A Spatial Harvest Model for Kangaroo Populations in Victoria

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Acknowledgment

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Contents

Tables

Figures

Summary

Context:

The implementation of a program for the commercial harvesting of kangaroos in Victoria has led to a requirement for a robust framework for setting harvest quotas to ensure the long-term ecological sustainability of the harvesting program. Kangaroo quotas are currently based on a simplified model of kangaroo population dynamics, and further model development is required so that more realistic policy options can be explored by managers.

Aims:

Using existing aerial survey data, relationships between the abundance of Eastern and Western Grey Kangaroos and environmental variables were investigated to predict grey kangaroo abundance, initial harvest thresholds, and quotas over a fine resolution grid across Victoria. The resulting grid of abundance values and environmental variables was then used to develop a spatially explicit population model for grey kangaroos in Victoria. This model was used to make predictions of future grey kangaroo abundances and the level of sustainable offtake from harvesting and culling programs at both the grid cell and population level.

Methods:

A spatially explicit model of the dynamics of grey kangaroos incorporating harvest data was developed for an area encompassing Victoria and adjacent areas of New South Wales, the Australian Capital Territory and South Australia. Besides being spatially explicit, the model incorporated additional complexities including kangaroo age and sex structure as well as dispersal.

Data on grey kangaroo counts from aerial line transect surveys conducted in 2018 were used to explore relationships between kangaroo density and environment variables using density surface models (DSM). Fitted DSM models were then used to approximate the spatially varying carrying capacity of kangaroos for the spatial model as well as to predict kangaroo densities across a fine grid within Victoria. The spatial model was used to predict the effect of different harvesting regimes (proportional offtake) on the kangaroo population to estimate the likely risk of different harvest regimes on the sustainability of the harvest program and the kangaroo population, by simulating population trajectories under each harvest regime over 50 years.

The risk of each harvest regime to the kangaroo population was expressed by the minimum total number of kangaroos contained in all grid cells covering Victoria (N_{min}). A detailed analysis was also conducted to determine the sensitivity of the model predictions to uncertainty in some of the key parameters of the model.

Results:

The most supported DSM model of the counts of grey kangaroos from aerial surveys contained variables related to the vegetation ‘greenness’ (as measured by the Normalised Difference Vegetation Index, NDVI) in the month prior to the surveys and land cover class. However, this model explained only 19% of the variance in kangaroo counts. Despite this, the predicted abundance of grey kangaroos in the kangaroo survey area (1 128 500) was similar to the design-based estimate in Moloney *et al*. (2019) (1 381 000) and had slightly better precision (coefficient of variation of 13.6% vs 15.7%).

Simulating the effects of various harvest regimes on grey kangaroo populations revealed that if harvest rates increased above 15%, the kangaroo population would be at high risk of falling to an unacceptably low level (i.e. < 50% of the population abundance without harvesting). However, with a strongly male-biased harvest strategy, ecological risks to the kangaroo population were greatly reduced. Estimates of ecological risk in the spatial model were sensitive to the assumptions made about carrying-capacity, the sex ratio of harvested kangaroos and the degree of assumed environmental stochasticity in the population vital rates.

Conclusions and recommendations:

- Based on the results of the spatial harvest model of kangaroos developed here, we recommend that the current conservative approach of setting annual harvest quotas at 10% of the estimated abundance in each harvest zone be maintained. The model results demonstrate that, under such a harvest regime, there is little chance of the population falling to an unacceptably low level.

- Aerial surveying of the kangaroo population should be undertaken at least every 3 years, using the methods presented in Moloney et al. (2018). If a harvest fraction greater than 10% is desired, then an increase in the frequency of monitoring to once a year, or once every second year is recommended.
- Ecological risks to grey kangaroo populations reduced substantially under a male-biased harvest strategy. The sex ratio of harvested kangaroos should therefore be included in the model to more accurately predict the ecological risk of the observed harvest.
- The locations of harvested kangaroos should be used to develop a model of spatially varying harvest rates that can be used to more accurately predict the likely harvest pressure on grey kangaroo populations in different parts of the state.
- The density surface model (DSM) used to predict kangaroo abundance and carrying capacity across the state could be improved by knowledge of the densities of kangaroos in forested habitats not currently subject to aerial surveys or harvest. Without good estimates of kangaroo densities in these areas, it is difficult to assess the contribution of these areas to the overall sustainability of the harvest program.
- Prediction of kangaroo abundance and carrying capacity in areas adjacent to the state border in NSW and South Australia would benefit from incorporation of aerial survey data from those state jurisdictions into the DSM model of kangaroo abundance. Future updates of the DSM model should explore the possibility of integrating interstate aerial survey data into the model, if these jurisdictions were willing to make it available.

1 Introduction

1.1 Overview

The adoption of a commercial kangaroo harvesting policy by the Victorian Government has led to a requirement for a robust framework for setting harvest quotas to ensure the long-term ecological sustainability of the harvesting program. Victoria's commercial harvesting program is regulated by the guidelines detailed in the *Victorian Kangaroo Harvest Management Plan* (DELWP 2020). The program enables authorised harvesters to take kangaroos for commercial purposes in designated areas of Victoria. The commercial take is limited by quotas set separately for seven commercial harvesting zones. The quotas are based on ecologically sustainable criteria (Scroggie and Ramsey 2019) and include kangaroos taken both from commercial harvesting operations and kangaroo control operations conducted under the Authority to Control Wildlife (ATCW) provisions of the *Wildlife Act 1975* (Vic.). Interim quota assessments have been based on quota setting approaches in other Australian jurisdictions, where quotas of between 10 and 15% of the surveyed population are typically in force.

The initial approach to quota setting was developed by Scroggie and Ramsey (2019) who used an aspatial, stochastic population model to examine the relationship between key demographic parameters of kangaroo populations, the proportional harvest quota, and resulting probabilities of population quasi-extinction. The results of this analysis supported the interim approach of applying a proportional quota of 10% as being ecologically sustainable across a wide range of plausible parameter combinations. The conclusion that this rate of harvest would be sustainable was considered conservative, as it was assumed that harvesting would be excluded from large parts of the state (such as heavily forested areas and conservation reserves), which would function as refugia. Furthermore, regular aerial monitoring of kangaroo populations in the state allows trends in abundance to be established. This means that the harvest quotas can be adjusted in response to observed changes in abundance. The use of a proportional (percentage-based) quota also reduces the absolute numbers of kangaroos harvested when abundance is low (for example, after droughts, bushfires or other stochastic events that reduce kangaroo abundance). For these reasons, the 10% proportional quota was considered highly precautionary, with only a very small risk of Victorian kangaroo populations dropping to unacceptably low abundances.

The stochastic population model developed by Scroggie and Ramsey (2019) includes some simplifying assumptions. First, the model disregards population age and sex structures, treating kangaroos as a single category of animals, with the processes of reproduction and survival subsumed by a single parameter describing the rate of population growth at a given time. Second, the model disregards the spatial distribution of kangaroos across the state and assumes that individual kangaroos have identical vital rates and the same risk of being harvested per year.

While such simple models are widely used in the analysis and management of harvested fish and wildlife populations, they lack details that may be important in decisions about harvesting programs. For example, harvesting may be preferentially directed at certain age-classes or one sex, so that the effects on population dynamics may need to account for differences in vital rates among age and sex classes in order to faithfully replicate the resulting population dynamics. It is also unlikely that the same population vital rates would apply across a large geographic area such as Victoria.

The development of population models that incorporate these additional aspects of population dynamics is desirable for two reasons. First, incorporating these complexities should allow us to describe the inherent dynamics of the population more accurately, making the model a more realistic representation of real kangaroo populations. Secondly, managers may wish to impose age-specific or age-preferential harvesting, or to impose different harvesting regimes (or exclude harvesting) in different parts of the state. Evaluating the outcomes of such management decisions necessarily requires models that can deal with age, sex and geographic variations in kangaroo populations. By constructing models that allow the analysis of population dynamics under different policies, an improved kangaroo harvest model can be used to directly evaluate and compare options that managers may wish to consider.

In this report we present the results of initial model development work intended to enhance the realism of the existing harvest model (Scroggie and Ramsey 2019). Specifically, we have incorporated age and sex structure into the model and structured the model so that spatial and temporal variation in population vital rates, carrying capacity and harvest rates can be readily incorporated. A limited exploration of some relevant harvest management scenarios is conducted, along with a detailed sensitivity analysis. We provide recommendations for additional scenario modelling and data collection that can contribute to further improvements in the model and its suitability for management decision-making.

1.2 Aims

- Using existing aerial survey data, investigate relationships between the abundance of the two species of grey kangaroos and biotic and abiotic environmental variables to predict kangaroo abundance, harvest thresholds, and quotas over a fine-resolution grid across Victoria.
- Using the grid of abundance values and environmental variables, construct a spatially explicit population model for kangaroos in Victoria that could be used to make predictions of future kangaroo abundances and the level of sustainable offtake from both harvest and other control activities at both the grid cell and population level.
- Use the model to help develop the Kangaroo Management Plan by identifying harvest zones and setting harvest rates.
- Based on the level of uncertainty in the predictions from the kangaroo population models, make recommendations on future kangaroo aerial surveys (and other necessary data collection), including scheduling and required monitoring effort.

2 Methods

The spatial harvest model was implemented using the spatially explicit population modelling software *steps* (Visintin *et al.* 2019; Visintin *et al.* 2020).The software was written using the statistical programming language *R* (R Core Team 2020) and provides flexible simulations of the dynamics of stage, age and spatially structured populations. Key components of the population biology of kangaroos were explicitly modelled using this software, with structural components and parameter values for the model informed by available information from published scientific literature together with expert opinion.

Because many aspects of the model are currently not well informed by published data, we have had to rely heavily on expert opinion to populate the model with parameter values. Importantly, much published data on the dynamics of kangaroo populations is derived from studies conducted in arid and semi-arid environments, which may not reflect the dynamics of populations inhabiting the temperate climates that predominate in Victoria. As a partial hedge against the risks inherent in such an opinion-driven approach, we have endeavoured to consider a range of plausible parameter values and run a sensitivity analysis that spans these ranges of values, as discussed below. This approach to examining the sensitivity of the model to assumptions is intended to identify critical uncertainties that could be targeted for further data collection and/or expert elicitation.

2.1 Spatial structure of the model

The entire south-eastern Australian mainland, up to 250 km beyond the state borders of Victoria, was included in the model of kangaroo population dynamics (Figure 1a). For simplicity, both species of grey kangaroo — the Eastern Grey Kangaroo (*Macropus giganteus*) and Western Grey Kangaroo (*Macropus fuliginosus*) — were modelled as a single, spatially structured metapopulation, without considering the geographic distributions of the two species, which includes a zone of overlap in north-western Victoria (Caughley *et al.* 1984a; Moloney *et al.* 2018). Given the generally similar biology and population dynamics of the two species, this was considered a reasonable assumption for the purposes of exploring the implications of different harvest policies, although in principle it would be possible to model both species separately (with differing dynamics if necessary) in an updated version of the model. The Red Kangaroo (*Osphranter rufus*) was not specifically considered in the model because it is not harvested commercially in Victoria (Scroggie and Ramsey 2019). In a sense, the model can be considered a generic model of grey kangaroo population dynamics, without a thorough consideration of differences between the two grey kangaroo species and the ecological interactions between them.

Kangaroos were harvested at the same rate throughout the study area (Figure 1b) with the exception of heavily forested areas, which were also not subject to aerial survey for kangaroos in Victoria (Moloney *et al.* 2018). For modelling the spatial dynamics of the kangaroo populations, the study area was divided into 50 km × 50 km squares (i.e. cells of 2500 km^2), with the population dynamics in each grid cell modelled separately (see below for details of how dispersal of kangaroos between cells was treated). For grid cells that partially overlapped the coastline, the assumed area of habitat within the cell (and hence it's carrying capacity) was reduced in proportion to the area of the grid cell that was located on land (Figure 1).

2.2 Modelling age and sex specific dynamics

For our demographic model we selected a structure with three age classes: juveniles, sub-adults and adults. This structure implies maturity of female kangaroos at approximately 2 years of age, which is roughly congruent with published accounts of ages at maturity in wild and captive populations of Eastern and Western Grey Kangaroos (Poole and Catling 1974; Poole 1983). A two-sex, age-structured model (Gerber and White 2014) was adopted, owing to the need to accommodate differing survival rates between the sexes, and likely male-biased harvesting of kangaroos by commercial operators (McLeod *et al.* 2004).

