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ORIGINAL ARTICLE

Land use and dingo baiting are correlated with the density of kangaroos in rangeland systems

Stuart J. DAWSON,[1,2] Tracey L. KREPLINS,[3] Malcolm S. KENNEDY,[4] Juanita RENWICK,[5] Mark A. COWAN[6] and Patricia A. FLEMING[1]

[1]Terrestrial Ecosystem Science and Sustainability, Harry Butler Institute, Murdoch University, Murdoch, Australia, [2]Department of Primary Industries and Regional Development (present address), South Perth, Australia, [3]Department of Primary Industries and Regional Development, Northam, Australia, [4]Queensland Department of Environment and Science, Australia, [5]Queensland Department of Environment and Science, Moggill, Australia and [6]Department of Biodiversity, Conservation and Attractions, Woodvale, Australia

Abstract

Rangelands worldwide have been subject to broadscale modification, such as widespread predator control, introduction of permanent livestock water and altered vegetation to improve grazing. In Australia, these landscape changes have resulted in kangaroos (i.e. large macropods) populations increasing over the past 200 years. Kangaroos are a key contributor to total grazing pressure and in conjunction with livestock and feral herbivores have been linked to land degradation. We used 22 years of aerial survey data to investigate whether the density of 3 macropod species in the southern rangelands of Western Australia was associated with: (i) land use, including type of livestock, total livestock, density of feral goats, type of land tenure, and kangaroo commercial harvest effort; (ii) predator management, including permitted dingo control effort, estimated dingo abundance, and presence of the State Barrier Fence (a dingo exclusion fence); and (iii) environmental variables: ruggedness, rainfall, fractional cover, and total standing dry matter. Red kangaroos (*Osphranter rufus*) were most abundant in flat, open vegetation, on pastoral land, where area permitted for dingo control was high, and numbers were positively associated with antecedent rainfall with a 12-month delay. Western grey kangaroos (*Macropus fuliginosus*) were most abundant on flat, agricultural land, but less abundant in areas with high permitted dingo control. Euros (*Osphranter robustus*) were most abundant in rugged pastoral land with open vegetation, where permitted dingo control was high. While environmental variables are key drivers of landscape productivity and kangaroo populations, anthropogenic factors such as land use and permitted dingo control are strongly associated with kangaroo abundance.

Key words: herbivores, livestock, macropods, overgrazing, rangelands, total grazing pressure

INTRODUCTION

Worldwide, the raising of livestock by people has led to conflict with predators, and in many cases leads to widespread lethal predator control (Berger 2006; Zimmermann *et al.* 2010; Ripple *et al.* 2014). Through

Correspondence: Stuart J. Dawson, Terrestrial Ecosystem Science and Sustainability, Harry Butler Institute, Murdoch University, 90 South Street, Murdoch WA 6150, Australia.
Email: stuart.dawson@dpird.wa.gov.au

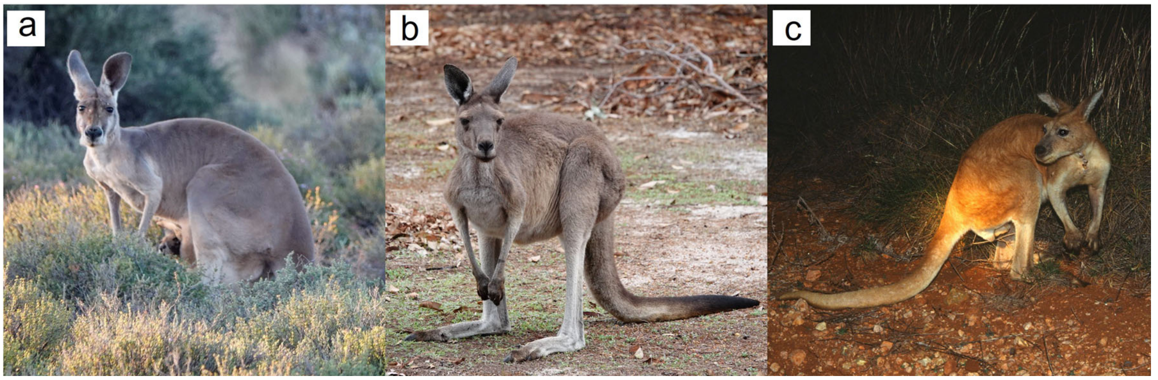

Figure 1 Three large kangaroo species are found in southern Western Australia. Each species shows different habitat preferences. (a) The xeric-adapted red kangaroo (*Osphranter rufus*) is capable of high mobility (Norbury *et al.* 1994), and populations are unevenly distributed with respect to vegetation and land use (Johnson & Bayliss 1981). (b) Western grey kangaroos (*Macropus fuliginosus*) appear to be more dependent on cover than red kangaroos (Caughley 1964) with a preference for habitat heterogeneity (Short *et al.* 1983). (c) Common wallaroos or euros (*O. robustus*) are sedentary and localized to rocky landscapes (Ealey 1967).

predator control to protect livestock, humans have manipulated predator–prey relationships and altered natural limitations on herbivore abundance (Schmitz *et al.* 2000; Berger & Conner 2008; Estes *et al.* 2011). Additionally, the introduction of free-standing water for livestock and altered vegetation to improve grazing can also benefit native herbivores (James *et al.* 1999; Smit *et al.* 2007; von Wehrden *et al.* 2012). In many cases, the consequent overabundance of herbivore species has caused degradation of rangelands (Katona & Coetsee 2019; Mills *et al.* 2020).

Kangaroo and common wallaroo or euro (hereafter collectively referred to as "kangaroos") populations have increased markedly since European colonization of Australia. Their increase in numbers is likely driven primarily by an increase in permanent water availability (James *et al.* 1999; Dawson *et al.* 2006; Fensham & Fairfax 2008), modification of vegetation (Newsome 1975), and broadscale control of wild dogs/dingoes (*Canis familiaris*; Jackson *et al.* 2017) (Caughley *et al.* 1980; Pople *et al.* 2000; Letnic & Crowther 2013). There are estimated to be, on average, a combined total 40 million red (*Osphranter rufus*; Fig. 1a), and grey (*Macropus giganteus* and *M. fuliginosus*; Fig. 1b), kangaroos in Australia, the vast majority of which are on rangelands in inland regions, used for pastoralism (Wilson & Edwards 2019).

Total grazing pressure (TGP) is the summed pressure applied by all grazers present in a system, which in the Australian southern rangelands (in semi-arid and arid Australia) includes livestock, kangaroos, unmanaged goats (*Capra hircus*), rabbits (*Oryctolagus cuniculus*), feral pigs (*Sus scrofa*), equids (*Equus* spp.), and dromedary camels (*Camelus dromedarius*) (Hacker *et al.* 2020). When combined with grazing by domestic livestock (representing the primary land use of many rangeland areas), populations of feral herbivores and kangaroos have resulted in unsustainably high TGP that can degrade landscapes and lead to negative outcomes for agriculture and biodiversity (Page & Beeton 2000; Mills *et al.* 2020; Fisher *et al.* 2021). There is some uncertainty around the degree to which kangaroos compete with sheep and cattle for fodder because of differences in diet (Pahl 2020b) and in the degree to which individual kangaroos contribute to grazing pressure (e.g. Grigg 2002; Pahl 2020a). Nevertheless, kangaroo populations, together with other unmanaged herbivores can contribute significantly to total grazing pressure of an area (Hacker *et al.* 2020).

