0.15	0.23	0.16
Eucalypt Saplings × Fire					0.50	0.18					0.43	0.19
Bare ground × Fire			−0.11	0.20	−0.07	0.19	−0.52	0.25	−0.02	0.19		
NDVI × Fire			0.20	0.26								

Fire is included as a factor, where pre-fire = 0 and post-fire = 1. We present the null model and the five models with the greatest AIC from the null model. The top five models sum to weight 0.95. Parameter estimates with confidence interval overlapping zero are in bold. Variance from the nested random effects was 0 for the transects and 0.65 for the transect segments. High segment variance was expected, because the July fire primarily affected the western half of the study system (Fig. 2).

(AIC = 544), and their cumulative weight summed to 0.95 (Table 4). Confidence intervals of slope estimates overlapped with zero in all five models, suggesting that fire had little effect on fairywren counts. The random effects for the transect surveys had no variance, and segments of transects had high variance ($\sigma^2 = 0.65$). High segment variance was anticipated, given that the July fire occurred predominantly along the west side of the study area and so affected the western segments of the transects (Fig. 2).

The vegetation fixed effects terms were interpreted as the effect of that vegetation type on fairywren counts, pre-fire. Of all vegetation fixed effects, bare ground was included in four out of the top five models with a consistently negative estimate of slope, suggesting that red-backed fairywrens avoided habitat with extensive bare ground. Eucalyptus saplings were not important to fairywrens' use of habitat, appearing in two out of the five models with inconsistent slopes that did not differ from zero. Short gamba grass was also in two out of the five models, with a slightly positive estimate of slope that barely differed from zero. Mid-height non-gamba grasses appeared only in model three, with a positive estimate of slope that

did not differ from zero, again indicating that this factor was not important to the fairywrens' use of habitat.

The vegetation-fire interaction term can be interpreted as the effect of that vegetation type on fairywren counts, post-fire. For the models with notable interaction terms, non-gamba grass and bare ground had strongly negative estimates of slope, whereas eucalyptus saplings had positive slope estimates, suggesting that after fire, fairywrens avoided non-gamba grass and bare ground while occupying habitats with eucalyptus saplings.

Interaction plots for the optimal model (Table 4, Model 1) are shown in Fig 3. Bare ground had an overall negative effect on the occurrence of fairywrens, and the magnitude of the negative effect increased after fire. NDVI was negatively associated with the occurrence of fairywrens before fire but this switched to a positive relationship after fire. In light of the other patterns in our data and our own observations in the field, we interpret these relationships to indicate that red-backed fairywrens avoided dense stands of mature gamba grass before the fire and occupied areas of less dense gamba and other (often

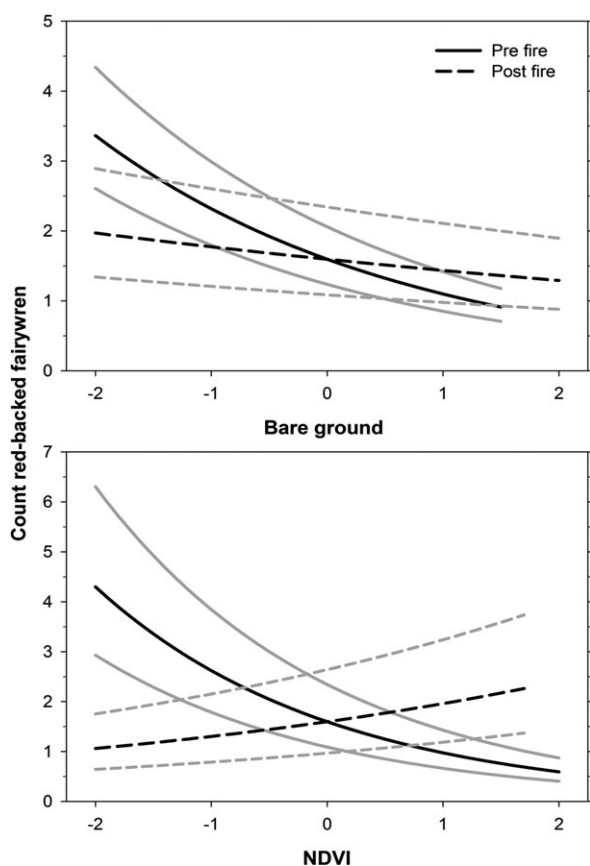


Fig. 3. Interaction plots for the optimal population-level model (Table 4, model 1). The top plot shows the estimates for bare ground and the bottom plot shows estimates for NDVI. Grey lines denote the $\pm 95\%$ CI.

native) grasses. Following the large fire, those mature stands of gamba grass burned, and the fairywrens sought refuge in remaining vegetative areas, which included stands of saplings and areas of regrowth.