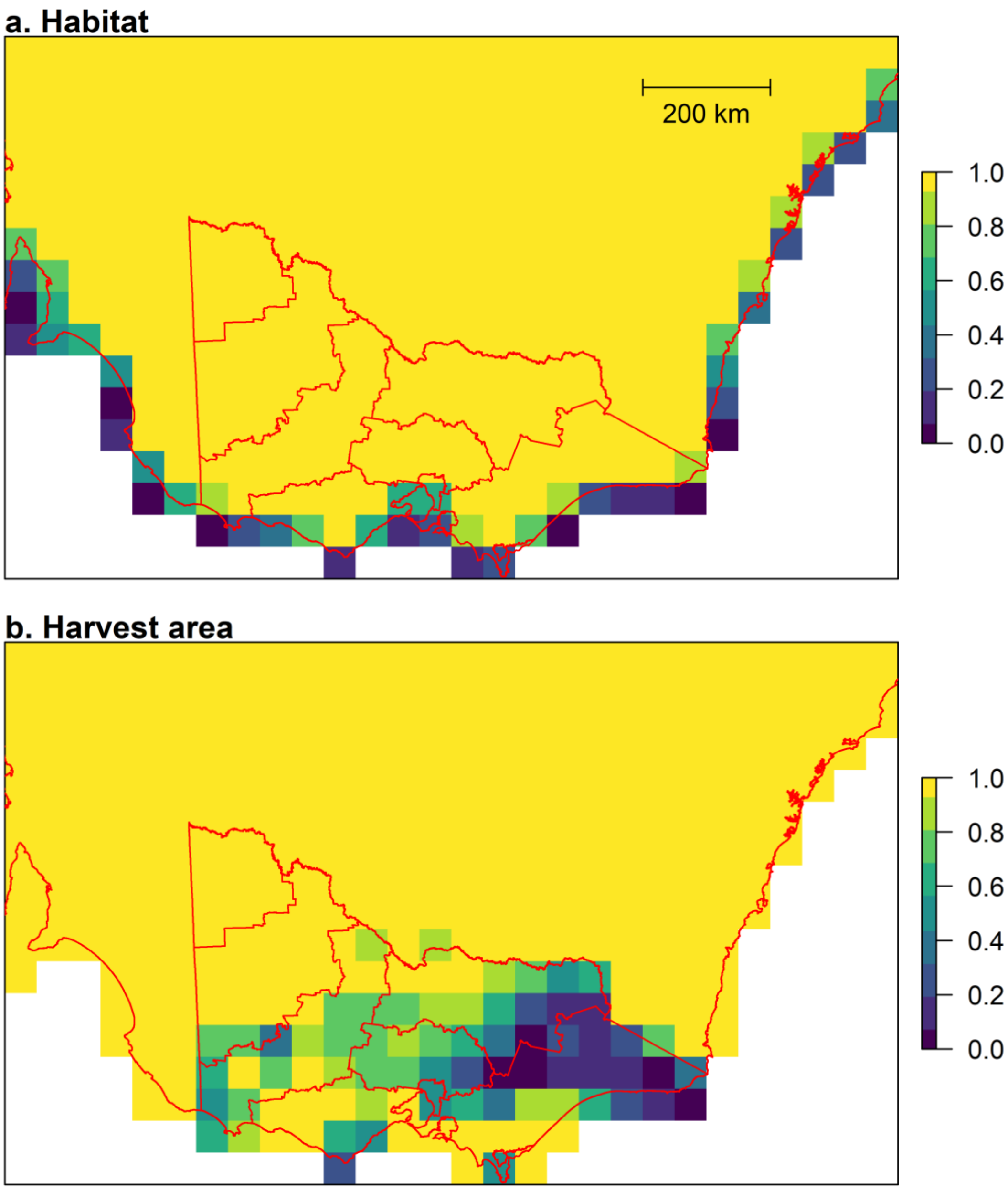

Figure 1. Map of the study area, showing (a) the proportions of assumed suitable kangaroo habitat for each 50 × 50 km cell, and (b) the proportion of habitat in each grid cell available for harvesting. (Heavily forested areas were assumed to be excluded from harvesting; these are shown in the darker blue colours.) The overlaid red lines are the coastline, the Victorian state borders, and the boundaries of the seven kangaroo harvest management zones.

It was assumed that the number of individuals in the adult male stage did not materially affect recruitment rates of juveniles (i.e. all mature females are able to find a mate regardless of local population density), which seems a reasonable assumption under most circumstances given the polygynous mating system of kangaroos (Rioux-Paquette *et al.* 2015; Montana *et al.* 2020). The dynamics of transition between life history stages (survival and recruitment) specified in our model can be described by the matrix equation:

$$\mathbf{n_t} = \mathbf{A}\mathbf{n_{t-1}}$$

where $\mathbf{n_t}$ is a column vector containing the number of individuals *N* in each life history stage (juvenile, sub-adult and adult), and sex (male, female) at time *t* years.

For computational convenience, and to simplify the model, both sexes of juvenile kangaroos are contained in a single compartment of the model. The matrix $\mathbf{A}$ specifies the vital rates (age and sex-specific rates of survival *S* and fecundity *F*) for each component of the population, as well as the proportion of males among the juveniles recruiting to the subadult population each year (ρ). This matrix equation can be more fully described as:

$$\begin{bmatrix} N_{\mathrm{j}} \\ N_{\mathrm{sm}} \\ N_{\mathrm{am}} \\ N_{\mathrm{sf}} \\ N_{\mathrm{af}} \end{bmatrix}_t = \begin{bmatrix} 0 & 0 & 0 & 0 & F \\ \rho S_{\mathrm{jm}} & 0 & 0 & 0 & 0 \\ 0 & S_{\mathrm{sm}} & S_{\mathrm{am}} & 0 & 0 \\ (1-\rho)S_{\mathrm{jm}} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{\mathrm{sf}} & S_{\mathrm{af}} \end{bmatrix} \begin{bmatrix} N_{\mathrm{j}} \\ N_{\mathrm{sm}} \\ N_{\mathrm{am}} \\ N_{\mathrm{sf}} \\ N_{\mathrm{af}} \end{bmatrix}_{t-1}$$

where the two column vectors specify the numbers of individuals in each age class at times *t* and *t* – 1*,* and the matrix specifies the vital rates (survival and fecundity) of the three age classes and two sexes of kangaroos as follows: S_{jm} = annual survival of juvenile males*,* S_{jf} = annual survival of juvenile females*,* ρ = proportion of male offspring among recruits to the juvenile stage, S_{sm} = annual survival of sub-adult males*,* S_{am} = annual survival of adult males*,* S_{sf} = annual survival of subadult females*,* S_{af} = annual survival of adult females*, F* = annual fecundity.

Under the set of vital rates specified in the transition matrix above**,** the annual maximum rate of increase (λ) of the population is given by the first eigenvalue of the matrix $\mathbf{A}$ (Caswell 2008)**.** We used the available literature and expert opinion to parameterise the transition matrix with the most likely values, as well as specifying broad yet plausible ranges for each parameter (see below). The matrix **A** was parameterised with vital rates that could be assumed to apply under good conditions at very low (near zero) population density, and therefore the associated estimate of the rate of increase (λ), reflects the maximum plausible rate. At higher densities the rates of survival and fecundity would be lower, as competition for resources reduces survival and reproductive rates below their maximum values (see section 2.2.2 below, for details of our approach to modelling density dependence in the populations). Where the maximum likely values of certain vital rates were poorly known, we chose values partly by checking the maximum rate of increase (λ) against published accounts of actual rates of increase in kangaroo populations at low-densities (Caughley *et al.* 1984b; Bayliss 1985a; Bayliss 1985b; Cairns and Grigg 1993). Collectively, these studies show that populations of both Red and Western Grey Kangaroos in the arid zone can increase at more than 20% per year (λ = 1.2). We adjusted the vital rates in our transition matrix so that the implied maximum rate of increase approximated this value, which should ensure that the dynamics of the stochastic model will not overestimate the maximum rate of increase, even if our estimates of the maximum likely values of some vital rates are too high or low.

Survival rates in wild kangaroo populations are not well known. Limited available evidence, including age structures derived from shot samples (Wilson 1975), suggests higher survival rates among females, leading to often markedly female-biased sex ratios among adult kangaroos (Norbury *et al.* 1988; Stirrat 2009). Such biased sex ratios may also be a consequence of male-biased harvesting in areas where kangaroos are culled, although other causes of mortality such as road kills are also known to be male-biased (Coulson 1997). We considered it likely that rates of survival among juveniles and sub-adults would be lower than those among adults, although reliable data on the survival rates of these life history stages are limited. Observed survival rates among juvenile kangaroos are generally low. Kirkpatrick (1985) reported survival rates of 0.5 for juvenile Eastern Grey Kangaroos in southern Queensland, while (Coulson *et al.* 2014) reported a survival rate of 0.54 among juveniles in a Victorian population of the same species. Neither of these populations were at low abundance, suggesting that where resources are not limiting, survival rates could be appreciably higher. Accordingly, we assumed a maximum survival rate for juveniles of 0.75 and explored the sensitivity to a wider plausible range of 0.65 – 0.85 (Table 1).

Similarly, there are few published studies of survival among sub-adult kangaroos. Arnold *et al.* (1991) reported a very low survival rate (0.27) for sub-adult Western Grey Kangaroos in Western Australia, but it is unclear whether this rate is broadly typical. We assumed that high survival rates for sub-adults at low population densities and in the absence of resource limitation were plausible (males 0.85, females 0.9), but also considered the implications of a broader range of values in our sensitivity analysis (see section 2.4).

It is likely that survival rates of both juveniles and sub-adults in particular will be strongly influenced by predation by feral Dogs and Dingoes (Caughley *et al.* 1980; Choquenot and Forsyth 2013), and Red Foxes (Banks *et al.* 2000), and that the impacts of such predation will vary in space and time, and in response to management of predator populations. Our model does not explicitly account for the varying impacts of predation on survival rates.

Rates of fecundity in kangaroo populations can vary markedly, depending on resource availability (Bayliss 1985a; Bayliss 1985b; Cairns and Grigg 1993), but maximum per-capita rates of recruitment to the juvenile stage of the population are unlikely to be much more than one juvenile offspring per female per year under typical conditions. Under very good environmental conditions a minority of females may be able to produce two young in a single year. Births of twins are very rare in grey kangaroos, and twins are seldom successfully raised to maturity (Norbury 1986). Accordingly, we assumed that the maximum likely per-capita recruitment rate was 1.2 juveniles per adult female, with a plausible range of 0.9 – 1.4 (Table 1).

Sex ratios among pouch young and juvenile kangaroos are generally close to parity (Poole and Catling 1974; Poole 1975; Norbury *et al.* 1988), although for Eastern Grey Kangaroo populations there is evidence that larger and older mothers produce more sons (Le Gall-Payne *et al.* 2015). We assumed that 50% of juveniles recruited to the subadult stage each year would be males, but in our sensitivity analysis we also considered scenarios where this ratio was slightly biased in either direction, to account for both differing sex ratios at birth and differential survival of pouch young (Table 1).

Table 1. Assumed vital rates (and plausible ranges) for the demographic parameters of Grey Kangaroo populations in south-eastern Australia. These are projected rates that would be expected to occur under good environmental conditions at very low population density. The ranges are the plausible ranges within which the true value will be found.

Parameter	Symbol	Likely value	Range	Sources
Age at reproductive maturity (female)		2	Fixed	Poole and Catling (1974), Poole (1983)
Age at reproductive maturity (male)		2	Fixed	
Juvenile survival (both sexes)	S_j	0.75	0.65 – 0.85	Kirkpatrick (1985): EGK 0.5 Coulson *et al.* (2014): EGK 0.54
Sub-adult survival (male)	S_{sm}	0.85	0.75 – 0.95	Arnold *et al.* (1991)
Adult survival (male)	S_{am}	0.9	0.8 – 0.95	Expert opinion
Sub-adult (female)	S_{sf}	0.9	0.8 – 0.95	Expert opinion
Adult survival (female)	S_{af}	0.95	0.85 – 0.98	Expert opinion
Per-capita recruitment	F	1.2	0.9 – 1.4	Expert opinion
Proportion of male offspring at time of recruitment to the juvenile stage	ρ	0.5	0.45 – 0.55	Poole and Catling (1974), Norbury *et al.* (1988), Le Gall-Payne *et al.* (2015)
Global temporal stochasticity of the vital rates (percentage of each value)	σ	0.2	0 – 0.3	Expert opinion

2.2.1 Assessment of recent kangaroo abundance

During September and October 2018, aerial surveys using line-transect distance sampling (Buckland *et al.* 1993) were used to estimate kangaroo densities across Victoria (Moloney *et al.* 2018). A total of 3182 km of transects were flown within three hours of sunrise or sunset in an easterly or westerly direction (flying away from the sun) at a height above ground of 200 feet (about 60 m), at a speed of 50 knots (about 90 km/h). A five-zone survey pole was used on either side of the aircraft, allowing observed kangaroos to be placed into one of five distance classes (0–20 m, 20–40 m, 40–70 m, 70 100 m and 100 150 m). The species, size and distance class of the first observation of each group of kangaroos observed was recorded. Because of the difficulty in accurately discriminating between Eastern and Western Grey Kangaroos from the air, the two species were treated as a single 'Grey Kangaroo' group. For further details of the aerial survey methodology see Leathbridge and Stead (2017).