The grazing pressure applied by unmanaged herbivores can limit the effectiveness of management actions to achieve rangeland regeneration (Norbury & Norbury 1993). Examples from the Gascoyne region of Western Australia (WA) indicate that, following removal of sheep, the density of kangaroo dung increased 6-fold (Norbury & Norbury 1993), suggesting that kangaroos move into areas with increased fodder availability. In addition to contributing significantly to TGP, kangaroo populations experience heavy mortality during drought with associated, and widely publicized, poor welfare outcomes (Wilson & Edwards 2019). Managing TGP in pastoral landscapes requires greater understanding of the factors determining population dynamics of each kangaroo species, including land use, the kangaroo commercial harvest effort, the impact of predator abundance, and environmental variables. Here, we briefly explore each of these potential drivers.

Land use and management

There is some evidence that grazing by livestock has modified the understorey of the rangelands to the benefit of kangaroos (Newsome 1971, 1975). Grazing by sheep in the Pilbara has resulted in an increase in *Triodia pungens*, which, once mature, is avoided by sheep but beneficial for euros (*Osphranter robustus*; Fig. 1c), contributing to an increase in euro abundance (Newsome 1975). Similarly, the creation of subclimax grassland by ruminant livestock in central Australia lead to greater availability of green pick (i.e. new growth promoted by rainfall), which benefits red kangaroos (Newsome 1971, 1975). Since the seminal work carried out by Newsome (1971, 1975), the rangelands sheep flock has largely been replaced with cattle, driven by declining demand for wool, increasing price of alternative commodities, and in some areas, dingo predation (Allen & West 2013; Forsyth *et al.* 2014); however, kangaroo populations remain high. Research published in 1982 showed that in south-eastern Australia, kangaroo densities were greater in pastoral areas than intensive wheat and sheep farming areas or within ungrazed natural vegetation such as mallee (Short & Grigg 1982). This difference has been attributed to the lack of shelter trees in cleared wheat and sheep holdings as well as the intense control effort by these farmers, while natural vegetation contains few palatable grasses and an absence of water points (Short & Grigg 1982). Despite recognized habitat preferences of kangaroos, some studies have not detected differences in kangaroo habitat use between land tenures, which typically reflects land use (Jonzén *et al.* 2005; Letnic & Crowther 2013).

Production of livestock grazing in Australia has required installation of artificial water points (AWPs) (Ealey 1967; James *et al.* 1999). Sheep and cattle must drink more frequently than kangaroos (Dawson *et al.* 1975), and therefore do not move as far from water as kangaroos (Fensham & Fairfax 2008). The proliferation of AWPs is believed to be a cause of the increase in kangaroo abundance within the southern rangelands over the past century (James *et al.* 1999). However, there is some uncertainty about the role of AWPs in influencing kangaroo distribution and abundance, with food availability, landscape features and predation frequently being identified as limiting macropod densities rather than water availability (reviewed in Lavery *et al.* 2018). However, Lavery *et al.* (2018) also identified a lack of experiments assessing the role of AWP on macropod density at appropriate spatial and temporal scales.

Throughout much of the Australian southern rangelands, kangaroos are harvested commercially for meat and leather. The primary goal of the industry is to provide kangaroo products to consumers, but ecologically-sustainable commercial harvest of kangaroos also provides an alternative management approach to reducing the damage caused by over overgrazing (Grigg 1987; Read *et al.* 2021). Conservative harvest quotas have been in place to allay concerns regarding the exploitation of kangaroos. As a result, after 40 years of monitoring, there is no evidence that commercial kangaroo harvest threatens populations of the 4 harvested species (Ampt & Baumber 2006; Lunney *et al.* 2018; Read *et al.* 2021).

Dingoes

The dingo is Australia's largest terrestrial predator. While sheep production is incompatible with dingoes (Thomson 1984; Allen & Sparkes 2001; Fleming *et al.* 2001), the effect of dingoes on cattle enterprises is more complex (Allen 2015; Prowse *et al.* 2015). The widespread control of dingoes has been synonymous with the spread of sheep grazing throughout agricultural and pastoral regions of Australia. There are currently 2 landscape-scale barrier fences in Australia intended to reduce dingo impacts on sheep production: the State Barrier Fence in south-western Australia and the Dingo Barrier Fence in eastern Australia. Dingoes are now less common on the sheep/agricultural sides of these fences (Pople *et al.* 2000; Woolnough *et al.* 2005).

Ecological theory suggests that herbivore numbers are directly linked to primary productivity (bottom-up), as well as being controlled by predators (top-down) (Choquenot & Forsyth 2013; Letnic & Crowther 2013). The relative strength of top-down regulatory processes is expected to be weaker in areas where productivity is unpredictable and stochastic (Morgan *et al.* 2017). Theoretical and field-based studies have concluded that the abundance of kangaroos can be determined by dingo predation. Caughley *et al.* (1980), Pople *et al.* (2000), Letnic and Crowther (2013), and Rees *et al.* (2017) describe field-based studies comparing areas either side of the Dingo Barrier Fence. Such natural experiments often have confounding factors, with land capability and productivity likely to have determined the location of the fence in the first place. For example, differences in vegetation structure and complexity (Mills *et al.* 2020) or fractional vegetation cover (Fisher *et al.* 2021) have been directly attributed to kangaroo overgrazing as a consequence of lower dingo density on the "inside" of the Dingo Barrier Fence. However, Newsome *et al.* (2001) examined one area surveyed by Caughley *et al.* (1980), but included multiple years of data, and concluded that landscape differences in productivity explained kangaroo numbers, obscuring any potential impacts of dingo predation. Manipulation experiments are likely to have the greatest ability to demonstrate the relationships between kangaroos and dingoes. Two studies monitored kangaroo populations over time following the introduction (Moseby *et al.* 2019; albiet within a fenced reserve) or removal (Thomson 1992) of dingoes; both studies found that dingoes had some regulatory effect on kangaroo populations. While these field-based studies show dingoes can play a regulatory role on kangaroo populations, the effect of predation on kangaroo density is not independent of plant biomass, habitat and land management (e.g. Newsome *et al.* 2001) suggesting the relationship is far from well understood. Nevertheless, some cattle graziers have ceased control of dingoes, anticipating regulation of kangaroos and reduced TGP (Emmott 2021; Pollock 2019), providing additional field trials.

Environmental factors

Population growth rate of various kangaroo species have been strongly linked to rainfall (Cairns & Grigg 1993; Letnic & Crowther 2013; Lunney *et al.* 2018). Increases in kangaroo density in response to rainfall show a lagged response, reflecting increased reproduction rate in response to vegetation growth and standing dry matter (Cairns & Grigg 1993; Lunney *et al.* 2018). However, negative responses can be more immediate. Kangaroo mobility increases in drought conditions, presumably to find resources (Norbury *et al.* 1994), and there can be dramatic reductions in kangaroo density through death during drought (Ealey 1967; Caughley *et al.* 1985; Newsome *et al.* 2001; Wilson & Edwards 2019; Zanker 2021). Authorities use rainfall to predict population size in years between aerial surveys, which is then used to set harvest quotas by the WA Department of Biodiversity, Conservation & Attractions (DBCA 2019).

