**Balancing overpopulation and conservation targets to optimize koala management strategies**

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Abstract

The koala (*Phascolarctos cinereus*) is Australia’s largest arboreal folivore that inhabits eastern and south-eastern Australia. While its populations are in decline in areas of New South Wales and Queensland, high and increasing densities in the Mount Lofty Ranges of South Australia raise concerns of overbrowsing. This challenge highlights the need for optimized fertility-control strategies to balance sustainable population management with ecological, ethical, and logistic complexities. Demographic models are valuable tools for predicting population dynamics, but their accuracy hinges on reliable estimates of population density, often influenced by biases in expert-elicited and citizen-science data. We developed and combined a point-process model, an ensemble species distribution model, and a demographic model to project koala populations in the Mount Lofty Ranges over the next 25 years to assess the efficiency and cost-effectiveness of fertility-control interventions. We tested two hypotheses: (1) koala distribution is driven by rainfall, temperature, and native vegetation, with summer rainfall boosting habitat suitability, and (2) spatially targeted fertility intervention is more cost-effective than generalized strategies due to subpopulation connectivity. Accounting for sampling biases and local densities, our models estimate that highly suitable areas in the Mount Lofty Ranges are determined by rainfall, temperature, and vegetation. Without intervention, this population could increase by ~10% in 25 years. Fertility control focusing on adult females was the most cost-effective (~AU$28 million) strategy, although this scenario was slower at reducing population size compared to an intervention also sterilizing female back young. While the choice of sterilization scenario has minimal impact on overall costs, ethical considerations and long-term conservation goals such as population density thresholds will have more influence on managing expenses effectively.

**Keywords**: matrix population model, fertility control scenarios, spatial prioritisation, inhomogeneous Poisson process

Introduction

The koala (*Phascolarctos cinereus*) is Australia’s largest extant arboreal folivore and the only remaining species within the Phascolarctidae (Black *et al.* 2014). While during the late Pleistocene (~ 126,000 years ago) the species ranged from the eastern states to south Western Australia, today its natural range is restricted to the eastern states (i.e., Queensland, New South Wales, Victoria, and Australian Capital Territory), and a small portion of the southern and eastern regions of South Australia (Shabani *et al.* 2019). Although an increasing incidence of drought and heat waves is likely to have restricted the past suitability of koala habitat (Adams-Hosking *et al.* 2011; Briscoe *et al.* 2016), extensive land clearing and the international fur trade following European settlement eventually precipitated the extinction of the species in South Australia in the 1920s (Menkhorst 2008).

Koalas were re-introduced to Kangaroo Island in 1923 and 1925 from Victoria (Masters *et al.* 2004; Wedrowicz *et al.* 2017). The translocated animals on Kangaroo Island established a population that grew to > 5000 by 1994 (revised to 27,000 in 2001) (Masters *et al.* 2004; Duka & Masters 2005). Subsequent translocation of koalas from Queensland, New South Wales, and Victoria occurred prior to 1940 to the Mount Lofty Ranges (Melzer *et al.* 2000), but the population became classified within a few decades as ‘overabundant’ in some areas because of high defoliation rates of preferred food trees. In some cases like in Victoria, high-density populations have caused complete and wide-spread canopy defoliation, eventually causing not only mass starvation of koalas (Menkhorst, 2008; Whisson, Dixon, Taylor, & Melzer, 2016), but also a decline in avian species richness (Whisson *et al.* 2016; Whisson, Orlowski & Weston 2018). Similarly, in densely inhabited patches of the Mount Lofty Ranges, overbrowsing of *Eucalyptus* spp. (especially manna gum *E. viminalis*) (Lee & Martin 1988) has caused the loss of trees to the point where this reduced food source, along with frequent human-wildlife conflicts (e.g., domestic dog attacks and vehicle collisions), likely place the koala population in the Mount Lofty Ranges at (or at least near) local carrying capacity (Sequeira *et al.* 2014).

