

The Influence of Environmental Heterogeneity on Winter Ranging in the Red-Backed Fairy-Wren, *Malurus melanocephalus*

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Abstract

The decline in food and cover that accompanies the tropical dry season can cause animals to shift and expand their home ranges. However, range expansion is problematic for territorial species. In birds, this challenge can be overcome via seasonal fission-fusion, a pattern in which birds combine individual breeding season territories in the nonbreeding season and travel as a flock over their combined range. Such behavior is present in a variety of birds and may have environmental, trophic, and social causes. Here we investigate a potential environmental cause in one such bird, the red-backed fairy-wren (RBFW) *Malurus melanocephalus*. We used spatial analysis of home ranges, movement logs, and fire history to see whether access to unburned habitat was associated with seasonal fission-fusion. RBFWs showed a strong preference for unburned habitat. However, two other predictions—that there would be a positive relationship between home range size and sociality and that flock size would be larger in unburned areas—were not supported. Our results suggest that fusion into large flocks did not occur at our site or had not begun in earnest during the study period. Fusion probably takes off in the late dry season and could potentially be driven by access to unburned habitat. This conclusion is suggested by RBFW's preference for unburned habitat, though other environmental and trophic factors are likely to drive group fusion as well.

Introduction

In tropical savannas, seasonal variation in solar radiation causes rain to fall mainly during a distinct "wet" season. The "dry" season, by contrast, is marked by a near-total lack of rain and, as a consequence, fire is often an important phenomenon at this time (Shine & Brown, 2008 and Molles, 2013). This high seasonality is associated with annual fluctuations in the availability of food, cover, and other resources that can shape animal behavior. For birds, important changes in the dry season include 1) the withering of ephemeral vegetation (Shine & Brown, 2008), 2) the loss of deciduous leaves that are used for foraging and cover (Shine & Brown, 2008), 3) a decrease in insect abundance with decreasing moisture levels (Janzen, 1980), and 4) the alteration of habitat by fire, which can reduce cover and create a mosaic of different habitat types (Brawn et al., 2001). Birds often respond to these phenomena by changing patterns of space use. For instance, avian responses can involve long-distance migration in response to insect scarcity (Jahn

et al., 2010), local movement out of food-limited areas (Smith et al., 2011), range-shifting in direct response to fire (Murphy et al., 2010 and Valentine et al., 2007), or nomadic, nonterritorial space use (Brown & Long, 2007). Birds may also adapt to seasonal stresses by foraging collectively (Emlen, 1952) or expanding their home range to forage over a wider area (Hatchwell et al., 2001).

Home range expansion, however, presents a challenge for territorial species, whose available home ranges may be constrained by the presence of neighboring territories. In some birds, "floating" appears to be a consequence of territoriality, with floaters forced to move frequently between already-occupied territories by the constant threat of eviction (Brown & Long, 2007). Another option for sedentary, territorial species to increase their home range is a "fission-fusion" strategy, in which discrete breeding season territories are combined ("fusion") in the nonbreeding season (Griesser et al., 2009). Birds from the various territories then travel together as flocks



Figure 1. (A) Male (left) and female (right) RBFWs with color-bands. (B) Habitat before (right) and after (left) fire, which reduces cover necessary for foraging and security. Photo credit: S. Lantz and P. Phillips.

across their combined range. As the breeding season returns, the flock breaks up into its component parts ("fission") which return to their former territories, sometimes with a slight reshuffling of members (Griesser et al., 2009).

Seasonal fission-fusion is well exemplified by the cooperatively-breeding Australian apostlebird *Struthidea cinerea* (Griesser et al., 2009), though similar patterns, often referred to as "winter flocking," are common in a variety of temperate bird species (Odum, 1942 and Quay, 1982). Proposed causes of this pattern include the foraging benefits of flocks, such as increased prey flushing or vigilance (Pulliam, 1973, Pyke, 1984 and Krause & Ruxton, 2002), and social factors such as the opportunity to form connections and exchange members (Griesser et al., 2009). Birds may also be adapting behaviorally to the spatial attributes of their habitat. Flocking has been generally related to periods of unfavorable conditions such as drought (Emlen, 1952) or to resource distributions that are indefensible and unstable (Gill, 1995). Corvids, for instance, forgo individual territories in favor of flocks when food supplies become patchy and unreliable (Verbeek, 1973).

