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Title:
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Date:
2022-08-01

Citation:
Young, A. R., Selwood, K. E., Benshemesh, J., Wright, J. & Southwell, D. (2022). Remotely sensed vegetation productivity predicts breeding activity and drought refuges for a threatened bird in semi-arid Australia. Animal Conservation, 25 (4), pp.566-581. https://doi.org/10.1111/acv.12763.

Persistent Link:
https://hdl.handle.net/11343/336297

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Article type : Original Article

Remotely-sensed vegetation productivity predicts breeding activity and drought refuges for a threatened bird in semi-arid Australia

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Short title: Drought refuges of malleefowl breeding activity

Word count: 4995 (excluding abstract, references, tables, and figures)

Abstract

Refuges play a critical role protecting species against the effects of climate change. Managing high priority refuges could improve species resilience and facilitate dispersal during periods of environmental change. In this study, we identified drought refuges in semi-arid Australia for a threatened bird, the malleefowl (*Leipoa ocellata*). Using a Poisson regression model, we quantified the effect of remotely-sensed vegetation indices, rainfall, soil moisture and site-characteristics on malleefowl breeding activity at 144 sites surveyed from 2000 to 2017 during and after drought. We tested the effect of two vegetation productivity indices on malleefowl breeding activity – the Normalised Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI) – averaged across three temporal and three spatial scales during the mound building and incubation stage of the breeding cycle. We found that NDVI and EVI were better predictors of malleefowl breeding activity than soil moisture and winter rainfall. The model with the lowest AIC value contained NDVI averaged over three months (June - August) and a 1 km radius. Malleefowl breeding activity had a strong positive association with NDVI (0.42 ± SE 0.03) and a negative association with slope (-0.34 ± SE 0.03) and vegetation patch size (-0.23 ± SE 0.02). We found the proportion of refugia (top 20% of predicted breeding activity) in protected areas was highly variable, decreasing from 42% in an extreme wet year (2011) to 14% in an extreme drought year (2007). Expanding the reserve network to include refugia predicted to occur in the south of the semi-arid Victoria could improve resilience of malleefowl to climate change. We demonstrate how remotely-sensed vegetation indices combined with citizen science data can identify where to protect native vegetation with high, stable productivity. Our approach could be applied to a broad range of species in semi-arid regions vulnerable to climate change.

Keywords: climate change, drought refuges, satellite imagery, vegetation indices, NDVI, remote sensing, malleefowl, semi-arid

Introduction

Dubbed the Anthropocene era, biodiversity declines characterise the 21st century (Butchart et al., 2010). Threats to biodiversity continue to escalate with climate change expected to add additional pressure on species and ecosystems (Steffen et al., 2009). The risk of climate change to biodiversity is both pertinent and challenging for conservation practitioners to manage directly at both landscape and local levels. However, identifying and protecting places that facilitate species persistence during periods of historical drought (Bennett &

Provan, 2008) or extreme weather events (e.g. Milstead et al., 2007; Selwood, Cunningham, & Mac Nally, 2019) might help improve the resilience of species to future global environmental change (Keppel et al., 2012; Keppel & Wardell-Johnson, 2012; Morelli et al., 2016).

Habitat refuges facilitate the persistence of biota by providing conditions buffered against the impacts of threats or disturbances (Selwood & Zimmer, 2020). Climate refuges, in particular, maintain more favourable abiotic conditions (e.g. microclimate) and/or greater resource availability (e.g. food, water, habitat) compared to the broader landscape during climatic disturbances (Bennett & Provan, 2008; Keppel et al., 2012) or changing conditions (Bennett & Provan, 2008; Ashcroft, 2010). In the current changing climate, areas that have provided a climate refuge for species in the past may represent high conservation value areas to target future management (Keppel & Wardell-Johnson, 2012). Identifying potential refuges can inform the optimisation of conservation actions, which is especially important given disturbances are expected to increase in frequency and intensity due to climate change (Steffen et al., 2009; Garnett et al., 2013; Morelli et al., 2016; Reside et al., 2019).

Species in arid and semi-arid regions of the world may be more vulnerable to climate change due to a reliance on already low levels of water availability (Collins et al., 2013; Dai, 2013). Remotely-sensed vegetation indices are increasingly being used to identify areas with higher and more stable vegetation productivity and water availability (Mackey et al., 2012; Gould et al., 2015). For example, recent studies have identified refuges using such methods in Australia (Selwood et al., 2015; Nimmo et al., 2016), the Mediterranean (Dubinin et al., 2018; Marcelino et al., 2020), South America (Marengo & Bernasconi, 2015; Bozkurt et al., 2017), West Africa (Sarr, 2012), the United States of America and Mexico (Seager et al., 2007; Wehner et al., 2011). Remotely-sensed vegetation indices provide great potential for identifying refuges across a variety of taxa because: they are likely to provide more proximal measures of factors driving populations compared with measures such as rainfall; they are relatively easy to access online, and; they have high spatial and temporal resolution (Andrew & Warrener, 2017).

Two remotely-sensed vegetation indices commonly used to assess ecological responses to environmental change are the Normalised Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) (Pettorelli et al., 2005). Both are based on ratios of reflected visible red and near-infrared light, with NDVI being more chlorophyll sensitive, and

EVI more responsive to canopy structural variations (Huete et al., 2002). NDVI and EVI are correlated with vegetation productivity and density, and hence have been used increasingly to measure drought-induced vegetation degradation in arid and semi-arid regions (Berry, Mackey, & Brown, 2007; Hope, Fouad, & Granovskaya, 2014). NDVI and EVI have also been directly linked to a variety of animal responses, including breeding activity (Saino et al., 2004; Marcelino et al., 2020), species richness and community composition (Evans, James, & Gaston, 2006; St-Louis et al., 2009) and assemblage stability during drought (Selwood, Cunningham, & Mac Nally, 2019). However, there exists an opportunity to compare and explore the predictive ability of NDVI and EVI at alternative spatial and temporal scales.

In this study, we explored the utility of NDVI and EVI at explaining breeding activity for a threatened Australian bird, the malleefowl (*Leipoa ocellata*). Malleefowl is a ground-dwelling bird endemic to the arid and semi-arid regions of southern Australia and provides a good case study due to its breeding behaviour and sensitivity to rainfall. The species builds large mounds out of soil and organic matter to incubate its eggs (Frith, 1956). Winter rainfall during mound building and incubation strongly influences breeding activity (Walsh et al., 2012; Benshemesh et al., 2020) because rainfall initiates exothermic decay of the vegetative material within the mounds (Frith, 1956). Rainfall also influences vegetation condition, which may in turn affect the direct provision of food, shelter from predators and nesting material (Frith, 1959; Gillam, 2008; Parsons, Short, & Roberts, 2009). Given the frequency and severity of drought is expected to increase across much of the species range, identifying proximal drivers of breeding activity and where high levels of breeding activity are maintained through periods of drought is crucial for future management (Brereton, Bennett, & Mansergh, 1995).