The conundrum of managing translocated koala populations is a challenge because they are simultaneously cherished by the public that see these koala in South Australia as ‘native’ species, and those who view them as an introduced pest that causes overbrowsing (Phillips 2000; Masters *et al.* 2004). This results in mixed messages: although the species is listed as *Endangered* in Queensland, New South Wales and Australian Capital Territory under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC 2023), and as *Vulnerable* as a whole in Australia under the IUCN Red List of Threatened Species (IUCN 2024), the species is not yet listed as *Vulnerable* under national legislation, nor in any special conservation category in South Australia. Because even the proposal to cull koala populations (commonly applied to other native wildlife causing environmental damage) is politically and ethically contentious (Duka & Masters 2005), there has been applications of alternative management strategies such as fertility control and translocation. For example, between 1997 and 2015, the South Australian Government sterilized > 12,500 koalas on Kangaroo Island and translocated 3,801 individuals to the south-eastern mainland of South Australia (Melzer *et al.* 2000; Duka & Masters 2005; Molsher 2017). However, the associated costs, poor welfare outcomes, and logistical constraints restricted these management options to small areas with a low potential for immigration (e.g., islands) (Massei & Dave 2014), where density targets have been set at ~ 0.70 koalas ha-1 (National Parks and Wildlife South Australia 2002; Ramsey, Tolsma & Brown 2016). While proactive fertility control strategies in mainland regions could help avoiding drastic subsequent interventions (Whisson *et al.* 2016), the potential costs of these interventions in the Mount Lofty Ranges remain unknown.

Demographic models can inform population control by predicting population growth and long-term viability under different climatic and management scenarios (e.g., Jenouvrier et al. 2009; Hunter et al. 2010; Huang and Karczmarski 2014), or to determine the efficient reduction of problematic species (e.g., Govindarajulu et al. 2005; Venning et al. 2021). These models require a realistic estimate of initial population size, modified over time by various processes such as birth, death, and/or immigration and emigration (Caswell 2001). Despite the development of hundreds of field techniques designed for different species and survey conditions (Bookhout 1994), collecting distribution and abundance data can still be time-consuming, costly, and logistically challenging (Hauser, Pople & Possingham 2006). To overcome some of these challenges, data collected by experts can be supplemented with volunteer citizen science initiatives (Silvertown 2009). For example, the *Great Koala Counts* in South Australia (2012 and 2016) provide data for estimating koala densities and population size, and to gauge public opinion on koala management in the Mount Lofty Ranges (Sequeira *et al.* 2014; Hollow *et al.* 2015) .

While citizen science expands sampling effort (spatially and temporally), and provides new opportunities for cost-efficient data collection, it is also the source of two main methodological challenges. The first arises because volunteers frequently collect data opportunistically and subjectively (Fourcade *et al.* 2014), thereby creating sampling biases in species distributions (Crall *et al.* 2010). Moreover, observers differ in their ability to recognize target species and the time spent to find them resulting in a range of detectability biases (Isaac *et al.* 2014). At fine spatial scales (e.g., 100s of metres), such biases can produce misleading population estimates (Sicacha-Parada *et al.* 2021). The real analytical challenge is to avoid assuming that opportunistically collected data represent the true distribution of any species. Because environmental conditions determining species occupancy result from a hierarchical selection process (Johnson 1980), opportunistically collected data are conditional on observer presence and detection ability (Cretois *et al.* 2021). As such, any estimates of habitat selection inferred exclusively from citizen-science data only partially measure the true distribution of a species. The *Great Koala Count* data in South Australia were biased toward unsealed and sealed roads (Sequeira *et al.* 2014), which is problematic to estimate realistic population distribution and abundance (Hughes *et al.* 2021) and limit empirically guided discussion on how to manage koala populations.