Aims of this study

Control of dingoes and provision of AWPs across Australian southern rangelands are likely to have removed important limitations to kangaroo populations that are now only food limited (Bayliss 1987; Cairns & Grigg 1993) and contributing significantly to TGP. In this study, we analyzed 22 years of aerial monitoring data from the southern rangelands of WA to test whether the density of 3 kangaroo species (red kangaroo, western grey kangaroo, euro) is associated with:

1. Environmental and management factors
2. Dingo control
3. Presence of the State Barrier Fence

MATERIALS AND METHODS

Kangaroo surveys

Since 1994, aerial surveys for red and western grey kangaroos and euro kangaroos have been used by DBCA to estimate abundance and inform setting of the annual harvest quota. Survey transects are flown at 0.5-degree latitude intervals (Fig. 2). The survey is broken into 4 monitoring zones: northern, central, south-eastern and south-western. As the present study is focused on the southern rangelands, only the central and south-eastern zones were analyzed (Table S1, Supporting Information). The central zone contains the Murchison, Gascoyne, Yalgoo, Avon Wheatbelt, and Geraldton Sandplains IBRA regions, and the southern-eastern zone contains the Murchison, Coolgardie, Nullarbor, Great Victoria Desert, Mallee, and Esperance Sandplains IBRA regions (Thackway & Cresswell 1995). The smaller south-western block is generally surveyed annually, while each of the larger monitoring blocks is surveyed every 3 years on a rotational basis; for example, the south-eastern zone was surveyed in 1996, the central zone in 1997, and the northern zone in 1998. As a note, from 1981 until 1993, a triennial aerial survey of WA was conducted by the then Australian Nature Conservation Agency; however, the raw data were not available and we have therefore not included these data in the present study.

The aerial survey technique is described in detail in Pople and Grigg (1999). Broadly, fixed-wing aircraft are flown along transects at 100 knots, at 76 m (250 feet) above ground level (AGL), with a 200-m-wide strip searched for the 3 species of kangaroo (DBCA 2018). A "cell" represents 5 km of flown transect, which is equivalent to surveying 1 km^2. Standard correction factors are applied for temperature and vegetation type (Table S2, Supporting Information).

Land use and management

Land use category is likely to incorporate elements of other factors such as availability of grasses for foraging or availability of drinking water. For example, much of the variation in the availability of AWPs is likely to

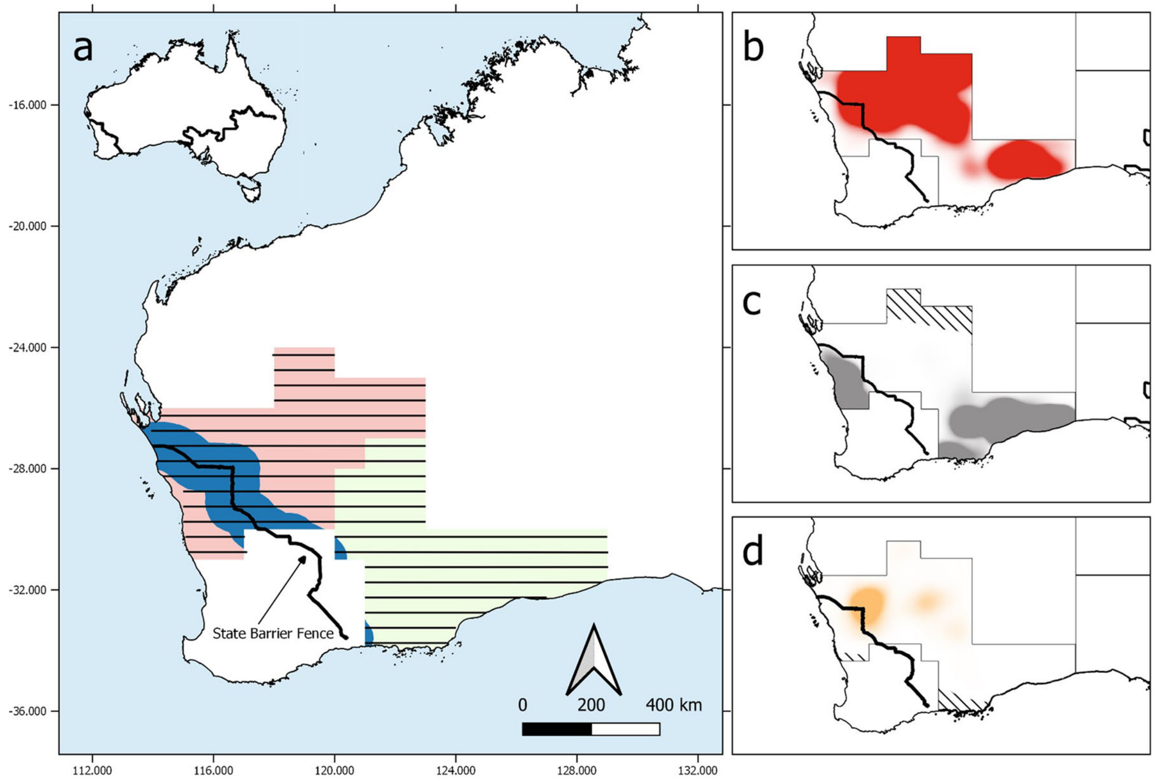

Figure 2 (a) Location of the kangaroo density survey transects (horizontal black lines), in the central (pink shading), and south-eastern (green shading) monitoring zones, flown on a triennial basis across Western Australia. Inset the 2 dingo barrier fences: the Western Australian State Barrier Fence and the Dingo Barrier Fence running across 4 states in eastern Australia. Right hand panel: heat maps indicating the areas of greatest density of (b) red kangaroos (*Osphranter rufus*) (red), (c) western grey kangaroos (*Macropus fuliginosus*) (grey), and (d) euros (*O. robustus*) (orange), over the period 1996 to 2018. All 3 species occur outside of the study area but shaded areas show locations with greatest density within the study area. Areas to the southwest of the State Barrier Fence are referred to as "inside," while areas to the northwest are "outside." Hatched areas indicate parts of the study area that were outside the distribution of western grey kangaroos and euros (c,d). State Barrier Fence dataset is shown by the blue area in plot (a).

be tied to land use; pastoral land generally has abundant AWPs for livestock, agricultural land may also have many AWPs (unless the operation is predominantly grain growing), while reserve and government land generally have no AWP or they have been turned off. Land use and management type were assumed to be constant at the individual property level over the study period. Across the entire survey, 61% of survey cells were on pastoral land, 7% on agricultural land, and 31% on government land and reserves (i.e. conservation estate, unallocated crown land, and miscellaneous reserves). Livestock type and livestock numbers were extracted from Australian Bureau of Statistics census data at the level of Local Government Area (LGA). Goats are also recorded during aerial surveys. To investigate the potential for a competitive effect on kangaroos by goats, the density of goats, averaged at the level of LGA, was tested.

Dingo density estimate

To assess the impact of the dingo predation on the density of kangaroos, we created 3 spatial data layers.

