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Climate change indirectly reduces breeding frequency of a mobile species through changes in food availability

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Citation: Mastrantonis, S., M. D. Craig, M. Renton, T. Kirkby, and R. J. Hobbs. 2019. Climate change indirectly reduces breeding frequency of a mobile species through changes in food availability. Ecosphere 10(4):e02656. 10.1002/ecs2.2656

Abstract. Trends of environmental change are influencing the behavior of many species across the world, while highly mobile species are disproportionately impacted by climate change and human modification. Here, we investigate the mechanisms behind climate change effects on the reproductive traits of highly mobile, West Australian bird taxa, the forest red-tailed black cockatoo *Calyptorhynchus banksii naso* (FRTBC). Using a dataset of annual breeding frequency spanning 19 yr, in combination with hydrological, climatological, and remotely sensed data, we modeled the effects of environmental variation on the annual breeding frequency of FRTBCs. We found several significant relationships between annual breeding frequency of FRTBCs and environmental variation. While the model, which included a proxy for the availability of the cockatoo's primary food source and the previous season's rain, explained 49% of annual breeding frequency, there were also direct and indirect effects of heatwaves and forest productivity. Forest red-tailed black cockatoo breeding appears to be linked to the spatiotemporal availability of its primary food sources, the fruit from the tree species, marri *Corymbia calophylla* and jarrah *Eucalyptus marginata*. However, Western Australia is experiencing significant climate change, with increases in temperature and declines in rainfall altering the phenologies of these species, while declining rainfall is affecting the vegetation structure of the region. As drought events and temperatures are anticipated to increase over the region, it is expected that the food resources during the breeding season for cockatoos will become increasingly limited in time and space, thus threatening the persistence of this iconic species. This scenario is likely to be representative of many other situations where wide-ranging species rely on patchy food resources in a changing environment. As global biodiversity is increasingly threatened, this study presents timely evidence illustrating how climate change is affecting the persistence of a threatened, mobile species, and what the implications are for mobile species around the world.

Key words: climate change; ecological modeling; heatwaves; hydrology; mobile species; remote sensing; reproductive behavior.

Received 4 February 2019; accepted 11 February 2019. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Climate change leaves a clear fingerprint on ecosystems and influences the behavioral traits of species (Both et al. 2006, Burrows et al. 2014). Additionally, changes in local or regional climate have been directly observed to impact on the survivorship and persistence of many species (Bildstein et al. 1990, Both et al. 2006, Plummer et al. 2015). This is particularly concerning for species that time vital biological functions with climatological and phenological cycles (Keast and

Marshall 1954, Plummer et al. 2015). These functions are often antecedent to natural events in the environment, and certain stimuli (such as rain or temperature) often trigger behaviors, such as reproduction or migration (Keast and Marshall 1954, Runge et al. 2014, Plummer et al. 2015). Long-term or punctuated climatic changes, such as droughts or increasing temperature, can significantly alter ecological regimes, directly or indirectly, causing a species to decline, shift its range, or adapt its behavior (Burrows et al. 2014, Runge et al. 2014, Plummer et al. 2015). Moreover, species that are highly mobile are disproportionately threatened by biophysical changes that may result from climate change, or from human modification of the environment (Both et al. 2006, Runge et al. 2014). This is because many mobile species breed infrequently and their reproductive behavior is closely related to natural cycles and resource availability in a given space for a period of time (Wyndham 1982, Areta et al. 2013), and these resources can be significantly altered by processes such as rising temperatures and declining rainfall (Both et al. 2006, Cameron 2009). Changes in temperature can shift fruiting and flowering events of vegetation, which may be the primary food supply during the breeding season for many species (Wale et al. 2012, Johnstone et al. 2013*a*). Therefore, a mismatch between the timing of breeding and peak food availability can lead to significant declines in populations, as well as affecting food chains and ecosystem functions (Both et al. 2006). For example, rainfall patterns have been observed to influence the abundance of glossy black cockatoo *Calyptorhynchus lathami* juveniles in Australia, where high rainfall years are associated with greater proportions of fledglings in the population (Cameron 2009). This is because higher rainfall results in greater availability of the glossy black cockatoos' food source, indicating that any regional hydrological changes will likely affect the population dynamics of this mobile species by directly altering food availability. Climate change also affects the population dynamics, ranges, and behaviors of other mobile species. Monarch butterfly *Danaus plexippus* populations that winter in relictual fir forests of central Mexico are threatened by habitat contraction due to warming temperatures (Oberhauser and Peterson 2003). The projected loss of suitable wintering habitat due to climate change is expected to cause significant declines in the eastern migratory sub-population, and these threats will be exacerbated due to logging activities across central Mexico (Brower et al. 2002). Caribou *Rangifer tarandus* in the Arctic time parturition to coincide with the annual peak of resource available, which occurs at the onset of the plant growth season. As plant phenology is altered due to climate change, a trophic mismatch has occurred during the caribou's breeding period, resulting in increased offspring mortality and greatly reduced offspring production (Post and Forchhammer 2007).