We reconstructed and projected koala population dynamics across the Mount Lofty Ranges over the next 25 years to evaluate the relative cost-effectiveness of possible fertility-control interventions. By combining habitat suitability and unbiased density estimates, we tested two hypotheses: (1) koala population distribution is primarily driven by a combination of rainfall, temperature, and availability of native vegetation. We expect that increasing summer rainfall improves habitat suitability by mitigating the impact of rising temperatures, drought, and fire risks. However, extreme and low temperatures challenge the koala’s ability to regulate body temperature, making habitat selection and the availability of specific native tree species essential for survival. (2) Spatially targeted fertility control is more cost-effective than specific fertility-control strategies, as it optimizes resource allocation and enhances the impact of population control efforts (Margules & Pressey 2000; Pepin, Davis & VerCauteren 2017). We anticipate that while some strategies might quickly reduce population size to meet density targets, their higher implementation costs could make them sub-optimal.

To test these hypotheses, we overcame the aforementioned methodological limitations by developing an approach to estimate the initial, unbiased population size of the koala population in the Mount Lofty Ranges, and then constructed a demographic model to (*i*) project the effectiveness of various sterilization intensities on the long-term patterns of projected abundance, and (*ii*) estimate the costs associated with three sterilization strategies: (1) no intervention, (2) only adult females sterilized, and (3) female back young and their mothers sterilized together at capture (see details in Methods). More specifically, we first developed an inhomogeneous Poisson process that accounted for the biases in uneven sampling effort in the two *Great Koala Counts* that we coupled with a habitat-based distribution model to estimate spatially averaged local densities across the Mount Lofty Ranges as a function of environmental conditions. We then used the resultant density estimates to calculate the initial unbiased population size in the demographic model to test the effectiveness of different sterilization scenarios on reducing abundance relative to their associated costs. Ultimately, we identified the relative yearly costs of these sterilization scenarios to provide the cheapest and most effective means of achieving population control over the next three decades.

Methods

Study area

The Mount Lofty Ranges (35° S, 138.7° E) of South Australia is a region adjacent to the capital city of Adelaide, including the Adelaide Hills and Fleurieu Peninsula. The region receives 400–1100 mm rainfall annually within an otherwise semi-arid landscape (Westphal *et al.* 2003). From its total area of 5000 km2, only ~ 10–18% of native woodlands remain (Bradshaw 2012), with overstoreys dominated primarily by eucalypt species (*Eucalyptus baxteri*, *E. fasciculosa*, *E. leucoxylon*, *E. obliqua* and *E. viminalis*). The rest of the region is devoted primarily to urban and peri-urban residential housing, pasture, plantations, cropland, vineyards, and orchard agriculture (Bryan 2000; ForestrySA 2014). There are no records of koalas in this region during the Holocene (~ 12,000 years ago) prior to European invasion (Robinson, Spark & Halstead 1989); instead, the current population is derived from deliberate translocations from Kangaroo Island (Melzer *et al.* 2000; Duka & Masters 2005), as well as escaped animals from Cleland and Belair Wildlife Parks (Robinson & Bergin 1978).

**Koala distribution data**

Koala occurrence data were collected during two events of the *Great Koala Counts* on 28 November 2012 and 26–27 November 2016, mainly in Adelaide and the Mount Lofty Ranges of South Australia (Sequeira *et al.* 2014; Hollow *et al.* 2015; Sbrocchi *et al.* 2015). As part of these surveys, citizen scientists were tasked with searching for koalas on the specified days of the surveys and to report both sightings and non-sightings (i.e., presences and absences). Reports could be made through the Great Koala Count website (koalacount.ala.org.au), or in near-real time via Apple® and Android® smartphone apps adapted from existing mobile applications created to feed citizen-science data to the *Atlas of Living Australia* (ala.org.au) (Stenhouse *et al.* 2020). Data collected included: (*i*) location (longitude and latitude, recorded by mobile GPS), (*ii*) a photograph for sighting validation, (*iii*) search effort in minutes, (*iv*) descriptions of activity of the observed koala(s) (e.g., *sleeping*, *sitting*, *eating*, *climbing*, *drinking*, *walking*, *dead*, *other*), (*v*) whether participants expected to spot a koala in the area, (*vi*) location type (e.g., *private garden*, *public park*, *roadside*, *on road*, *other*), (*vii*) sighting frequency in the area, (*viii*) species of tree in which koala was sighted, (*ix*) presence/absence of offspring, (*x*) tree health (e.g., *dead*, *lots of leaves*, *scarce leaves*, etc.), and (*xi*) any additional comments. We quality-checked all records by removing duplicates or obviously erroneous entries (e.g., other species), resulting in a total of 3026 recorded sightings across the Mount Lofty Ranges (Table S1).