1. *Restricted Chemical Permits as a surrogate of permitted dingo control*. We used the Department of Primary Industries and Regional Development (DPIRD) Restricted Chemical Permit (RCP) database, a record of all granted permits and the property they are associated with, to calculate the percentage of each LGA in which poison baiting or trapping with strychnine was permitted for 2010–2020 (this was the only period for which electronic data was available) at the level of LGA. This does not necessarily imply that control was undertaken in these areas, only that a permit existed for control. We extrapolated from these available data back to the beginning of the study period. LGAs

where dingo control had only recently commenced (areas "inside" the State Barrier Fence where broadscale control only commenced since 2013) were assumed to have had no dingo control prior to 2010. LGAs with consistently high (approx. >75% RCP-permitted area) dingo control were assumed to have consistent dingo control since 1996; average percentage RCP-permitted area for 2010–2020 was therefore extrapolated back for 1996–2009. For LGAs with a consistent increase in the percentage of the RCP-permitted area, the average value over a shorter period (2010–2012) was extrapolated back for 1996–2009.

2. *Dingo density*. We estimated dingo density across the study area in the years 1996–2018 using the approach of Woolnough *et al.* (2005). To create our estimate of dingo density, we conducted interviews with 4 DPIRD staff directly working on dingo management in WA for ∼20 years each, who also consult broadly with land managers over time to monitor vertebrate pests. For each LGA, participants were asked to estimate the density of dingoes as absent (0), rare (1), medium (2), or common (3) for each year between 2003 and 2018. An average value was then calculated across the 4 experts for each LGA for each year. Each kangaroo-monitoring transect point was assigned a value for dingo density for the matching time point.
3. *State Barrier Fence*. We recorded which side of the State Barrier Fence data were collected for each 5-km length of transect.

Environmental factors

We recorded terrain ruggedness and vegetation cover for each 5-km length of aerial transect. Rainfall (in the previous 12 and 12–24 months) and total standing dry matter (TSDM) (in the previous 12 and 12–24 months) were calculated at the level of LGA (details in Table 1, and Table S1) . The coordinates of the start of each 5 km-length of transect were used as a survey point for extracting environmental information from Geographic Information System (GIS) input layers for each year of the study (Table 1). The previous year's kangaroo density in the relevant monitoring zone was included as a covariate.

Statistical analysis

Two datasets were analyzed for each kangaroo species (6 datasets in total):

1. Full survey dataset. As red kangaroos are found throughout the survey area, the entire survey area was analyzed for this species. The analysis included a smaller area for western grey kangaroos and euros, including only those locations where these species are likely to occur (Fig. 2).
2. State Barrier Fence dataset. A separate analysis was conducted on datapoints from within 100 km of the State Barrier Fence (Fig. 2), allowing a finer scale comparison of the effect of the fence between relatively similar areas.

Prior to inclusion, each dataset was filtered to exclude missing values, which were generally due to data gaps in layers. All input variables were scaled (each value has the mean for that variable subtracted and is then divided by the standard deviation) before being included in analysis.

Kangaroo data were collected as count data, but integers were converted to a continuous scale after correction for temperature and vegetation. The data were highly zero-inflated (>80% zeros). Given these characteristics, a GLM with a Tweedie link was fitted for each species, using the "tweedie" package (Dunn 2017) in R (R Core Team 2018). The Tweedie distribution allows for highly zero-inflated continuous data, with true zeros, to be used without the need for dramatic data filtering or pooling to fit the assumptions of alternative distributions, and the variable power of the Tweedie link can be specified for each individual model in order to optimize fit (Dunn & Smyth 2005). When fitting the model, we used log-transformed kangaroo density (+1) to achieve best fit. We compared alternative models using the derived Tweedie-AIC value (Dunn 2017).

A single interaction term, *land use x 12-month lagged-rainfall*, was included in all models as the availability of AWPs on pastoral land makes it likely that rainfall will have minimal effects on drinking water for kangaroos on pastoral land (compared with relative absence from reserves and public estate). A global model was fitted for each for the 6 datasets (full and State Barrier Fence subset data for each of the 3 species), containing all 15 independent variables plus the *land use x 12-month lagged rainfall* interaction term (Table 1). All combinations of the variables within the global model were fitted using the *dredge* function in the "MuMIn" package (ver. 1.43.17) (Barton & Barton 2020) in R. Variance Inflation Factors (VIF) were calculated for each variable in the fitted global model using the *vif* function in the "car" package (Fox *et al.* 2007) in R. Variable pairs that resulted in a VIF > 3 were specifically excluded from *dredge* analysis, so that models containing collinear variables were not fitted (all excluded combinations specified in Table S3, Supporting Information). Model averaging was performed on the top models (all models within Δt-AIC < 2 of the best model).

Table 1 Layers used to extract environmental and anthropogenic data as covariates to model the density of red kangaroos (*Osphranter rufus*), western grey kangaroos (*Macropus fuliginosus*), and euros (*O. robustus*). Details relating to sources and scale of data in Supporting Information

Variable name	Description
Kangaroos (dependent variables)	
Separate density estimates for red kangaroo (RK), western grey kangaroo (GK), and euro (E)	The number of individuals recorded in a 5 km-length of transect (~1 km^2), after correction for temperature and vegetation
Land use and management	
Livestock type	Proportion of total DSE that are sheep in Local Government Area (LGA)
Livestock density	Dry sheep equivalent per km^2 in LGA
Goat density	Average goats per km^2 in LGA
Land use	The type of land tenure under which the individual property is held, aligning broadly with the type of management: (1) pastoral, (2) agricultural/grain-growing, (3) government/reserve
Previous kangaroo harvest	Kangaroos harvested per km^2 in that Management Zone in the previous calendar year
Dingoes	
Percentage of LGA covered by Restricted Chemical Permits (RCP)	RCP-permitted area as % of the total LGA area
Density of dingoes	Average of 4 expert rankings for each year for each LGA
State Barrier Fence	Inside (southwest of fence) or outside (northeast of fence)
Environmental	
Terrain ruggedness	The standard deviation of elevation within a 5-km radius
Vegetation cover	Mean tree cover within a 5-km radius
Rainfall	Rainfall decile in the 12 months prior to survey
Lagged-rainfall	Rainfall decile lagged 12 months (12–24 months prior to survey) across each LGA
Total standing dry matter (TSDM)	Average TSDM in previous 12 months across each LGA
Lagged-TSDM	Average TSDM in lagged previous 12 months (12–24 months prior to survey) across each LGA
Previous kangaroo density	Individuals per km^2 in the previous year across each LGA

Forest plots of the model-averaged beta estimates (±95% confidence intervals) of each predictor variable were made using "ggplot2" (Wickham 2016) in R. For visualization, graphs were also made using a fitted model that contained all significant predictors from model averaging, where significant predictors were those for which the 95% confidence interval did not overlap zero. Individual relationships were also plotted using the *ggeffect* function in the "ggeffects" package (Lüdecke 2018) in R. This method is useful when displaying fitted models with multiple explanatory variables, as it holds other variables constant (at an average or median value) while displaying the effect of the variable in question (Lüdecke 2018). All plots weare back-transformed to be plotted on the original scale of the variables displayed.

