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# The impacts of fire on the home range and social connectivity of a tropical passerine

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The impacts of fire on the home range and social connectivity of a tropical passerine

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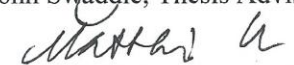The College of William and Mary

by

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Williamsburg, VA
April 24, 2015

# I. Abstract

Fire, a pervasive influence on many landscapes worldwide, can have a range of impacts on flora and fauna. We studied the impact of fire in Northern Territory Australia with a focus on the red-backed fairy-wren (*Malurus melanocephalus*, hereafter RBFW). While previous studies have demonstrated that RBFWs are negatively impacted by fire, the exact mechanisms are generally unknown. We examined the relationships between fire, social connectivity, and home range utilization, factors which appear to be highly connected in the lives of RBFWs. We utilize a combination of visual tracking and radio telemetry data collected during the dry seasons of 2013 and 2014 to examine these relationships. Analyses conducted using home range maps constructed in ArcGIS revealed that fire alters habitat utilization primarily through changes to vegetative structure. While these changes appear to be short term, fire has the potential to alter RBFW distributions over time by shifting the habitat from a heterogeneous patchwork currently utilized by RBFWs to a system dominated by invasive gamba grass (*Andropogen gyanus*). In addition, fires alter the social structure of RBFWs through direct displacement after fires. These findings provide additional information on the impacts of fire on specific species, deepening our understanding of the impacts of fire in Northern Australian. Because fires are likely to become more prevalent in the coming future as a result of climate change, understanding species dynamics with fire will become increasingly important.

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# V. Acknowledgments

There are several people who deserve acknowledgement and thanks for their contribution to this project. First, I would like to thank my advisor John Swaddle for his support and guidance in all my research pursuits. Second, I would like to thank Matthias Leu for helping me through many of the complicated nuances of ArcGIS when I lost my way and for guiding me to mixed models. I would also like to thank Brent Kaup for his assistance in reviewing my thesis as a member of my committee.

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# 1. Introduction

Across the globe, from Australia to the American southwest (Westerling et al. 2006) and the Mediterranean (Pausas 2004), ecosystems have evolved and differentiated as a direct result of repetitive fire events. Flammable ecosystems generally comprise boreal forests, eucalypt woodlands, shrublands, grasslands, and savannas; though grasslands and savannas in more humid regions are the most frequently impacted. Repeated fire events are important because they can shape the evolution and development of biomes across continents (Bond and Keeley 2005). Fire acts as a disturbance event, similar to herbivory, in that it causes widespread, but selective, removal of vegetation (Bond and Keeley 2005). It also has drastic effects on soil composition through a decrease in nutrients such as nitrogen and phosphorus, and an altered composition of organic matter (Bond and Keeley 2005; Knicker 2007).

The direct changes brought about by fire have driven the formation and survival of the ecosystem in Northern Australia, especially over the last few thousand years. Over a five year period from 1997-2001, an average of 373,000 km$^2$, or 19% of the tropical savannas, were burned per year. In the past, Aboriginal people undertook extensive burning across most of Northern Australia throughout the dry season and even into the wet season. This practice had a number of important ties to resource management and social values, but ecologically tended to create patchy, diverse habitats (Russell-Smith *et al.* 2003). In contemporary times, the fire regime has changed as a result of more modern fire management practices, meaning that most fires now occur later in the dry season when the fuel load is higher and that fire is completely suppressed in certain areas where human settlement and pastoralism are prevalent. While many ecosystems, such as the eucalypt dominated savannas, have evolved resiliency to frequent, low

intensity fires, frequent late-season burns can have strong negative impacts in terms of mortality and biomass production (Bowman *et al.* 1988; Williams *et al.* 1999).

Fire regimes have changed additionally in modern times because of the introduction of Gamba grass (*Andropogen gyanus*), an invasive from Africa. Gamba grass recovers more quickly than native grasses to fires, perpetuating its spread, and creating a dangerous grass-fire cycle (D'Antonio and Vitousek 1992). In this cycle, the proliferation of dense stands of gamba grass increases fire intensity, rate of spread, and frequency, and has drastic impacts on the vegetation and community composition of an ecosystem (Rossiter *et al.* 2003).

These complex changes to the fire regimes in Northern Australia and the accompanying potential for ecosystem change mean that is important to understand the impacts and ramifications for diverse life forms. Study of the impacts of fire on specific species is particularly important given the widespread reduction in faunal populations occurring across Northern Australia (Woinarski *et al.* 2001).

Animals react to fire in a variety of ways (Woinarski *et al.* 2001; Baldwin 2005; Bechtoldt and Stouffer 2005), implying that the study of a variety of taxa, populations, and habitats is necessary to understand the potential impacts of different fire management schemes on wildlife in the Northern Territory. One species, the red-backed fairy-wren (*Malurus melanocephalus*, hereafter RBFW, Figure 1a), represents a suitable species for studying the effects of fire. These tropical passerines have been well-studied, have a highly variable social structure, and reside in areas frequently disturbed by fire events.

Figure 1a: a male and a female RBFW

RBFWs are also subject to high social and environmental variability (Webster *et al.* 2010). Male RBFWs have two types of plumage, a non-breeding brown which superficially matches that of the females, or a red and black nuptial plumage which is correlated with higher breeding success (Rowley and Russell 1997; Karubian *et al.* 2009). Because the molt to dull or bright plumage occurs before or during the early breeding season, and is regulated by environmentally mediated testosterone levels (Karubian *et al.* 2011), conditions during the dry season can have a large impact on the trajectory of a male's breeding season. This is a time of extreme social instability, when birds form large flocks, young males disperse from their natal territories, and older birds experience increased mortality (Webster *et al.* 2010). Because this social upheaval, coupled with a lack of rains and increased frequency of fire, can have drastic impacts on the breeding season, the dry season presents an important opportunity for studying the influence of environmental factors on RBFW social structure and habitat use.

We primarily sought to understand three related factors of the dry season: 1) RBFW social connectivity; 2) RBFW home range size and use; and 3) the extent of burning in the habitat. The first factor, social connectivity, is defined, for our purposes as the number of other birds which an individual RBFW associates with across the non-breeding season. RBFWs are

known to expand their social circles beyond that of the breeding pair and to associate in flexible flocks of up to 20 during the non-breeding season (Chan and Augusteyn 2003). Flocking behavior in birds can have numerous potential explanations including decreased risk of predation (Whitfield 2003), and increased foraging success in accordance with optimal foraging theory (Pyke 1984), or through information sharing (Templeton and Giraldeau 1995). Alternatively, flocking may serve a social purpose by allowing for dispersal and exchange of group members (Griesser *et al.* 2009).

In other bird species, group size directly relates to the size of a bird's home range (Chan and Augusteyn 2003; Langen and Vehrencamp 1998). For our purposes, home range is defined as the area in which a bird moves about to perform normal activities such as food gathering, resting, and mating (Bas *et al.* 2005). This differs from the territories held by RBFWs during the breeding season in that it is not necessarily a fixed space from which a male will actively exclude competitors (Maher and Lott 1995). The size of a RBFW territory may relate to environmental conditions such as food availability and competition, though previous studies have shown little relationship between territory size and the size of a family unit in previous studies (Chan and Augusteyn 2003).

To date, research on RBFW home ranges outside of the breeding season has been lacking (see Nakamura *et al.* 2010). However, studies suggest that fires during this time may have an impact on the distribution of RBFWs within the habitat, causing them to disperse to unburned habitat in the short-term and to utilize burned habitat in combination with adjacent unburned habitat once regrowth begins (Murphy *et al.* 2010). This would suggest that RBFWs increase the size of their home range in response to fire.

An increase in home range size in response to fire may come about through a number of mechanisms, including resource constraints, alteration of habitat structure, and social disturbance. Territorial expansion may be a response to decreasesd food availability; RBFWs are obligate insectivores (Webster *et al.* 2010), and arthropod composition may decrease 80-90% immediately following a fire event due to habitat loss and direct mortality (Radford and Andersen 2012). Insect populations in habitats which consistently experience fire events are highly resilient and bounce back quickly (Andersen and Muller 2000). Previous studies have found that RBFWs utilize burned habitat for foraging about one month following a fire (Nakamura *et al.* 2010). Therfore the change in distribution of home ranges needs additional explanation.