A further issue in the conservation of mobile species is that current biodiversity management strategies are inadequate for conserving these species as they transcend the geopolitical boundaries of traditional protection (Woinarski et al. 1992). Conservation plans are generally static in time and space and are not appropriate for species that undertake seasonal or dispersive movements (Dhanjal-Adams et al. 2017). Peaks in resource availability often coincide with populations congregating in a single location or engaging in specific activities such as foraging and breeding. Hence, resource loss from human modification, or changes to resource availability due to climate change, during these key periods can result in disproportionate impacts to population abundance (Dhanjal-Adams et al. 2017). Thus, in the face of change and uncertainty, protection for critical ecological elements such as breeding and stopover sites, networks, functional resources, and habitat should become a priority for the conservation of the world's mobile species (Runge et al. 2014). Yet, assessing the environment and, subsequently, a species' persistence is challenging, as it requires systematic environmental and autecological data spanning many years to determine any significant temporal trends. Previous studies have successfully identified causal relationships between climate change and certain behaviors and dynamics, such as range shifts and population abundance in mobile bird species (Bildstein et al. 1990, Both et al. 2006). However, very little research has explicitly focused on the frequency of successful breeding events over time and their variation due to environmental processes and climate change.

The forest red-tailed black cockatoo *Calyptorhynchus banksii naso* (FRTBC) is a vulnerable subspecies of black cockatoo that is endemic to

southwest Western Australia (SWWA; Chapman 2008). The FRTBC is a highly mobile species, and previous studies have reported that the adults travel long distances (>20 km/d) from their nests in search of food and water, and these movements are changing due to altered water and food availability in SWWA forests (Johnstone et al. 2013*a*). The FRTBC form monogamous pairs, and after breeding occurs, the juveniles are dependent on the parents for roughly eighteen months to two years after fledging (Johnstone et al. 2013*b*). Previous studies have shown that breeding occurs across all months of the year with peaks in autumn (April–June) and spring (August–October) and breeding frequency varies significantly between years (Johnstone et al. 2013*a*). Breeding may occur during periods that coincide with the fruiting of the FRTBC's Principal feed trees, the marri *Corymbia calophylla* and jarrah *Eucalyptus marginata*, and fruiting quality or quantity may be the primary factor influencing breeding frequency. Over the last six decades, the FRTBC has disappeared from approximately 30% of its former range, leaving a patchy distribution across SWWA (Johnstone et al. 2013*a*). The FRTBC range contraction is most likely due to climate change, food availability, and habitat loss over the SWWA (Cameron 2007). The SWWA has experienced a significant decline in rainfall and streamflow since the 1970s (Petrone et al. 2010, Grigg 2017), while drought events and severity have been increasing throughout the forests of SWWA, potentially impacting on FRTBC food quality and quantity (Ruthrof et al. 2015). Furthermore, temperatures across the SWWA have, on average, increased by approximately one degree since the 1970s (Hughes 2003), further affecting the ranges and habitat quality of many species and impacting on natural ecological processes, such as the flowering and fruiting phenologies of myrtaceous trees (Law et al. 2000, Chen et al. 2011, Wale et al. 2012).

This paper seeks to explore the mechanisms behind FRTBC breeding variation and examine potential links between breeding frequency and regional environmental change over time. It is hypothesized that the yearly variation in breeding frequency of the FRTBC is controlled by variation in environmental processes such as rainfall, temperature, or vegetation structure and phenology. More broadly, we use the FRTBC as a focal species to illustrate the impacts of climate change on mobile species, and what the management implications are for similar species.