Social group-level habitat-use

Though we could not test for quantitative differences among social groups, we found that habitat use did not vary with fire. Red-backed fairywren groups were generally found in low-density areas with bare ground, non-gamba grasses, and cycad species. They also used areas with short gamba grasses. However, according to our grass height classifications (Table 1), short gamba grasses are functionally and structurally similar to non-gamba grasses. Pre-fire groups avoided dense areas with mature gamba grasses and understory cycads (Fig. 4a). Post-fire groups avoided areas of mid-height non-gamba grasses (Fig. 4b). Group identity (a random effect in the linear mixed-effects models) explained a substantial amount of variation in our data (pre-fire = 0.17,

post-fire = 0.32), indicating variation in habitat use among social groups.

Effects of fire on home range size

We tracked fifteen social groups for an average of 13 days (SD = 7) and gathered 103 (SD = 35) locations per group (Table 2). Home range sizes were not correlated with number of locations (5% isopleth, $F_{1,13} = 0.090$, $P = 0.769$; 50% isopleth, $F_{1,13} = 0.171$, $P = 0.686$), number of colour-banded individuals in the social group (5% isopleth, $r_s = 0.076$, $df = 15$, $P = 0.787$; 50% isopleth, $r_s = 0.033$, $df = 15$, $P = 0.909$), or tracking duration (5% isopleth, $F_{1,13} = 1.01$, $P = 0.333$; 50% isopleth, $F_{1,13} = 0.002$, $P = 0.969$).

Neither the overall home range size (5% isopleth) nor the core home range size (50% isopleth) changed pre- and post-fire (5% isopleth, $t_{1,14} = 1.21$, $P = 0.245$; 50% isopleth, $t_{1,14} = 1.25$, $P = 0.231$). Both pre-fire and post-fire, home range cores were greener than locations in the outer area (pre-fire, $F_{1,545} = 140.1$, $P < 0.001$; post-fire, $F_{1,865} = 49.8$, $P < 0.001$; Fig. 5), indicating that red-backed fairywrens centralized their home ranges around the greenest habitat regardless of fire events.

DISCUSSION

While fire reduces available habitat, red-backed fairywrens did not systematically alter the size or location of their home ranges in response to decreased vegetative substrate. Instead, fairywrens centralized around photosynthetically productive habitat within their original home range. Contrary to Nakamura *et al.* (2010), who observed relocation of home ranges following fire, we found fairywrens exhibited flexibility and/or resiliency by using unburned areas within their original home range. Our observed lack of relocation may be due to the magnitude of the July fire. While 65% of our site was burned, thousands of hectares of the surrounding habitat were also impacted by the fire, leaving substantially less remaining biomass available for relocation. Despite the poor flying ability of red-backed fairywrens (Murphy *et al.* 2009) and dependence on highly combustible tropical savanna habitat, there was no mortality among our radio tracked individuals and no effect of fire on fairywren counts, suggesting no immediate decrease in population size in response to fire in accordance with Murphy *et al.* (2010). Though survival following fire may be a function of fire intensity, we tracked red-backed fairywrens through a late season gamba-fuelled fire with scorch heights of over 18 m (N. Sommer, unpublished data, 2014), which was the largest fire at the study site in 10 years (R. Luxton,