Sampling biases and density estimates

Given the potential sampling biases that need to be corrected to produce reliable inferences, citizen-science datasets can be treated as point patterns that have been degraded by many factors such as sampling effort, detectability, or misidentification. The South Australian *Great Koala Count* datasets are no exception, with three main sources of biases identified (Sequeira *et al.* 2014). First, the data are strongly clustered around the frequently visited Cleland Wildlife Park, where a local peak in the density of koala detections describes a higher probability of detection the closer the observer is to the park. The second bias is also related to the presence of a national park, although the effect is not as pronounced as for Cleland — observers appear more likely to detect a koala inside compared to outside a national park. Finally, the distance to the nearest road is also a strong driver of variation in sampling effort (Sequeira et al. 2014), such that the closer an observer is to the road, the higher the detection likelihood.

Here, we described the spatial pattern of the censused koala population across the Mount Lofty Ranges using an inhomogeneous Poisson point-process model assuming that (*i*) individual koalas do not have strong social interactions that could affect their spatial distribution (i.e., spatial locations are independent), (*ii*) koalas do not live in large groups, (*iii*) they are not aggressively territorial, and (*iv*) the probability to detect a given koala is conditional on local environmental conditions but independent of the probability of detecting any another individual koala in the area. This point process can account for the distance an observer is from a koala-detection hotspot (i.e., Cleland Wildlife Park), whether the observer is inside or outside a national park, or the distance an observer is from the nearest road.

The homogeneous Poisson process () is a suitable model when the points are ‘randomly’ (i.e., the location of each point does not depend on the location of its neighbours) distributed in space (Illian *et al.* 2008). This process is characterized by two fundamental properties: (*i*) the number of detections in any subset of the study area follows a Poisson distribution with mean , where (intensity or point density) = the mean number of points per unit area, and = a neutral symbol referring to the area (in km2), and (*ii*) the number of detections in disjoint subsets within generate independent variables (for an arbitrary value of ).

In an inhomogeneous Poisson process, varies with location on , which in our case translates into a change in sighted koala density across the Mount Lofty Ranges driven by the heterogeneous sampling effort of citizen scientists. Therefore, by estimating we obtain an average estimate of the density of the koala population across the Mount Lofty Ranges while accounting for biases in sampling effort and assuming that each koala has only been counted once. Based on these two fundamental properties, the probability of detection of a sighted koala in non-overlapping areas follows an inhomogeneous Poisson point process:

eq. 1

where , and the intensity function can be estimated using a likelihood function:

eq. 2

where = the probability of a koala detection at a given location as a function of (*i*) the distance to the density hotspot (i.e., Cleland wildlife Park), (*ii*) the probability of being inside or outside a national park, and (*iii*) the distance to the nearest road, such that:

eq. 3

where represents the decreasing probability of a koala detection as a function of = the distance from to the nearest road, and = the decreasing probability of a koala detection as a function of , such that the greater the distance is from a hotspot of detection , the less likely it is to detect a koala. We also assumed that a koala cannot be missed at a short distance (e.g., < 10 m) from the observer and that the koala will not try to escape and avoid detection as the observer is approaching. The probability of detecting a koala inside and outside a national park is:

eq. 4

with being the indicative function that is located inside a park (= 1 if true otherwise = 0) and the indicative function that is located outside a park (= if true otherwise = 0). The parameters , and are estimated by maximum likelihood: here, 0.26, 0.18 and 7 ×10-4.