We explored the dry season (winter) flocking of a sedentary, territorial bird, the red-backed fairy-wren *Malurus melanocephalus*. The red-backed fairy-wren (hereafter, RBFW) is a non-migratory, cooperatively-breeding passerine found in the seasonal savannas of northern Australia. In the wet season, the birds

establish breeding territories as pairs or small families (Webster et al., 2008). Males develop a variety of sexual signals (Karubian et al., 2009) and they display and sing to defend the boundaries of their territory (Rowley & Russell, 1997). These boundaries erode as the dry season progresses, with RBFWs forming relatively large, loose flocks (Rowley & Russell, 1997, Schodde, 1982, Lord, 1956 and MacGillivray, 1914), in contrast to their breeding season groups of 2-3 individuals. As the dry season goes on, the size of these flocks may increase up to 30 or 40 individuals at some sites, but the birds re-segregate into small groups or pairs again for the next breeding season (Schodde, 1982). From this evidence, it appears that a seasonal fission-fusion model is applicable to RBFWs.

While flock benefits and social factors may both contribute to seasonal fission-fusion in this species, we investigated a potential environmental cause: habitat heterogeneity. RBFWs are insectivorous and require tall grass or other cover for foraging and security. In the dry season, a general decrease in insect abundance coupled with the loss of ephemeral vegetation and the prevalence of fire are likely to create a patchy distribution of these essential resources. Food availability and vegetative structure are factors that contribute to habitat choice in birds and are affected by fire history (Brawn et al., 2001 and Woinarski & Recher, 1997). We focused on the patchiness that is directly attributable to past fires, which create a mosaic of different vegetative structures that can persist for years after a fire (Brawn et al., 2001 and Valentine et

al., 2007). At our site, more recently burned areas have been found to contain less grass cover, and the presence of this vegetation is a significant predictor of RBFW presence (Hinton, 2013).

We hypothesized that seasonal fission-fusion is a response to patchiness in the environment, as it allows birds to expand their potential range by foraging together and thus gain access to unburned areas. By flocking together under the seasonal fission-fusion model, birds would reap the benefits of aterritoriality through larger home ranges and increased access to unburned areas. There should be more birds in larger flocks in these areas than in burned areas. Under this model, the size of the territory a bird gains access to should be related to how many other birds it joins with (Griesser et al., 2009); that is, how socially connected that bird is. To test this hypothesis, we made the following three predictions about habitat use and flocking behavior during the dry season. 1) There will be a positive correlation between the size of an individual bird's home range and that bird's social connectivity. Social connectivity would be quantified by degree, the number of unique connections to other birds, and by average flock size. 2) Birds will spend more of their time in unburned areas than in burned areas. 3) Average flock size will be larger in unburned areas, as the larger flocks are more likely to gain access to this desired habitat and thus more likely to be found there.

Methods

We studied a color-banded population of RBFWs in a core area of 4 km² at Coomalie Farm (13.00°S, 131.18°E), located roughly 100 km south of Darwin in Australia's Northern Territory. The site is within the seasonal tropics, experiencing a dry season with little to no rain from May to September and a wet season involving heavy rain and flooding from October to April (Australian Bureau of Meteorology, 2013 and Shine & Brown, 2008). The site comprises a mosaic of savanna-woodland habitats including paperbark woodlands, monsoon forests, bamboo thickets, rocky hillsides, palm/cycad woodlands and open savannas of native and invasive grasses. Common genera include *Eucalyptus*, *Melaleuca*, *Erythrophleum*, *Cycas*, *Pandanus*, *Corypha*, *Themeda*, *Heteropogon*, and the invasive West-African gamba grass *Andropogon gayanus*, which has become well-

established. Controlled burns and natural fires occur regularly in the dry season. We collected data from June 3rd to August 3rd, 2013.

We made standardized and opportunistic observations of 13 male RBFWs chosen for proximity to the research station. We elected to focus only on males to control for the effect of sex and because males are the sex that enforces territorial boundaries in the wet season (Rowley & Russell, 1997). Standardized observations involved locating and observing each individual on three separate occasions throughout the season, at least once in the morning (between 6:00 and 12:00) and once in the afternoon (between 15:00 and 19:00). All included observations lasted at least 5 minutes and ended either after 30 minutes had elapsed or when the bird was lost and not found again within the 30 minute window. We observed all birds for between 60 and 90 minutes total across the three observations.