All analyses were performed in the R statistical environment (version 3.5.2; R Core Team 2018).

RESULTS

Overall

Red kangaroos were observed over the entire study area, a total of 13 440 individual 5 km-length cells (i.e. 13 440 km^2). Abundance of red kangaroos was highly variable between years in the central monitoring zone (Fig. 3);

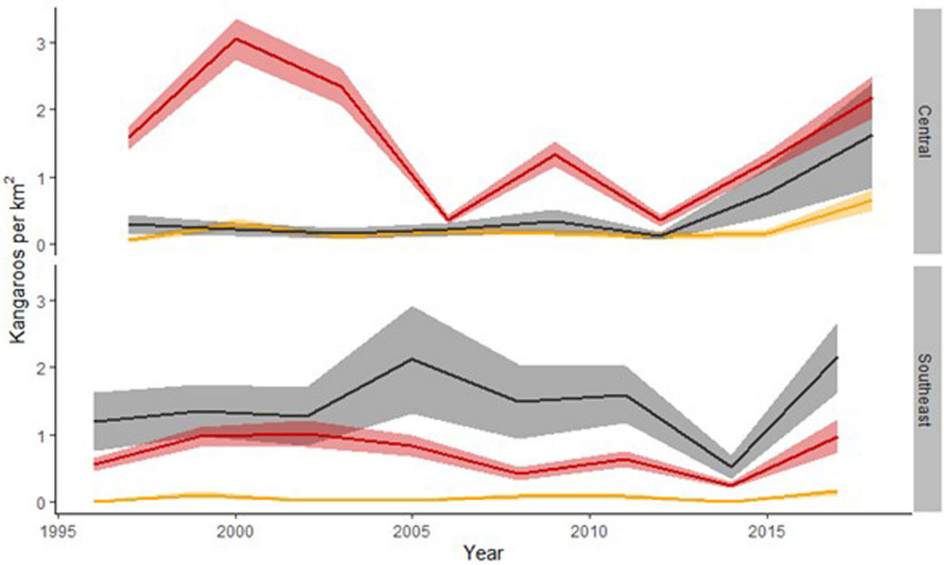

Figure 3 The mean density of red kangaroos (*Osphranter rufus*, red line), western grey kangaroos (*Macropus fuliginosus*, grey line), and euros (*O. robustus*, orange line) in the central and southeast monitoring zones of Western Australia. Shaded areas indicate 95% confidence intervals.

there was a maximum population size of approximately 1 189 886 (95% CI: 1072 777–1 306 996) red kangaroos in 2000, and a minimum of 139 270 (95% CI: 105 044–173 496) in 2012. Western grey kangaroos were distributed over 11 639 km^2 of the survey area. Their numbers were highly variable between years in the southeast monitoring zone (Fig. 3) with greatest density in southeast and northern parts of the study area (Fig. 2). Euros were distributed over 12 909 km^2 of the survey area, with greatest numbers found in the northwest parts of the study area.

Full dataset

The density of red kangaroos was greatest on pastoral land and lowest on agricultural land (Figs 4,5). The density of red kangaroos was positively associated with the number of red kangaroos harvested in the previous year. Red kangaroos were positively associated with the RCP-permitted area, that is, there were more red kangaroos in locations where there was more likelihood of toxic baiting for dingoes. However, dingo density was not retained in the top models and there was no significant effect of the presence of the State Barrier Fence. There was some evidence of preference for flat ground (negative relationship with terrain ruggedness) and red kangaroos were more common in areas with less vegetation cover (Figs 4,5). Red kangaroo density was positively correlated with 12-month lagged-rainfall (Figs 4,5).

Western grey kangaroos were most abundant on agricultural land, and least abundant on reserve and government land (Figs 4,5). The density of western grey kangaroos was positively associated with the number of western grey kangaroo harvested in the previous year (Figs 4,5). Western grey kangaroos were less abundant in areas with a greater RCP-permitted area, which likely reflects that grey kangaroos were more common across agricultural land rather than pastoral land (Figs 4,5). Dingo density and presence of the State Barrier Fence were not retained in the top models. Western grey kangaroos preferred flat ground (indicated by the negative relationship with terrain ruggedness) (Figs 4,5).

Euro density was not significantly different between the 3 land use types and euro density was negat with number of euros harvested in the previous year. Euros were more common in areas with greater RCP-permitted area (dingo density and presence of the State Barrier Fence were retained in the top models but were not significant factors) (Figs 4,5). Euros prefered rugged terrain (Figs 4,5) and were more common in areas with less vegetation cover (Figs 4,5).

It was notable that the density of the 3 species was not correlated with feral goat, livestock, or estimated dingo densities, the presence of the State Barrier Fence, rainfall

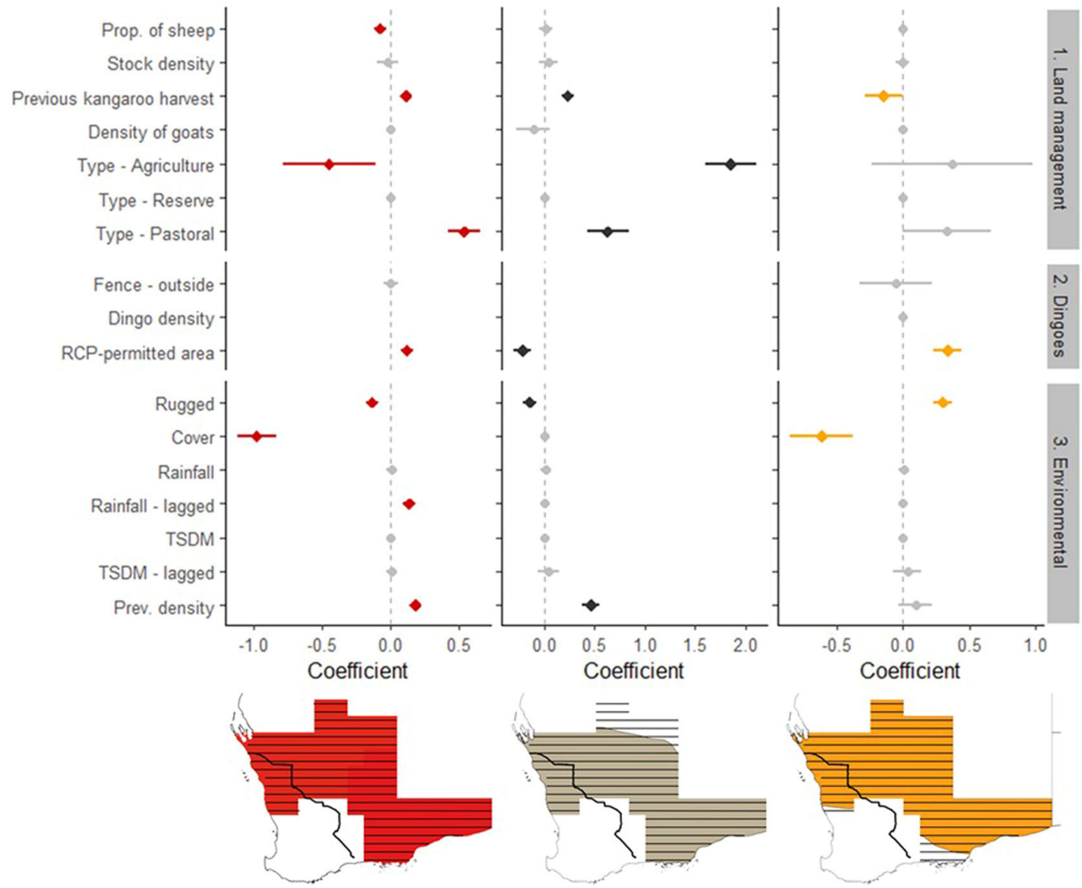

Figure 4 Model-averaged beta values of explanatory variables on the density of red kangaroos (*Osphranter rufus*), western grey kangaroos (*Macropus fuliginosus*), and euros (*O. robustus*). Bars indicated the 95% confidence intervals, and bars that overlap zero are considered to be non-significant predictors (grey points and bars). The maps at the bottom indicated the area over which data was included.

in the previous year, or the current or 12-month-lagged TSDM.