Methods

FRTBC breeding data

Forest red-tailed black cockatoo breeding events were recorded from 1993 until 2011 across the northern jarrah forest of SWWA, as per the methods in Johnstone et al. (2013*b*), with surveys conducted over both Swan and Murray River catchments (Fig. 1). Forest red-tailed black cockatoo presence was established by locating feeding residue or listening for calls. Once located, lone males were followed back to their nests and nest trees were recorded using a GPS. Breeding events were confirmed by observing females at the entrance to nest hollows during the day, and, if the female was fed by a male in the evening and subsequently returned to its nest to incubate, it was considered a successful breeding attempt. A total of 143 unique trees were surveyed over the 19-yr period, and the recorded frequency of breeding was highly variable between years. A total of 175 total breeding events were observed during the study period, with 104 and 71 events observed over the Swan and Murray River catchments, respectively. On average, there were 5.83 breeding events per year with a standard deviation of 5.86, while breeding events ranged from 0 to 21. Yearly survey efforts remained constant over the study period; however, knowledge of nesting trees increased over time as additional nesting sites were discovered.

Climate and environmental data

Numerous environmental covariates were prepared for data analysis, and the variables, data sources, and data types are summarized in Table 1. Previous research has linked rainfall to cockatoo breeding (Cameron 2009, Saunders et al. 2013). Thus, rainfall variation was hypothesized to be the primary factor driving FRTBC breeding frequency. As breeding data were spread over two catchments—the Swan and Murray River catchments, with differing hydrological regimes, they were spatially separated across these catchments to explore any relationships between rainfall (as well as other environmental changes) and FRTBC reproduction