We detected focal birds by heading to the area where that bird was last seen and walking a transect through the habitat, using roads, telegraph lines or forest edges as boundaries. Transect boxes were between .004 and .01 km², and we sampled from opposite corners heading towards the center on lines spaced 50 m apart. If no birds were detected by sight or sound within the transect box, we transected the adjacent habitats by the same procedure. When a bird was found we started a timer and noted its location. We recorded the time when a bird arrived at and left a specific location to the nearest 15 seconds. As the bird or birds moved we followed behind them along the path they had taken, keeping a distance of at least 30 m and recording the GPS coordinates of each of their former locations as we passed through them. We attempted to determine the number of birds present and the identity of each bird within the 30 minute period. Opportunistic observations were made throughout the season at various times of day, including the identity, time and location of the bird as well as any other positively identified birds present.

The habitat within the study area was divided up into one of five "burn types" based on the most recent fire that had occurred. Fire typically destroys the grass and shrub layer but spares large trees, depending on severity. Grass begins regenerating soon after the burn, causing habitats that have only burned months apart to be quite different in vegetation structure. Within our

study area, there were four fires within the past year: one in July and August 2013, during our field season, one in May 2013, one in December 2012, and one in July of 2012. Habitat that did not burn within the last year was considered “unburned”. The unburned area represented a mosaic of areas that burned between one and several years ago and others that were never allowed to burn due to their proximity to dwellings.

We quantified the social connectivity of our birds by degree and flock size. Degree is the total number of unique interactions a bird had with other birds, as seen in all observations. An interaction was defined as two birds clearly associated either by proximity (perching or moving within 5 m of each other) or by activity (displaying to each other, singing, and responding). The network also included connections made when birds were caught together. Flock size was the number of connections made within the 30 minute directed observation window, averaged over the three observations. The 5 minute minimum for directed observations ensures that the birds were indeed traveling together and not merely briefly associated.

Analysis

To test for a relationship between home range size and social connectivity, we used the “minimum bounding geometry” tool of ARCGIS Explorer 10.1 (ESRI 2012) to create Minimum Convex Polygons (MCPs) drawn from all of the opportunistic sightings across the season and the initial sighting locations from the standardized observations. We used logistic regression to compare home range sizes in m² to degree and flock size.

To test for a preference for burned areas, we compared the amount of time that birds spent in each burn type to the expected amount under a null preference via a Chi-Square analysis. MCPs were overlaid with a map of the different burn types at our site. We laid points from standardized observations, containing the amount of time spent at each point and the flock size, onto this map to determine which burn type each point was in. All birds were then summed to give a distribution of their collective time among the five possible burn types. To calculate the expected distribution, we calculated the area of the intersection of each bird's home range with each burn

type, giving the percentage of the home range made up of each burn type. Under a null preference, there would be no relationship between the burn type and where the birds spend their time, so the expected time was proportional to the percentage of each burn type within the total home range.

For prediction 3, we calculated average flock size between burn areas by dividing the initial sighting points for the three standardized observations into “Unburned” and “Burned.” Because only two different burn types were represented (July and December 2012) among these points, they were combined as simply “burned.” We then calculated the average of the flock size for each category, and compared via a two-tailed Student's *t*-test.

Results

Prediction 1

The average home-range size was 50,019 m² ($\pm 7,684$ m², $n=13$; Fig. 2). We did not detect a significant relationship between total degree of social connectivity and home range size (linear regression; $F=1.642$, adjusted $r^2=0.051$, $d.f.=1, 11$, $p=0.227$) or between average flock size and home range size (linear regression; $F=1.993$, adjusted $r^2=0.076$, $d.f.=1, 11$, $p=0.186$), though both putative relationships were positive.

Prediction 2

The distribution of time that birds spent in various burn areas was significantly different than expected (chi² test; $\chi^2=558.6$, $d.f.=4$, $p<<0.001$; Fig. 3), with birds spending more time than expected in unburned areas and less time in every type of burned area.

Prediction 3

There was no significant difference between average flock size in burned or unburned areas (2-tailed Student's *t*-test; $t=0.874$, $d.f.=37$, $p=0.388$). Overall average flock size was $2.66 (\pm 0.31, n=13)$ birds.