State barrier fence dataset

Data from the State Barrier Fence subset was collected between 1996 and 2018, representing 2870 km^2 of sampling for all 3 species. As this scale, there were no marked differences in density for the 3 species.

Within 100 km of the State Barrier Fence, red kangaroos were positively associated with average livestock density, but negatively associated with increased proportion of sheep grazing (i.e., red kangaroos were more common in areas with cattle) (Fig. 6). Similar to the full analysis, red kangaroos were most common on pastoral land and more common where there was a greater proportion of RCP-permitted area (Fig. 6). Red kangaroos were negatively associated with vegetation cover, and positively associated with terrain ruggedness (Fig. 6).

Within 100 km of the State Barrier Fence, western grey kangaroos were most abundant on agricultural properties and least abundant on pastoral properties (Fig. 6). They were also negatively associated with 12-month-lagged rainfall (Fig. 6).

Within 100 km of the State Barrier Fence, euros were negatively associated with the previous euro harvest, but positively associated with the previous euro density (Fig. 6). Consistent with the larger dataset, euros were more common in rugged-terrain areas.

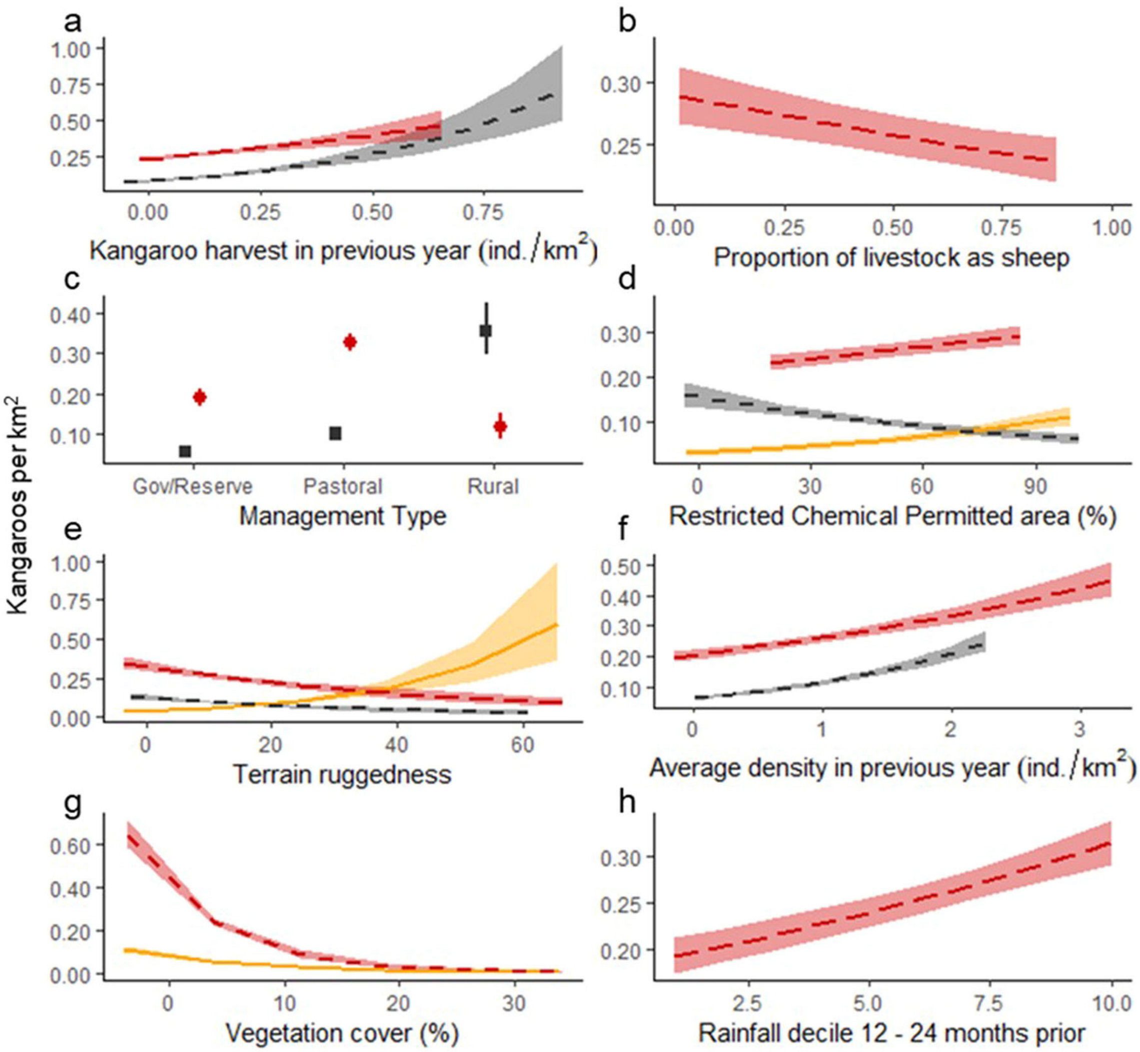

Figure 5 The effect of land use variables (a–c), dingo management (d), and environmental variables (e–h) on the density of red kangaroos (*Osphranter rufus*), western grey kangaroos (*Macropus fuliginosus*), and euros (*O. robustus*). Only those variables that were significant after model averaging are included here, and are only shown for the species in which they were retained in the top models. While euro density was significantly associated with harvest in the previous year, the low harvest effort means that the relationship was not included in the plot (a).

DISCUSSION

The long-term degradation of rangelands around the world presents a significant threat to biodiversity and livelihoods of livestock producers (Harris 2010; Bedunah & Angerer 2012). In Australia, there is a renewed focus on understanding the contribution of kangaroo populations to TGP, and the impact that this has on rangeland health and livestock production (Mills *et al.* 2020; Emmott 2021; Fisher *et al.* 2021). Broadly, the habitat associations identified in this study for the southern rangelands of Western Australia were similar to those recorded previously for red kangaroos (Newsome 1975; Short *et al.* 1983), western grey kangaroos (Short *et al.* 1983), and euros (Ealey 1962). However, density of these kangaroo species also varied with land management practices and potential dingo control (estimated as the proportion of land covered by Restricted Chemical Permits for dingo control). Here we discuss the basic habitat requirements of each of the 3 species investigated in this study, followed by an exploration of the potential impact of land use, commercial kangaroo harvest, and dingo control on their abundance.