RBFWs are known to decrease in abundance in response to the removal of understory vegetation, such as shrubbery, which they utilize in foraging, nesting, and as cover from predation (Valentine *et al.* 2007). The patchy distribution of suitable vegetation and food resources created by fires may force RBFWs to alter their social behavior from that of socially monogamous pairs and family units to that of flocking birds. Larger flocks are often seen post-fire, likely taking advantage of foraging opportunities in vacated territories with suitable habitat (Krebs and Davies 1981). Conversely, RBFWs often maintain smaller group sizes and territories in areas of more suitable habitat (Nakamura *et al.* 2010), suggesting that fire represents a significant disturbance in the lives of these birds. Whether by changes to food abundance, habitat structure, or social pressure, disturbance by fire can be an influential force on many areas of avian life. Birds affected by fires may have decreased body size and nestling survival rates during the breeding season (Murphy *et al.* 2010), suggesting that careful fire management may be instrumental in maintaining the well-being of this and other species.

Based on previous literature, we predict that the factors discussed above, 1) RBFW social connectivity; 2) RBFW home range size and use; and 3) the extent of burning in the habitat, are highly interrelated (Figure 1b). As burn intensity increases, resources such as food and habitat will decline in availability, forcing RBFWs to leave the area in search of more suitable habitat; however, because wrens utilize recently burned areas when foraging, an expansion of territory size will occur. Birds will be found most frequently in areas with the least damage from burns and least frequently in areas with more intense burns. These effects will lessen with time, so that birds will spend more time in areas that have remained unburned in more recent years. Because we predict that birds will increase their home range size in response to burning, we also predict that they will increase their social connectivity due to instability in the environment in addition to the normally higher levels of social interaction as compared to the breeding season. We, therefore, predict that social connectivity will increase with intensity of burn and decrease with time since burning.
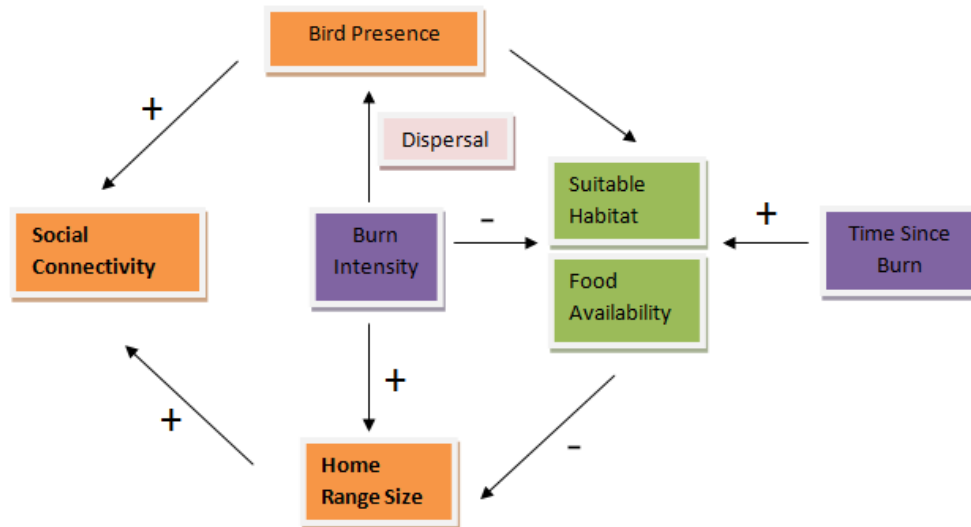


Figure 1b: A summary of the relationships between the factors under examination in the relationship between fire and RBFW home range size and social connectivity.

To determine the relevance of these predictions, we formulated a number of research questions. These are as follows:

I.  What influence does burn intensity have on the utilization distribution of RBFWs within their home ranges?

II.  Do RBFWs alter their home range utilization in response to alterations to habitat structure post fire?

III.   Do changes to bird distribution and habitat use lessen with time since a burn occurred and do birds concentrate activity more in areas which have been untouched by recent burns?

IV.  Does increased territory size correlate with increased social connectivity, as predicted if birds gain access to more territory through increased social interaction during the dry season?

V.  Does the fire history of a home range correlate with differences in social connectivity?

## 2. Methodology

**2.1 BACKGROUND**

2.1.1 Project Information

All field data were collected as part of an International Research Experience for Students program funded by the National Science Foundation (NSF-IRES, Award Number 1131614). This was a three year project intended to study the behavioral ecology of the RBFW, while encouraging students to formulate their own research projects.

2.1.2 Study Site

We studied a population of RBFWs at Coomalie Farm (13.0667° S, 131.0167° E) in Northern Territory, Australia. This area experiences climate patterns characteristic of tropical

areas, with a dry season from May to September and then a wet season from October to April,

bringing heavy rains and flooding (Australian Government Bureau of Meteorology 2011). The

Coomalie Farm site was comprised of many ecosystem types, including eucalyptus groves,

bamboo thickets surrounding year-round creeks, grasslands, and forests of paperbarks, cycads,

and fantail palms. All of these areas were at risk in the dry season from controlled and natural

burns. During the 2013 study season, only natural fires occurred, while multiple anthropogenic

and natural fires occurred during the 2014 season at the site.

2.1.3 Study Population

The population of wrens at Coomalie has most recently been part of an ongoing study

beginning in 2012, but was formerly part of a Japanese study from 2006-2007 (Nakamura *et al.*

2010). Most adults in the population were caught during the non-breeding seasons and marked

with individual combinations of three colored leg bands as well as a numbered aluminum band

from the Australian Bird and Bat Banding Scheme (ABBBS).

**2.2 DATA COLLECTION**

2.2.1 Home Range Mapping

Data were collected during two years. During the dry season of 2013, we collected data

by visually tracking focal birds, while during the dry season of 2014, we followed birds using

radio telemetry.

In 2013, we focused on the males in the population, most of which maintained red and

black nuptial plumage throughout the non-breeding season or began to acquire nuptial plumage

by early August. We collected these data during the non-breeding season from early June to early

August 2013. Morning observations occurred between 0630 and 1100. Afternoon observations

took place between 1500 and 1900.

To locate groups, we systematically searched areas where birds had been observed previously. During the non-breeding season, RBFWs fly over areas with more loosely-determined boundaries than their breeding season territories (Rowley and Russell 1997). However, they can generally still be found within a certain range. Upon arriving at the site, two observers listened for the bird's distinct songs or contact calls. If birds were not immediately found, observers walked a transect following the diagonal of an assigned rectangle and stopping roughly every 50 m for one minute to listen for birds. We repeated this process until finding birds or until each observer reached the center of the rectangular transect. Upon finding birds, both observers joined at the location for the observation.

While observing groups of birds, we attempted to stay at least 30 m away in order to minimize influence on their movements and behavior. Beginning with the first confirmed sighting of a bird, we recorded the location of the bird with a GPS, the time, and the type of vegetation that the bird perched on. This same information was recorded every time the bird left a specific substrate and flew to a new location. We required all observation periods to last a minimum of five minutes and cut off the observation at thirty minutes. During this time, we attempted to observe and record the color bands for every bird present in the group. After our initial observations, we confirmed the sex of the birds in the group using plumage information from previous breeding seasons and designated one of the known males as a focal male for each area. The focal male was generally designated as the first male observed in that group. For all subsequent observations, we observed that focal male's movements preferentially over other birds in the group. We performed observations of each focal male's group on at least three different occasions, two in the morning during peak activity and one in the afternoon. This

allowed us to capture the birds range at different times of day, rather than during one particular

time period.

We, along with other members of the research team, also opportunistically collected

location data for color-banded birds during the course of other studies. These data gave us

plumage color, GPS points, time, date, and substrate. These points supplemented the detailed

home range maps created from our focal observations.

2.2.2 Radio telemetry

During the dry season of 2014, 19 individuals (15 male, 4 females of 15 different

established social groups) were fitted with radio transmitters (LB-2X, Holohil Systems Ltd.,

0.31g) using elastic figure eight harnesses (Rappole and Tipton 1991) (Figure 2a). We ensured

that all birds were appropriately sized (mean mass = 6.63g, SD =  0.29) and monitored each bird

upon release for signs of impaired movement or flight.