Specifically, we identified drought refuges for malleefowl by modelling the influence of remotely-sensed vegetation productivity, rainfall, soil moisture and other environmental variables using an 18-year dataset of breeding activity from 144 sites in southern Australia. We investigated the following questions: 1) what spatially mapped site covariates drive malleefowl breeding activity?; 2) is NDVI, EVI, soil moisture or rainfall a better predictor of breeding activity?; 3) which temporal and spatial scales of NDVI, EVI, rainfall, soil moisture explain the most variation in breeding activity?, and; 4) what proportion of potential drought refuges for malleefowl intersected with protected areas during an extreme drought from 1997 – 2009? This study is one of the first to explore the influence and predictive ability of vegetation productivity indices on the breeding activity of wide-ranging semi-arid species.

With drought predicted to increase across the malleefowl range (Brereton, Bennett, & Mansergh, 1995), locating and protecting potential refuges is important for managing the species in the face of climate change. Our approach will become increasingly relevant to taxa in semi-arid around the world.

Materials and methods

Study area and species

Malleefowl are large (1.8 – 2.2 kg), terrestrial ground-dwelling birds distributed in semi-arid and arid regions of southern Australia (fig. 1.a). They predominantly occur in native shrublands and woodlands characterised by cool, wet winters (June – August) and hot, dry summers (December – February). The distributional range of malleefowl has declined since European colonisation (Parsons, 2008; Garnett, Szabo, & Dutson, 2011; Benshemesh et al., 2020) as a result of habitat clearing for agriculture. The species now occupies remnant habitat patches sometimes amongst agricultural land and continues to be threatened by feral herbivores, introduced predators and changed fire regimes (Frith, 1962; Benshemesh, 2007; Parsons, Short, & Roberts, 2008). Subsequently, the species is listed as Vulnerable both nationally (Birdlife International, 2016) and under the International Union for the Conservation of Nature (IUCN). Common management strategies include fox baiting, fire management, herbivore control and revegetation (Benshemesh, 2007; Office of Environment and Heritage, 2015), however, the benefits of these management actions are highly uncertain and the focus of considerable research (Hauser et al., 2019).

Malleefowl is one of three avian species in Australia that build terrestrial mounds to incubate their eggs. Mounds are 3-6 m in diameter and are filled with leaf litter which undergoes exothermic decay to assist egg incubation (Frith, 1962). Mound preparation usually begins in early winter from June onwards, followed by egg laying between September and January (Neilly et al., 2021). Rainfall is required to wet the leaf litter and initiate decay (Frith, 1956, 1959), although excessive rainfall is also detrimental (Brickhill, 1987; Priddel & Wheeler, 2005). Malleefowl are generalist feeders consuming seeds, fruits, vegetative material and insects (Harlen & Priddel, 1996; Reichelt & Jones, 2008). Vegetative material is an especially important food source in winter months when mounds are being prepared (Benshemesh, 1992). During the nesting season, malleefowl are observed maintaining a close distance to their mounds; Frith (1959) noted the males strayed less than 100 m from the mound and females less than 250 m in breeding season, while Booth (1987) observed an average home range size of 4 km^2 with high range overlap with other pairs.

Breeding activity data

Malleefowl are the focus of a large-scale citizen scientist monitoring program across four states of southern Australia: Western Australia (WA), South Australia (SA), Victoria and New South Wales (NSW) (Fig. 1) (Benshemesh, 2007). Sites are monitored annually following a standardised protocol (National Malleefowl Recovery Team, 2016). Volunteers locate all known mounds within a site (typically 4 km^2) and record the number of mounds being used for breeding during the egg-laying period. Mound activity status (active or inactive) is uploaded remotely to the National Malleefowl Monitoring Database before being screened by members of the National Malleefowl Recovery Team. We extracted the number of mounds used for breeding at 144 sites from 2000 to 2017 from this database (Fig. 1a). Further information about the monitoring protocol is provided in Appendix S1.

Environmental covariates

We collated static and temporally dynamic topographic and environmental variables thought to influence the behaviour, biology, and habitat preferences of malleefowl. Our choice of variables was limited to those mapped consistently across southern Australia, excluding some variables known to influence breeding activity such as time since fire and biotic threats. While time since fire can be mapped at broad scales, there were inconsistences across the jurisdictional boundaries and the recorded fire scars did not align with on-ground observations. We extracted the following static variables from the centre of each monitoring site: slope and topographic position index (TPI) calculated from the Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) (Gallant et al., 2009) which may influence rainfall run-off, and; soil clay content for influencing soil moisture and fertility. We obtained a map of major vegetation groups across Australia from the National Vegetation Information System (NVIS). We identified the broad vegetation types at existing monitoring sites and assumed these types were representative of the vegetation inhabited by malleefowl. In total, seven vegetation types contained monitoring sites: Acacia woodlands, Callitris woodlands, Mallee woodlands, Acacia shrublands, other shrublands, hummock grasslands and mallee open woodlands. We calculated the size of native vegetation patches containing sites using our vegetation layer as patch size has been previously shown to influence malleefowl breeding activity (Benshemesh et al., 2020).

We collated a range of temporally dynamic variables related to water availability and vegetation productivity. We obtained daily rainfall and soil moisture at 5 km (Jones, Wang, & Fawcett, 2009) from 2000 – 2017 and obtained 16-day Terra MODIS imagery (MOD13Q1) processed for NDVI and EVI from the United States Geological Survey (USGS) at 250 m resolution (Didan, 2015). In addition, south-eastern Australia was subject to one of the worst droughts in recorded history from 1997 to 2009, known as the Millennium Drought, or Big Dry (Verdon-Kidd & Kiem 2009). We classified sites in south-eastern Australia (NSW, Victoria and SA, fig.1) as being in drought or not using this time period. A more detailed description of each variable, the source, and justification for their selection is presented in Table 1.

Alternative temporal and spatial scales

We calculated rainfall, soil moisture, NDVI and EVI across a range of temporal and spatial scales based on the scales relevant to the breeding biology and behaviour of malleefowl. We summed daily rainfall and averaged soil moisture over three alternative temporal scales during the breeding season: one month (July), three months (June – August) and five months (May – September). These temporal periods were chosen because July tended to have the highest rainfall at the monitoring sites; three months because it captures the winter period when rainfall dominates in arid Australia (Morton et al., 2011), and; five winter months to be consistent with temporal rainfall windows adopted in previous studies (Benshemesh, Barker, & MacFarlane, 2007; Benshemesh et al., 2020; Walsh et al., 2012). We also averaged NDVI and EVI across these three spatial scales: a 250 m, 1 km and 5 km radius around the centroid of each site. These scales were chosen to match the reported home range of malleefowl and previous studies and match the scale of monitoring sites (Frith, 1959; Booth, 1987; Parsons, Short, & Roberts, 2009). We could not test alternative spatial scales of rainfall and soil moisture because they were only available at 5 km resolution.