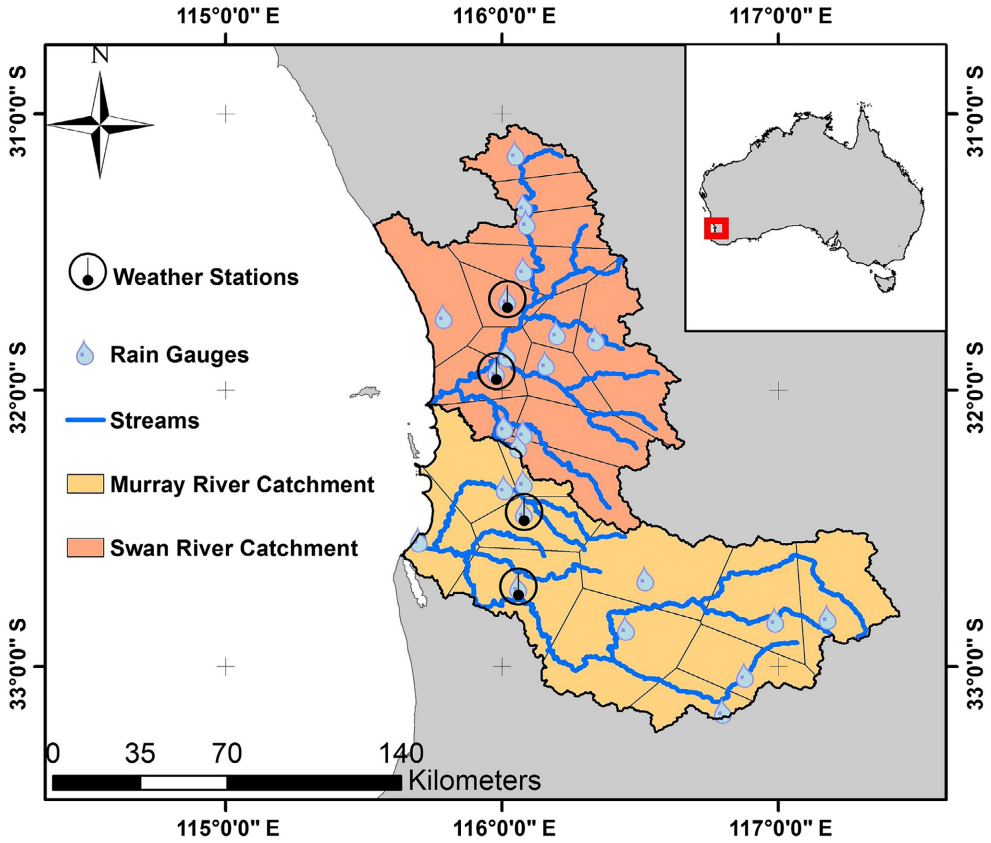

Fig. 1. Map of the southwest Western Australia study area depicting the Swan and Murray River catchments. Rain gauges and their corresponding Thiessen polygons are depicted as water droplets. Stream networks are depicted as blue hydrolines, and Bureau of Meteorology weather stations are depicted as black temperature gauges.

Table 1. The environmental variables used in this study to model the response of yearly FRTBC breeding frequency.

Variable	Description	Source
Catchment	Regions of the study area	Geoscience Australia
Breeding frequency	The response variable of FRTBC breeding events	Johnstone et al.
Burnt area	Total area of burnt vegetation (km^2)	Landsat
Extreme weather events	Frequency of tornadoes, and hail and storm events	BOM
Heatwaves	Frequency of 3 or more days above the 95th percentile for maximum temperature	BOM
Honey production	The yield of wild honey produced by apiarists (tonnes)	Wescobee Honey
Leaf area index	The projected area of leaves over a unit of land (m^2/m^2)	Landsat
Maximum temp	Mean maximum temperature (°C)	BOM
Minimum temp	Mean minimum temperature (°C)	BOM
NDVI	Normalized difference vegetation index	Landsat
Rain	Spatially aggregated total precipitation (mm)	BOM
Streamflow	Volume of water passing through monitored streams (GL)	BOM

Notes: BOM, Bureau of Meteorology; FRTBC, forest red-tailed black cockatoo. Data span the length of the study period (1993–2011) and are representative for the entire extent of both the Swan and Murray River catchments.

(Fig. 1). Rainfall data were sourced from the Bureau of Meteorology (BOM) rain gauges, which have been monitored since the early 1900s. Due to the relative sparseness of rain gauges across the landscape, it was determined that rainfall for the region would be aggregated across space and time. Aggregated rainfall for each year over each catchment was calculated using the following equation (Davie 2008):

$$R_t = \sum_{i=t}^{n} \frac{r_{i,t} \times a_i}{A}$$

where R_t is the spatially aggregated rainfall over a catchment in year t, $r_{i,t}$ is the rainfall at gauge i (mm) in year t, a_i is the area of the unique Thiessen polygon (the area closer to the corresponding gauge than any other gauge) surrounding rain gauge r_i (km^2), and A is the total area of the catchment (km^2). Yearly standard errors in rainfall were also calculated to determine whether within-year variation in rainfall might be influencing breeding frequency. To further explore how water availability and flux may be influencing FRTBC breeding, streamflow (Q, gigaliters) was sourced from BOM hydrological reference stations, and was aggregated across the Swan and Murray River catchments, and totaled for each year.

Previous studies have shown how local vegetation conditions (such as primary productivity) can influence breeding in migratory birds, where years of high normalized difference vegetation index (NDVI) were correlated with increased clutch sizes (Saino et al. 2004). Yearly vegetation condition and structure were estimated over both catchments from remotely sensed, historical Landsat 7 ETM+ imagery. Band sets for each year from both the winter (June–August) and summer (December–February) seasons, to account for any phenological variation, were geometrically co-registered and then corrected to top of atmosphere reflectance using the following equation (Chander et al. 2009):

$$\rho_\lambda = \frac{\pi \times L_\lambda \times d^2}{ESUN_\lambda \times \cos\theta}$$

where ρ_λ = Planetary TOA reflectance (unitless), π = Mathematical constant equal to ~3.14159, L_λ = Spectral radiance at the sensor's aperture ($W/(m^2\ sr\ \mu m)$), d^2 = Earth–Sun distance (astronomical units, AU), $ESUN_\lambda$ = Mean exoatmospheric solar irradiance ($W/(m^2\ \mu m)$), θ_s = Solar zenith angle (°). A simple dark object subtraction (Chavez 1988) was applied to the TOA reflectance imagery to calculate the reflectance at the base of the atmosphere. Bands were then corrected using linear regression and mosaicked before being masked over each of the study catchments. NDVI was then calculated using the following equation (Lillesand et al. 2014):