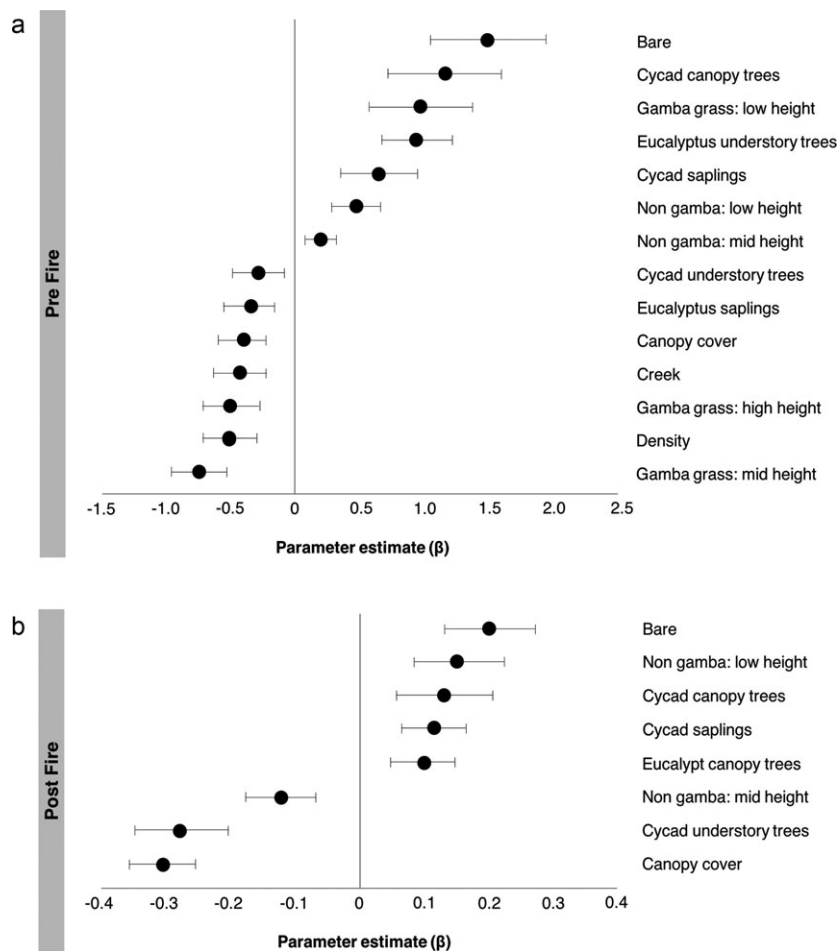


Fig. 4. Parameter estimates derived from group-level red-backed fairywren habitat use models pre-fire (a) and post-fire (b). We used generalized linear mixed models to examine the telemetry-derived use of vegetation, with 273 vegetation plots collected within our study site. We report the parameter, its regression coefficient (β), and 95% CI. Parameters whose CI overlapped with zero were excluded from this figure.

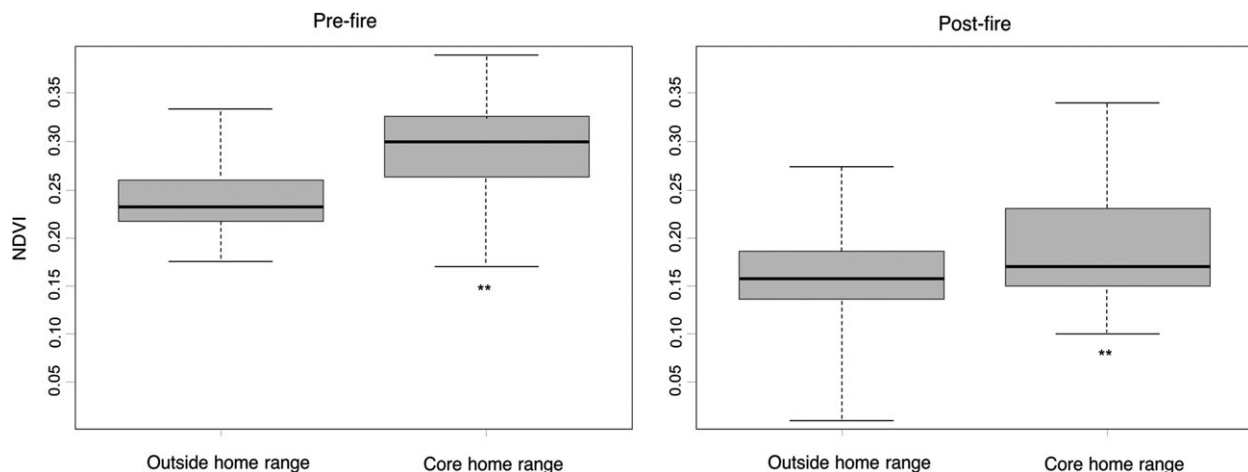


Fig. 5. ANOVA of NDVI by core and outer core distinction, with group identity as a random factor for pre-fire and post-fire locations. “Core” is within the 50% isopleth and “outer” is beyond the 5% isopleth. For both pre-fire and post-fire, the home range core areas are greener than the outer areas (** $P < 0.05$).

personal communication, 2014). These findings suggest that red-backed fairywrens are, at least in the short-term, resilient to fire perturbation.

One hypothesis for the mechanism of resiliency to intense fires could relate to our observation that social groups of red-backed fairywrens avoided areas dominated by mature gamba grass before the July fire. Because gamba is dense, with three times the biomass per unit area of other grasses (Rossiter *et al.* 2003), we initially hypothesized it may offer passerines additional cover from predators. Red-backed fairywren avoidance of gamba grass does not appear to be driven by decreased prey availability (Parr 2010), though more data are needed to substantiate this conclusion. Gamba grass is more combustible than native grasses and prey availability may be greater in unburned areas at our study site (Rose *et al.* 2014). Hence, we posit that the density of gamba grass is likely a deterrent to red-backed fairywrens. As gamba grass increases the intensity of fires (Rossiter *et al.* 2003; Setterfield *et al.* 2010), the combined trend of red-backed fairywrens avoiding dense gamba grass and gamba grass fuelling more intense fires implies that the fairywrens on our study site prefer habitat that is less likely to burn intensely, which would promote short-term survival following fire events.