Figure 2a: Radio transmitter attached to a female RBFW. Photo credit Sam Lantz.

Each bird was tracked for multiple sessions, with the objective to collect 10-15 location

points per session. Points were taken using a Garmin GPS every five minutes, for a total session

time of at least 50 minutes. Tracking occurred using an AOR 8200 MkIII wide-range receiver

and either a Yagi 3-element antenna or Telonics H-antenna. The point was collected only if the location was absolutely certain through visual, vocal, or coaxial confirmation or if there was approximate certainty via vocalization, previous location, or localized signal. If the location of the bird could not be determined with certainty, that location was recorded as a miss. At each point, we collected bands of accompanying individuals, behaviors, and height and type of vegetation in use at each point collection. We staged tracking sessions to ensure sampling from different periods of the day.

2.2.3 Vegetation Surveys

During both 2013 and 2014, we conducted vegetation surveys in areas where wrens had been previously observed, based on transect surveys, opportunistic sightings, or telemetry data. In addition to the designated "use" points, 100 additional points were generated per year at random locations throughout the core area of the site in order to survey vegetation character in areas where birds were absent (Fig 2b). These were categorized as "non-use" points. In 2014, an additional 50 plots were added. These plots were resurveys of use or random plots taken after a fire event. In each plot, a 10 m by 10 m plot was established around the central point and divided into four quadrants. Pairs of researchers then recorded the visibility within each quadrant by having one partner count the number of visible squares on a checkerboard held at DBH height by the other partner at the edge of the plot. Canopy cover was determined using a makeshift densiometer from the center of the plot. We also recorded species, height, and diameter at breast height (DBH) of all trees present, as well as the height and DBH of all snags, or burned trees.
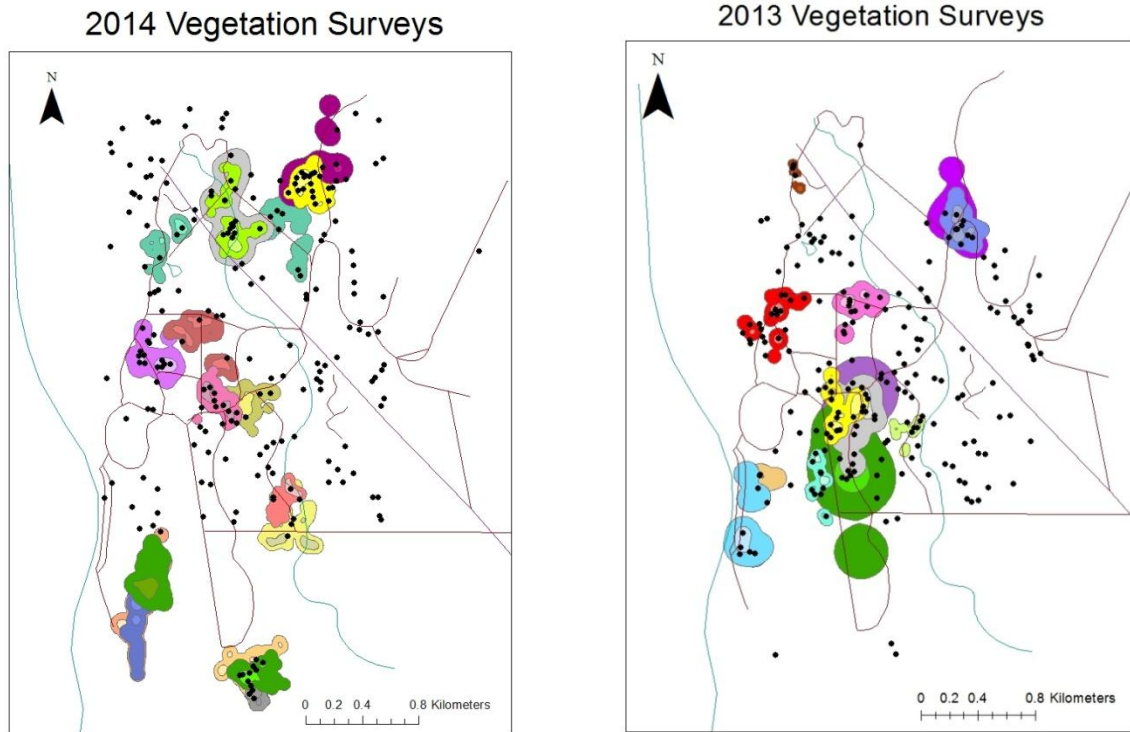
Figure 2b: Vegetation Surveys: The map on the right shows all available vegetation plots for the 2014 season, including the random and use plots, as well as the post-burn plots. The map on the left shows all available vegetation plots for the 2013 season, including both random and use plots. Vegetation surveys are shown as large black dots overtop a map of individual male home ranges.

We estimated percent ground cover of various categories (Table 2a). These characteristics help to describe the overall vegetation within plots. For the purpose of analysis, the four quadrants in each vegetation survey were averaged as proportions to produce a single value for that plot, for each groundcover category. The categories of percent groundcover were then condensed into a few primary categories (Table 2a).

Table 2a: This shows all the types of vegetation metrics evaluated as well as the original categories from which they were condensed.

| Ground Cover Vegetation Metrics | |
|---|---|
| Gamba grass | % of ground covered by invasive gamba grass, divided into heights of >2 m, 1-2 m, and 1 m |
| Native grasses | % of ground covered by all grasses other than gamba grass, divided into heights of >2 m, 1-2 m, and 1 m |

| Bare ground | % of ground covered by no vegetation, metal, charring, rock, pavement, unpaved roads, or termite mounds |
|---|---|
| Cycad saplings | % of ground covered by the broad, leaved area of cycad or pandanus saplings |
| Saplings | % of ground covered by saplings less than DBH height |
| Bambooo | % of ground covered by burned or unburned bamboo |
| Shrubs | % of ground covered by shrubs, turkey bush, or other non-specific greenery |
| Pandanus | % ground covered by the broad area of pandanus taller than 1m |
| Creek | % ground covered by all water types-creek or billabong |
| Logpile | % of ground covered by all fallen trees |

2.2.4 Fire Data

I obtained MODIS (Moderate Resolution Imaging Spectroradiometer) imagery of fire scars for both 2013 and 2014 from the Northern Australian Fire Information (NAFI) website (http://www.firenorth.org.au/nafi3/). These files provide maps of fires at a 250m resolution for each month (Figure 2c). The data provided in these files is limited in that the satellite may be unable to capture fires which are small, burn for short periods of time, or are covered by clouds. We know of a number of small fires which occurred at our study site throughout the year which are unavailable on NAFI, meaning that we may be missing the impacts of small fires on the birds. However, as it is difficult to collect data on the exact boundaries of these smaller burns, we have opted to use the MODIS imagery.
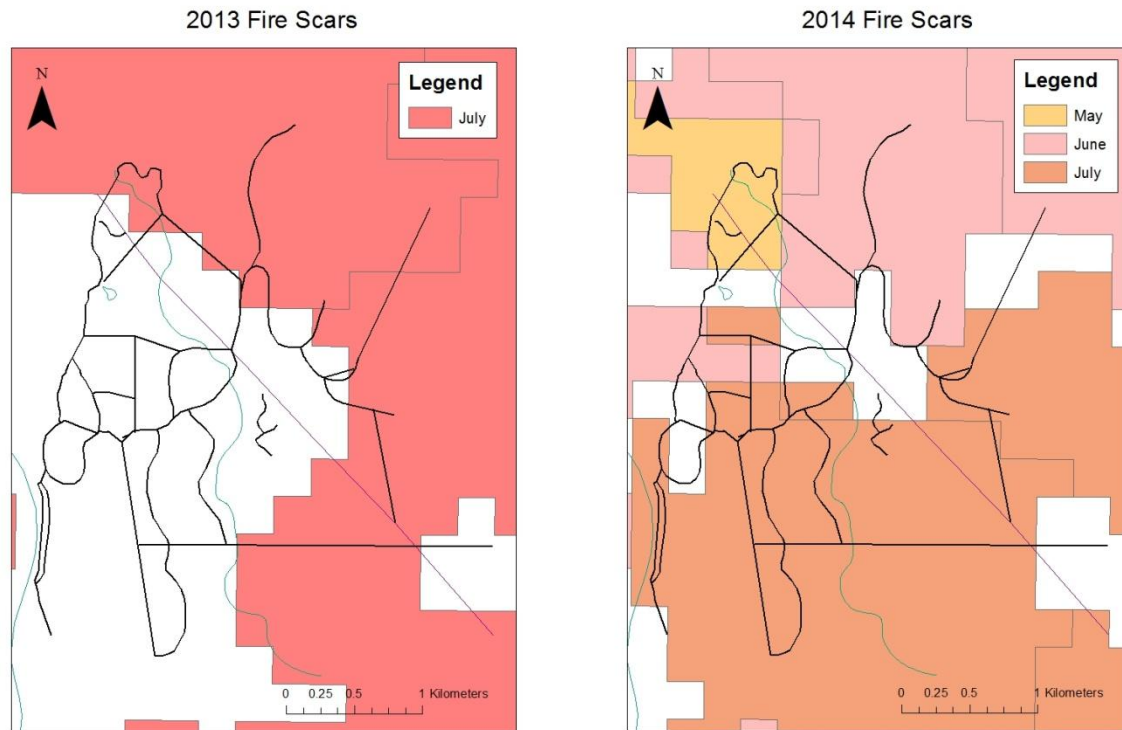
Figure 2c: MODIS Fire scar maps obtained from NAFI for 2013 and 2014.