Discussion

The predicted correlation between home range size and social connectedness did not occur. Neither degree nor flock size showed a significant relationship to home range size, though both relationships were

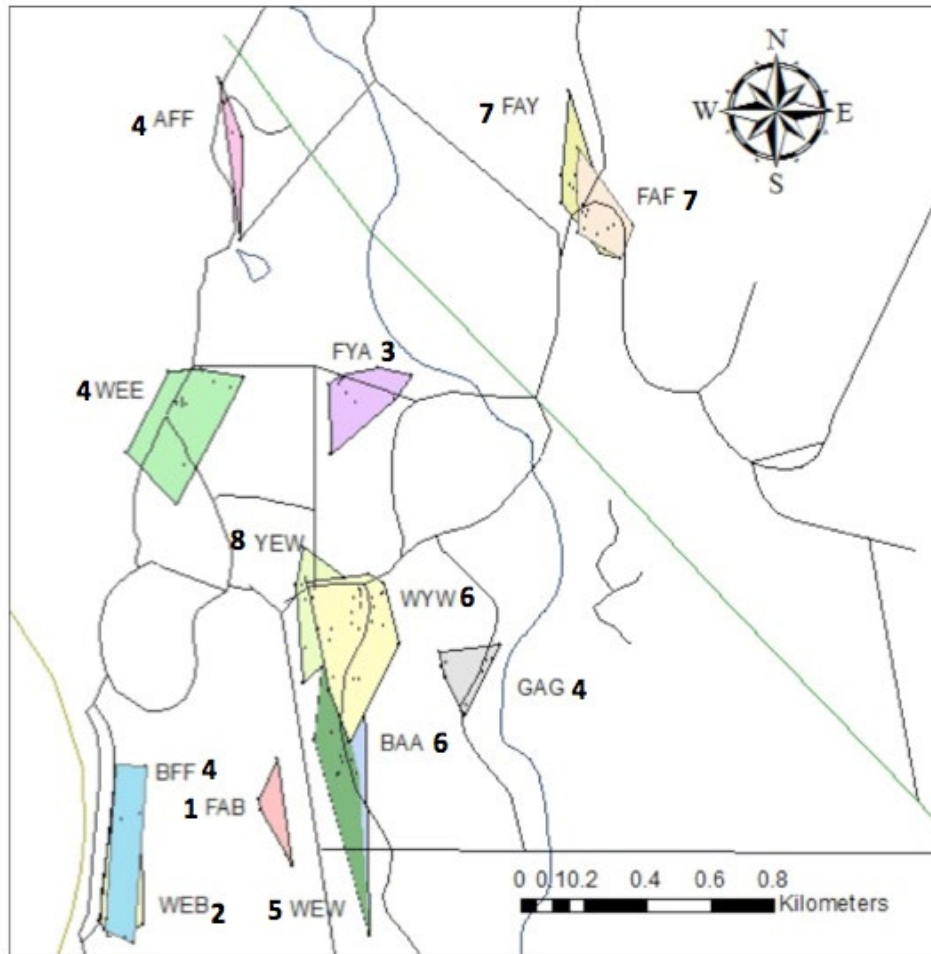


Fig. 2 Home ranges of 13 males RBFWs, labeled by their individual color-band designations (YEW, for instance). Lines represent roads. The social connectivity of each bird is given by the bold-face number next to their color-band designation. For size comparisons, the home range of WEE is roughly 90,000 m², that of BFF 50,000 m², and that of AFF 13,000 m².

positive. This failed hypothesis implies that forging social connections is not directly related to increasing range in the middle of the dry season. It may also be that any relationship between the two was clouded by the RBFW's tendency to remain in unburned patches (Fig. 3), so that the range we observed was much smaller than the birds' potential range. As males are the defenders of territory, it is possible that what is truly important is the number of social connections a bird makes to other males.