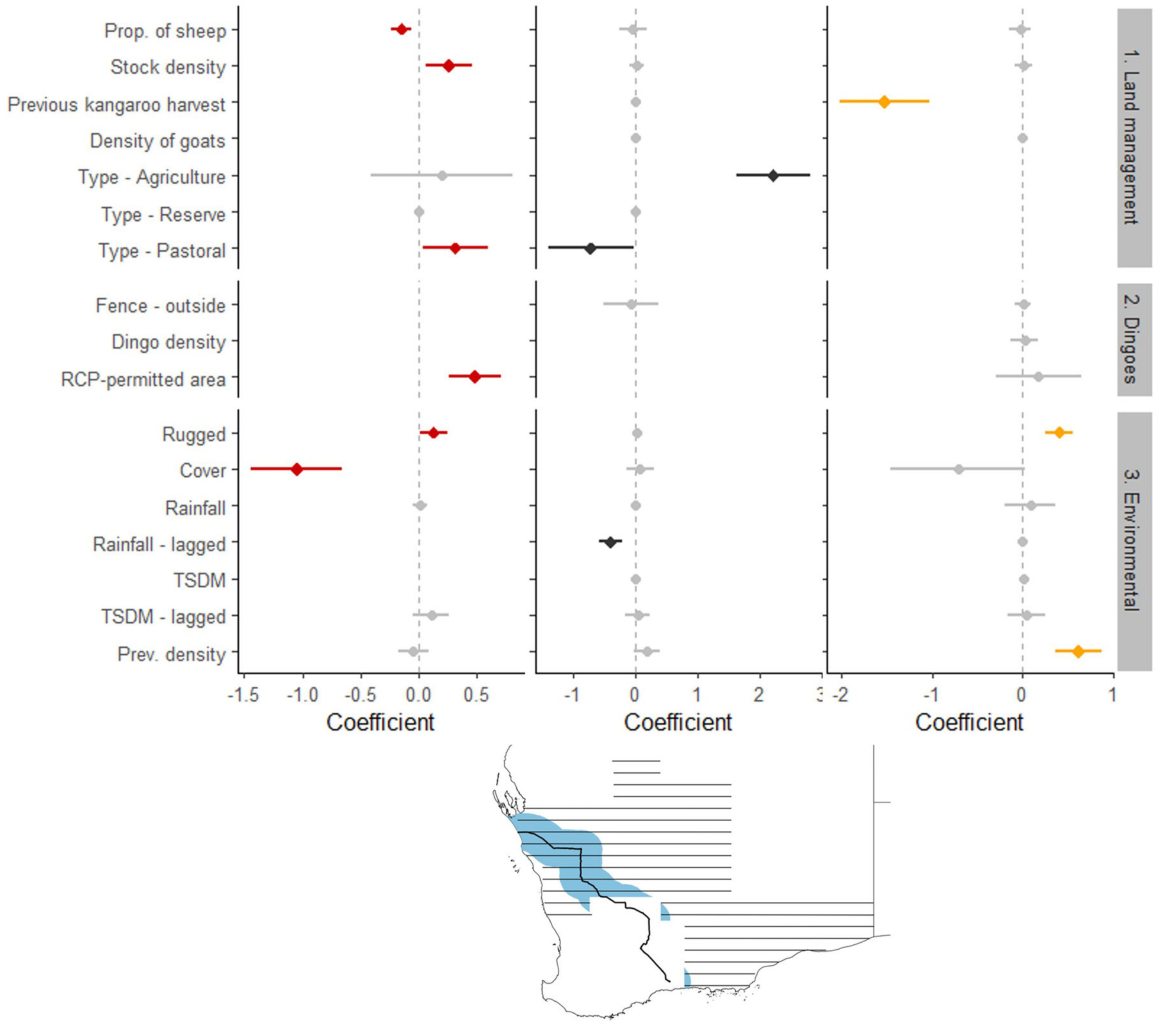

Figure 6 Model-averaged beta values of explanatory variables retained in the top model set (Δt-AIC < 2) on the density of red kangaroos (red), western grey kangaroos (grey), and euros (orange) at points within 50 km of the state barrier fence (area shown in blue in the map below). Bars indicated the 95% confidence intervals, and bars that overlap zero are considered to be non-significant predictors (light grey points and bars). Variables are sorted from most negative estimates on the bottom, to positive estimates at the top.

While red kangaroos are the most broadly distributed macropod species in WA, their density is lower than recorded in eastern Australia (Short *et al.* 1983). Red kangaroos are primarily grazers, favoring open plains where grasses predominate, and are therefore less common in woodlands and shrublands (Short *et al.* 1983). This habitat preference is reflected in the greater density in areas with low vegetation cover and low terrain ruggedness. The rate of increase of red kangaroo populations is known to be driven by primary productivity, which in turn is driven by antecedent rainfall (Bayliss 1987; Cairns & Grigg 1993). Here, we were unable to directly calculate the annual rate of increase, as each area was only surveyed every 3 years. To account for this temporal non-independence, we included the modeled previous density, and the 12-month lagged rainfall, both of which were positively associated with red kangaroo density. We found that the density of red kangaroos was greatest on pastoral land, and lowest on agricultural land. It is likely that rather than avoiding agricultural land, the natural distribution of red kangaroos tends to end at the western boundary of the pastoral zone, which is approximately the 250 mm isohyet (Short *et al.* 1983). After swamp wallaby (*Wallabia bicolor*), red kangaroo is the second most common prey consumed by dingoes across Australia (Doherty *et al.* 2019; Fleming *et al.* 2022).

The distribution and density of western grey kangaroos is largely driven by climatic factors, such as the seasonality of rainfall, preferring areas with winter rain (May–October) (Short *et al.* 1983). As the winter-rainfall regions of WA are less subject to stochastic rainfall driven resource pulses than the arid zone, it is likely that temporal changes in rainfall and pasture availability are insufficient to be a significant driver of western grey kangaroo density (we found no evidence for an effect of rainfall on this species). Areas dominated by winter rainfall largely correspond to the "wheatbelt," the grain-growing region of southwest WA (Short *et al.* 1983), with the notable exception of high western grey kangaroo densities across the Nullarbor region.

Euros are colloquially known as "hill kangaroos," and in the present study displayed their well-documented preference for rugged-terrain country, including rocky outcrops and breakaways (Ealey 1967). Euros are highly selective for grasses (Ellis *et al.* 1977), which may account for their preference for grazing in more open areas, as opposed to the often shrub-dominated woodlands.