2.2.5 NDVI Data

NDVI (Normalized Difference Vegetation Index) measures vegetative productivity

through the analysis of near-infrared (NIR) and visible (VIS), allowing us to determine the

changes to vegetative structure following a fire event (Diaz-Delgado *et al.* 2003). I obtained

imagery from the MODIS Terra MOD13Q1 satellite from the USGS Glovis website

(http://glovis.usgs.gov/), which provides measures of NDVI for the entire Earth at 250m. These

images are available at intervals of 16 days, meaning that they did not always line up perfectly

with fire events, but were generally useful for determining NDVI within a week of the fire event.

2.2.6 Social Connectivity

To determine social connectivity, we considered the total number of birds our focal males

interacted throughout the season to obtain a degree of connectivity. This method does not

consider differences in interaction, meaning that even if a bird spent substantially more time with one individual than another, both individuals would count for one interaction.

## 2.3 QUANTITATIVE ANALYSES OF FIELD DATA

### 2.3.1 Mapping in ArcGIS

In order to examine if fire history is related to territory size, we first constructed range maps using ArcGIS ArcMap 10.1 software (ESRI 2012). We used the points taken opportunistically throughout the season to construct the home ranges, as this allowed us to map the fullest extent of available knowledge on each bird's movements.

To examine how specific birds budgeted their time within burned and unburned areas, we created Kernel Density maps using Geospatial Modelling Environment (Spatial Ecology 2012). These maps allowed us to visualize the home range of a bird with particular emphasis on the areas in which they spend the most of their time, also known as a utilization distribution. We created Gaussian kernels with a CVh bandwidth and a cell size set at 10 m (Figure 2d). The CVh bandwidth applies the likelihood cross-validation smoothing parameter, which produces kernel estimates with better fit and less variability than alternative parameters, especially with smaller sample sizes, and is recommended when determining high-use areas using data with a lack of independence between locations (Horne and Gatton 2006), which was especially applicable to the 2013 data. While the least-squares cross-validation (LSCV) bandwidth has been the default for most ecological analyses and is useful in determining  home range size and discrete patches of high use (Gitzen *et al.* 2006), we believe it inappropriate for use in this study. The increased rate of failure for LSCV as clumping increases makes it difficult for use with RBFWs, which at times have small ranges in which the repeatedly visit certain areas.
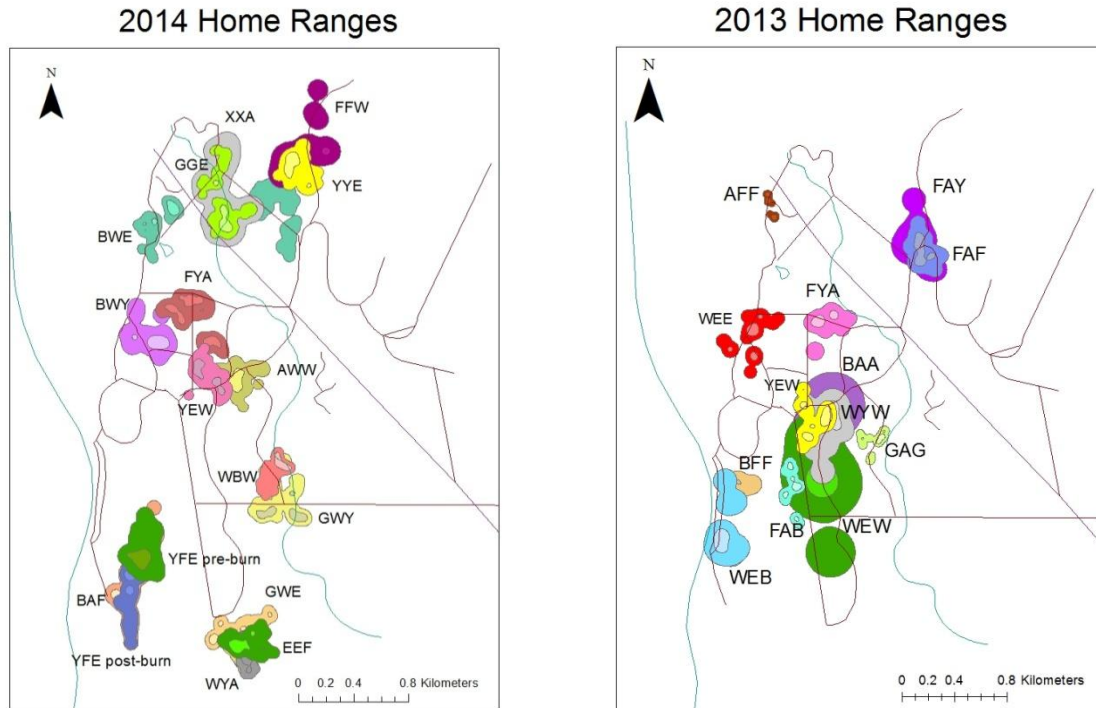
Figure 2d: Map of All Home Ranges for focal males during 2013 and 2014. These maps shows 50% and 99% isopleths resulting from kernels constructed using CVh bandwidth with a cell size of 10 for each focal male.