Since the aerial survey consisted of spatially referenced transect lines, we used density surface modelling (DSM) to estimate grey kangaroo densities in Victoria. DSM is a two-stage spatial model that seeks to construct a relationship between spatially varying abundance and corresponding environmental variables, in order to predict abundance or density over the entire study region, not just the areas sampled (Miller *et al.* 2013).

A detection function was fitted to the distance data to estimate the average detection probability $\hat{p}_k$. This detection probability was then incorporated into a generalised additive model, with the observed counts of individuals as the response and the environmental covariates as the potential explanatory variables. The model for the observed counts at each transect location was therefore

$$E(n_k) = \hat{p}_k e_k \exp\left[\beta_0 + \sum_j f_j(z_{jk})\right]$$

where β_0 is an intercept term and f_j are (possibly smooth) functions of the covariates z_{jk}.

The overall sampling effort e_k (transect length) and the detection probability $\hat{p}_k$ were fitted in the model as an offset, which effectively corrects the expected counts for both imperfect detection and sampling effort (Miller *et al.* 2013). To facilitate the spatial modelling of the observed kangaroo counts, we divided the study area into 10 × 10 km cells. The locations of kangaroos in each cell were then summed to give a total count per cell. The sampling effort within each cell was derived by subdividing the kangaroo transects into the segment that occurred in each cell and calculating its length (km).

Potential covariates used as explanatory variables to model the spatial distribution of kangaroo counts were likewise derived for each 10 × 10 km cell. The covariates examined in the DSM included biotic variables (e.g. vegetation 'greenness') and abiotic variables (temperature and rainfall) (Table 2). Temperature and rainfall were derived from BioClim (https://www.worldclim.org/bioclim), which consists of a set of global climate layers for the period 1970–2000 at a spatial resolution of approximately 1 km (30 seconds of latitude or longitude). We included BioClim layers relating to mean annual rainfall (mm) (AnnRain) and temperature seasonality, which is measured by the standard deviation in annual temperature (TempSeas) (Table 2) with values for each 10 km cell calculated by averaging the BioClim cell values. Two variables representing vegetation 'greenness' were also used, both derived from remotely sensed Normalized Difference Vegetation Index (NDVI) imagery obtained from Google Earth Engine (Gorelick *et al.* 2017). The first was the average NDVI from the month immediately prior to the aerial surveys (31 August 2018 to 30 September 2018) (NDVI) and the second was the length of the growing season (length of 'greenness' period) during 2018 (Green_period). We also included a variable for land cover (Landcover) using the national land cover dataset derived from satellite imagery at a spatial resolution of 250 m (https://ecat.ga.gov.au/geonetwork/srv/eng/catalog.search#/metadata/83868). This dataset classifies landcover into 34 categories, from bare ground (1) to forest (34), with the average of the values occurring within each 10 km cell used as a continuous variable in the analysis. Increasing values of the landcover variable thus represent vegetation succession from grassland/farmland (low) to forest (high). We constructed a suite of plausible models using combinations of these variables and compared their relative fit to the data using AIC (Burnham and Anderson 2002a). The model with the lowest AIC has higher support than the alternative models examined and hence, was then used to predict kangaroo abundance.

Table 2. Variables used in the density surface model (DSM) to investigate relationships with kangaroo abundance.

Variable	Description
AnnRain	Mean annual rainfall (mm)
TempSeas	Temperature seasonality (℃ standard deviation)
Landcover	34 land cover classes (treated continuously)
Green_period	Length of the 'greenness' period during 2018 (growing season)
NDVI	Average NDVI during the month prior to the aerial surveys

All models were fitted using the *dsm* package (Miller *et al.* 2020) in R (R Core Team 2020). Potential non-linear relationships were explored by including smooth functions of continuous variables in models using thin-plate regression splines available in the *mgcv* package (Wood 2006), which is utilised by *dsm*. Smooth functions of variables were indicated by s( ) enclosing the respective variable. The variance of overall kangaroo abundance was estimated using the parametric moving-block bootstrap method in *dsm* (Miller *et al.* 2013)

2.2.2 Carrying capacity, density dependence and environmental stochasticity

The stochastic population model included a carrying capacity for the population, expressed as the number of kangaroos per square kilometre. This can be considered the density above which the kangaroo population will decline because of resource limitation. In the model, this density-dependent effect is implemented by rescaling the values in the transition matrix **A** with a multiplying scalar, so that the effective rate of increase (λ) is less than 1 when abundance is above the carrying capacity. The scalar value is chosen to make the relationship between the rate of increase and local abundance follow the Beverton-Holt equation for density dependence (Beverton and Holt 1957), which is the discrete-time analogue of the continuous-time logistic equation for density dependence.

At any given time, observed densities can be above or below longer-term carrying capacities. Directly inferring carrying capacities from observational data generally requires long-term time-series observations of abundance, which are currently lacking for Victoria. The most recent estimates of abundance of kangaroos in Victoria (Moloney *et al.* 2018) calculated densities of kangaroos in each of seven harvest management zones across the state. In this report, we update these estimates using DSM methods to infer the relationships between environmental covariates and kangaroo abundance (see above). Importantly, however, both these approaches to estimating kangaroo abundance did not include survey data for kangaroos in heavily forested parts of the state that are unsuitable for aerial survey.

Carrying capacity will vary in space and time, but we have little information on which to make reliable inferences about this other than our observation that abundance varies markedly across the state. We might, in general, expect that carrying capacities in arid parts of the state such as the Mallee would be lower than in more mesic regions. Carrying capacity might also increase during periods of higher rainfall, and might also depend on spatial and temporal variation in land use (cropping, grazing), native vegetation types, and competition with other native and introduced herbivores, including livestock. We currently lack a sound basis for directly estimating carrying capacity in space, other than to assume that DSM estimates of abundance are at least partly informative about local carrying capacity. As part of our sensitivity analysis, we considered models with carrying capacities varying between 0.8 and 8 times the current abundance estimated from the DSM analysis. We also assumed that, while carrying capacities vary in space, they do not vary in time.

Temporal variation in vital rates is dealt with indirectly by applying random stochastic variation to the population vital rates (Table 1). This is intended to simulate temporal environmental variability in vital rates attributable to year-to-year variation in environmental variables such as food availability, weather and other unmodelled biotic and abiotic drivers of population rates. At each time step, stochastic variation in the vital rates of the transition matrix $\mathbf{A}$ were encoded in the model by multiplying the assumed values by a positive stochasticity factor. The resulting matrix of stochasticities was then used to perturb the values of the transition matrix **A** by drawing values from a normal distribution. Stochasticity factors up to 0.3 were considered plausible.

2.2.3 Dispersal

At each annual time step, animals in each 50 × 50 km grid square were allowed to disperse between cells. Movement was modelled using a negative exponential dispersal kernel. Scale parameters of the dispersal kernel (equivalent to the mean distance moved per year) were set to values from 10 to 100 km. Lower values for the scale of the dispersal kernel can be considered more conservative when assessing the risks of alternative harvest policies, as higher rates of dispersal will tend to compensate for local (cell level) quasi-extinctions caused by over-harvesting, or by environmental or demographic stochasticity.

2.2.4 Harvest regimes

Harvest fractions spanning 0% to 25% of the current population in each grid cell were considered in our analysis. It was also assumed that harvesting would have different levels of male bias, ranging from 50% to 90% of males. Commercial kangaroo harvesters tend to prefer to take males because of their larger, higher-value carcasses, although the proportion of males taken varies with availability. As a simplifying assumption, it was assumed that the harvesting regime was identical across the entire study area, including adjacent areas of South Australia, New South Wales and the Australian Capital Territory. The only exceptions to this were that harvesting was excluded from heavily forested habitats in Victoria (the same areas that have not been subject to aerial surveys for kangaroos), which function as harvest refugia. This is a rather imperfect representation of spatial variation in harvesting pressure across south-eastern Australia. However, the model has been designed to easily simulate scenarios where the harvesting policy varies in space or time, or both. See Discussion for further exploration of this issue.

2.3 Stochastic risk analysis of different harvest rates

With all other model parameters set close to the mid-point of their plausible ranges (see Table 1 for assumed values) we systematically varied the harvest rate parameter between 0% and 25% in order to examine resulting impacts on risk. We also considered carrying capacities of 1, 2, and 4 times the DSM estimate of abundance derived from the aerial surveys. Under each assumed harvest rate, we ran 250 replicate simulations of the model, each with a duration of 50 years. For each replicate simulation we determined the minimum total number of kangaroos (N_{min}) occupying all the 50 × 50 km grid cells covering Victoria only, as an inverse measure of ecological risk. This is a narrow definition of risk for this range of harvest rates, as it ignores uncertainty in all other model parameters and is thus conditional on the assumed parameter values used; see the sensitivity analysis below for our approach to dealing with this shortcoming, and exploring the implications of a more diverse set of parameter values.

2.4 Sensitivity analysis

To explore the implications of uncertainty in the full range of parameter values, a global sensitivity analysis of the stochastic model was undertaken using a model emulation approach (Prowse *et al.* 2016). This approach involves generating stochastic predictions from the model across a random sample of parameter values (5000) drawn from their plausible ranges using Latin-hypercube sampling (McKay *et al.* 1979). For each resulting combination of parameters, a single realisation of the stochastic harvest model was simulated over a 50-year interval. N_{min} was recorded for each simulation.

Following Prowse *et al.* (2016), we then used a boosted regression tree model (BRT) (Elith *et al.* 2008) model to emulate the relationship between the input parameter values of the simulations and N_{min}. The BRT was fitted to data from a random 80% sample of the 5000 simulations, with the remaining 20% of simulations retained as a testing dataset to evaluate the predictive accuracy of the BRT. Fitting of the BRT was carried out using the *R* package *dismo* (Hijmans *et al.* 2017), with learning rates, tree numbers and step sizes in the model being manually tuned to maximise the predictive accuracy of the fitted model.

To examine the global sensitivity of N_{min} to each parameter, we estimated variable importance scores (Elith *et al.* 2008) for the fitted BRT. Variable importance scores provide a summary measure of sensitivity to each parameter, expressed as a percentage. Variables with high global sensitivity in this analysis can be considered high priorities for further refinement by collecting additional data, as the values that they are assigned in the model have disproportionately large effects on the modelled ecological risks. We also used the BRT to assess the partial and joint relationships between N_{min} and selected parameters identified as having large amounts of influence on risk, as revealed by their variable importance scores. This was accomplished by plotting univariate and bivariate partial dependence plots for the model (Friedman and Meulman 2003; Elith *et al.* 2008). Important interaction terms in the BRT model were identified using the procedures described by (Elith *et al.* 2008), using the functions provided for that purpose in the *R* package *dismo* (Hijmans *et al.* 2017).

3 Results

3.1 Spatial variation in abundance

A total of 4707 grey kangaroos were observed on the 3182 km of transects during the aerial survey (Moloney *et al.* 2018). A half-normal detection function with second order cosine adjustments was selected after comparing the fit of the half-normal and hazard rate distance functions, with up to third order cosine adjustments. The estimated detection function was monotonic, decreasing as distance from the transect increased (Figure 2). A goodness-of-fit test indicated that the model was an adequate fit to the data (p = 0.40).

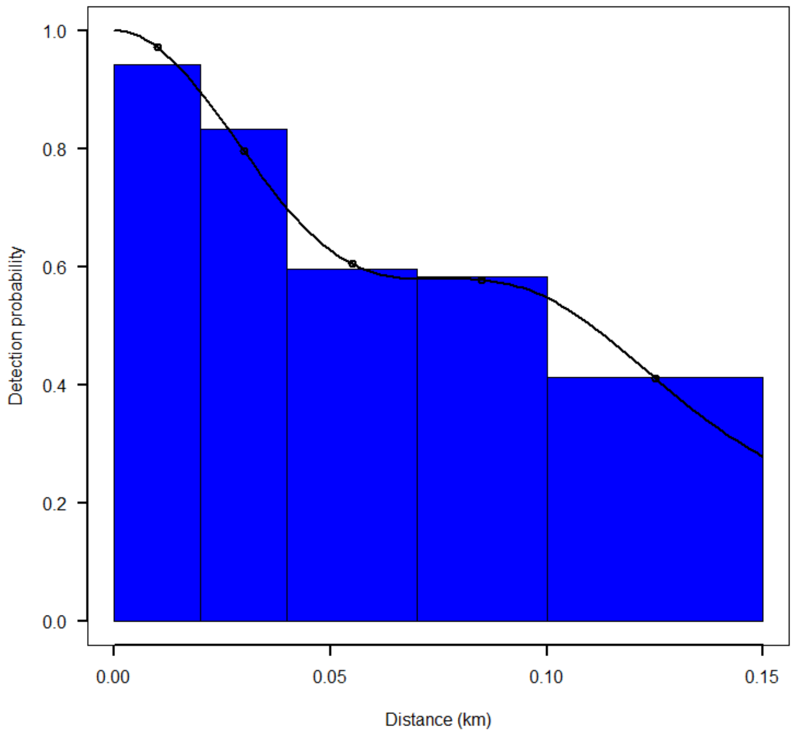

Figure 2. The fitted half-normal detection function estimated from distances recorded between the aerial observer and grey kangaroos during the 2018 aerial survey.