Data analysis and modelling

We extracted the environmental covariates for each site-year using the ‘raster’ package in R (Hijmans, 2017) and centred each variable at their mean, scaled by the standard deviation (Zuur et al., 2009). We tested all continuous covariates for collinearity using Spearman's rank correlation coefficient as less than |0.7| for pair combinations (Dormann et al., 2013). Only NDVI and EVI were highly correlated with each other and were thus never included in the same competing model (Appendix S3). We assumed the count of active malleefowl mounds for each site-year followed a Poisson distribution given by:

$$y_{ij} \sim Pois(\lambda_{ij}) \qquad (1)$$

where y_{ij} is the count of active mounds at site i in year j. To test the effect of covariates, we fitted a generalised linear mixed regression model (GLMM) using the 'lme4' package in R (Bates et al., 2015). We fitted our model in two steps. First, we fitted a model (hereafter our 'base model') containing all covariates except for the temporally dynamic variables (NDVI, EVI, rainfall and soil moisture), given by:

$$\log\left(y_{ij}\right) = \alpha S + \beta_1 \mathrm{DRT}_{i,j} + \beta_2\,\mathrm{PTCH}_i + \beta_3 \mathrm{TPI}_i + \beta_4 \mathrm{CLAY}_i + \beta_5 \mathrm{SLP}_i + \beta_6\,\mathrm{VEG}_i \qquad (2)$$

where y_{ij} is the count of active malleefowl mounds at site i in year j, α is a random intercept by state (S), β_1 is the effect of drought for the specific site i and year j, β_2 of patch size, β_3 of topographic position index, β_4 of percentage soil clay content, β_5 of slope and β_6 of vegetation type. In the second step, we added NDVI, EVI, soil moisture and rainfall separately for each alternative spatial and temporal scale to develop a candidate set of models. For example, we considered nine separate models with NDVI each containing different combinations of the three temporal and three spatial scales. This analysis resulted in a total of 24 competing models in our candidate set (Appendix S4). We ranked all candidate models by their AIC value and considered the best model as the one with the lowest AIC (Akaike, 1974). We calculated the conditional R^2 value for each model using the 'MuMin' package in R (Nakagawa & Schielzeth, 2013) and tested the spatial autocorrelation of the model residuals using Moran's I (Moran, 1948) in GeoDa (Anselin, Syabri, & Kho, 2006) (Appendix S5).

Predictive mapping

We predicted malleefowl breeding activity across the state of Victoria, Australia (Fig. 1), using the top ranked model with all spatial variables re-sampled to 1 km resolution to align with malleefowl movement and range sizes during breeding season (Frith, 1959; Booth, 1987). For the covariate vegetation type, we reclassified "other shrublands" as "mallee woodlands and shrublands" because there were no "other shrublands" sampled within Victoria and therefore the model had no data upon which to predict. We focused on Victoria because this state was severely affected by the Millennium drought and has the highest spatial and temporal coverage of monitoring sites. To explore the variation in breeding activity between drought and non-drought periods, and the location of potential drought refuges, we predicted breeding activity for each year during and after the Millennium Drought (2000 – 2017). We clipped predictions of breeding activity to the species range (Benshemesh et al., 2018) to avoid extrapolating too far beyond the sampled environmental space. We also clipped predictions by our reclassified vegetation layer so that predictions were only made to suitable habitat. To identify drought refuges, we compared predicted breeding activity at two scales: 1) in a single extreme drought (2007) and non-drought (2011) year, and: 2) during (2000 - 2009) and after (2010 – 2017) the Millennium drought. Finally, we calculated the proportional overlap of the top 20% of predicted malleefowl habitat in drought and non-drought periods with the existing network of protected reserves in Victoria (Commonwealth of Australia, 2018).

Results

Static and dynamic predictors of breeding activity

There was strong support for the addition of NDVI, EVI, soil moisture or rainfall to the base model (Appendix S4). All except one spatial and temporal combination of NDVI resulted in models with the lowest AIC values, suggesting NDVI is a better predictor of malleefowl breeding activity than EVI, soil moisture or rainfall (Table 2; Appendix S4). The model with the lowest AIC value contained NDVI averaged over 3 months (June - August) and a 1 km radius (Table 2). There was considerable support for the next best model (ΔAIC = 2.76), which contained NDVI averaged over 3 months and a 250 m radius (Table 2). Spatial resolutions of 5 km were not included in the top set of competing models. There was weaker support for EVI as a predictor of breeding activity compared to NDVI, although both vegetation condition indices outperformed soil moisture and winter rainfall (Appendix S4). There was no consistent ranking of soil moisture and rainfall; the order depended on the temporal resolution of each variable (Appendix S4).

Our top ranked model in terms of AIC suggested a positive relationship between NDVI and malleefowl breeding activity (0.42 ± SE 0.03) (Fig. 2 and 3). We also found a positive association between malleefowl breeding activity and each of EVI, soil moisture and rainfall in the top-ranked models with these variables. Malleefowl breeding activity was negatively associated with slope (-0.34 ± SE 0.03) and vegetation patch size (-0.24 ± SE 0.02); however, there was little evidence for associations between breeding activity and soil clay content (0.04 ± SE 0.02), drought (0.05 ± SE 0.04) and topographic position index (-0.003 ± SE

0.02). Malleefowl breeding activity was highest in the vegetation categories *Acacia* forests and woodlands (1.67 ± SE 0.25) and *Acacia* shrublands (0.83 ± SE 1.65), although there was considerable uncertainty surrounding these categories as they were sampled less than other categories (Fig. 2).

Location of drought refuges in Victoria

On average, breeding activity was similar in drought compared to non-drought years, likely due to high inter-annual variation in breeding activity within each period (Fig. 3 and 4). In Victoria, breeding activity during drought years was predicted to be highest in small, isolated patches of suitable vegetation types. These patches occurred most frequently in the south and east of the species known range (Fig. 4). Little Desert, to the north-west of Victoria (Fig. 1.a), proved to be an important refuge, except during 2007. Other large, protected areas such as Murray Sunset National Park and Big Desert were not identified as areas of high breeding activity. Focusing on the areas with the top 20% of the breeding activity and assuming these areas represent refuges, we identified only 23% and 22% of drought and non-drought refuges occurred in existing protected area networks, respectively. By contrast, in extreme drought (2007) and wet (2011) years, we found 14% and 42% of refuges were found in existing protected areas, respectively (Fig. 4.c-d).