For each kernel, we drew polygons at the 50% and 99% isopleths (Figure 2e). The 99% isopleth is the recommended because it most accurately reflects space use at the furthest extents of the animals home range (Marzluff *et al.* 2004), while the 50% isopleth allows us to investigate where wrens dedicate most of their time. When evaluating factors such as proportion burned and social connectivity in relation to the area of the home range, we utilized the 99% isopleth as the best measure of total area. The variation in methodology between 2013 and 2014 created some differences in mean home range area. While the means did not differ largely at the 50% isopleth, differences increased at the edges of the home range, with 2013 ranges having much higher variation than 2014 ranges (Figure 2f). In order to perform a mixed model analysis we also drew all isopleths from 1-99% (Figure 2e).
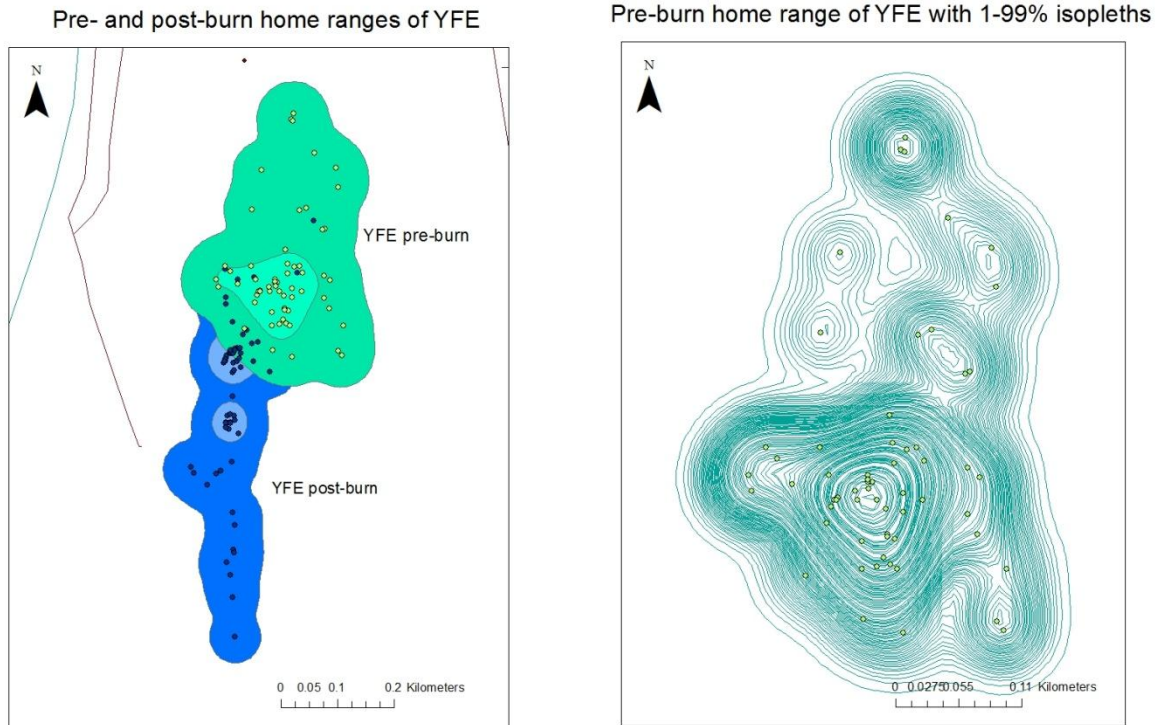
Figure 2e: Home ranges of YFE. The figure on the left shows the pre- and post-burn home ranges of YFE drawn at the 50% and 99% isopleths. The figure on the right shows the pre-burn home range of YFE drawn with all isopleths from 1-99% as is utilized in our mixed model analysis.
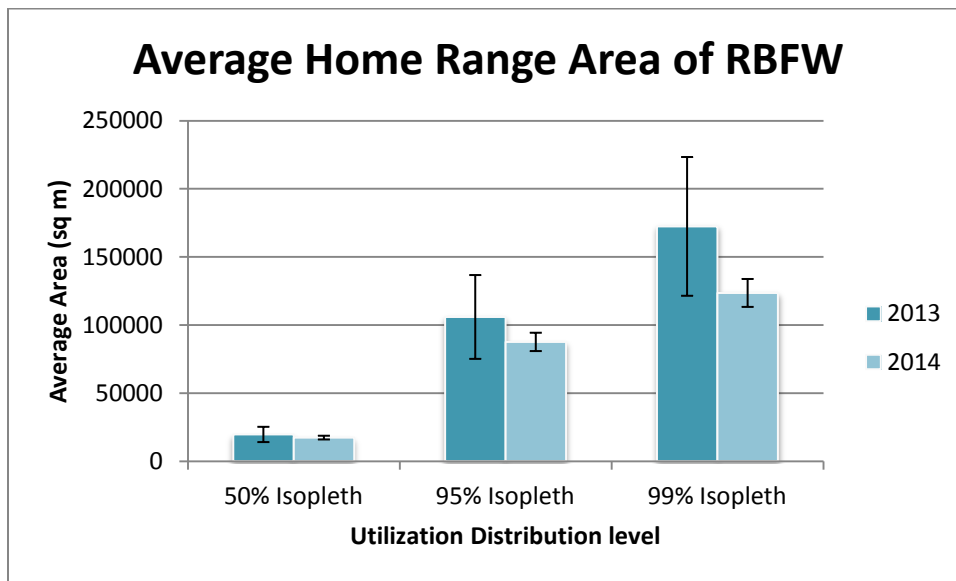


Figure 2f: Average Home Range Areas of RBFWs at the 50%, 95%, and 99% isopleths. Error bars represent standard error.

2.3.2 Statistical Analysis

*2.3.2a: Influence of burn severity on RBFW home ranges*

For this analysis, we extracted NDVI values at use and non-use vegetation points. We first determined that NDVI did differ with fire at our study site by comparing before and after values for vegetation plots within a burned area using a paired-sample *t*-test. We performed an independent-sample *t*-test to determine if there was a difference in NDVI between areas the birds did or did not utilize. We performed a bivariate correlation in PASW Statistics (SPSS Inc. 2009) of NDVI and isopleth in order to evaluate the relationship between burn severity and bird distribution. In addition, we calculated the average NDVI for each home range and performed partial correlations of NDVI and home range size while controlling for social connectivity.

*2.3.2b: Influence of habitat structure and burn history on RBFW home range*

First, we determined wren habitat use preferences. We established this by analyzing the condensed vegetation plot covariates for both years in a Principle Components Analysis. Then, we performed a paired *t*-test to compare the principle component values for use and non-use plots to evaluate what habitat metrics acted most strongly on the RBFW habitat use. Finally, we ran a mixed-effects model to determine which variables, vegetation, burn intensity, or time since burn, best explained RBFW utilization distributions. For this model, we employed use vegetation plots, determining which utilization distribution isopleth the plot was located in, the time since burn at that area, the NDVI value of the plot, as well as all vegetation parameters for that particular plot (see Table 2a). The model first determines a null model describing the variation that exists simply as a result of differences between home ranges. Subsequent models which include vegetation parameters can then be compared against this null model to determine which parameters best explain variation in utilization distributions by comparing AIC values.

*2.3.2c: Relationship between time since burn and home range*

To gauge the relationship between time since the last burn and area use, we first

classified burns as having been 0 months, 1 month, or 2 months from the time at which the birds

ranges were mapped. Any areas which did not overlap with one of these categories, were

considered unburned recently. We evaluated each of these variables as well as the total burned

area in the home range using a partial correlation with the area of the home range, while

controlling for the total birds associated with across the season. For the 2013 season, only a

single burn, occurring in July was visible from the MODIS fire data for our site; therefore, the

2013 season is evaluated only in terms of total burned area.

*2.3.2d: Relationship of home range size and social connectivity*

In order to determine the relationship between connectivity and territory size, we

compared the degree of connectivity to the area of the focal male's territory, mapped as the 99%

isopleth of the kernel of each male's territory. We compared these variables in a partial

correlation, controlling for time since the last burn in each home range.

*2.3.2e: Relationship of social connectivity and burn history*

We compared the relationship between home range and fire history by doing a partial

correlation of the time since the last burn, as described above, and the degree of connectivity,

while controlling for the size of the home range at the 99% isopleth.

# 3. Results

**3.1 INFLUENCE OF BURN SEVERITY ON WREN HOME RANGES**

3.1.1 Paired samples T-test of NDVI in burned and unburned areas

Following a time period in which a fire occurred, there were significant differences in the

NDVI for areas both within ($t(72) = 12.4$, $p < 0.001$) and external ($t(147) = 11.9$, $p < 0.001$) to

burned habitat. This suggests that NDVI varies across the site in a relatively uniform manner and may be unrelated to fire.

3.1.2 Independent samples T-test of NDVI in use and non-use areas

There was no significant difference in NDVI between use (M = 0.477, SD = 0.038) and non-use (M = 0.484, SD = 0.039) areas (t(217)= 1.42, p = 0.158), suggesting that wrens do not use areas of different NDVI across the site.

3.1.3 Correlation of NDVI and isopleth

A bivariate Spearman's correlation revealed a weak negative relationship between isopleth and NDVI (r(143) = -0.289, p < 0.001).  This indicates that for lower isopleths, which are closer to the center of the home range, the NDVI is higher than at the edges of home range. Therefore, RBFWs are using the most productive cores of their home ranges. While this correlation is weak, the low p-value suggests that the relationship is not the result of chance.