Because of the large extra Poisson variation in the observed counts of kangaroos, the counts were modelled with the Tweedie distribution (Candy 2004) rather than a Poisson distribution, as the former resulted in a much better fit to the data. Based on the potential covariates available to use in the DSM (Table 2), initial exploratory analysis indicated that smooth functions of NDVI, Landcover, and Green_period and linear functions of AnnRain and TempSeas explained significant variation in DSM models, so these were used in further analyses. Five plausible models were constructed using various combinations of these variables to model the spatial distribution of grey kangaroos (Table 3).

The results of model selection for the five DSM models indicated that Model 1, including the smooth effects of both average NDVI in the previous month and landcover class, was the most supported by the data, being the model with lowest AIC. However, this model explained only 19% of the deviance in the data (Table 3). Model 2, which included linear effects of mean annual rainfall (AnnRain) and temperature seasonality (TempSeas), was the next most supported model, having a difference in AIC of 8.1 with the most supported model and explaining 18% of the deviance in the data.

A check on the adequacy of Model 1 by plotting the deviance residuals against the theoretical quantiles (quantile-quantile plot) indicated the bias in predicted kangaroo counts was highest at high observed counts. A plot of the randomised quantile residuals against fitted values indicated no obvious residual trends (Figure 3). The predicted marginal effects of each variable used in Model 1 are shown in Figure 4.

Table 3. Details of models fitted to counts of kangaroos on line transect segments within 10 × 10 km cells to estimate the spatial distribution and abundance of grey kangaroos. Non-linear smooth functions of variables are indicated by s() enclosing the respective variable.

Model	Variables	AIC*	ΔAIC*	%Deviance
1	s(NDVI) + s(Landcover)	1746	0.0	19.1
2	AnnRain + TempSeas	1754	8.1	17.8
3	s(Landcover)	1759	12.9	14.3
4	s(NDVI)	1762	15.7	15.8
5	s(Green_period)	1776	29.4	11.0

* AIC = Akaike's Information Criterion, ΔAIC = difference between AIC and the model with the lowest AIC (Model 1, in bold).

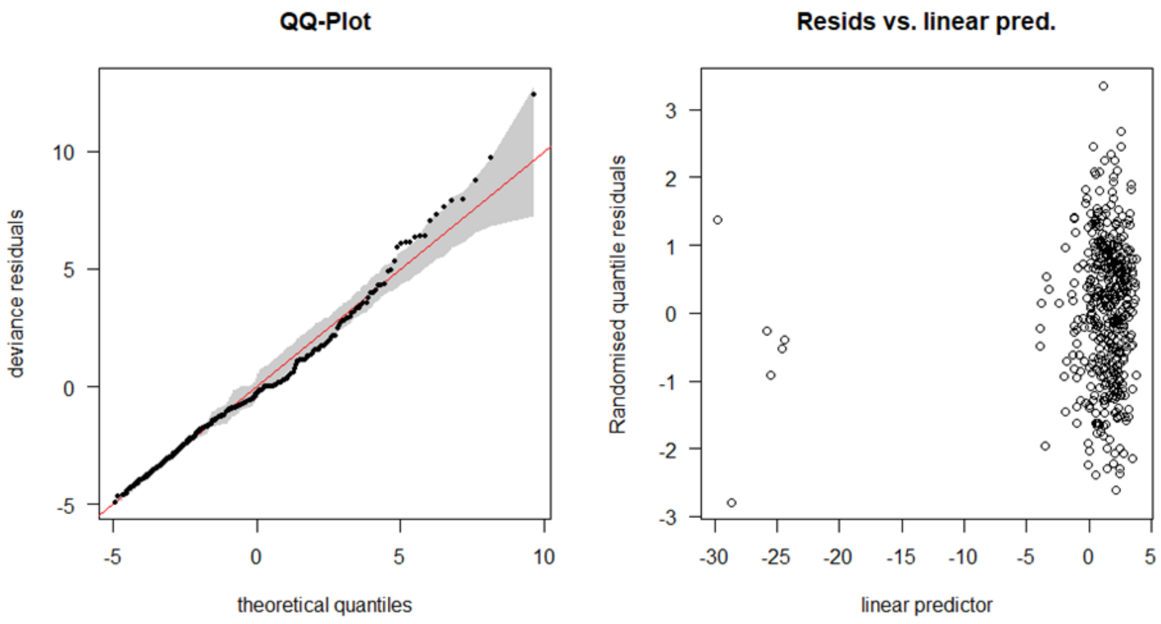

Figure 3. Quantile–quantile plot (left) and randomised residual plot (right) for the most supported DSM model, model 1.

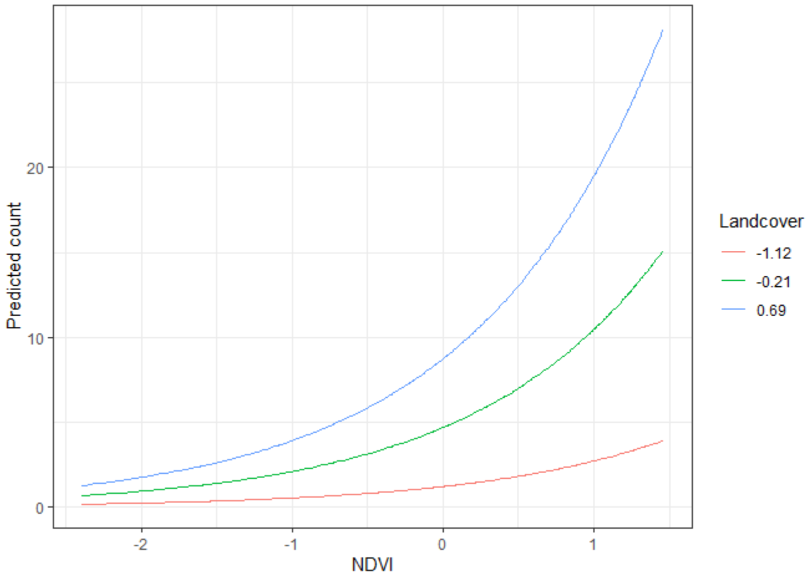

Figure 4. The marginal effects of NDVI and Landcover variables on the predicted counts of kangaroos on transect segments in each cell. Increasing values of Landcover indicate increasing succession from grasslands to forest.

The prediction of kangaroo abundance was restricted to the kangaroo survey area within the 10 × 10 km cells, totalling 160 562 km^2 across the study area. This area consisted of habitat that was outside the densely forested parts of the state and subject to aerial kangaroo surveys (Scroggie *et al.* 2017). Predictions from Model 1 indicated a population estimate of 1 128 500 grey kangaroos (95% CL; 865 500 – 1 471 400) (Figure 5). This was similar to the design-based estimate in Moloney *et al*. (2019) (for grey kangaroos only) of 1 381 000. The coefficient of variation (CV), a measure of relative error, was also lower compared with the CV of the overall kangaroo population estimate given in Moloney *et al.* (2018) (13.6% vs 15.7%).

Predictions of kangaroo abundance were used to inform the likely carrying capacity of the kangaroo study area used in the spatial kangaroo model (Figure 6) by aggregating the predictions at the spatial scale (50 × 50 km) used for the stochastic population model. These predictions were also extended beyond the Victorian borders to avoid edge effects in the spatial harvest model.

3.2 Stochastic risk analysis under different harvest rates

Figure 7 shows the time-series of abundances of kangaroos from 250 runs of the stochastic simulation model under different harvest rates (0–25%) and different carrying capacities (between one and four times the most recent estimated abundance) and with all other model parameters set close to their mid-points. These simulations show that as the harvest rate increases, the abundance of kangaroos tends to decrease, particularly at harvest rates above 15%. For each simulated population trajectory, the minimum abundance was calculated, and the distributions of this quantity for each harvest rate are given in Figure 8, along with the mean (N_{min}) across all 250 simulation runs. The stochastic estimates of N_{min} can be taken as a measure of inverse ecological risk for each of the harvest rates under consideration, with the distributions of values around the means representing the uncertainty. N_{min} progressively decreases as the harvest rate goes up, indicating that higher rates of harvesting can be expected to result in a greater chance of the kangaroo population falling to an unacceptably low level over the course of 50 years.

It is important to stress here that the results of these simulations are conditional on the values taken by all the other parameters in the model, which were set close to the mid-points of the assumed plausible ranges (Table 1). The global sensitivity analysis (see below) explored how these estimates of risk might be impacted by changes in the assumed parameter values.

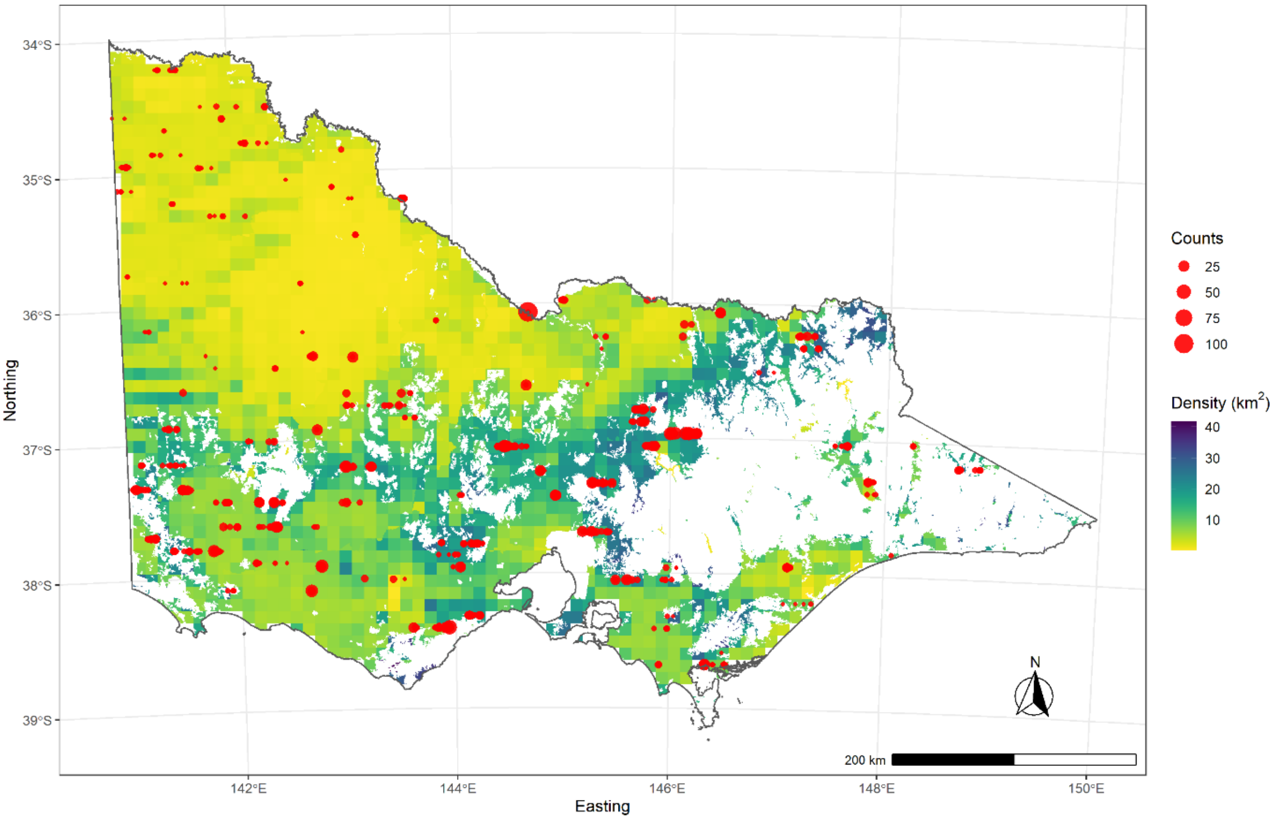

Figure 5. Densities of grey kangaroos within the area subject to aerial surveys (kangaroo survey area) predicted by the DSM model. Red circles show the locations and counts of kangaroos observed along transects during the 2018 aerial survey.