$$\text{NDVI} = \frac{\rho_{\text{nir}} - \rho_{\text{red}}}{\rho_{\text{nir}} + \rho_{\text{red}}}$$

where ρ_{nir} is the reflectance in the near-infrared band (unitless), and ρ_{red} is the reflectance in the red band. Leaf area index (LAI, the projected area of leaves over a unit of land) for both catchments was formulated using the following relationship which was derived from a previous study across the jarrah forest (Waring and Running 2007, Macfarlane et al. 2017):

$$\text{LAI} = 4.45 \times \text{NDVI}^{1.42}$$

Fire plays an important role in Australian ecosystems and has been shown to impact on the abundance and occurrence of bird species (Woinarski 1990). The extents of fire-affected regions for both catchments were derived from difference normalized burn ratios (DNBR):

$$\text{DNBR} = \text{prefireNBR} - \text{postfireNBR}$$

where prefire and postfire NBR's data were derived from data between the Western Australia fire seasons (October–May), and normalized burn ratios (NBR) were calculated as follows (Leon et al. 2012):

$$\text{NBR} = \frac{\rho_{\text{nir}} - \rho_{\text{swir}}}{\rho_{\text{nir}} + \rho_{\text{swir}}}$$

where ρ_{SWIR} is the reflectance in the shortwave-infrared band (unitless). Recently burnt and regenerating vegetation was delineated from the DNBR data using 0.25 and −0.25 cutoff, respectively.

Changes in regional temperatures have been shown to impact the reproductive response of bird species (Both et al. 2006). Thus, mean maximum and mean minimum temperatures (°C) were sourced from BOM weather stations and aggregated across each of the catchments from 1960 to 2017 (Fig. 1). Extreme climate events (sourced from BOM weather stations over each catchment), which were the yearly frequency of severe wind gusts, tornadoes, and damaging hail and storm events, were included as potential covariates, as these types of events have been shown to impact the populations of the Carnaby's black cockatoo (Saunders et al. 2011). Additionally, the yearly frequency of heatwaves was hypothesized to be an important factor on FRTBC breeding, as extreme heat has been shown to negatively impact on the reproductive cycles and outputs of eucalypt species, and such tree species provide the primary food sources for the FRTBC. Heatwaves occurring during flowering periods could significantly reduce the proportion of flowers that develop into fruit and provide food for the FRTBC (Setterfield and Williams 1996, House 1997). Heatwaves are defined by BOM as "...three or more days of unusually high maximum temperatures in any area." In this study, we considered a heatwave to be three or more consecutive days of temperatures above the 95th percentile for the respective catchment, which was determined to be 37.7°C and 34.8°C for the Swan and Murray River catchments, respectively.

Food availability is one of the primary factors influencing breeding for many bird species (Martin 1987). However, there were no data on FRTBC food quality/quantity for the region over the study period, nor were there data on feed tree flowering and fruiting; hence, we included honey production across SWWA as a proxy measure for the quality of flowering and fruiting in different years. Monthly honey production data (tonnes) for the SWWA (from 1992 to 2012) were sourced from Wescobee Honey. Wescobee Honey is the second largest exporter of honey in Australia and refines and distributes wild honey that has been harvested by apiarists who establish their hives among the jarrah and karri forests of the SWWA (Wescobee Honey 2018). We used the honey production data (the total monthly yield of wild honey) during February and March, the primary months of marri flowering as a proxy for regional marri flowering magnitude. The fruit from marri trees is the FRTBC's Principal food source (Johnstone and Kirkby 1999), and as flowering magnitude generally results in higher fruit production in subsequent years (House 1997), it was hypothesized that higher honey production would correspond with higher food production and therefore higher FRTBC breeding frequency. Very few other plant species flower during February and March, and none flower in abundance; thus, we were confident this provided an accurate proxy of annual variations in marri flowering intensity.