Dingoes

Numerous studies have concluded that predation by dingoes regulates the abundance of kangaroo populations, and that widespread dingo control in food production landscapes for livestock protection has alleviated kangaroo population control through predation (Caughley *et al.* 1980; Pople *et al.* 2000; Letnic & Crowther 2013). While kangaroo populations are significantly influenced by bottom-up processes, when macropod density is high enough to support dingo populations, kangaroos may be regulated by a top-down predator–herbivore feedback loop (Choquenot & Forsyth 2013). As such, suppression of dingo populations is hypothesized to result in increased kangaroo populations that are limited only by pasture availability (Choquenot & Forsyth 2013). We assessed the effect of dingoes on kangaroo populations using 3 variables: the RCP-permitted area, an estimate of dingo density, and presence of the State Barrier Fence. Red kangaroos and euros were positively associated with the RCP-permitted area (note that this is not actual control effort, but a surrogate measure of likely dingo control effort). This result could be interpreted as suggesting that the extent of dingo control is associated with an increase in red kangaroo and euro density, as revealed by numerous previous studies (Caughley *et al.* 1980; Pople *et al.* 2000; Choquenot & Forsyth 2013; Letnic & Crowther 2013). By contrast, western grey kangaroos were negatively associated with RCP-permitted area. We note as a caveat, that such correlations do not demonstrate causation, and the inverse relationships for red kangaroos and euros *vs.* grey kangaroos also clearly demonstrate that the correlations are not a direct response to anticipated dingo control. An alternative explanation posits that these relationships reflect habitat features and land use other than dingo abundance, where there are different levels of reliance on dingo control for pastoral versus agricultural (i.e. largely crop-growing) lands, as noted by Newsome *et al.* (2001).

There are other important caveats with these dingo datasets. The relationship between the RCP-permitted area and dingo density can be weak and highly variable. For example, in recent years, baiting in the southern rangelands of WA seems to be particularly ineffective (Kennedy *et al.* 2021) compared to previous studies (Thomson 1986). Consequently, greater investment in dingo control does not necessarily result in fewer dingoes (Kreplins *et al.* 2018; Kennedy *et al.* 2021). Furthermore, obtaining an RCP does not necessarily mean dingo control was actually carried out on the ground. Well-organized community biosecurity groups encourage and enable landholders to gain RCPs to the maximum extent allowed, but landholders may never actually carry out dingo control (T. Kreplins, personal observation).

Density of dingoes is extremely difficult to quantify at the site-scale, let alone gaining an understanding across multiple years at the regional scale. Our approach of interviewing DPIRD employees was based on that used by Woolnough *et al.* (2005), and was undertaken because there are no recent regional estimates of dingo density in Western Australia. Such an approach is naturally limited by the knowledge and memory of interviewees, the scale at which density is estimated, and subject to individual biases. Nevertheless, we believe that observed trends in dingo density over the period of the study are likely to represent coarse trends, even though these broadscale temporal changes in estimated dingo density ultimately proved uninformative as predictors of kangaroo density.

When limiting our analysis to areas within 100 km of the WA State Barrier Fence, we found no evidence of a difference in density on either side of the fence, and a positive correlation between RCP-permitted areas on red kangaroo density only. Most studies that have investigated the effect of dingo predation on kangaroo populations have relied on comparison across the Dingo Barrier Fence in Queensland, New South Wales, and South Australia, inferring that differences in kangaroo populations are driven by dingo density (Caughley *et al.* 1980; Pople *et al.* 2000; Letnic & Crowther 2013; Rees *et al.* 2017). In contrast with recent studies on the Dingo Barrier Fence in eastern Australia (Mills *et al.* 2020; Fisher *et al.* 2021), we found no significant differences in density on either side of the WA State Barrier Fence for 3 kangaroo species. It is possible that the difference in dingo density within 100 km of the fence was insufficient to effect a difference in kangaroo population control. Dingo control effort is high on both sides of the WA State Barrier Fence and the fence has some known locations where it is permeable to dingoes (e.g. road crossings). The few remaining pastoral enterprises running sheep on the "outside" are generally within 100 km of fence, and properties "inside" the fence running small livestock (i.e. sheep) have seen incursions by dingoes through the fence for over 10 years (Pacioni *et al.* 2018). As such, dingoes are present, but subject to relatively high control effort, on both sides of the WA State Barrier Fence. Another important observation is that the fence itself acts as a barrier to kangaroo movements and can effectively concentrate animals in its immediate vicinity (Bradby *et al.* 2014; Vlachos 2020).

Commercial harvest of kangaroos

There was no evidence that commercial harvesting had a negative effect on the density of red and western grey kangaroos in the southern rangelands of WA. In fact, there was a significant positive relationship between the numbers of kangaroos harvested in the previous calendar year and the density of red and western grey kangaroos. This result is likely an artifact of commercial shooters targeting areas of high density, which remain at high density the following year.

Grigg (1987) postulated that kangaroo harvesting would reduce grazing pressure, resulting in lower TGP and better long-term grazing practices. However, we found no evidence of a relationship between kangaroo density and kangaroo harvesting, which is unsurprising given that the conservative harvest quota of 15–17% has been met in only 2 years since 1972 for red kangaroos, and 3 years since 1983 for western grey kangaroos (DBCA 2018). At current harvest rates, the commercial kangaroo harvest appears to provide no regulatory effect on kangaroo populations, and is far from presenting a threat, as suggested by Ben-Ami *et al.* (2010).

In contrast to red and western grey kangaroos, there was a significant negative relationship between the harvest of euros and their density. There has been no commercial harvest of euros in WA since 2009 (DBCA 2019), largely due to the small number of euros taken annually and the significant cost of the monitoring required to continue to support a commercial harvest under a Wildlife Trade Management Plan. The negative relationship is likely an artifact of no harvest in the second half of the time series analyzed in the present study corresponding with an increase in euros due to some factor unrelated to the harvest.

CONCLUSIONS

In the present study, we analyze and present results from one of the largest annual, broadscale surveys of a group of native species in Australia, comparable with the Eastern Australian Waterbird Survey (Kingsford *et al.* 2020). Results of macropod monitoring surveys across Australia are rarely interrogated or reported in the scientific literature. This lack of reporting is particularly concerning for macropods given their important ecological roles in virtually all Australian ecosystems and the acknowledged impacts of their overabundance. Given most jurisdictions in Australia conduct regular macropod monitoring of some scale, we implore researchers to use these existing datasets to build on our understanding of long-term landscape-level change in Australian ecosystems.

Red kangaroos, western grey kangaroos, and euros select habitat according to environmental factors such as terrain ruggedness and vegetation cover. In addition, all 3 species were significantly impacted by anthropogenic factors, including livestock grazing, abundant artificial water, and potential dingo control (RCP-permitted area). Red and western grey kangaroos were more abundant in food production landscapes (pastoral and agricultural land, respectively), than reserves, while euros demonstrate their preference for more rugged terrain.

Addressing our central question regarding the potential impact of dingo control on density of these macropods, red kangaroos and euros were more abundant in areas with greater RCP-permitted area, which would support an assumption of regulation of their populations via dingo predation. However, western grey kangaroos showed the opposite pattern. We conclude that 'bottom-up' processes are likely to be the primary drivers of kangaroo populations in the southern rangelands. Given the species differences in response to the extent of dingo control, we conclude that there is little evidence for a causative relationship between dingo control and macropod density.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Layers used to extract environmental and anthropogenic data as covariates to model the density of red kangaroos (*Osphranter rufus*), western grey kangaroos (*Macropus fuliginosus*), and euros (*O. robustus*), including sources and scale of data

Table S2 Standardized correction values, used during surveys of Western Australia to correct for vegetation and temperature (e.g. Department of Biodiversity, Conservation and Attractions 2018)

Table S3 Combinations of independent variables that were excluded from dredge analysis due to collinearity (VIF > 3)

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