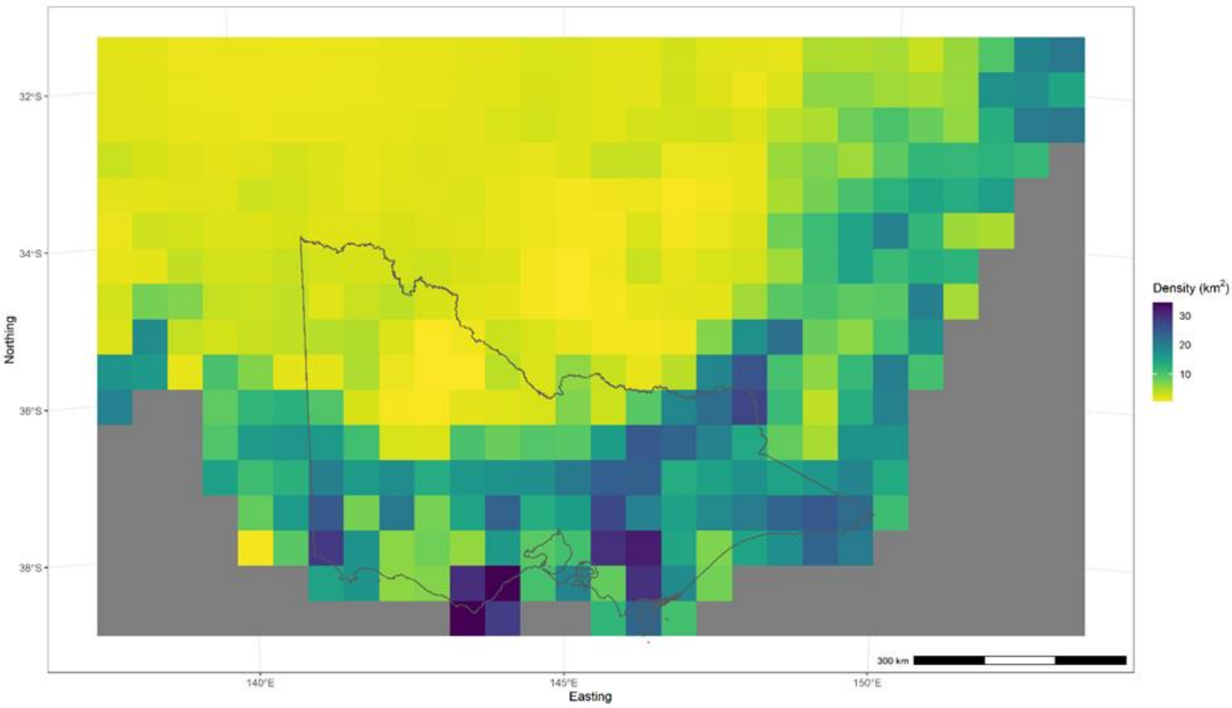

Figure 6. Densities of grey kangaroos within the study area predicted by the DSM model, and used in the spatial kangaroo model. Densities are aggregated to a grid cell size of 50 km × 50 km to match the spatial resolution of the stochastic harvest model.

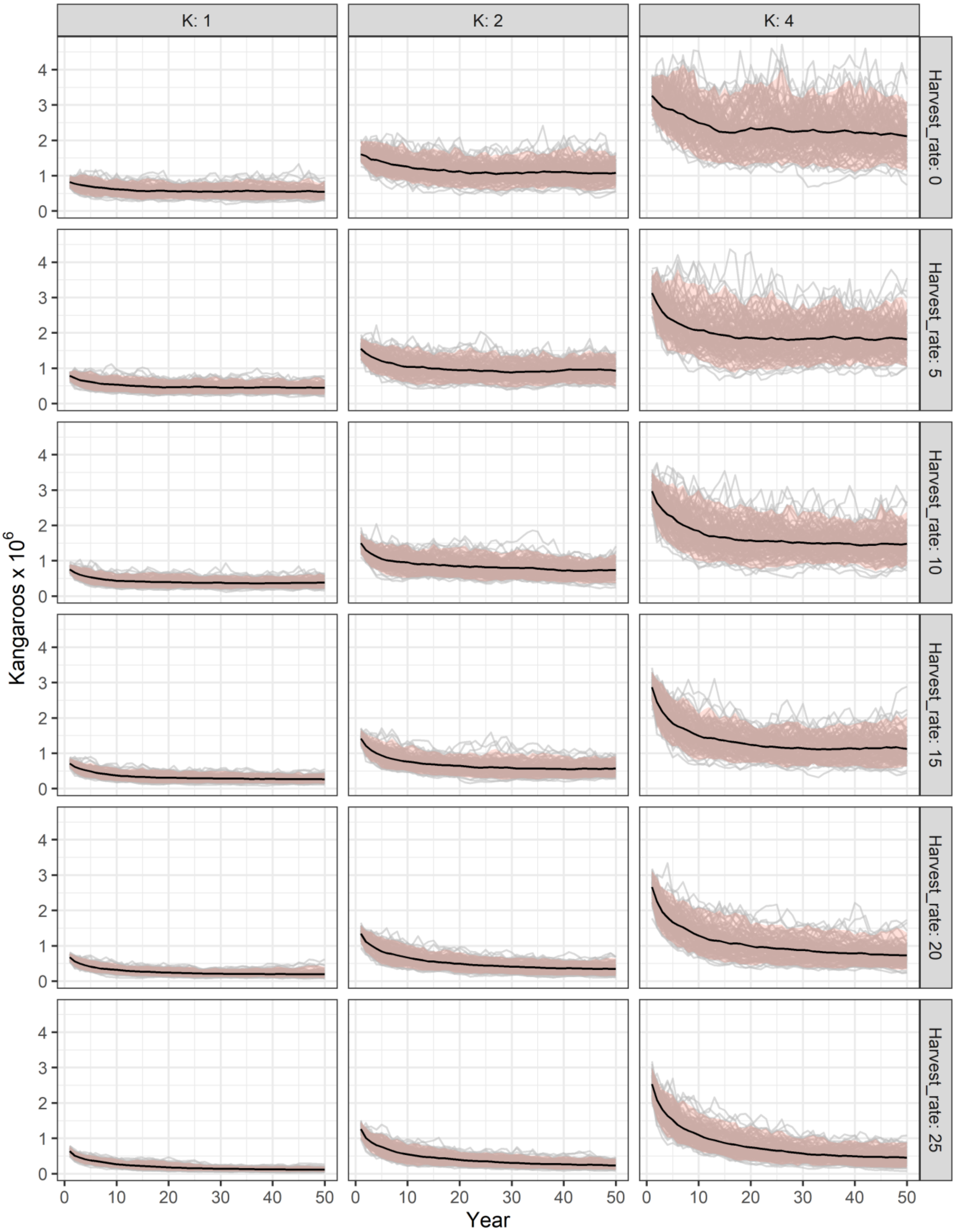

Figure 7. Stochastic simulation results under a range of harvest scenarios for the Victorian kangaroo population. Each panel shows the abundance trajectories (grey lines) for 250 runs of the stochastic simulation under harvest rates between 0 (no harvesting) and 25% per annum over a period of 50 years, and for carrying capacities (*K*) 1, 2 and 4 times the recent Victorian kangaroo abundance estimate. The red shaded area is the bound of the 95% quantiles for simulated total kangaroo abundance at each timestep. Only kangaroos within the borders of Victoria are included in this plot, although the simulation itself encompassed a larger part of south-eastern Australia to avoid edge effects.

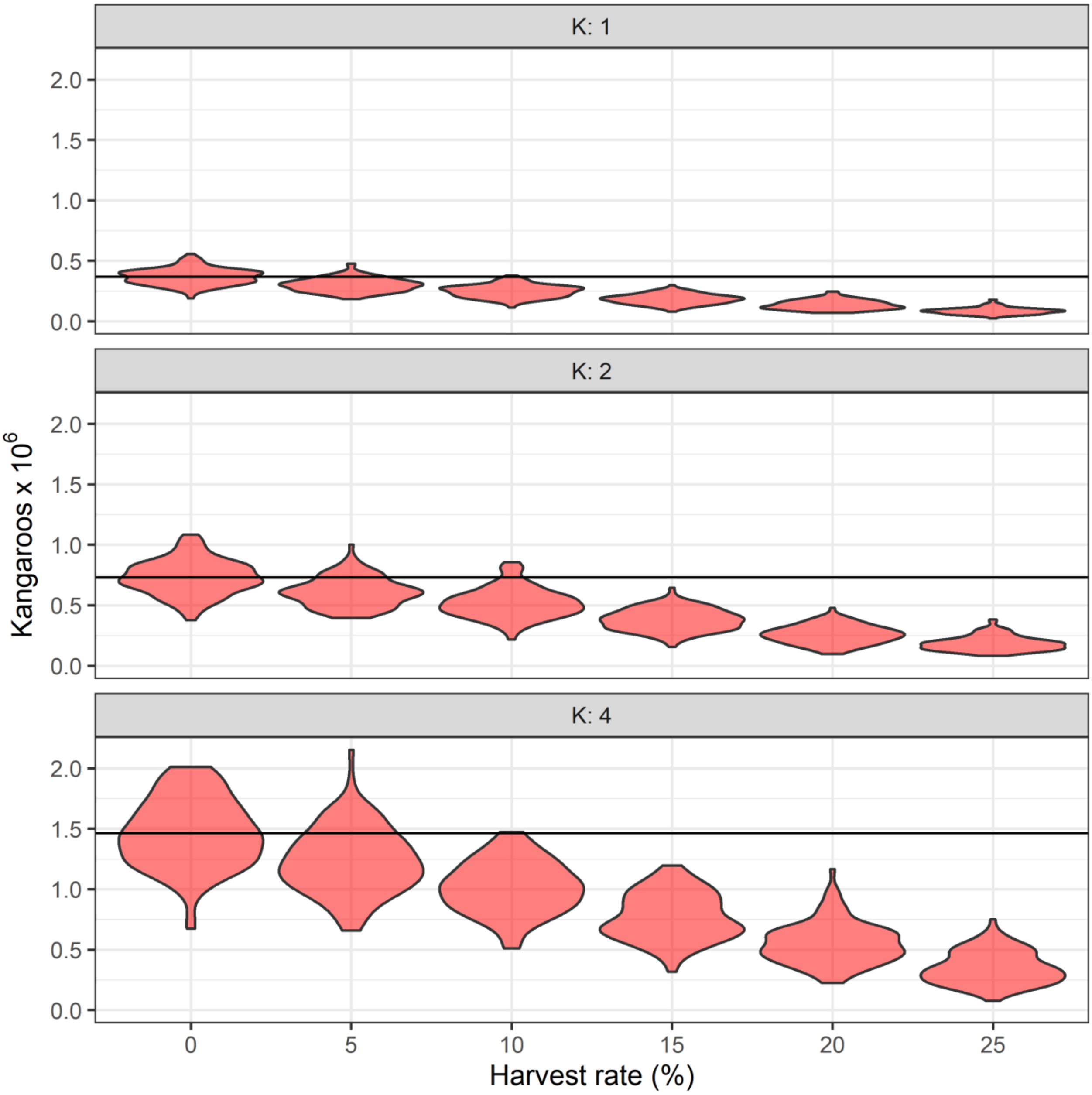

Figure 8. Distributions of minimum abundance of kangaroos (N_{min}) in Victoria over 50 years for 250 stochastic simulations of the kangaroo harvest model at a range of proportional annual harvest rates between 0% and 25%, and for three different carrying capacities (K) that were 1, 2 and 4 times the most recent estimate of abundance. The horizontal lines represent the mean N_{min} when the harvest rate is 0 (i.e. a baseline measure of risk in the absence of harvesting), to allow comparison with the expected distributions of N_{min} under different harvest rates.

3.3 Sensitivity analysis

The model emulation approach to sensitivity analysis was highly effective at predicting the inverse risk measure N_{min} based on parameter values of the stochastic simulation model. The fitted BRT model accurately predicted N_{min} in an independent, hold-out sample of 500 simulations, with the root mean square error (RMSE) of the predictions being 0.19 million kangaroos (Appendix 1). Visual comparison of the simulated and predicted values of N_{min} showed excellent calibration of the model, with a highly linear relationship between the stochastic estimates, and those of the BRT (Appendix 1). While the stochastic simulation approach should be considered the gold standard for assessing alternative management scenarios and parameter values, the emulation approach based on boosted regression tree modelling of the results of a sample of simulation runs makes the evaluation of risks associated with a wide variety of parameter values and management scenarios computationally feasible within a short period of time. Running the 5000 simulations required for the global sensitivity analysis took approximately six hours on a notebook PC with 32 GB of RAM and a 2.11 GHz quad-core processor.

The global sensitivity analysis revealed that our selected measure of risk (N_{min}) was most sensitive to the fraction of the kangaroo population harvested (H_frac), the population carrying capacity (K), the sex ratio of the harvested animals (H_ratio) and the degree of environmental stochasticity in the vital rates (stoch). The population vital rates (survival and fecundity) had relatively little influence on estimates of risk across the ranges of values considered. Similarly, risk was affected little by the assumed value for the dispersal rate (Figure 9).