We calculated a confidence interval for using a parametric bootstrap approach (Manly 2006). We first simulated 1000 independent inhomogeneous Poisson processes of sighted koalas based on the estimated parameters , and , such that each inhomogeneous Poisson process follows the same spatial pattern and characteristics as the dataset (i.e., *Great Koala Counts*). We then estimated for each of the simulated inhomogeneous Poisson processes the parameters based on equations 1–3, which results in a vector of 1000 estimates per parameter. We subsequently calculated the confidence interval for each parameter ( , and ) as the quantiles at 0.025 and 0.975 of the values in each vector.

Species distribution model

*Model overview*

We used an ensemble of nine correlative species distribution models to estimate koala habitat suitability across the Mount Lofty Ranges as a function of nine environmental variables (see *Environmental variables*). Correlative species distribution models predict and map species habitat suitability by estimating the statistical relationship between *in situ* occurrence (i.e., koala observations from the *Great Koala Count*) and the environmental conditions of those locations. This statistical relationship is needed to capture the envelope of all suitable environmental conditions for a species to survive, reproduce and thrive, which represents the realized environmental niche of the species (Guisan, Thuiller & Zimmermann 2017).

Among the broad range of available statistical algorithms to predict species distributions, we used an ensemble modelling approach based on nine widely used algorithms: artificial neural networks, generalized additive models, generalized linear models, boosted regression trees, flexible discriminant analysis, multivariate adaptive regression splines, maximum entropy, random forest, and species-range envelopes. Each algorithm returns a map of suitable habitat for the species (i.e., nine in total) that are used to generate a weighted-mean consensus map (i.e., the relative contribution of each algorithm on the final map depends on their relative performance — see *Model training, performance, and projections*). This approach integrates statistical models of different complexities and statistical properties when projecting a species through time (Araújo & New 2007; Elith *et al.* 2011) and ensures that several possible projections are considered for mapping both the main trend (i.e., mean, median, or some other percentile) and the overall variation (and thus uncertainty) across all models (Fig. S3).

Some of the algorithms used in the ensemble modelling approach require either presence/absence or presence only data. We discarded the absence data collected in the *Great Koala Counts* because of their unreliability. Indeed, true absences are usually estimated based on repeated survey and using multiple methods (Woosnam-Merchez *et al.* 2012), which was not the focus of the Great Koala counts (e.g., most people only started their survey when they spotted their first koala). Therefore, we generated a total of 2000 pseudo-absences by randomly sampling points within the study area where koalas were not recorded (Barbet-Massin *et al.* 2012).

*Model training, performance, and projections*

We first randomly split our dataset (including pseudo-absences) into 80% training and 20% validation subsets. To account for the stochasticity in pseudo-absence generation, we repeated this process 20 times, thus generating 20 different training and evaluation datasets. We then computed each of the nine models independently and applied *k*-fold cross-validation (Fielding & Bell 1997) to evaluate performance using the 30% validation subset.

We evaluated model performance for each repetition using the area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS), two intuitive metrics to assess the predictive performance of species distribution models transposed into presence-absence mapping (Swets 1988; Allouche, Tsoar & Kadmon 2006). From the relative suitability map generated by each model for each repetition, we determined a threshold maximizing TSS (which includes both sensitivity and specificity) (Guisan, Theurillat & Kienast 1998) below which we considered the species ‘absent’. This threshold method is commonly used to transform continuous probabilities of suitability into probabilities of presence/absence in species distribution models (Nenzen & Araújo 2011).