RBFWs were observed to spend more time in unburned areas than expected. This is likely related to a need for dense cover. Past research at our site has shown that grass cover is negatively related to the time since fire (Hinton, 2013); in another site, fire decreased shrub abundance in the short term and plant diversity in the long term (Valentine et al., 2007). At our site,

grass cover predicted RBFW presence better than any other factor (Hinton, 2013), while in the other site shrub abundance predicted RBFW presence (Valentine et al., 2007). Other authors have noted an aversion to burned areas on the part of RBFWs (Woinarski et al., 1999 and Valentine et al., 2001) that is likely related to reduced shrub and grass foraging opportunities (Woinarski et al., 1999) and the risk of predation in such habitats (Braithwaite & Estbergs, 1987). RBFWs are preyed upon by a number of avian predators observed at our site such as butcherbirds (*Cracticus spp.*), kookaburras (*Dacelo spp.*), and pheasant coucals (*Centropus phasianinus*) (Rowley & Russel 1997). RBFWs would be highly vulnerable in the denuded landscape of a recently burned area.

However, recently-burned areas do not necessarily have lower arthropod abundance, another

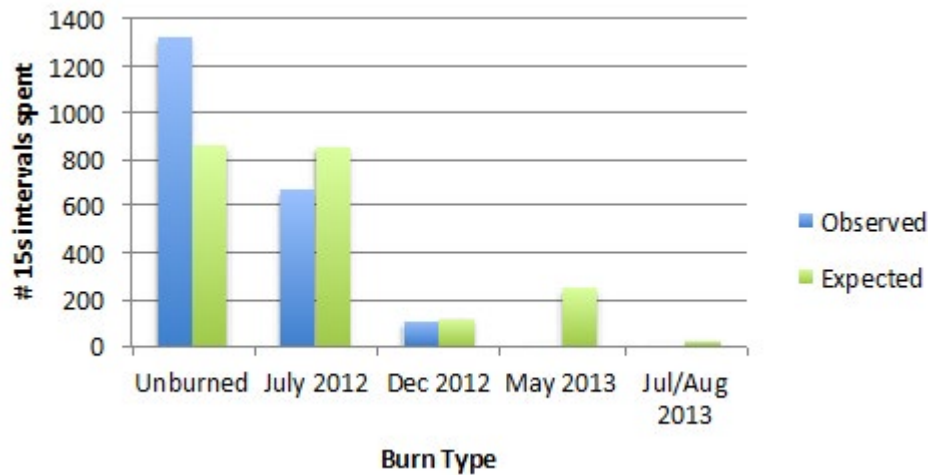


Fig. 3 Distribution of time spent by birds across different burn types. Birds spent significantly more time than expected in unburned areas and less time in all areas burned within the last year. The recentness of a burn, and hence the severity of vegetation loss, increases from left to right.

predictor of RBFW presence (Hinton, 2013 and Rose, 2014), and the reduced vegetation may make it an easier place for some birds to forage. Arthropod abundances may persist through fires because insects are drawn to the new green vegetation that grows soon after a fire (Force, 1981). Insectivorous birds as a whole (though not RBFWs) have been shown to be more abundant in burned areas than unburned ones (Valentine et al., 2007).

We found no support for our prediction that average flock size would be larger in unburned areas. In fact, at 2.66 birds, average flock size was comparable to that during the breeding season, when territories consist of a breeding male and female and occasionally an auxiliary male (S. Lantz, *pers. comm.*). This pattern indicates that fusion was not yet occurring at the time of sampling. More sampling time would have been useful for this question, as only two burn types (July and December 2012) were represented in the initial observation points used. Many more initial points were located in unburned areas than in any type of burn because unburned habitat made up the majority of habitat area and because RBFWs have a demonstrated preference for unburned habitat. It is possible that, as adjoining territories probably have similar compositions of burned and unburned areas, a flock composed of the combined members ranging over a combined territory may not encounter unburned areas at any higher rate than they would have separately. At

the observed flock sizes of five or below, flocks probably represent adjoining family groups.

Our prediction about the relationship of sociality to home range size was a basic prediction of fusion in the fission-fusion model. The fact that this hypothesis did not materialize indicates that fusion was not occurring for most of our observation period. Our observations were made during the middle of the dry season (July-August), while RBFW groups increase in size over time with the largest groups occurring in the late dry season (September) (Schodde, 1982). At the stage in which we sampled, the birds may not have begun to form the kind of large, cross-territorial flocks that we expected. Until the last week of observations, flocks never had more than five birds, which represented at most the members of two to three individual territories and perhaps only one territory. However, in the last week of sampling we recorded flock sizes of 9 and 13 birds (possibly a result of a recent fire, discussed below). These results indicate that birds at our site maintained fairly discrete territories aggregating into large flocks only towards the end of the non-breeding season, if at all. This pattern also explains why there was no difference in flock size between burned and unburned areas; that difference is a prediction from fusion, which was not occurring at this time. The low density of birds at our site (S. Lantz, *pers. comm.*) may preclude large flocks like those observed at other sites from forming. At the

RBFW densities seen at Coomalie Farm, a flock of 20-30 RBFWs would need to be composed of birds from across several square kilometers.