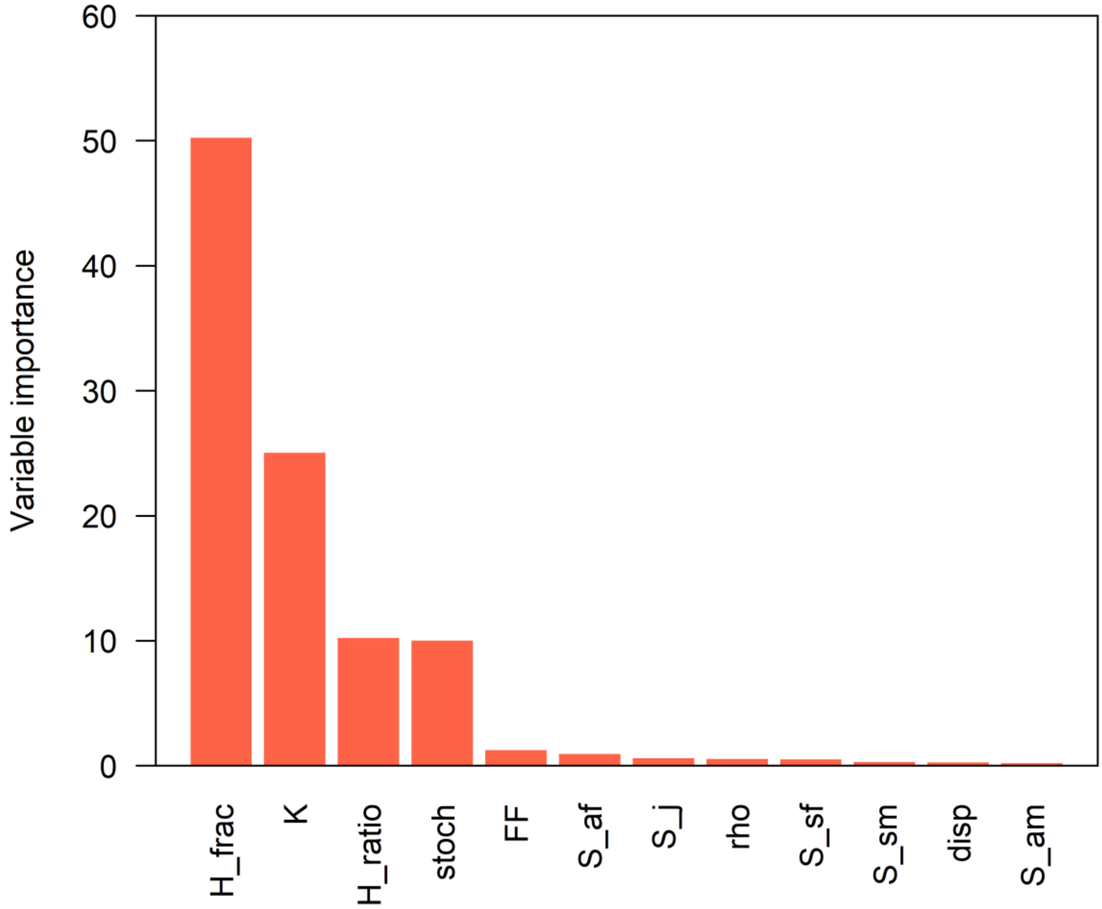

Figure 9. Variable importance plot for the variables considered in the global sensitivity analysis. Large variable importance values imply that the variable has a disproportionately large effect on conservation risks. H_frac – harvest rate, K – carrying capacity, stoch – environmental stochasticity, H_ratio – harvest sex ratio, S_j – juvenile survival, S_af – adult female survival rate, FF – per capita fecundity of adult females, rho – sex ratio of juveniles, S_am - survival of adult males, S_sf – survival of sub-adult females, disp – dispersal rate, S_sm – survival of subadult males.

The effects of those variables identified as having the largest impacts on risk (Figure 9) are further illustrated in the univariate partial dependence plots (Figure 10). As the proportional harvest rate increased, the expected minimum number of kangaroos (N_{min}) decreased markedly, with the expected value of N_{min} being approximately 1.5 million less at the highest proportional harvest rate (40%) considered in the sensitivity analysis, relative to a scenario where no harvesting was conducted.

Conversely, higher values of the population carrying capacity (*K*) were associated with much higher expected minimum abundances, while high levels of environmental stochasticity were associated with a greater risk of abundance falling to low levels (Figure 10). The risk associated with high harvest rates was somewhat mitigated when the sex ratio of harvested animals was biased towards males. Risks were relatively insensitive to population vital rates (survival and fecundity), with the most important vital rates being fecundity and the survival rates of adult females. Increases in both these survival rates were associated with higher N_{min}, but these effects were small relative to the effects of harvest rate, carrying capacity, environmental stochasticity and harvest sex ratio (Figure 10).

The relationships revealed in the univariate dependence plots for the BRT (Figure 10) are expanded on in some bivariate partial dependence plots of the most important interactive effects on risk in the BRT (Figure 11). The effect of harvest rate (H_frac) on N_{min} is clearly negative, but the strength of this effect depends strongly on interactions with other variables. For example, at high assumed carrying capacities (Figure 11a) and low environmental stochasticity (Figure 11b), and when the harvest is biased towards males (Figure 11c), a given proportion harvest rate will result in a higher N_{min}, and hence a lower level of ecological risk. The impact of harvest sex ratio (H_frac) also interacted with the carrying capacity (Figure 11d), with greater risks of low N_{min} where carrying capacity was low and harvest was not male-biased.

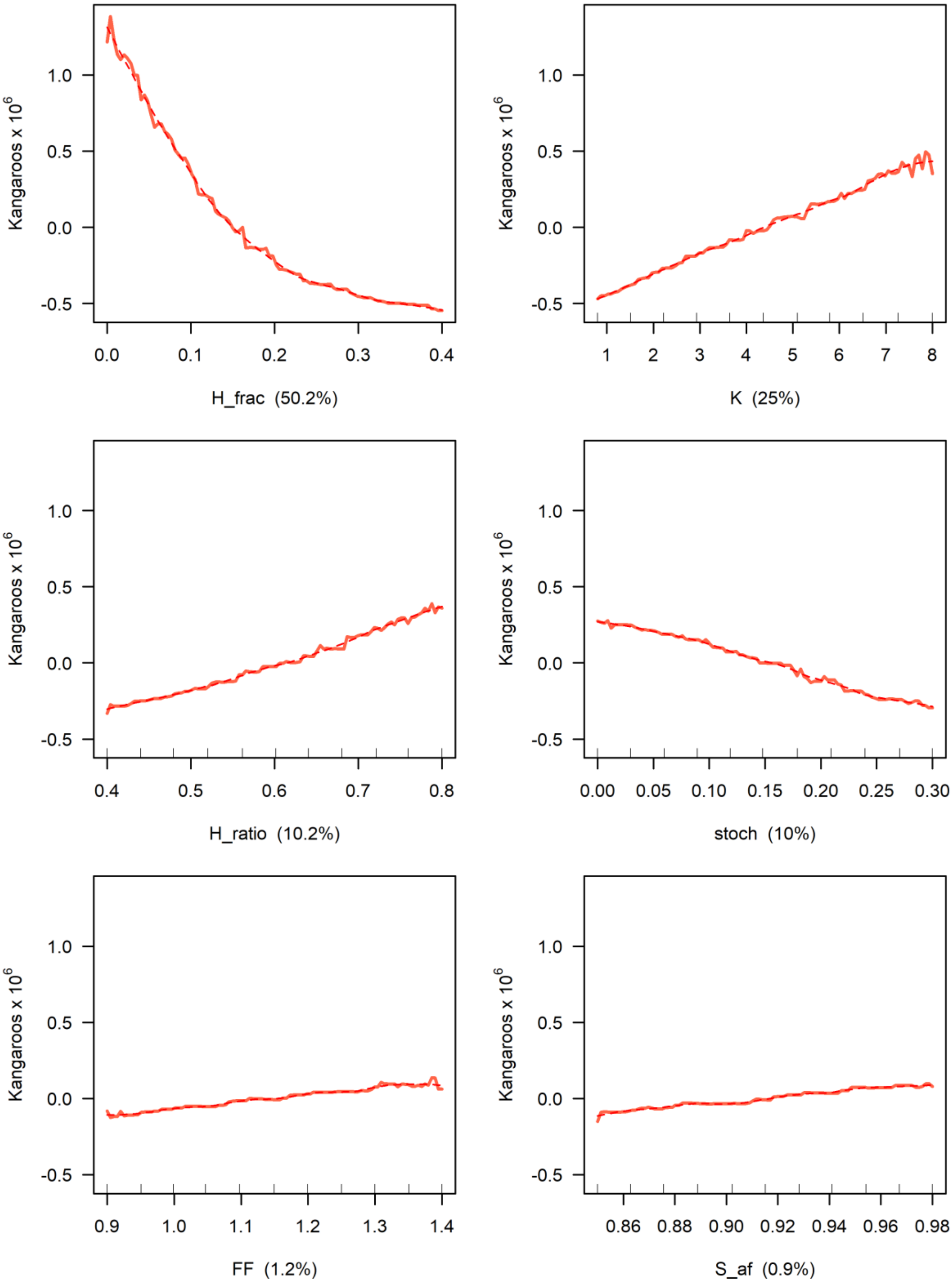

Figure 10. Univariate partial dependence plots (Friedman and Meulman 2003) derived from the boosted regression tree model showing the predicted relationship between the six most important variables influencing conservation risks (expressed as N_{min} – minimum population size over 50 years) for our simulated harvested kangaroo populations. H_frac – proportional harvest rate, K – population carrying capacity, stoch – environmental stochasticity, H_ratio – sex ratio of harvested animals, S_j – survival rate of juveniles, FF –per capita annual fecundity of adult females at low density. Each plot assumes that all other variables in the model are held constant at their means.

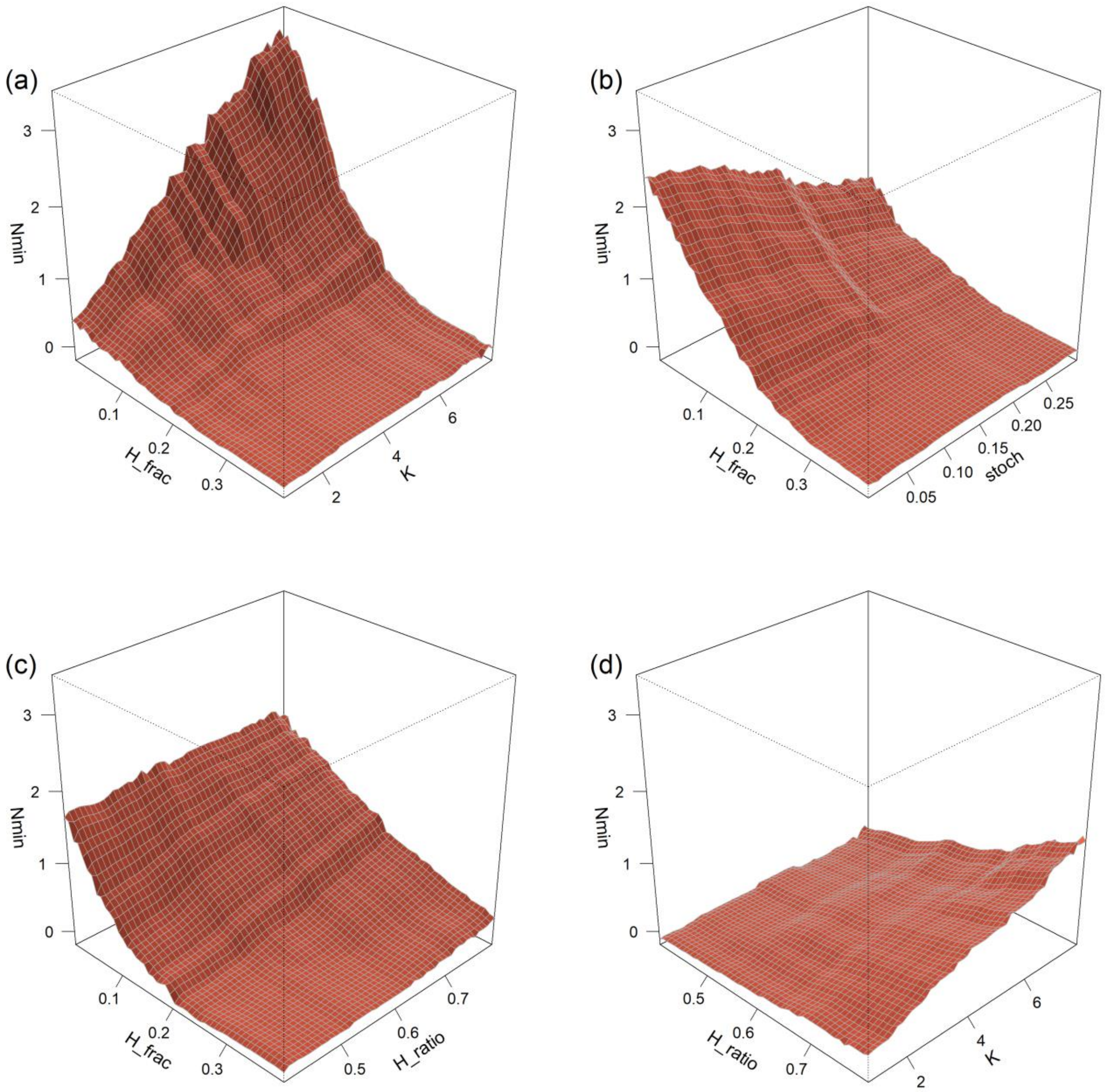

Figure 11. Bivariate interaction plots showing the joint effects of pairs of variables identified as having strongly interactive effects on ecological risk in the boosted regression tree model.