We projected to the complete study site and averaged predictions for each model across the 20 repetitions. We then generated the final ensemble projection averaging the predicted occurrences across all models, while weighting each model contribution to the average based on its respective TSS (Thuiller *et al.* 2009), assuming that TSS is more reliable than AUC as a measure of accuracy when using dichotomous presence/absence data (Allouche, Tsoar & Kadmon 2006). Models with higher TSS thus had a greater contribution to the ensemble estimate.

*Environmental variables*

The ensuing nine environmental variables used as predictors to build our species distribution models predicting koala habitat suitability were: (1) minimum temperature (°C), (2) distance to water bodies (m), (3) average rainfall for November (mm), (4) total water index, (5) likelihood of native vegetation being present in the grid cell (%), (6) distance to roads (m), (7) solar exposure (megajoules m-2, MJ m-2), (8) water vapour pressure (in hectopascals, hPa), and (9) elevation (m). We obtained spatial data on vegetation, topographic water features, transport infrastructure (distance to roads), and elevation from the Department of Environment and Water, Government of South Australia (data.sa.gov.au, Fig. S1). From the Australian Government Bureau of Meteorology (bom.gov.au), we obtained 20-year monthly averages (from 1993 to 2012) of minimum temperature, water vapour pressure, solar exposure (no data for November 2009), and rainfall. We used the distance to inundated areas as proxy for the availability of drinking water, considering only year-round and seasonally inundated areas (water bodies). We also included the density of watercourses (i.e., rain watercourses) within each grid cell as a proxy for food quality (i.e., possibly reflecting leaf water content). We calculated the variance inflation factor for all climate variables and ensured that all variables returned a variance inflation factor < 10 to minimize multicollinearity.

*Variable importance and response curves*

We estimated the individual contribution of all variables in the species distribution models (Thuiller *et al.* 2009) for each of the nine statistical algorithms based on their present-day projection as a benchmark. We then ran these algorithms with one environmental variable changed (randomly reshuffling that variable’s values) while maintaining the others in the observed order. We then calculated Spearman’s *ρ* between the new prediction and the benchmark prediction as a metric of relative variable importance (high *ρ* indicates that the randomized variable has little effect on final predictions). We repeated this process for each environmental variable in all 20 training datasets (10 iterations per variable). We subsequently calculated the mean and standard deviation of variable importance for each variable across the 10 iterations per algorithm, and then calculated the ensemble predictions using the TSS-weighted average of the nine model algorithms.

We evaluated the responses of the species distributions to the gradients of explanatory variables based on the response curves derived from each model. We generated response curves by holding *k* - 1 variables constant at their mean value while the variable of interest contains 100 points varying from the maximum to the minimum of its range. Here, the variation in predictions for these 100 cells only reflects the effects of one selected variable. Thus, a plot of these predictions visualizes the modelled response to the variable of interest, contingent on the other variables held constant.

*Abundance estimates*

With no specific information available for koalas, we assumed a simple linear relationship between relative habitat suitability index (0 = lowest; 1 = highest) and density, following the assumption that the relationship increases linearly with the highest habitat suitability score corresponding to the average population density estimated by the inhomogeneous Poisson process. Summing over all 1-km2 grid cells provides an estimate of the total population size within the 3080-km2 Adelaide–Mount Lofty ranges study area.

Sterilization demographic model

*Model overview*

We developed a 13 × 13 age-classified (Leslie) matrix population model (i.e., a 12-year age-classified model produces a 13 × 13 matrix including the 0–1 year transition based on the longevity reported for koalas) (Smith 1979) to simulate the effect of fertility control for the koala population in the Mount Lofty Ranges. We gathered input data from previously published studies on wild koala populations across Australia — for fertilities, we acquired median values from Rhodes *et al.* (2011) (Fig. S4), and for survival, we combined data from Penn *et al.* (2000); Dique *et al.* (2003); Lunney *et al.* (2007); Rhodes *et al.* (2011) (Table S1). The model ran over a 24-year period that describes the koala’s population dynamic from 2016 (i.e., date of *Great Koala Count 2* used to calculate the absolute population size) until 2040.