Discussion

Identifying refuges that can sustain species during disturbance periods is crucial for conserving biodiversity in changing environmental conditions (Garnett et al., 2013; Morelli et al., 2016). There is a growing body of literature demonstrating that vegetation productivity is a good predictor of stability and persistence of animal populations, including during periods of drought (Selwood et al., 2015, 2018; Nimmo et al., 2016). Indices such as NDVI and EVI, which are strongly related to vegetation productivity, can indicate variation in resource availability over time and climate conditions, such as drought. Such indices are available in high resolution at spatial and temporal scales that can be matched to species observations and key periods of activity. We demonstrated that: 1) remotely-sensed vegetation indices are better predictors of malleefowl breeding activity than soil moisture or rainfall, and; 2) the spatial and temporal resolution of the indices influence the ability to predict breeding activity. Our findings show that remotely-sensed indices - particularly NDVI - are promising tools for identifying temporally dynamic habitat quality and drought refuges for semi-arid zone species, which will be useful for prioritising conservation efforts under different climate conditions.

Importance of NDVI

We suggest two potential explanations for why NDVI is a better predictor of malleefowl breeding activity than rainfall and soil moisture. First, rainfall data is interpolated at coarse resolutions (5 x 5 km) from sparsely distributed weather stations, which are possibly too broad to appropriately capture rainfall patterns (Berry, Mackey, & Brown, 2007). Such interpolations are notably inaccurate in arid regions of Australia where patchy rainfall is common (Morton et al., 2011; Tozer, Kiem, & Verdon-Kidd, 2012). In contrast, NDVI is measured at higher resolutions and is therefore more likely to represent the spatial and temporal variation of water availability more accurately in and around monitoring sites. Second, measures of vegetation greenness, such as NDVI, are closely related to vegetation productivity (Schloss et al., 1999), so NDVI likely integrates information on not only about the amount of rainfall, but also the rainfall absorption, run-off and soil nutrients which influence vegetation growth. Thus, NDVI may better represent the essential resources for malleefowl survival driven by vegetation productivity, whereas rainfall is only directly essential for the initiation of breeding activity (Frith, 1959).

The role of NDVI at explaining avian abundance, richness and assemblage composition has been well-documented around the world (Hurlbert & Haskell, 2003; Evans, James, & Gaston, 2006; St-Louis et al., 2009; Albright et al., 2010; Selwood et al., 2018). However, the relationship between NDVI and breeding activity has not been widely tested (except see Saino et al., 2004; Marcelino et al., 2020), but may provide a more proximal indicator of environmental change than abundance or occupancy. Breeding activity might also be easier to detect over shorter timeframes than species richness, abundance or occupancy, providing earlier indication of environmental change (Selwood, McGeoch, & Mac Nally, 2015). Another advantage of measuring breeding activity is that it is considerably easier to repeatedly collect across a broad range compared to abundance or occupancy, increasing the temporal and spatial resolution of sampling. Indeed, a key reason behind the success of the malleefowl monitoring program is that monitoring is sustained almost entirely by volunteers across large spatial scales (Benshemesh et al., 2018). Despite these advantages, further research is needed to investigate the effect of vegetation productivity indices on even more proximal metrics, such as clutch size, hatching success or juvenile survival, which are likely to be even more sensitive to disturbance events like drought.

While NDVI is the most widely used remotely-sensed vegetation index, in part due to its accessibility and ease of use, other indices may also be useful. We found that NDVI outperformed EVI in all the models tested. EVI tends to outperform NDVI in areas with high biomass because it is more sensitive to canopy variations, while NDVI and EVI tend to be well correlated in more arid areas (Huete et al., 2002). In arid and semi-arid areas, other vegetation indices, which we did not test, may offer further potential for predicting faunal responses. For example, the arid-specific Soil Adjusted Vegetation Index (Huete, 1988) correlates well with vegetation in India (Vani and Mandla, 2017) and South Australia (Jafari, Lewis, & Ostendorf, 2007), and the Normalised Difference Moisture Index (NDMI) has been used to locate drought microrefugia in the United States (Cartwright, 2018) and Western Australia (Andrew & Warrener, 2017). The utility of such measures on predicting habitat refuges in semi-arid areas warrants further attention.

Temporal and spatial scales

Testing alternative temporal and spatial scales of environmental variables is often overlooked in modelling species distributions and responses, despite its importance in influencing local environmental conditions (Hewitt, Thrush, & Cummings, 2001; Austin & Van Niel, 2011). Our results suggest that NDVI averaged over a three-month winter period was the best predictor of malleefowl breeding activity compared to one- or five-months. This temporal window likely reflects a critical time prior to and during breeding when malleefowl improve their body condition before laying eggs in spring and summer (Frith, 1962; Neilly et al., 2021). For example, NDVI during the breeding season has been positively associated with metrics of breeding success in kestrels, due to food availability and female body condition (Marcelino et al., 2020). In some cases, NDVI measured over longer time periods or with substantial temporal lags might improve predictions of how species respond to environmental change. For example, annual estimates of NDVI were used to predict the response of arid birds during drought in North America (Cady et al., 2019). We did not consider longer temporal windows for our dynamic variables because they have been found to have a negligible effect on malleefowl breeding activity (Benshemesh et al., 2020).

We found NDVI averaged across a 1 km radius was a better predictor of malleefowl breeding activity compared to 250 m or 5 km, although there was not overwhelming support for the top model. One explanation might be that a 1 km radius is better represents of the home range and habitat usage of malleefowl in sites during the mound building and incubation stage of the breeding cycle. While malleefowl are thought to move around relatively larger areas (Parsons, Short, & Roberts, 2009), breeders are known to spend a considerable time tending to their mounds during the temporal windows considered (Neilly et al., 2021). The wider 5 km radius consistently underperformed compared to the smaller spatial scales; however, this larger resolution will likely become more important before and after the breeding season. Further studies that track the movement of malleefowl throughout the year, especially during mound building and egg incubation, may elucidate the most appropriate spatial scale of environmental drivers of breeding activity.

Influence of site-characteristic covariates

We found that site characteristics added to the explanatory power of the model to varying degrees. Soil clay content had a moderate positive influence on breeding activity within the known range, contrasting previous research which suggests malleefowl prefer lighter soils (Frith, 1959; Parsons, Short, & Roberts, 2009). However, higher clay soils have been previously suggested to allow malleefowl to continue breeding during droughts, whereas mounds on sandier soils were abandoned (Frith, 1959; Priddel & Wheeler, 2005). Patch size was negatively associated with breeding activity, which is consistent with previous studies (Benshemesh et al., 2007; Benshemesh et al., 2020) but contrasts distributional modelling (Parsons, Short, & Roberts, 2009). The negative association between patch size and breeding activity is thought to occur because smaller patches of native vegetation have been retained on fertile land in agricultural areas (Benshemesh, Barker, & MacFarlane, 2007; Benshemesh et al., 2020). They also possibly have longer fire return intervals than larger patches, which benefits malleefowl (Parsons & Gosper, 2011). The other DEM-derived site variables (slope and TPI) had little influence on breeding activity, likely due the broad scale of our analysis and generally the flatness of the terrain monitored.