Though our data do not speak directly to an environmental cause of seasonal fission-fusion, the occurrence of fusion late in the dry season potentially implies environmental factors. As the dry season progresses, vegetation continues to wilt and fires become more frequent and intense (Shine & Brown, 2008 and Gill & Williams, 1996). All of the changes associated with the dry season become more severe with time. Conditions at the beginning of the dry season may be harsh enough to inhibit reproduction, but not harsh enough to drive birds to form large flocks. This explanation corresponds well with a general trend among birds to form flocks in lean times (Emlen, 1952). The preference we found for unburned areas can be explained by birds spending more time on the unburned parts of their own home range. However, as the season goes on, even unburned areas will become leaner, perhaps necessitating fusion to secure access to good habitat. The strong preference for unburned habitat we found at least suggests that habitat access could be important enough to change territorial behavior.

There are other ways in which the environmental patchiness of the dry season could contribute to fusion. The benefits of flocking, such as multiple sets of eyes and shared information, are especially useful in a patchy environment (Pulliam, 1973). By traveling together, birds increase the likelihood of any individual coming upon good habitat and sharing that resource once it is found (Pulliam, 1973 and Krause & Ruxton, 2002). Flocks also confer protection against predation (Krause & Ruxton, 2002), which may be especially important in the denuded landscape of the dry season where prey are more easily detected (Braithwaite & Estbergs, 1987). Predation pressure may become more intense throughout the dry season as good habitat defoliates or burns away. However, it is also possible that RBFWs face less overall predation pressure in the dry than the wet season, as predators are raising their chicks and hunting more to support them in the wet season (Griesser et al., 2009).

The direct effects of fire may also be driving the pattern of flock formation late in the dry season. Fire directly pushes birds out of their territories and into

those of other birds (Murphy et al., 2010), potentially causing them to form a flock or share a territory. Social factors may also play a role in flock formation, as RBFWs have a very high rate of extra-pair paternity (Webster et al., 2008). This process involves both males and females forging many connections with potential future mates outside of their territory, which might be facilitated by flocking and interacting in the nonbreeding season.

A major limitation of our study was the short observation time for each bird. If time and observer availability are issues, we suggest that obtaining detailed estimates of the home ranges and movement patterns of a few focal birds is preferable to sparse records of many birds. Frequent directed observations could provide an estimate of home range over a 2-3 week timeframe. Such estimates could then show how ranges are changing from the breeding to the nonbreeding season, throughout and into the end of the dry season. We predict that such an analysis would show that early dry season territories are larger than breeding season territories. Though flock size should also increase, it is possible that the relationship we predicted between home range size and sociality will not materialize. The low density of birds at our site may allow them to expand their home ranges without pushing against the boundaries of other territories, thus eliminating the need for fusion. The implementation of radio-tracking for RBFWs is a crucial future development that will greatly increase the accuracy of home ranges and the scale at which we can track their movements. It will also be important to develop more fine-scale measures of habitat quality than fire-history maps. The Normalized Difference Vegetation Index (NDVI) from satellite images and the use of LiDAR scans from aerial transects can provide incredibly detailed renderings of ground cover and help identify suitable habitat and how it changes over time. The combination of these fine-scale techniques will allow an unprecedented glimpse into how environmental conditions drive habitat-use and ranging in birds.

Conclusion

We found a significant preference by RBFWs for unburned habitat. Flock sizes were shown to be the same between burned and unburned areas. We did not find the predicted positive relationship between social

connectivity and home range. Our results indicate that sampling occurred too early and too infrequently to capture fusion at its full extent. We suggest that the preference for unburned areas and the late-season increase in flock size indicate that access to habitat could be driving ranging patterns in this species, though there are other environmental explanations. The direct effects of fire and the sociality of the species may also explain fusion. Future research should examine home ranges and RBFW movement more extensively throughout the dry season and within the breeding season to better understand ranging patterns and their causes.

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