To combine the survival estimates across available studies, we developed a resampling approach where we first compiled the median and upper/lower limits of age-specific survival per study (i.e., ± 1.96 reported standard errors or confidence limits provided), and then standardized these uncertainties by back-calculating a standard deviation for each class per study. From this dataset, we randomly resampled 10,000 medians and standard deviations per age class (interpolating missing data for a given age class from the mean of values for that age class), and then beta-sampled age-specific survival probabilities per iteration using the resampled medians and standard deviations. To smooth the stochastically resampled survivals, we applied an exponential association function:

eq. 5

where *si,x* = is the smoothed survival probability for age *x* in iteration *i*, and *ai*, *bi*, and *ci* are constants per iteration *i*. From the 10,000 estimates of *a*, *b*, and *c*, we took the mean and upper and lower 95 percentiles per age *x* from which we resampled stochastically following a beta distribution in the matrix projections (Fig. S2). Our model was female-only, assuming a pre-census design and a 1:1 sex ratio (McLean 2007; Ellis *et al.* 2010).

For each projection scenario (see *Projection scenarios and associated sterilization costs*), we stochastically resampled the age-specific fertilities assuming a 3% standard deviation (Rhodes et al. 2011) and the survival probabilities from the smoothed mean values (± 5% standard deviation, see Eq. 5). We assumed a Gaussian distribution around the mean of fertility and a *β* distribution for survival probability (Table 1). We calculated the population’s stable age distribution from the deterministic matrix (Caswell 2001), and then multiplied this stable age structure by an initial population size of 32,231 – 38,119 individuals (see Results).

*Projection scenarios and associated sterilization costs*

Baseline (no-intervention) — To provide a realistic baseline expectation of population trajectory for comparison to the sterilization interventions, we used the population size estimated from the inhomogeneous Poisson point-process ensemble distribution model as the founding population size, and expressed all subsequent projections as a proportion of that initial abundance. Because the Mount Lofty Ranges are bounded by habitat that is largely unsuitable for koalas (Sequeira et al. 2014; Whisson & Ashman 2020), making immigration or permanent emigration unlikely, we assumed a closed population structure.

We included a logistic compensatory density-feedback function by reducing survival as the population approached carrying capacity of the form:

eq. 6

where Smod is the proportion of realized survival (survival modifier) as a function of population size *N*, and the constants a = -107, *b* = 0.00216, and *c* = 34.7 (Fig. S2). Here, we assumed that survival probability would decline as the population approached a carrying capacity that we assumed was 20% higher than the current population size to allow for additional dispersal into suitable habitats in the Mount Lofty Ranges not currently occupied or at low density.

We also invoked a catastrophic mortality function at a probability of 0.14 generation-1 based on Reed *et al.* (2003) (generation length = 6.75 as inferred from the deterministic matrix), where each event would reduce the population by 50% (stochastically resampled assuming a 5% standard deviation).

Sterilization scenarios — We examined two main sterilization scenarios that represent the two extreme of fertility control options: (i) only adult females sterilized, and (ii) female back young and their mothers sterilized together at capture. For the first scenario, where only adult females are targeted and sterilized, we adjusted the baseline model with incrementing proportional sterilization of females (expressed as reductions in overall fertility) randomly selected from the adult portion of the age structure. The second scenario is predicated on the notion that capturing adult females with female back young and sterilizing both mother and daughter would be more efficient and effective than adult-only sterilizations.

This is because with about 46.5% of the koala population in the Mount Lofty Ranges infected with chlamydial disease (Fabijan et al. 2019), many females are likely infertile (Robbins et al. 2019), making their sterilization unnecessary. Since detecting and capturing individuals is the most time-consuming and expensive part of the process (not the sterilization itself), focusing on females proven fertile (those with back young) would optimize the cost-benefit by avoiding the sterilization of already chlamydia-infertile females (Hynes et al. 2019). This approach, however, presents ethical challenges related to authorizing sterilization of back young.