Management implications

Refuges offer strategic locations to protect formally and target management actions. Current protected areas have been unable to protect birds in Australia (Rayner et al., 2014), and against droughts internationally (O’Farrill et al., 2014). Accounting for refuges in reserve network design can optimise ecosystem protection (Scott et al., 1993). Many refuges for malleefowl breeding activity are currently unprotected, particularly refuges during the extreme drought year of 2007, and may be assets to the protected area network.

Priority management actions for malleefowl could focus on refuges during drought periods, although conserving the refuges integrity during non-drought periods is also imperative. Improving native vegetation cover and condition in drought refuges as well as managing fire regimes may improve the resilience of malleefowl populations during periods of stress. especially on private, unprotected land (Parsons, Short, & Roberts, 2008; Garnett, Szabo, & Dutson, 2011). The potential for populations to resist and recover from drought or other disturbances will also be hampered by pressures from feral predators and competitors which may intensify around refuge areas (Hradsky et al., 2017; Wilson, Zhuang-Griffin, & Garkaklis, 2017). Managing herbivores, such as feral goats, deer and rabbits, and pigs, is therefore likely to improve the integrity of refuge areas for malleefowl under climate change or drought (Benshemesh, 2007; Garnett, Szabo, & Dutson, 2011; Office of Environment and Heritage, 2015). Targeted management of malleefowl refugia should consider landscape connectivity to maintain gene flow and allow the species to track their climatic niche between existing protected areas (Noss, 2001; Garnett et al., 2013; Stralberg et al., 2019). The differences refuge locations between extreme years and the entire drought period of highlight that both temporal scales should be explored.

We identified potential drought refuges for a single species; the malleefowl, and a single stressor; droughts. Expanding our approach to include multiple species and other stressors is an important area of future research and would enhance effective ecosystem conservation (Garnett et al., 2013; Reside et al., 2014, 2019). If the frequency and intensity of droughts increases under climate change as expected, promoting resilience through protected areas is vital to conserving biodiversity (Chambers, Hughes, & Weston, 2005; Garnett et al., 2013). Our approach of identifying drought refuges from high and stable vegetation productivity using readily available remotely-sensed indices could easily be applied to other systems around the world. The board applicability is particularly important given an estimated 15-37% of species inhabiting 20% of the worlds terrestrial surface are in at risk due to climate change (Thomas et al., 2004). In particular, counting for refuges in reserve network design is an important method globally to minimise the impact of anthropogenic climate change (Araújo et al., 2004) and is being investigated in North America (Stralberg et al., 2019), Australia (Graham et al., 2019) and Europe (Araújo et al., 2011).

Conclusion

Based on data from a large, citizen-science monitoring program, we found that the malleefowl breeding activity is strongly associated with remotely-sensed indices, especially NDVI. Vegetation productivity, readily available through remotely-sensed data, holds great promise to help locate refuges under periods of environmental change. With the rapidly improving availability and quality of satellite-derived data, this framework of spatial analysis to identify drought refuges could be applied to other species and stressors to create a holistic view of refuge locations across a landscape. Incorporating knowledge on the location of potential refuges into conservation plans will enhance decision-making, including new protected areas and targeted management actions, aimed at supporting the persistence of species in the face of changing climate conditions.

Acknowledgements

This research was funded by the Australian Government's National Environmental Science Programme's Threatened Species Recovery Hub and the Parks Victoria's Research Partners Program. All fieldwork was conducted under a DELWP permit (number 10008024). Data on the malleefowl breeding activity was provided by the National Malleefowl Recovery Team and collected largely by volunteers. We thank Rohan Mott, Brendan Wintle and three anonymous reviewers for constructive feedback on draft manuscripts. We also thank Roozbeh Valavi for advice regarding spatial analysis and Michael Gooch for the use of the image in the graphical abstract.

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Table 1. List of environmental covariates used to model the breeding activity of malleefowl (*Leipoa ocellata*) in Australia, the covariates abbreviations used in the model equations, and the rationale for selecting the covariates with respect to malleefowl, resource availability and drought refuges.

Covariate	**Source**	**Resolution**	**Rationale**	**Supporting literature**
Dynamic variables				
Normalised Difference Vegetation Index (NDVI)	16-Day Terra Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Indices (MOD13Q1) Version 6 (Didan, 2015) downloaded from the United States Geological Survey (USGS) through National Aeronautics and Space Administration (NASA) (https://lpdaacsvc.cr.usgs.gov/appeears/). Available from 2000 onwards.	250 m	Vegetation provides essential resources, including food, shelter, and nesting material. NDVI is easy to source pre-processed online for managers and has been used globally, including for arid species.	*General:* Mackey et al., 2012, Gould et al., 2015, Andrew & Warrener, 2017, Selwood et al., 2018 *Malleefowl specific:* Harlen and Priddel, 1996, Benshemesh, 2007, Reichelt and Jones, 2008
Enhanced Vegetation Index (EVI)	16-Day Terra Moderate Resolution Imaging Spectroradiometer (MODIS) Vegetation Indices (MOD13Q1) Version 6 (Didan, 2015) downloaded from the United	250 m	Vegetation provides essential resources, including food, shelter, and nesting material. EVI is easy to source pre-processed online for managers, however it tends to be more effective in high	*General:* Hope et al., 2014 *Malleefowl specific:* Harlen and Priddel, 1996, Benshemesh, 2007, Reichelt and

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	States Geological Survey (USGS) through National Aeronautics and Space Administration (NASA) (https://lpdaacsvc.cr.usgs.gov/appeears/). Available from 2000 onwards.		productivity areas.	Jones, 2008
Soil moisture (%) at root zone depth (10-100cm) (SM)	Australian Water Resource Assessment Landscape (AWRA-L) through the Bureau of Meteorology (BoM) (http://www.bom.gov.au/water/landscape/#/sm/Actual/day/-40.14/117.47/4/Point////2019/10/18/)	5 km	Soil moisture at root depth is a more direct indicator of water available for vegetation growth and illustrates the presence of water to initiate decomposition inside mounds.	*General:* Luoto et al., 2004; Gould et al., 2015 *Malleefowl specific:* Parsons et al., 2009
Cumulative sum of rainfall (mm) (RAIN)	Australian Water Availability Project (AWAP) through the Bureau of Meteorology (BoM) (http://www.bom.gov.au/jsp/awap/rain/index.jsp)	5 km	Rainfall has been observed as a key driver in malleefowl breeding activity. The winter period captures majority of rainfall in arid regions. Cumulative rainfall indicates water availability to initiate decomposition inside mounds and impacts vegetation growth.	*General:* Gould et al., 2015, Selwood et al., 2015, 2017 *Malleefowl specific:* Benshemesh et al., 2007, 2020, Gillam, 2008, Parsons et al., 2009, Walsh et al., 2012
Static variables				