Statistical analysis

We used generalized linear modeling to investigate relationships between the environmental predictors described above (the independent variables) and breeding frequency (the number of breeding events in each year, the dependent variable). We assumed a Poisson error distribution and a log link function to account for the fact that the dependent variable was count data (Zuur et al. 2007). Initial data visualization indicated that breeding frequency might be higher in years where there had been moderate (rather than high or low) rainfall two years prior and breeding frequency and so linear and quadratic terms were included for rain to account for this possible non-linear relationship. In general, yearly breeding frequency was observed to be increasing over time, and year was included in the model as a continuous predictor to account for any effect of increasing survey efficiency over time. Terms for all environmental parameters at lags of one ($t - 1$) and two ($t - 2$) years were included in the models to allow for any time lag in response to environmental cues. Prior to statistical investigation, variance inflation factor (VIF) analysis was performed on continuous variables to assess collinearity, and terms with a VIF value above 10 were iteratively excluded from formal analysis (Zuur et al. 2007). Some covariates, namely NDVI (collinear with LAI) and Streamflow (collinear with Rainfall), were subsequently removed from the pool of model parameters. Following this, all predictor variables were mean-standardized so that model parameter estimates would be comparable (Gelman 2008). To avoid overfitting and to determine the most parsimonious set of model predictors, a full subset

selection, using an exhaustive search with a maximum parameter threshold of 3, was applied to the dataset under Bayesian inference criterion (James et al. 2013). The pseudo-R^2 (1 − (residual deviance/null deviance)) of each of the five best models was estimated to show how much variation is being explained by each. After accounting for the yearly time lags, there were 30 observations available for statistical inference. Models were tested for overdispersion, and it was found that that the model fits were significantly overdispersed ($P = 0.001$), and so a quasi-Poisson error distribution was assumed to correct for this issue. Further regression analysis, using a simple linear model, was conducted on the honey production data to determine whether any environmental predictors were influencing wild honey yields. The threshold of statistical significance was considered to be $P < 0.05$. All spatial data manipulation and analysis were undertaken in ArcGIS Desktop version 10.6 (Environmental Systems Research Institute 2017), and statistical modeling and data manipulation were undertaken in R version 3.5.1 (R Core Team 2018). Data visualization was performed using ggplot2 package (Wickham 2016), while subset selection was performed using the leaps package (Lumley 2017).

Results

The five best models included combinations of Year, Rain, Honey production, Heatwaves, and Burnt area (Table 2). These models show that the non-linear effect of $\text{Rain}_{(t-2)}$ was a significant term (Fig. 2a). Honey $\text{production}_{(t-1)}$ was a highly significant predictor in several models and had a strong positive effect on annual breeding frequency (Fig. 2b). Even though Year was shown to have a significant positive effect on breeding frequency, the other environmental parameters remained significant when included

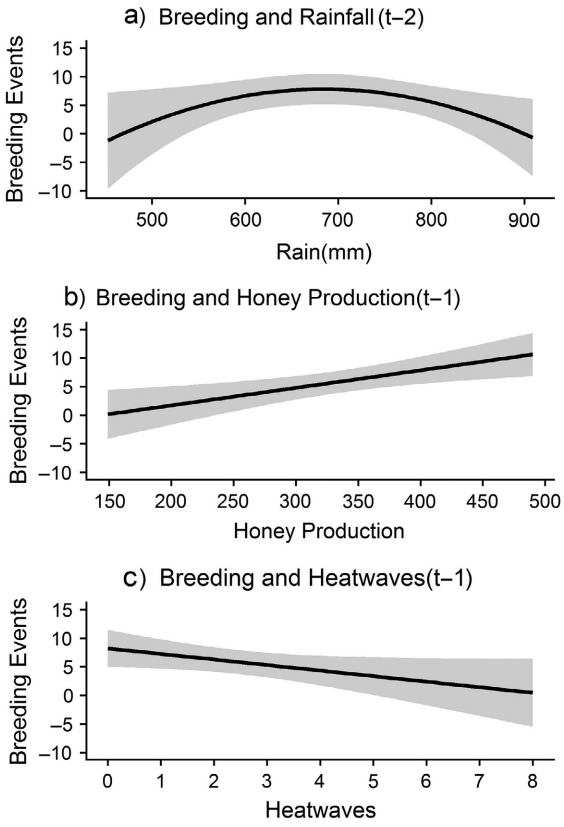

Fig. 2. The significant univariate relationships between forest red-tailed black cockatoo breeding frequency and environmental covariates. Panel (a) depicts the relationship between breeding events and rainfall, panel (b) represents the relationship between breeding events and honey productions, and panel (c) represents the relationship between breeding events and heatwaves. Black lines represent the univariate linear model fits, and the gray bands represent the 95% confidence intervals.