The population-level and social group-level models consistently showed that after fire, red-backed fairywrens use habitat characterized by saplings, and do not use habitat with mid-height gamba grass. From our ordination analysis and field observations, saplings occurred in low-density areas without mature grasses. After fire, habitat with standing saplings is unburned, and relative to surrounding areas, characterized by high NDVI. This is consistent with our findings from both models. Mature non-gamba grass was included in both the population-level and social group-level models, and while it had a consistently positive effect, its pre-fire influence on fairywren populations was negligible. In contrast, the direction switched and magnitude increased after fire for both models (population and social group-levels). One possible hypothesis for the apparent avoidance of mature non-gamba grass after fire may relate to disturbance avoidance; after experiencing an intense fire in the dry season, red-backed fairywrens may switch their habitat use away from the remaining and highly combustible substrate to reduce risk of repeated disturbance. This is a speculative explanation for the switching and should be the focus of future research.

How red-backed fairywrens associate with bare ground appears to differ among birds at the population-level compared with the social group-level. The population-level model shows a consistent avoidance of habitat with bare ground, whereas the group-level shows consistent use. If we interpret the two models

separately, at the population-level, fairywrens are broadly using photosynthetically productive substrate before fire, and specifically using habitat with saplings after fire. At the group-level, fairywrens use of bare ground can be interpreted in conjunction with vegetative density. Habitats occupied by social groups are fairly heterogeneous, including trees, saplings, and non-gamba grasses; heterogeneous areas have not been invaded by gamba grass. The inconsistent association with bare ground could be further explained by the considerable variation explained by group identity in our models.

The substantial variation explained by group identity indicates differences in habitat use among social groups. Anecdotally, for the two fairywren groups that were tracked both before and after fire, use of green (NDVI) and dense habitat appeared consistent between the two flocks, but use of gamba-dominated habitat differed. High variation between flocks for habitat use indicates there is some potential for local behavioural adaptation in response to an invasive species, or sufficient flexibility in habitat use to cope with intense fires.

Following a fire, gamba grass is often the first successor, inhibiting the regrowth of other species and reducing habitat heterogeneity (Setterfield *et al.* 2010). Thus, fire may be promoting the spread of gamba grass, which could decrease preferred red-backed fairywren habitat availability over successive fire cycles. The rapid invasion of gamba grass (Setterfield *et al.* 2010), combined with predicted effects of climate change (Hughes 2003; Westerling *et al.* 2006), will likely lead to more frequent and intense fire regimes. Changing fire regimes could impact long-term trends of space use by red-backed fairywrens, with downstream implications for fairywren demography.

Red-backed fairywren population density at our study site declined from 2011–2015, as inferred from extremely low reproductive output and recruitment during this period (Karubian & Lantz, unpublished data, 2015). This decline coincided with the increased invasion of gamba grass, a series of years with relatively low rainfall, and frequent managed burns. These findings suggest that positive feedbacks between fire and gamba grass may be associated with a long-term decline in red-backed fairywren populations. However, we noted considerable variation in habitat use among groups, meaning not all social groups are equally impacted by the invasion or that many groups could switch their habitat use to lessen the negative effects of the invasion-induced change in local habitat. Group variation in preferences indicates that red-backed fairywrens, as a population, are flexible in their habitat use.

Flexible behavioural strategies are often considered adaptive in stochastic environments (Sol *et al.* 2002).

Red-backed fairywrens face both unpredictable ecological and social environments, with social group size and composition varying throughout the year (Webster *et al.* 2010). In a continuously changing social environment, red-backed fairywrens exhibit reproductive flexibility during the breeding season to increase reproductive success, with males switching social status from non-breeding auxiliary helpers to breeders (Karubian 2002; Webster *et al.* 2010). Similarly, flexibility in use of habitat during the non-breeding season might allow individuals to succeed in unpredictable environmental conditions. Increasing flexible habitat use would allow red-backed fairywrens to exploit multiple habitat types and increase the likelihood of population persistence, despite ongoing disturbance. The importance of flexible behavioural strategies in tropical passerines may increase as fire regimes in tropical savannas increase due to the dual impacts of the gamba grass invasion and climate change (Westerling *et al.* 2006).

There are known costs of specialist strategies in heterogeneous environments (MacArthur & Connell 1966; MacArthur 1972), therefore we predict that decreasing habitat heterogeneity due to the gamba grass invasion and fire will drive the red-backed fairywren towards increasingly flexible strategies. Controlled burns are consistently used as a short-term strategy to reduce standing biomass and curb the intensity of late season fires. However, as gamba grass is the primary successor after fire, current management practices may be promoting the spread of gamba grass and its associated ecological impacts. Our study emphasizes the need for finer-scale research to assess impacts of ecological disturbance on tropical passerines as the magnitude and direction of disturbance changes over time. Future studies should examine disparity between short-term and long-term responses to ecological disturbance, as previously understood dynamics may change with the changing climate.

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