Slope from horizontal (%) (SLP)	Created using the slope command in QGIS (version 3.16.3) from the 3 second (~30m) SRTM Digital Elevation Model (DEM) sourced from Geoscience Australia (Gallant et al., 2009). (https://www.clw.csiro.au/aclep/soilandlandscapegrid/index.html)	30 m	Slope angle increase rainfall runoff and less infiltration. Therefore, slope influences water available to both vegetation growth and malleefowl for decomposition inside the mound.	*General:* Williams et al., 2012; Pavey et al., 2014; Gould et al., 2015; Cartwright, 2018
Clay content in soil (%) (CLAY)	Soil and Landscape Grid of Australia through the Commonwealth Scientific and Industry Research Organisation (CSIRO) (https://www.clw.csiro.au/aclep/soilandlandscapegrid/index.html)	1 km	Soil composition and clay content have been observed as a key factor allowing malleefowl to breed during drought periods historically, suggested as increasing the water holding capabilities of the soil. Clay content in soil may also influence soil fertility. Both water holder capabilities and fertility influence vegetation growth. The soil texture may also influence the easy with which malleefowl can build their mounds.	*General:* Williams et al., 2012 *Malleefowl specific:* Frith, 1959 Gillam, 2008 Parsons et al., 2009
Drought as binary classification for the	Created using years of the Millennium drought (1997-2009) in	250 m	Droughts diminish resource availability. The Millennium drought impacts south-	*General:* Mac Nally et al., 2009

Millennium drought (DRT)	south-eastern Australia from Verdon-Kidd and Kiem (2009). Sites in WA were not identified as being in drought at any point.		east Australia: a key area of the malleefowl distribution. The Millennium drought is thought to have caused declines in malleefowl breeding activity.	Selwood et al., 2015, 2019 Cady et al., 2019 *Malleefowl specific:* Frith, 1959; Booth, 1987; Benshemesh, 2007
Patch size of continuous habitat (km^2) (PTCH)	Calculated from continuous habitat available to malleefowl, as classified by NVIS categories and expert judgement.	250 m	Breeding activity has been found to be higher in smaller patches. Area of continuous habitat could indicate the resources available.	*General:* Luoto et al., 2004 *Malleefowl specific:* Benshemesh et al., 2007, 2020, Walsh et al., 2012
Topographic Position Index (TPI)	Created using the TPI command in QGIS (version 3.16.3) from the 3 second (~30m) SRTM Digital Elevation Model (DEM) sourced from Geoscience Australia (Gallant et al., 2009). (https://www.clw.csiro.au/aclep/soilandlandscapegrid/index.html)	30 m	A low Topographic Position Index value represents valleys and gullies which are run-on areas and likely have higher moisture retention. A high value represents ridges or crests with higher run-off.	*General:1/1/0001 5:30:00 AM* Williams et al., 2012; Gould et al., 2015; Cartwright, 2018 *Malleefowl specific:* Frith, 1959

Vegetation type from the National Vegetation Information System (NVIS) major vegetation groups (version 5.1) (VEG)	Federal Department of the Environment and Energy (https://www.environment.gov.au/land/native-vegetation/national-vegetation-information-system/data-products)	250 m	Vegetation type relates to the species composition, canopy cover and strata structure. Variation in vegetation types impacts resource availability, and possibly flammability. NVIS vegetation categories in which malleefowl monitoring sites were located were *Eucalyptus* woodlands (NVIS 5), *Acacia* forests and woodlands (NVIS 6), *Callitris* forests and woodlands (NVIS 7), mallee woodlands and shrublands (NVIS 14), *Acacia* shrublands (NVIS 16), other shrublands (NVIS 17), hummock grasslands (NVIS 20) and mallee open woodlands and sparse mallee shrublands (NVIS 32). (See Appendix 2)	*General:* Luoto et al., 2004; Dickman et al., 2011 *Malleefowl specific:* Benshemesh, 2007; Gillam, 2008

Table 2. Comparison of the top five generalised linear mixed models for predicting malleefowl (*Leipoa ocellata*) breeding activity in terms of the Akaike Information Criterion (AIC), the difference in the AIC compared to the best model with the lowest AIC (Δ AIC), and percent deviance explained. The subscripts denote the temporal and spatial resolutions for NDVI. The base model denotes the model without NDVI, EVI, soil moisture or rainfall. Rainfall, soil moisture and EVI were not present in any of the top models.

Candidate models	**AIC**	**Δ AIC**	**Conditional R^2 value**
Count ~ DRT + PTCH + TPI + CLAY + SLP + VEG + $NDVI_{3,\ 1000}$ + (1 | STATE)	6478.76	0.00	0.64
Count ~ DRT + PTCH + TPI + CLAY + SLP + VEG + $NDVI_{3,\ 250}$ + (1 | STATE)	6481.52	2.76	0.65
Count ~ DRT + PTCH + TPI + CLAY + SLP + VEG + $NDVI_{5,\ 1000}$ + (1 | STATE)	6486.26	7.50	0.64
Count ~ DRT + PTCH + TPI + CLAY + SLP + VEG + $NDVI_{1,250}$ + (1 | STATE)	6493.61	14.85	0.65
Count ~ DRT + PTCH + TPI + CLAY + SLP + VEG + $NDVI_{5,250}$ + (1 | STATE)	6494.00	15.24	0.65
BASE: Count ~ DRT + PTCH + TPI + CLAY + SLP + VEG + (1 | STATE)	6755.59	276.83	0.58

a)