**3.2** RELATIONSHIP OF HABITAT STRUCTURE AND BURN HISTORY TO RBFW RANGE USE

3.2.1 Principal Components Analysis: 2013 and 2014 Vegetation Plots

PC1 explained 12.513% of the variance. As PC 1 increased, bare ground (0.822) increased while grass of 1-2m (-0.684) and less than 1 m (-0.691) decreased. PC 2 explained 11.743% of the variance. As PC 2 increased, grass less than 1 m (0.455) and visibility (0.496) increased while gamba greater than 2m (-0.702) and gamba grass 1-2 m (-0.814) decreased. PC 3 explained 8.269% of the variance. As PC 3 increased, eucalypts (0.580) and saplings (0.578) increased while shrubs (-0.548) and bamboo (-0.438) decreased. PC 4, which increased as canopy cover (0.507), bamboo (0.589), and creek (0.496) increased, explained 6.827% of the variance. PC 5 explained 5.879% of the variance and increased as cycad saplings (0.569)

increased but cycads decreased (-0.588). As PC 6 increased, shrub (0.546) increased while logs (-0.410) decreased, explaining 5.602% of the variance. PC 7 explained 5.464% of the variance and increased as saplings increased (0.709).

3.2.2 T-test: Use vs. Random Plots

PC 1 was more strongly represented in non-use plots (M = 0.227, SD = 1.01) than in use plots (M = -0.209, SD = 0.951). The difference was statistically significant, (t(478) = -4.88, p < 0.001), suggesting that RBFWs are more frequently found in patches of grass 2 m tall or shorter (Table 3a). PC2 was more strongly represented in non-use plots (M = 0.226, SD = 0.884) than in use plots (M = -0.208, SD = 1.06). The difference was statistically significant, (t(473.926) = -4.90, p < 0.001). Because PC2 is associated with a decline in gamba grass 1 m tall or taller, this suggests that wrens are associated with dense patches of tall gamba. PC4 was more strongly represented in use plots (M = 0.215, SD = 1.08) than in nonuse plots (M = -0.234, SD = 0.845). The difference was statistically significant, t(478) = 5.05, p <0.001. Bamboo, creek, and canopy cover increase with PC4, suggesting that RBFWs are more commonly observed in areas with tall bamboo stands. No other PCs varied significantly between use and non-use areas.

Table 3a: Interpretations of differences in PCs between use and non-use plots.

|      | Significance | Interpretation |
| --- | --- | --- |
| PC 1 | * | Wrens are associated with dense stands of native grass. |
| PC 2 | * | Wrens are associated with dense stands of tall gamba grass. |
| PC 3 | = | |
| PC 4 | * | Wrens are associated with creeks surrounded by tall, dense bamboo. |
| PC 5 | = | |
| PC 6 | = | |
| PC 7 | = | |

3.2.3 Mixed Model

Variation explained by differences in home range alone had an AIC of 1373.371. This is

considered the null model. The mixed model showed that the majority of variation in home

ranges was explained by NDVI ($\Delta$AIC = 17.749) with very little to no variation explained by

eucalypts, months since burn, saplings, or cycads. When variables were combined in multivariate

analysis, the model best explaining variation in home ranges included NDVI, and percent ground

cover of creek, shrub, pandanus, saplings, logpiles, all grasses, bamboo, and bare ground (AIC =

1244.073) Within the model, all variables which have influence on the utilization distribution

have a negative magnitude value (Table 3b). This means that they decrease as the isopleth value

increases. Therefore, these variables are more likely present in the center of the home range

where RBFWs concentrate most of their activity. The very large delta AIC ($\Delta$AIC = 129.298),

lends very strong support to the conclusion that RBFWs are more likely to be observed in areas

characterized by a variety of vegetation parameters with their home ranges centered in the most

productive regions.

Table 3b: Direction and magnitude of factors impacting RBFW utilization of home ranges.
Factors are arranged by significance in the model. Variables with negative slopes increase in
areas of high utilization. All variables below the dark black line have high variation and are less
reliable in interpretation.

| Variable | Magnitude | Standard error |
|---|---|---|
| NDVI | -122.0231 | 42.9317 |
| Shrub | -146.2227 | 55.6722 |
| Creek | -293.8500 | 122.5613 |
| Gamba grass 1-2 m | -142.3638 | 63.8101 |
| Bamboo | -81.7622 | 52.1070 |
| Bare | -83.0018 | 52.9618 |
| Other grass 1-2m | -102.1830 | 78.1729 |
| Gamba grass < 1m | -78.3145 | 60.7283 |
| Other grass <1m | -53.0366 | 63.1394 |
| Pandanus | 384.1716 | 579.6010 |
| Gamba grass >2 m | -42.9064 | 66.4332 |
| Logpile | -19.2091 | 69.4416 |
| Sapling cover | 1.9062 | 114.3751 |

**3.3 RELATIONSHIP OF TIME SINCE BURN AND HOME RANGE SIZE**

For 2014, bivariate correlations revealed a positive relationship between the total area of the home range and the proportion of habitat burned 1 month previously ($r(19) = 0.47$, $p = 0.042$). A positive correlation suggests that RBFWs expand their home range as the proportion within the home range of habitat burned one month previously increases. When running the same correlation controlled for social connectivity, the result was still present ($r(16) = 0.590$, $p = 0.010$), suggesting that social connectivity is not the primary factor in controlling for home range area. Bivariate correlations between the total home range area and the proportion of burned habitat in all other categories were not statistically significant (Table 3c). For 2013, the results of the correlation between the proportion of total burn in the home range and the total area of the home range was non-significant.

Table 3c: Results of correlation analyses comparing the relationship between proportion of area in burned habitat and the total area of a home range.

|  |  | 0 months | 1 month | 2 months | Total Burned |
|---|---|---|---|---|---|
| Total Area (2014) | Bivariate | $r(19) = 0.18$, $p = 0.46$ | $r(19) = 0.47$, $p = 0.042*$ | $r(19) = 0.151$, $p = 0.538$ | $r(19) = -0.152$, $p = 0.533$ |
|  | Partial | $r(16) = 0.136$ $p = 0.591$ | $r(16) = 0.590$ $p = 0.010*$ | $r(16) = 0.063$ $p = 0.803$ | $r(16) = 0.332$ $p = 0.179$ |
| Total Area (2013) | Bivariate | -- | -- | -- | $r(13) = 0.035$ $p = 0.910$ |
|  | Partial | -- | -- | -- | $r(10) = -0.280$ $p = 0.378$ |

## 3.4 RELATIONSHIP OF HOME RANGE SIZE AND SOCIAL CONNECTIVITY

There was no significant correlation between total area of the home range and the total number of birds associated with throughout the season for either 2014 ($r(19) = 0.161$, $p = 0.51$) or 2013 ($r(13) = 0.388$, $p = 0.190$). At our site, RBFWs do not appear to be increasing the number of birds they associate with as their home ranges expand in area.

## 3.5 RELATIONSHIP OF SOCIAL CONNECTIVITY AND BURN HISTORY

In comparing time since the last burn and social connectivity, higher proportions of burned areas within a home range correlated with decreased association with other birds in 2014 ($r(19) = 0.448$, $p = 0.054$), while the opposite relationship was true in 2013 ($r(10) = 0.548$, $p = 0.065$). These results reveal apparently contradictory findings on how social connectivity relates to the proportion of burned habitat in an area.

Higher proportions of the most recently burned habitat (0 months) within a home range also correlated with increased social connectivity in 2014 ($r(19) = 0.414$, $p = 0.078$). This suggests an increase in bird presence shortly after a fire. All other correlations were non-significant (Table 3d). Partial correlation of the proportion of total burn in the home range and the number of birds associated with was positive ($r(16) = 0.481$, $p = 0.043$) when controlling for the total area, suggesting that area is a controlling influence in these relationships.

Table 3d: Results of correlations comparing the relationship between proportion of area burned in a home range and the total number of birds associated with across a season.

|  |  | 0 months | 1 month | 2 months | Total Burned |
|---|---|---|---|---|---|
| Social Connectivity (2014) | Bivariate | $r(19) = 0.414$, $p = 0.078$* | $r(19) = 0.279$, $p = 0.248$ | $r(19) = -0.152$, $p = 0.533$ | $r(19) = -0.448$, $p = 0.054$* |
|  | Partial | $r(16) = 0.464$ $p = 0.052$* | $r(16) = 0.272$ $p = 0.274$ | $r(16) = -0.157$ $p = 0.534$ | $r(16) = 0.481$ $p = 0.043$* |
| Social Connectivity (2013) | Bivariate | -- | -- | -- | $r(13) = 0.520$ $p = 0.069$* |
|  | Partial |  |  |  | $r(10) = 0.548$ $p = 0.065$* |

# 4. Discussion

## 4.1 MAIN FINDINGS

The most important impacts of fire on RBFWs may be reduction of productive vegetative cover, including dense patches of grass, within RBFW home ranges. RBFW utilization distributions within their home ranges are best explained by a number of combined vegetation parameters, suggesting a preference for high habitat heterogeneity. Time since burn does

correlate positively with the size of home ranges at one month since the most recent burn, and also correlates with increased social connectivity at zero months since the most recent burn. These findings suggest the potential for fire to play a significant role in determining where we observed RBFWs.