Table 2. Results of the various generalized linear models fitted in this study to determine the relationships between FRTBC yearly breeding frequency and standardized environmental covariates.

Model	Burnt area	Honey $\text{production}_{(t-1)}$	$\text{Heatwaves}_{(t-1)}$	$\text{Rain}_{(t-2)}$	$\text{Rain}^2_{(t-2)}$	Year	R^2
1		<0.001 (0.51)				<0.000 (0.59)	0.56
2		<0.000 (0.59)		0.022 (5.823)	0.016 (−6.09)		0.49
3			0.006 (−0.49)	0.004 (8.77)	0.003 (−8.75)		0.41
4		0.016 (0.50)	0.303 (−0.20)				0.29
5	0.638 (−0.09)		0.049 (−0.42)				0.14

Note: Five model combinations, determined by full subset selection, with their respective parameter *P*-values and response estimates in brackets have been reported.

in a model with Year, indicating that these environmental parameters explained variation in breeding that was additional to that explained by the general increasing trend over time. The pseudo-R^2 of the model that included Rain and Honey production year was 0.49, suggesting that Rain and food availability (as represented by a proxy) are explaining approximately half the variability in yearly FRTBC breeding frequency. Moreover, when honey production was tested as the dependent variable, $Rain_{(t-1)}$ and LAI had significant positive effects ($P = 0.027$ and <0.001, respectively).

Discussion

Our model results indicated that FRTBC yearly breeding frequency was non-random and that yearly variation in breeding frequency was likely due to the availability or quality of food in any given year, which in turn appeared to be influenced by environmental factors, such as rainfall and forest productivity. This finding is in accord with previous research conducted on a wide range of bird species avifauna and their response to climate change. The magnitude of breeding by American white ibis *Eudocimus albus* was linked to the availability of their principal prey species (crayfish), which was in turn influenced by seasonal rainfall variability (Bildstein et al. 1990). In addition, the migratory behavior and range of the Eurasian blackcap *Sylvia atricapilla* were altered by increasing temperatures (Plummer et al. 2015), while the European Pied flycatcher *Ficedula hypoleuca* populations across the Netherlands were deleteriously affected by changes in the peak availability of their principal food source, caterpillars, due to climate change (Both et al. 2006). Among cockatoos, glossy black cockatoo reproduction is closely related to rainfall variation and conservation of this species must take into account the potential impacts of climate change, and Carnaby's cockatoos synchronize egg-laying with rainfall seasons, with alterations to regional hydrology predicted to affect the reproductive behavior of this threatened species (Cameron 2009, Saunders et al. 2013).

With regard to the FRTBC, it appears that the availability of their principal food, the fruit from marri and jarrah trees, is a primary driver of yearly breeding variation. This is congruent with the considerable research that has been conducted on factors influencing avian breeding, with the availability of food during the breeding season identified as one of the primary limiting factors of breeding magnitude (Martin 1987). Johnstone et al. (2013*a*) state that "[FRTBC] breeding occurred at times of fruiting of either the Principal feed trees, jarrah *E. marginata* or marri *C. calophylla*, so it does not depend solely on one or the other of these species." Though no direct data measuring eucalyptus fruiting trends are available, including the proxy of regional honey production into the model indicated a non-random effect between marri food availability and breeding. Honey production is a suitable proxy for the flowering and fruiting of the marri tree, as intense flowering is associated with an increased honey yield between February and March, the typical period of marri flowering for the region (Wale et al. 2012). This notion is supported by the fact that apiarists across south Western Australia capitalize on events of mass marri blossoming, which result in higher honey yields (Pancia 2018). Further, fruit maturation in eucalypts generally occurs 8–12 months after flowering and the abundance of fruiting in the subsequent year is directly correlated with flowering intensity (House 1997, Law et al. 2000). Thus, the peak availability of food for the FRTBC would occur in autumn and spring approximately 13–18 months after flowering, a notion that is supported by the data and results. The flowering and fruiting of eucalypts is associated with patterns of temperature, solar radiation, and the previous season's rainfall (House 1997). Often, seasonal fluctuations in temperature and rainfall correlate with flowering intensity and bud formation in the succeeding two years. Moreover, drought and extreme temperatures have been shown to negatively impact on reproductive processes of many eucalypts, often causing affected stands to abort floral bud initiation (House 1997, Law et al. 2000). Therefore, significant flowering years may not necessarily translate to significant breeding years, as droughts or heatwaves may interfere with bud formation and fruit production and the fact that heatwaves had a significant negative effect on breeding frequency in our model is consistent with this notion. Given that the region is experiencing increased temperatures and droughts, and we