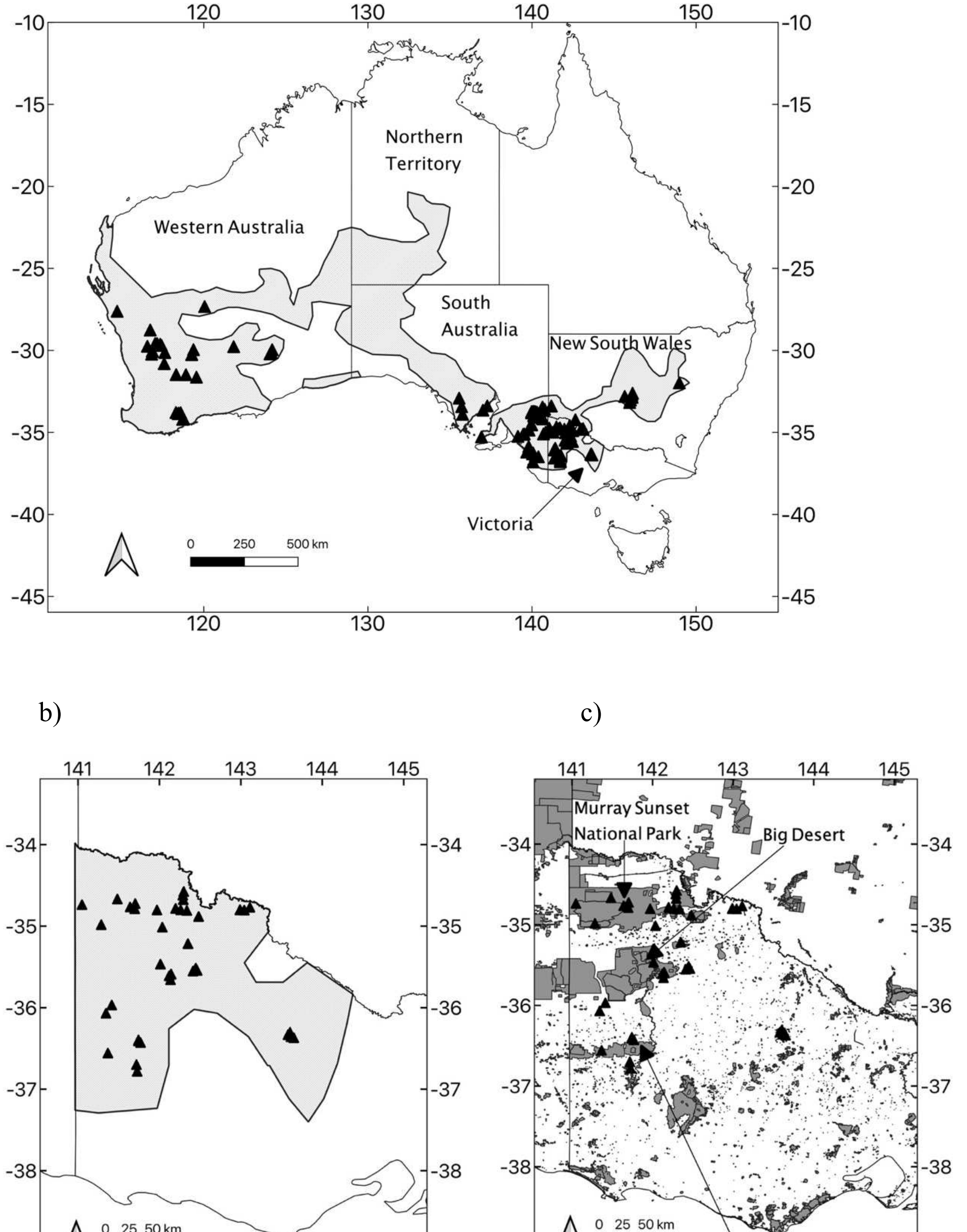

Figure 1. Location of the malleefowl (*Leipoa ocellata*) monitoring sites (black triangles) surveyed by the National Malleefowl Recovery Team in a) Australia (n = 144), b) Victoria (n = 47) and c) in Victoria with relation to the current reserve network. The grey shading represents the estimated current range of malleefowl (Benshemesh et al., 2018).

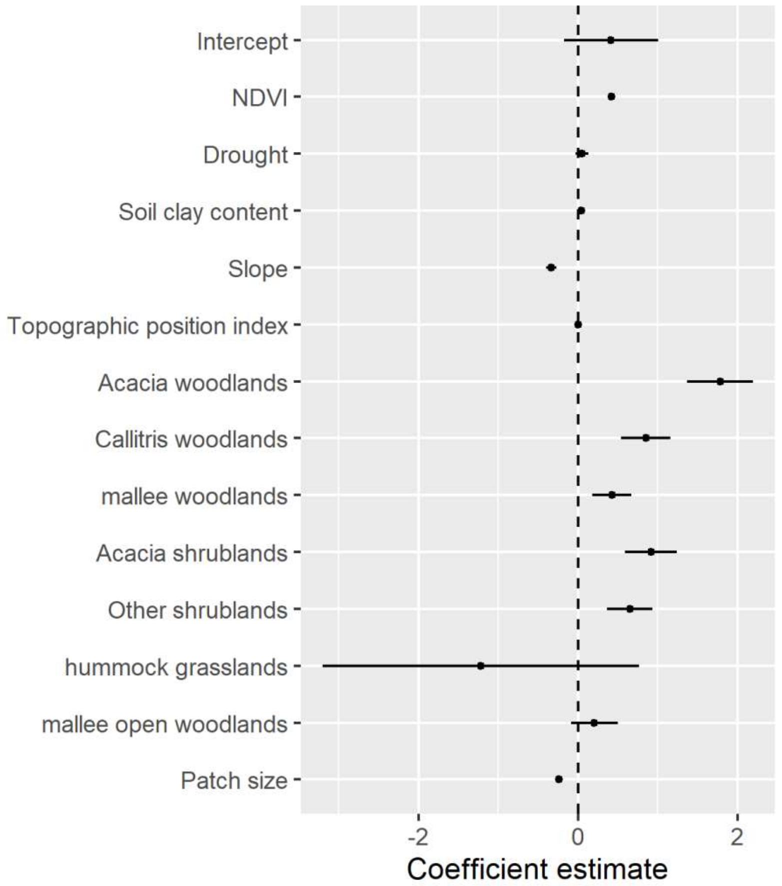

Figure 2. Coefficient estimates (x-axis) for the variables included (y-axis) in the generalised linear mixed model with the lowest AIC value (AIC = 6466), relating malleefowl (*Leipoa ocellata*). The black dots represent the mean of the predictor estimates, the horizontal lines are the 95% confidence intervals.