## 4.2 IMPORTANCE OF VEGETATIVE STRUCTURE IN RBFW HOME RANGES

According to the results of our study, NDVI varied significantly before and after fire events, both within and external to the burned area. This would suggest that NDVI relates more heavily to seasonal changes than to the impacts of fire on vegetation for the fires we examined. This could occur for a number of reasons. First, seed banks may sprout immediately after a fire (Auld and O'Connell 1991), causing a large spike in vegetative productivity, thereby masking fire-caused damage in satellite imagery. Alternatively, NDVI may be changing across the site as a result of seasonal changes to temperature and precipitation (Kawabata *et al.* 2001), rather than being driven by fire. Regardless, NDVI alone does not appear to be an appropriate means of measuring fire intensity, within the range of fires experienced by this site over the two years of our study. In light of this, we would suggest the addition of normalized burn ratio (NBR), which provides a more accurate measure of fire severity (Escuin *et al*. 2008), in future analyses. This analysis was not performed in this study due to logistical and time constraints.

Due to the lack of reliable correlation between NDVI and fire events, for the purpose of this discussion, we will utilize NDVI as another proxy of vegetative structure. Across the site, NDVI varied little between use and non-use sites; however, NDVI as a single variable explained most of the variation in the utilization distributions of home ranges. Space use within home ranges were negatively correlated with NDVI values, suggesting that NDVI decreases with

distance from the center of the RBFW home range. It therefore follows that RBFWs concentrate their activity in the most productive areas of vegetation within their home range.

Variation in RBFW home ranges was additionally explained by the combination of all grass types, though gamba grass of 1-2 m in height better explained variation than other grasses alone. Gamba was negatively associated with space use within the mixed model, suggesting that as use increased, gamba grass also increased. The same was true for native grasses, though the association was weaker. This may suggest some preference in utilization of gamba over native grasses.

In addition to grasses, utilization distributions within home ranges were explained by a large range of vegetation parameters. Our model found that, among groundcover categories, shrubs had the highest explanatory power. Shrubs negatively correlated with isopleth value, meaning they were more likely found in the central region of home ranges.  There has been some disagreement in the primary foraging substrate of RBFWs, with some studies aligning with our findings (Brooker *et al.* 1990), and others suggesting grasses (Murphy *et al.* 2009).These differences may be ascribed to site conditions.

For our site, the multivariate model of habitat utilization encompasses many different types of habitat, including grasslands, shrublands, creeks, and areas of new growth. While it may seem counterintuitive that wrens could occupy so many diverse types of habitat at once, this variation can be explained by habitat heterogeneity (Figure 4a). Essentially, the wrens are utilizing a multitude of habitat patches, with particular emphasis on the most vegetatively productive areas. The association of wrens with shrubs and gamba grasses over native grasses fits well with this pattern as green shrubs are likely to have the highest NDVI, followed by gamba which grows in taller, denser clumps than native grass.

Figure 4a: Examples of Habitat Heterogeneity.
The photo on the left shows an example of a mostly grassy area interspersed with native and gamba grasses as well as termite mounds. On the right is an example of a more forested area with patches of bare ground and short, native grass. RBFWs could inhabit both areas. Photo credit: Sam Lantz.

**4.3 IMPORTANCE OF FIRE HISTORY IN RBFW HOME RANGES**

We found moderate, positive correlation between the total area of the home range and the proportion of the habitat burned 1 month prior to collection of home range data. Because previous studies have shown that RBFWs will utilize burned areas about a month after a burn (Nakamura *et al.* 2010), the expansion in range may be due to an expansion into burned areas. There was likely no correlation to home range size at 0 months due to the flexible nature of wren ranges following a fire-related upheaval. They have not had the opportunity to establish a structured range, but are also limited by the extremely depleted vegetative structure of post-burn habitats (Kutt and Woinarski 2007). These relationships appear to stabilize within two months following the burn. This suggests that there may be limited impact of fires directly within a season as RBFWs seem to be responding to short-term cues. RBFWs appear to have the ability to utilize habitat relatively quickly following a fire event and to stabilize their home range size relatively quickly.

The quick recovery of RBFW habitats may relate to the ability of gamba grass to begin regrowth within a few days of fire (Bowden 1964). While quick restoration may prevent fire from exerting a strong influence on RBFW habitats in the short term, there is potential for fire to alter RBFW habitat use over longer time scales. Fire is known to increase gamba grass cover, causing a shift from native grasses over time (D'Antonio and Vitousek 1992). If vegetative cover is the defining factor in RBFW utilization distributions, then such a shift could have a dramatic impact on RBFW populations. Our analysis has shown that RBFWs are associated with dense patches of both native and gamba grass, with an apparent preference for gamba grass, so a shift to a gamba-dominated system may not necessarily cause RBFWs to shift their distributions. However, increased gamba may interfere with the patchy quality of the landscape, altering RBFW utilization patterns in a landscape traditionally defined by heterogeneity.

In addition, the capacity of gamba patches to burn with much higher intensity than other vegetation (Rossiter *et al.* 2003) may have the potential to negatively impact wrens. Recent studies of RBFW habitat utilization have found that wrens may be more frequently found in recently burned areas with very low vegetative productivity compared to their surrounding habitat (O'Toole 2014). This suggests that increased and more intense fires associated with gamba grass cover may not disrupt RBFW habitat usage. Our findings related to NDVI contradict these recent findings, meaning that a decline in vegetative productivity following intense fires could further displace RBFWs. Additionally, the selection by RBFWs of areas impacted by high intensity burning may place them in a location vulnerable to increased disturbance. In effect, a proliferation of gamba grass may create an ecological trap, in which RBFWs make maladaptive habitat choices based on reliable habitat cues (Schlaepfer *et al.* 2002).

An ecological trap would function in the long term to reduce fitness, even though a shift to gamba may appear beneficial if RBFWs select for patches of gamba over other vegetation. In the short term, the impacts of fire-induced vegetation changes on RBFWs are less clear from our study. It has been suggested that while wrens may utilize burned areas, they concentrate such action in or very near unburned patches (Murphy *et al.* 2010). Because the burned areas in this study were determined using satellite derived imagery at 250m, the scale was far too coarse to evaluate the presence or use of unburned patches within the burned habitat. It is, therefore, possible that the wrens were utilizing only the unburned habitat within the burned areas. Our observations of wrens in areas burned only days previous seems to suggest that this hypothesis may be inaccurate, though the patchy nature of our mapped home ranges leaves this as a possibility. Further study is needed in order to ascertain the actual utilization of patches of burned and unburned habitat in recently burned areas. Such information may be crucial in determining the true impacts of fire on habitat utilization.

**4.4 IMPORTANCE OF SOCIAL CONNECTIVITY IN RBFW HOME RANGES**

Social connectivity was positively correlated with the total proportion of burned habitat in a home range in 2013, but negatively correlated in 2014. This may, at first, seem contradictory; however, it makes sense considering that there was only a single large fire at the study site in 2013. Therefore, in 2013, the total proportion of burned habitat in a home range essentially reflects only the proportion of fire in the 0 months category. In 2014, social connectivity was positively correlated with the proportion of habitat burned zero months since the last burn. This is likely related to the immediate dispersal of RBFWs from burned areas (Murphy *et al.* 2010). Following a fire event, birds will be a tumultuous state of displacement,

which will force them into contact with their conspecifics. They will likely meet resident birds or

fellow fire refugees in the usable portions of a burned area.