4 Discussion

4.1 Assessment of ecological risks

Based on the results of the stochastic modelling presented in this report, we recommend that the current conservative approach of setting harvest quotas at 10% of the estimated abundance in each harvest management zone be maintained. The results of the stochastic simulation model suggest that under such a harvest rate there is little chance of the abundance of kangaroos falling to an unacceptably low level (Figures 7 and 8). It may be feasible in future to cautiously increase the harvest rate, but harvest rates above 15% are associated with considerably higher levels of risk of the population falling to abundances of less than 50% of those expected under a no-harvest scenario over 50 years.

Our global sensitivity analysis has revealed that our estimates of inverse risk are likely to be highly sensitive to the values taken by several model parameters. Risk was very sensitive to assumptions about carrying capacity, and it is notable that we do not have good estimates for that parameter. Estimation of carrying capacity from wildlife survey data is difficult because real-world biological populations are never truly at equilibrium and can be subject to large fluctuations above and below the carrying capacity. With longer-term time-series abundance data, estimation of population carrying capacity (and its spatial and temporal variability) may become feasible (Iijima and Ueno 2016), but at the present time the available kangaroo population monitoring data are inadequate for this purpose. While the aerial surveys, coupled with tools such as the distance surface models presented in this report, can provide reliable estimates of total abundance and its spatial variability, they provide only limited insight into the actual carrying capacity of the populations. Given that the sensitivity analysis has revealed that our assessments of ecological risk are strongly affected by assumptions regarding the carrying capacity, it is considered prudent to take a risk-averse approach by assuming that carrying capacities are on the low side of plausible values. Such a strategy can help to mitigate any risk of overallocation of harvest quotas.

Risks were also found to be quite sensitive to the sex ratio of harvested animals. With a strongly male-biased harvest, ecological risks were greatly reduced. This is not an unexpected result, given that rates of increase of biological populations are generally limited by the numbers of females in the population rather than males. As male-biased harvest substantially reduces ecological risk, it would be worthwhile to include the sex ratio of harvested kangaroos into the model to more accurately reflect the ecological risk of the observed harvest. Commercial harvesters are known to generally prefer to take male kangaroos (Wilson 1975; McLeod *et al.* 2004; Hacker *et al.* 2004), so it is likely that harvests will already be male-biased. Monitoring data on the age and sex structure of culled animals will provide valuable insight into the extent of the sex-bias in the commercial harvest, which can then help to inform updated ecological risk assessments using our spatial harvest model.

It is notable that the results of the sensitivity analysis showed that the estimates of risk were only marginally affected by the values of the population vital rates (survival, fecundity and offspring sex ratio), or by the value of the dispersal parameter. While survival rates of adult females and rates of fecundity had some impact on estimates of ecological risk, these effects were quite small relative to those of other model parameters such as carrying capacity, harvest rate and harvest sex ratio. While the model was insensitive to the rate of dispersal, it should be noted that the model assumed that vital rates and harvest pressure were homogenous across the study area. In a situation where vital rates and harvesting rates may vary in space, it might be expected that some parts of the study area would be population sinks, with mean rate of increase less than one in the absence of dispersal. Source-sink dynamics of this type could be expected to increase the sensitivity of ecological risk to rates of dispersal.

The low sensitivity of our assessments of ecological risk to estimates of population vital rates or rates of dispersal suggests that additional data collection to obtain better estimates of these parameters are low priorities for research. In contrast, the model would benefit greatly from improved estimates of environmental stochasticity, harvest sex ratio and carrying capacity.

4.2 Enhancements to the spatial harvest model

The spatial harvest model we present here is significantly more realistic than the earlier, aspatial population model of Scroggie and Ramsey (2019). However, there are several aspects of the model that remain over-simplified and could be enhanced to improve model realism and allow assessment of a wider range of management scenarios.

Firstly, our model assumes that the proportional harvest rate is the same in all parts of the state (except for heavily forested areas which were excluded from harvesting). However, it is expected that commercial harvesting activity and culling under ATCW will be concentrated in certain parts of each harvest management zone, either because kangaroos are more abundant, habitats are more suitable for hunting, or certain categories of land managers may be more willing to permit commercial harvesters to operate on their land. It may be possible to use harvest tag-return and ATCW approval data to develop a real-world spatial model of relative harvest intensity. The predictions of such a model could then be used in the stochastic harvest model to assess the impacts of spatially heterogeneous harvesting activity on the ecological sustainability of the kangaroo harvest program.

Our assessment of variation in kangaroo density across the state (and hence the carrying capacity) are based on aerial survey data collected only in unforested parts of the state. The density surface model of abundance attempts to extrapolate its predictions of abundance into forested habitats, but the accuracy of these extrapolations in unknown and untested. Little reliable information on kangaroo densities in forested habitats in Victoria exists. Consideration could be given to assessing the abundance of kangaroos in areas not currently subject to regular aerial counting. This would require an alternative survey methodology, as aerial survey methods are unsuitable for counting kangaroos in heavily forested habitat. As the number of kangaroos in these habitats is unknown, it is difficult to properly assess the contribution of this component of the kangaroo population to the viability of Victorian kangaroo population under the current harvesting regime. Kangaroos in the areas in question (forested areas, which are mainly on public land) are also not likely to be subject to much culling pressure, so forested areas presumably function as harvest refugia, and provide a source of immigrants into nearby areas subject to heavier culling pressure. However, without good estimates of abundance or carrying capacities in these areas it is difficult to assess their contribution to the overall sustainability of harvesting and culling programs.

We extrapolated from the DSM to estimate abundances (and hence carrying capacities) of kangaroos in adjacent areas of South Australia and New South Wales, based on the covariate values of the distance surface model. The South Australian and New South Wales governments conduct regular aerial surveys of kangaroo populations (Lunney *et al.* 2018; DEW 2019; DEW 2020). For future updates of the DSM it would be worthwhile to explore the possibility of integrating this interstate aerial survey data into the analysis, if those states were willing to make it available.

The spatial harvest model in its current form assumes that harvest quotas are based on an accurate and unbiased annual assessment of statewide kangaroo abundance. Under the recommended conservative harvest rate of 10%, statewide surveys should be undertaken at least every three years (Scroggie and Ramsey 2019). However, improvements to the predictions from the spatial harvest model will accrue more rapidly if monitoring is undertaken more frequently (e.g. annual or biannual monitoring). In reality, aerial surveys provide an imperfect estimate of kangaroo abundance and hence, model predictions based on these estimates will also contain errors that will be magnified as the frequency of monitoring reduces. For example, distance sampling estimates are likely to be low if a proportion of individuals are effectively undetectable (e.g. kangaroos that are hidden in thick vegetation at the time of the survey). Even if such sources of bias are accounted for, resulting estimates of abundance will still have a measure of uncertainty around them due to sampling error. For example, the harvest-zone level estimates of kangaroo abundance reported by Moloney *et al.* (2018) have coefficients of variation of between 23% and 48%. This means that proportionally calculated harvest quotas based on these population estimates may result in effective harvest rates that are higher or lower than the nominal figures, because of over or under-estimation of true abundance. For example, if kangaroo abundance is over-estimated from the survey data, then the resulting proportional harvest quota will be an over-allocation in proportional terms. For this reason (among others) we have deliberately taken a conservative approach to setting harvest quotas. Exploring the impacts of uncertain, biased or irregular abundance estimates on the ecological sustainability of the harvest program is a high priority for further enhancement to the stochastic harvest model.

At present the process for informing the spatial harvest model with data from aerial surveys of abundance and harvest return data is *ad hoc.* As further aerial survey and harvest data begin to accumulate, it may be possible to formalise the process of updating the spatial harvest model using these data. Statistical inference for the parameters of stochastic population models is not straightforward owing to the complexity of such models. While simple approaches which use available data to infer the values of individual parameters may be useful, an approach which uses the data to jointly update all parameters in the model would be desirable. Standard inferential approaches such as maximum likelihood estimation or Bayesian estimation using Markov chain Monte Carlo methods may be difficult to apply to complex stochastic models because of the intractability of the model likelihood. Approximate Bayesian computation (ABC) methods have been used successfully for inference in such cases (Scranton *et al.* 2014; Warne *et al.* 2019) and would be worth considering for Bayesian updating of the spatial harvest model as further aerial monitoring and harvest return data become available.

References

Arnold, G. W., Grassia, A., Steven, D. E., and Weeldenburg, J. R. (1991). Population ecology of western grey kangaroos in a remnant of wandoo woodland at Baker's Hill, southern Western Australia. *Wildlife Research* **18**, 561–575. doi:10.1071/wr9910561

Banks, P. B., Newsome, A. E., and Dickman, C. R. (2000). Predation by red foxes limits recruitment in populations of eastern grey kangaroos. *Austral Ecology* **25**, 283–291. doi:10.1046/j.1442-9993.2000.01039.x

Bayliss, P. (1985a). The population dynamics of Red and Western Grey Kangaroos in arid New South Wales, Australia. I. population trends and rainfall. *Journal of Animal Ecology* **54**, 111–125. doi:10.2307/4624

Bayliss, P. (1985b). The population dynamics of Red and Western Grey Kangaroos in arid New South Wales, Australia. II. the numerical response function. *Journal of Animal Ecology* **54**, 127–135. doi:10.2307/4625

Beverton, R. J., and Holt, S. J. (1957). 'On the dynamics of exploited fish populations'. (Ministry of Agriculture, Fisheries and Food, Canada: Ottowa.)

Buckland, S. T., Anderson, D. R., Burnham, K. P., and Laake, J. L. (1993). 'Distance sampling: estimating abundance of biological populations'. (Springer: New York.)

Burnham, K. P., and Anderson, D. R. (2002a). 'Model selection and multi-model inference: a practical information-theoretic approach'. 1st edition. (Springer: New York.)

Burnham, K. P., and Anderson, D. R. (2002b). 'Model selection and multimodel inference: a practical information-theoretic approach'. 2nd edition. (Springer: New York.)

Cairns, S. C., and Grigg, G. C. (1993). Population dynamics of Red Kangaroos (*Macropus rufus*) in relation to rainfall in the South Australian pastoral zone. *Journal of Applied Ecology* **30**, 444–458. doi:10.2307/2404185

Candy, S. (2004). Modelling catch and effort data using generalised linear models, the Tweedie distribution, random vessel effects and random stratum-by-year effects. *CCAMLR Science* **11**, 59–80.

Caswell, H. (2008). 'Matrix population models: construction, analysis, and interpretation' 2nd edition. (Sinauer Associates: Sunderland, Mass.)

Caughley, G., Brown, B., Dostine, P., and Grice, D. (1984a). The grey kangaroo overlap zone. *Wildlife Research* **11**, 1. doi:10.1071/WR9840001

Caughley, G., Grigg, G. C., Caughley, J., and Hill, G. J. E. (1980). Does dingo predation control the densities of kangaroos and emus? *Wildlife Research* **7**, 1–12. doi:10.1071/wr9800001

Caughley, J., Bayliss, P., and Giles, J. (1984b). Trends in Kangaroo Numbers in Western New South Wales and their relation to Rainfall. *Wildlife Research* **11**, 415–422. doi:10.1071/wr9840415

Choquenot, D., and Forsyth, D. M. (2013). Exploitation ecosystems and trophic cascades in non-equilibrium systems: pasture – red kangaroo – dingo interactions in arid Australia. *Oikos* **122**, 1292–1306. doi:10.1111/j.1600-0706.2012.20976.x

Coulson, G. (1997). Male bias in road-kills of macropods. *Wildlife Research* **24**, 21–25. doi:10.1071/wr96004

Coulson, G., Cripps, J. K., and Wilson, M. E. (2014). Hopping Down the Main Street: Eastern Grey Kangaroos at Home in an Urban Matrix. *Animals* **4**, 272–291. doi:10.3390/ani4020272

DELWP (2020). 'Victorian Kangaroo Harvest Management Plan'. Victorian Department of Environment, Land, Water and Planning, East Melbourne. Available at: http://agriculture.vic.gov.au/__data/assets/pdf_file/0011/495029/Kangaroo-harvest-management-plan-2020.pdf [accessed 12 June 2020]

DEW (2019). 2019 Quota Report for Commercial Kangaroo Harvest in South Australia. South Australian Department of Environment and Water, Adelaide. Available at: https://www.environment.sa.gov.au/files/sharedassets/public/plants_and_animals/abundant_species/2019-kangaroo-harvest-quota-report.pdf [accessed 19 June 2020]

DEW (2020). '2020 Quota report: Commercial kangaroo harvest South Australia'. Department of Environment and Water, South Australia, Adelaide.