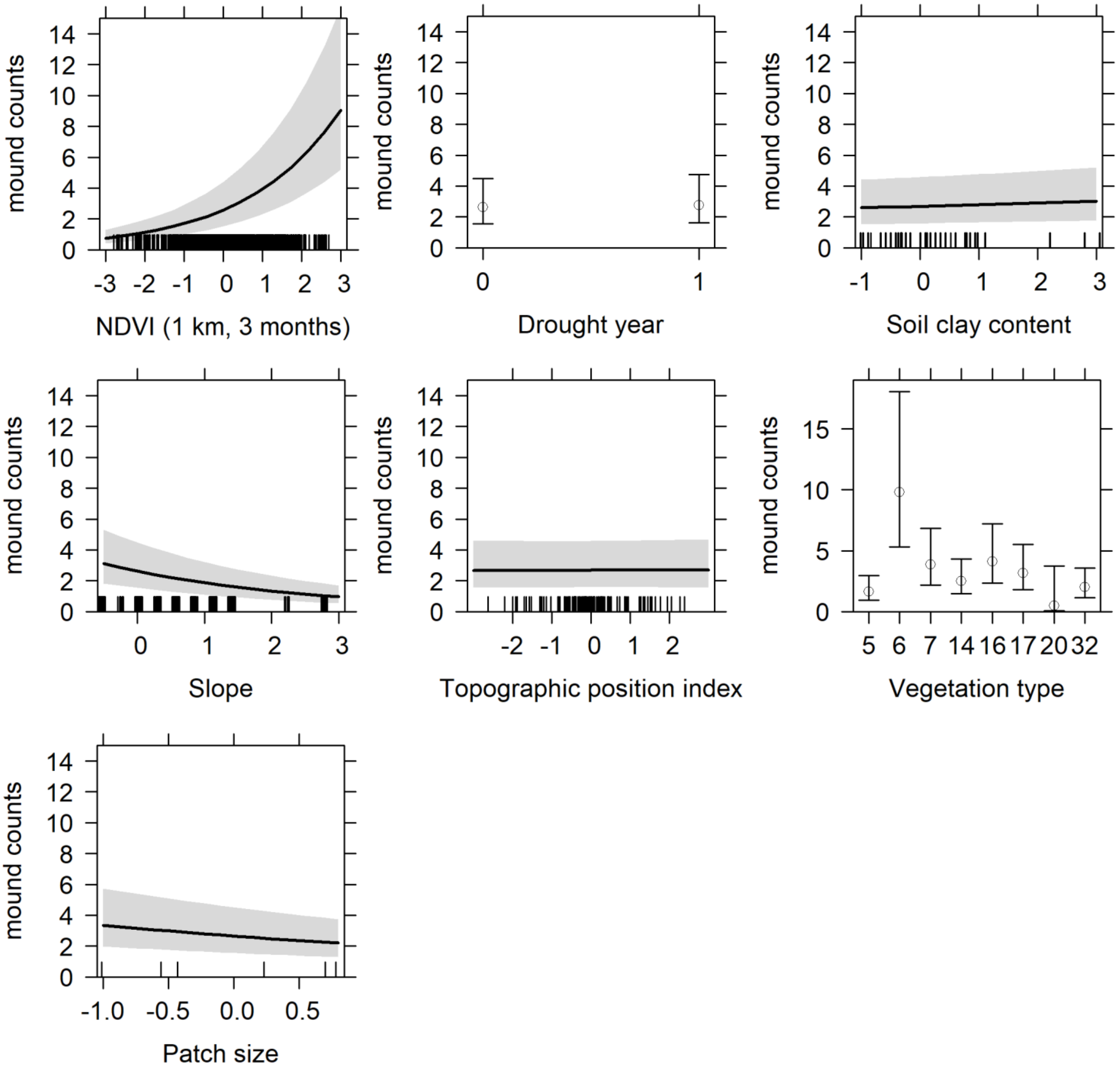

Figure 3. Relationship between the variables included in the best model (x-axis) and malleefowl breeding activity (y-axis). In panel (f) category 5 represents Eucalyptus woodlands, 6 Acacia forests and woodlands, 7 Callitris forests and woodlands, 14 mallee woodlands and shrublands, 16 Acacia shrublands, 17 other shrublands, 20 hummock grasslands and 32 mallee open woodlands and sparse mallee shrublands.

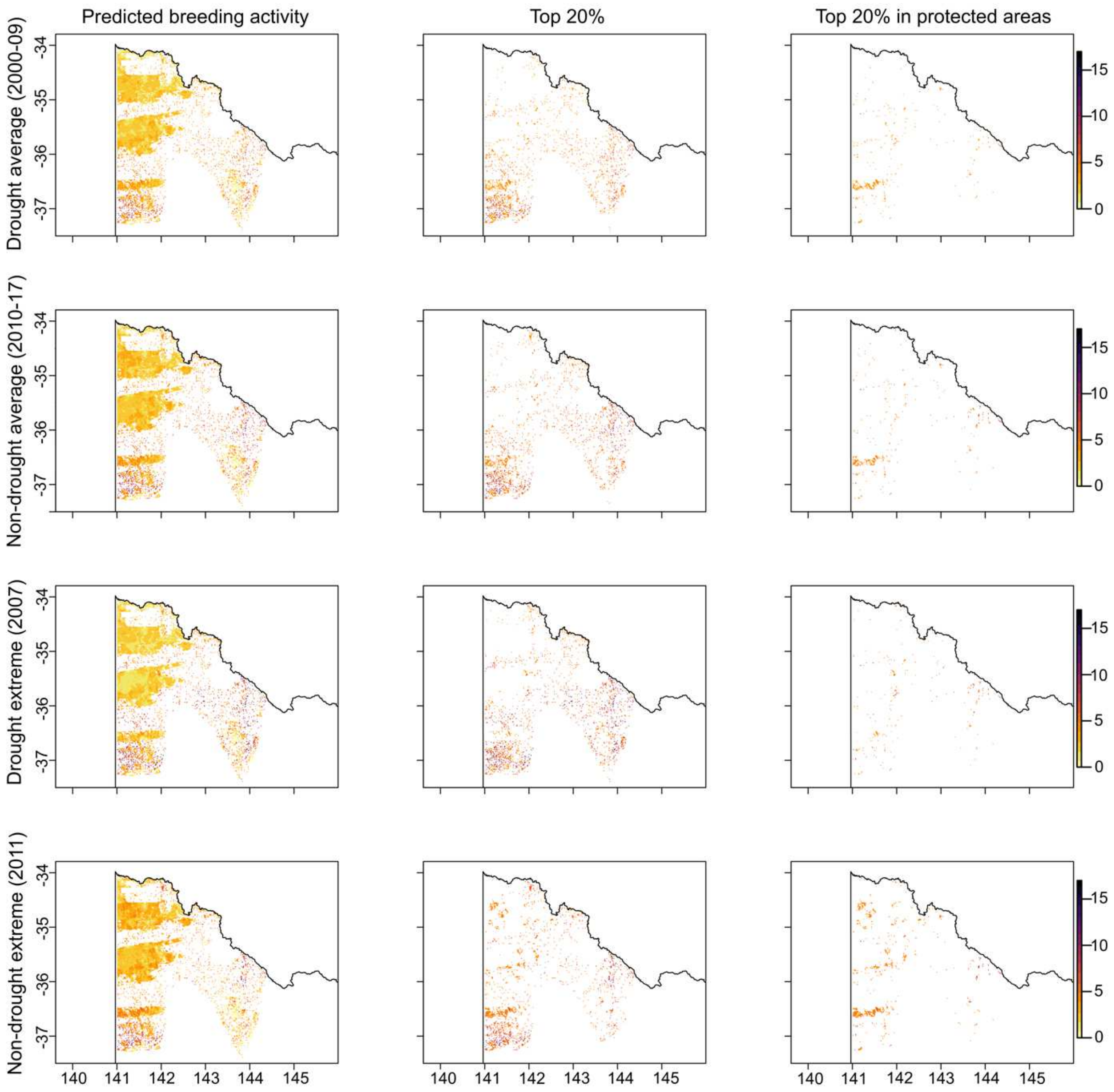

Figure 4. Predicted number of active malleefowl (*Leipoa ocellata*) mounds within the species known range and extant vegetation appropriate for malleefowl habitat in Victoria, Australia during and after the Millennium Drought. The rows depict 1) average drought conditions from 2000-2009, 2) average non-drought conditions 2010-2017, 3) an extreme drought year in 2007 and 4) and extreme non-drought year in 2011. The columns depict 1) the predicted breeding activity, 2) the top 20% of breeding activity, and 3) the overlap of the top 20% of breeding activity with the current reserve network.