have shown that these factors directly influence the availability of the FRTBC's food sources, there will likely be an impact on the overall abundance of the population, which will inevitably present complex conservation challenges for the species in the future.

Nevertheless, our statistical and ecological inference assumes, and is predicated on, the notion that wild honey yield is associated with eucalyptus flowering magnitude in Western Australia and thus the availability of the FRTBC's primary food source. Our inference is also limited by the generality of the environmental and breeding data. Because nesting trees were scattered over wide geographic extents, and no direct environmental data were recorded during the breeding survey, spatial aggregation of the hydrological, ecological, and climatological data was necessary for analysis. Thus, the variation in breeding events may not be adequately explained due to the mismatch between the spatiotemporal scale of the environmental variables and FRTBC breeding surveys. However, it is logical to assume there would be less chance of observing significant relationships given this spatiotemporal mismatch, yet there remain several significant trends in the data, which supports the notions that, at a broad scale, FRTBC breeding is influenced by the availability and flux of their food. The most significant limitation lies in the fact that eucalypt fruiting and flowering data are lacking for the region. Given that fruiting cycles of marri, and potentially jarrah, appear to be influencing FRTBC breeding frequency and that other studies have shown how avifaunal breeding often correlates to food availability, it is likely these data, rather than a proxy, would have greatly improved model outcomes. Regardless of these limitations, FRTBC breeding frequency appears to be linked to peak food availability, and food availability is a function of the climatological, hydrological, and ecological patterns across the region.

Knowledge of what is driving the breeding of this vulnerable, iconic species can aid in management and recovery plans across the region, allowing for predictions of population fluctuations that may occur from climate change. Feed trees are important for FRTBC breeding, and fruit production in feed species depends on the previous season's rainfall and temperature (Setterfield and Williams 1996, House 1997). Hence, climate change is likely to reduce food availability in the future. These risks from climate change are further accentuated as FRTBC habitat continues to be cleared for mining, logging, and urbanization (Cameron 2007), rendering spatially and temporally patchy food resources even patchier. The current recovery plan for threatened cockatoos in Western Australia mentions that climate change is a threat to these species (Chapman 2008). However, the recovery plan lacks any detail on the mechanistic effects of climate change on cockatoo populations, as well as any management considerations for future consequences. As hydrological and climatological regimes change across the region, the availability and distribution of the FRTBC's food sources will alter as a response. Therefore, the recovery plan needs to account for range shifts that will occur as the FRTBC changes its foraging activities, as well as population declines that may occur from a trophic mismatch between their breeding seasons and eucalypt fruiting periods.

In conclusion, our study highlights the importance of examining likely mechanisms underlying species' responses to climatic variation and change. In the case of the FRTBC, the effect of climate plays out through its impact on food resources, rather than on the species directly. Broadly, our study suggests that mobile species are challenging to protect and are particularly vulnerable to extinction, as they explicitly rely on spatially patchy and temporally transient resources, while climate change and human modification are altering the availability and extent of these critical resources (Runge et al. 2014). A key question arises as to how we can effectively manage the patchy and ephemeral resources that mobile species rely on, and mitigate the changes that will occur to their availability resulting from climate change. With climate trends expected to intensify across the world, the resources that mobile species utilize will likely become scarcer which will, in turn, increase their risk of extinction, presenting a complex conservation conundrum for the future.

Acknowledgments

We would like to thank the Australian Research Council for funding this research (ARC Linkage Grant 0882687).

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