Elith, J., Leathwick, J. R., and Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology* **77**, 802–813. doi:10.1111/j.1365-2656.2008.01390.x

Friedman, J. H., and Meulman, J. J. (2003). Multiple additive regression trees with application in epidemiology. *Statistics in Medicine* **22**, 1365–1381. doi:10.1002/sim.1501

Gerber, L. R., and White, E. R. (2014). Two-sex matrix models in assessing population viability: when do male dynamics matter? *Journal of Applied Ecology* **51**, 270–278. doi:10.1111/1365-2664.12177

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., and Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment* **202**, 18–27. doi:10.1016/j.rse.2017.06.031

Hacker, R., McLeod, S., Druhan, J., Tenhumberg, B., and Pradhan, U. (2004). 'Kangaroo management options in the Murray–Darling Basin'. Murray–Darling Basin Commission, Canberra.

Hijmans, R. J., Phillips, S., Leathwick, J., and Elith, J. (2017). ‘dismo: Species Distribution Modeling’. Available at: https://CRAN.R-project.org/package=dismo

Iijima, H., and Ueno, M. (2016). Spatial heterogeneity in the carrying capacity of sika deer in Japan. *Journal of Mammalogy* **97**, 734–743. doi:10.1093/jmammal/gyw001

Kirkpatrick, T. (1985). Biology for management. In ‘The kangaroo keepers' (ed. H. J. Lavery), pp. 135–160. (University of Queensland Press, Brisbane.)

Le Gall-Payne, C., Coulson, G., and Festa-Bianchet, M. (2015). Supersize me: heavy eastern grey kangaroo mothers have more sons. *Behavioral Ecology and Sociobiology* **69**, 795–804. doi:10.1007/s00265-015-1896-y

Leathbridge, M., and Stead, M. (2017). 'Victorian aerial kangaroo population survey: Insights and learnings from Victoria’s first state-wide kangaroo aerial survey'. Report to Department of Environment, Land, Water and Planning. (EcoKnowledge, Mylor).

Lunney, D., Purcell, B., McLeod, S., Grigg, G., Pople, T., and Wolter, S. (2018). Four decades of research and monitoring the populations of kangaroos in New South Wales: one of the best long-term datasets in Australia. *Australian Zoologist* **39**, 784–800. doi:10.7882/AZ.2018.040

McKay, M. D., Beckman, R. J., and Conover, W. J. (1979). A comparison of three methods for selecting values of input variables in the analysis of output from a computer code. *Technometrics* **21**, 239–245. doi:10.2307/1268522

McLeod, S., Hacker, R., and Druhan, J. (2004). Managing the commercial harvest of kangaroos in the Murray–Darling Basin. *Australian Mammalogy* **26**, 9–22. doi:10.1071/AM04009

Miller, D. L., Burt, M. L., Rexstad, E. A., and Thomas, L. (2013). Spatial models for distance sampling data: recent developments and future directions. *Methods in Ecology and Evolution* **4**, 1001–1010. doi:10.1111/2041-210X.12105

Miller, D. L., Rexstad, E., Burt, L., Bravington, M. V., and Hedley, S. (2020). 'dsm: Density Surface Modelling of Distance Sampling Data'. Available at: https://CRAN.R-project.org/package=dsm

Moloney, Paul. D., Ramsey, D. S. L., and Scroggie, M. P. (2018). State-wide abundance of kangaroos in Victoria: results from the 2018 aerial survey. *Arthur Rylah Institute for Environment Research Technical Report Series* No. 296. Arthur Rylah Institute for Environmental Research, Heidelberg. Available at: https://www.wildlife.vic.gov.au/__data/assets/pdf_file/0030/415596/Statewide_kangaroo_report_2018_FINAL.pdf [accessed 26 August 2019]

Montana, L., Rousseu, F., Garant, D., and Festa-Bianchet, M. (2020). Siring success in kangaroos: size matters for those in the right place at the right time. *Behavioral Ecology* **31**, 750–760. doi:10.1093/beheco/araa020

Norbury, G. L. (1986). Twins in the western grey kangaroo (*Macropus fuliginosus*) in north-western Victoria. *Australian Mammalogy* **10**, 33.

Norbury, G. L., Coulson, G. M., and Walters, B. L. (1988). Aspects of the demography of the western grey kangaroo, *Macropus fuliginosus melanops*, in semiarid northwest Victoria. *Wildlife Research* **15**, 257–266. doi:10.1071/wr9880257

Poole, W. E. (1983). Breeding in the Grey Kangaroo, *Macropus giganteus,* from widespread locations in eastern Australia. *Wildlife Research* **10**, 453–466. doi:10.1071/wr9830453

Poole, W. E. (1975). Reproduction in the two species of grey kangaroos, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest). I. gestation, parturition and pouch life. *Australian Journal of Zoology* **23**, 333–353. doi:10.1071/zo9750333

Poole, W. E., and Catling, P. C. (1974). Reproduction in the two species of grey kangaroo, *Macropus giganteus* Shaw and *M. fuliginosus* (Desmarest) I. Sexual maturity and oestrus. *Australian Journal of Zoology* **22**, 277–302. doi:10.1071/zo9740277

Prowse, T. A. A., Bradshaw, C. J. A., Delean, S., Cassey, P., Lacy, R. C., Wells, K., Aiello-Lammens, M. E., Akçakaya, H. R., and Brook, B. W. (2016). An efficient protocol for the global sensitivity analysis of stochastic ecological models. *Ecosphere* **7**, e01238. doi:10.1002/ecs2.1238

R Core Team (2020). 'R: A Language and Environment for Statistical Computing'. (R Foundation for Statistical Computing: Vienna, Austria.) Available at: https://www.R-project.org/

Rioux-Paquette, E., Garant, D., Martin, A. M., Coulson, G., and Festa-Bianchet, M. (2015). Paternity in eastern grey kangaroos: moderate skew despite strong sexual dimorphism. *Behavioral Ecology* **26**, 1147–1155. doi:10.1093/beheco/arv052

Scranton, K., Knape, J., and de Valpine, P. (2014). An approximate Bayesian computation approach to parameter estimation in a stochastic stage-structured population model. *Ecology* **95**, 1418–1428. doi:10.1890/13-1065.1

Scroggie, M. P., Moloney, P. D., and Ramsey, D. S. L. (2017). Design of an aerial survey to estimate the abundance of kangaroos in Victoria. *Arthur Rylah Institute for Environment Research Technical*

Report Series No. 280. Arthur Rylah Institute for Environmental Research, Heidelberg. Available at: https://www.environment.gov.au/system/files/consultations/14b5b0e9-3473-48b8-b4b6-17de025c2f7d/files/kangaroo-pet-food-trial-survey.pdf [accessed 26 August 2019]

Scroggie, M. P., and Ramsey, D. S. L. (2019). Kangaroo harvest quotas for Victoria, 2020. *Arthur Rylah Institute for Environment Research Technical Report Series* No. 308. Arthur Rylah Institute for Environmental Research, Heidelberg. Available at: https://www.ari.vic.gov.au/__data/assets/pdf_file/0019/453502/ARI-Technical-Report-308-Kangaroo-harvest-quotas-Victoria-2020.pdf [accessed 21 April 2020]

Stirrat, S. C. (2009). Age structure, mortality and breeding in a population of agile wallabies *(Macropus agilis)*. *Australian Journal of Zoology* **56**, 431–439. doi:10.1071/ZO08060

Visintin, C., Briscoe, N. J., Woolley, S. N. C., Lentini, P. E., Tingley, R., Wintle, B. A., and Golding, N. (2020). STEPS : Software for spatially and temporally explicit population simulations Ed L. Graham. *Methods in Ecology and Evolution* **11**, 596–603. doi:10.1111/2041-210X.13354

Visintin, C., Golding, N., Woolley, S., and Baumgartner, J. (2019). ‘steps: Spatially- and Temporally-Explicit Population Simulator’. Available at: https://CRAN.R-project.org/package=steps [accessed 6 November 2019]

Warne, D. J., Baker, R. E., and Simpson, M. J. (2019). ‘Rapid Bayesian inference for expensive stochastic models’. *arXiv:1909.06540 [q-bio, stat]*. Available at: http://arxiv.org/abs/1909.06540 [accessed 18 September 2019]

Wilson, G. R. (1975). Age structures of populations of kangaroos (Macropodidae) taken by professional shooters in New South Wales. *Wildlife Research* **2**, 1–9. doi:10.1071/wr9750001

Wood, S. N. (2006). ‘Generalized additive models: an introduction with R’. (Chapman & Hall/CRC: Boca Raton, Florida, USA.)

Appendix

Assessing calibration of the boosted regression tree model

The predictions of N_{min} from the boosted regression tree model used to conduct the sensitivity analysis were compared to those generated from the stochastic simulation model by plotting them against each other (Figure A1). The data used to fit the BRT, and a separate set of holdout (evaluation) data are shown in different colours. If the BRT is well calibrated we would expect the stochastic and predicted estimates to be nearly equal, and for the points on the graph to be distributed along the diagonal equivalence line. Minor divergences from the diagonal indicate the excellent predictive accuracy of the BRT. The general alignment of the distributions of the test and training data reinforce the predictive accuracy of the model.

The root mean square error (RMSE) for the training data was 0.11 million kangaroos, while for the independent testing data (not used to fit the BRT) the RMSE was 0.19 million kangaroos.

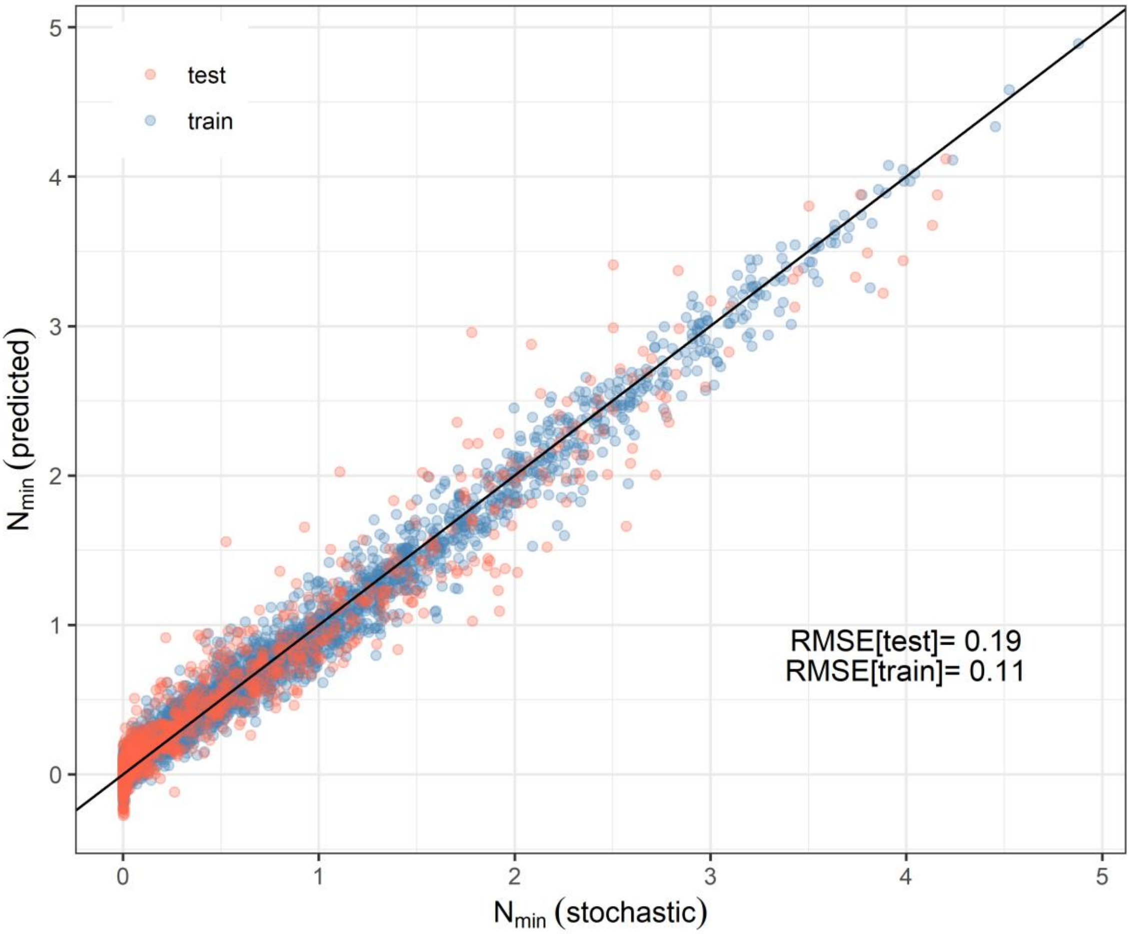

Figure A1. Calibration of the boosted regression tree model for *N*$_{min}$ with test both (holdout) and training data superimposed. The *x*-axis shows the estimated minimum number of kangaroos over a 50-year interval for each scenario evaluated using the stochastic harvest model, while the *y*-axis gives the same evaluation of risk using the boosted regression tree model trained on a sample of 4500 stochastic simulations.

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