    The positive correlation of social connectivity to the total proportion of burned habitat in

2013 is backed by previous literature which suggests that RBFWs will maintain smaller ranges

and group sizes when suitable habitat is available (Nakamura *et al.* 2010). The conflicting,

negative correlation from 2014 may suggest that the unsuitable habitat created through burning

has little relation to social connectivity. Several factors may explain this result, namely the extent

to which fire covered the area during the 2014 season. Because such a high proportion of the

vegetative structure has been degraded, there is little available suitable habitat. This likely forces

high numbers of birds into small, usable patches, increasing the population density. Given the

complex relationhship between fire history and social connectivity, it is difficult to say if

RBFWs might be expanding their home ranges and social connections in response to a decline in

suitable habitat following a fire.

    While social connectivity was correlated with the proportion of burned habitat in a home

range, there was no correlation between connectivity and home range size. These findings

corroborate the results of previous studies which suggest that RBFW territory size is unrelated to

unit size and may instead by constrained by ecological factors (Chan and Augusteyn 2003).

    While social connectivity appeared to play a small role in relation to home range size, it

should be noted that the potential for social interactions may be limited in comparison to other

studies. The density of RBFWs at our site is rather low. While other studies have reported flocks

as large as 20 during the non-breeding season (Chan and Augusteyn 2003), no bird in either 2013

or 2014 associated with more than eight birds throughout the entire season. This allows for

substantially less variability and may mute the effect of social interactions. Because social

interactions may play an important role in mitigating the relationships between RBFWs and their environment (Pyke 1984; Whitfield 2003), it is important to ascertain the exact nature of these limitations.

**4.5 REWORKING OUR ORIGINAL HYPOTHESES**

We originally hypothesized that social connectivity and burning worked as somewhat equal and, at times, reciprocal forces in characterizing RBFW home ranges. Investigation of the actual RBFW home ranges has forced us to alter this initial idea. Vegetative structure must be emphasized as the most important factor influencing RBFW distribution. Fire, on the other hand, has impact primarily through alteration of the vegetative structure or through direct displacement of birds. The vegetation is also likely to be altered by external factors related to seasonality, such as rains. The direct influence of fire on RBFWs remains uncertain due to the conflicting nature of our results with existing literature. In this context, social connectivity plays a small role in influencing home range (Figure 4b). Further research is needed to effectively quantify the direct impacts of fire on RBFWs and to ascertain the role of seasonality in these relationships.
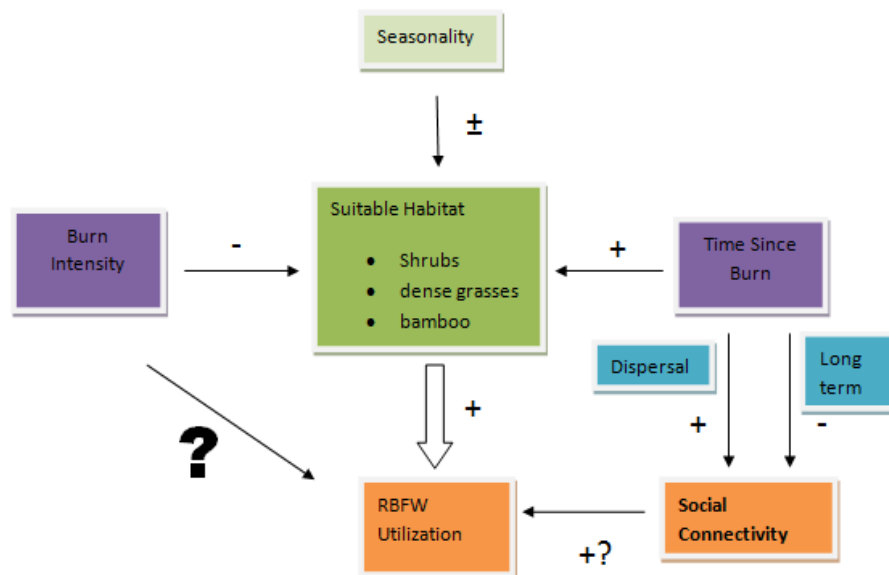


Figure 4b: The relationships between fire, social connectivity, and RBFW home range utilization as implied from the results of this study. Positive impacts are indicated by blue arrows while

negative relationships are shown in red. The strength of the relationship is indicated by the outline of the arrow.

## 4.6 LIMITATIONS OF THIS STUDY AND IMPLICATIONS FOR FUTURE RESEARCH

Although this study has provided many insights into the relationships between fire history, social connectivity, and  home range, many questions still remain. Looking forward to future studies which may attempt to address these questions, certain limitations of this study should be considered. First, it was very difficult to draw any meaningful conclusions from the 2013 data. Most of the limitations associated with this data set originate with the sampling method. While manual tracking of birds can be an effective means of obtaining data, there are several problems which radio telemetry helps to eliminate. Most of the time my field partner and I spent collecting data was focused on simply finding our focal males, a task made difficult by the association of RBFWs with dense vegetation. This difficulty can be easily corrected with radio telemetry, as the long wavelength signals allow for penetration of dense vegetation (Hedin and Ranius 2002).This allows for more time in the field spent collecting locations of RBFWs, providing for a more accurate and statistically sound estimation of kernels (Millspaugh *et al.* 2006). We therefore believe that future studies on RBFW habitat use and responses to fire should make use of radio telemetry unless specific behavioral observations are desired.

A second important limitation of this study has already been mentioned in brief but deserved additional discussion. All of our fire data for this study came from satellite imagery of fire scars at a scale of 250m. This did not allow us to evaluate the impacts of smaller, less intense fires, which we knew to occur, on RBFWs. Because of this limitation, our results must be taken with a grain of salt. These smaller fires, while not big enough to appear on MODIS imagery, may still be damaging enough to force RBFWs into short-term migration and to alter the vegetative

structure for months to come. Ground measures of these small fires proved difficult to collect and accurately quantify, and were consequently stopped. Future studies should evaluate efficient means of detecting and mapping smaller fires so that the effects of such events can be quantitatively measured in RBFW studies.

In allowing for more accurate measurement of RBFW locations and the effects of small-scale fires, the dynamics between fire and environmental factors in shaping RBFW habitat utilization can be more thoroughly understood.

## 4.7 APPLICATIONS OF FINDINGS ON A MULTI-SPECIES AND GLOBAL SCALE

The findings of this study demonstrate that fire may not play an entirely negative role in shaping the habitat utilization of RBFWs, as has been previously thought. Instead, RBFWs respond more strongly to vegetative cues and are able to readjust their range extent within several weeks of a fire. This suggests that as long as there are available adjacent patches of suitable habitat, wrens may still be able to forage in burned areas, limiting the impact of fire. While this may be the case, previous studies have shown that fire events may have a negative impact on RBFW breeding success in the subsequent breeding season (Murphy *et al.* 2010). Therefore, the use of burned habitat by RBFWs may constitute an ecological trap in which seemingly suitable habitat actually has a negative impact on long-term fitness (Schlaepfer *et al.*2002). As such, more study is necessary to verify such a relationship at other sites and to determine how dry season home ranges relate to breeding season territories.

In the meantime, other species must be examined to understand whether they also exhibit similar patterns of habitat utilization. If burning has little impact on the ranging behaviors of other species within a season, this could have implications for the management of controlled burning. However, I would hesitate to make any quick recommendations about burning practices

based on the results of this study as it simply shows that RBFWs are capable of using large areas of burned habitat, but has no analysis of the availability of unburned patches within those areas. Previous literature on the impacts of fire have emphasized the importance of landscape heterogeneity in the survival and abundance of RBFWs and other species (Fuhlendorf *et al.* 2006; Murphy *et al.* 2010; O'Toole 2014), suggesting that fires which maintain a patchy landscape may be important. Our research supports these findings by providing evidence that RBFWs may be able to utilize burned areas, though the long-term population impacts are still uncertain. As such, it is our recommendation that research be increased on the long-term dynamics of fire on not only RBFWs, but other species as well.

Such research may become increasingly important in the coming years as fires are increasing and predicted to continue increasing in Northern Australia due to global climate change (Pitman *et al.* 2007). As fires increase, a nuanced understanding of the implications across the ecosystem becomes increasingly important, as changes to the fire regime can drastically shift community assemblages (Valentine *et al.* 2007). Because similar trends of increased fires are occurring across the world (Pausas 2004; Westerling *et al.* 2006), this principle applies beyond Northern Australia. We need to understand our fire-dominated ecosystems in order to conserve them in a changing and uncertain future.

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