*Costs*

For both models, sterilization is achieved through subcutaneous hormone implants. These implants release hormones over a prolonged period, interfering with the normal reproductive processes and effectively preventing the animal from breeding. This method presents the main advantages of being non-surgical and reversible (unlike surgical sterilization such as spaying or neutering that are permanent, so that the animal can regain its reproductive capabilities if desired. Cost estimates are based on $30 hour-1 labour cost, 0.83 hours koala-1 search/capture and $27 cost for each hormone implant (modified from Delean, Prowse and Cassey (2013)).

Results

Using the inhomogeneous Poisson point process model, we estimated an average of 160 koalas km-2 (95% confidence interval: 104–123 km-2) when not constrained by environmentally driven habitat suitability. By rescaling these estimates (i.e., average estimate + confidence intervals) proportionally to habitat suitability, we obtained a total population estimate of 32,851 (32,231–38,119) koalas across the entire study area. The densest areas (up to 160 km-2, Fig. 1a) are centred around Cleland Conservation Park and Belair National Park, extending to Mount Barker, Lobethal, and Gumeracha, in the areas of highest habitat suitability (Fig. 2a) and cover an area of approximately 5576 km2 (Fig. 1a). This density then decreases sharply with distance from this highly suitable core area (> 100 km-2; Fig. 1a), especially north of Gumeracha. Some low-density populations (< 25 km-2, Fig. 1a), are estimated toward the Fleurieu Peninsula in some local areas such as Onkaparinga National Park, Kangarilla, and Prospect Hill that present some low habitat suitability for the species (0.5 – 0.75, Fig. 2a).

The ensemble habitat suitability models showed a high predictive power (ROC = 0.99; Fig. 2a). The presence of suitable koala habitat is mostly predicted by rainfall, minimum temperature, and the probability of a cell containing native vegetation (Table 1). More specifically, the highest habitat suitability was in areas with a high annual rainfall (> 75 mm) (Fig. 3b) and warm minimum temperature (> 10 °C, Fig. 3c), and > 90% native vegetation (Fig. 3d). Based on these habitat suitability estimates, capping the koala population density to 0.7 koalas ha-1 (= 70 koalas km-2) would result in > 10% of the total area occupied by koalas identified as overpopulated (Fig. 1b). If remained unmanaged (i.e., no fertility control), we estimate an increase in the population of ~ 36,088 individuals ([95% confidence interval: 32,231 – 46,474], Fig. S4) over the next 25 years. Not only would this increase the number of koalas in already overpopulated areas, but new areas of excessive population will appear (e.g., Northeast of Mount Compass and Onkaparinga National Park, Lobethal, etc.) with > 12% of current koala distribution predicted to be overpopulated (Fig. 1c).

Fertility control implemented to keep koala density ≤ 0.7 ha-1 in the Mount Lofty Ranges, accounting for habitat suitability, requires a total population (i.e., males and females) < 30,194 individuals (green horizontal line, Fig. 3a,b). Both fertility control scenarios tested have different impacts on the speed of reduction in total population size (i.e., blue line in Fig. 3a,b) depending on the annual effort of sterilization. They both lead to a decrease in the total population as the yearly proportion of sterilized individuals increases (but so does the confidence interval around the total population estimates). However, sterilizing adult females only slows down the rate of population reduction (Fig. 2a) compared to sterilizing adult females and female back young (Fig. 3b). This results in a higher yearly proportion of adult females only sterilized (~12%, Fig. 3a) compared to sterilizing adult females and female back young (~ 8%, Fig. 3b) to match this conservation target. Sterilizing between 6% and 8% of individuals, irrespective of scenario, would merely keep the population density constant at its present value, which means there would still be an of excess of 2657 individuals (i.e., orange area, Fig. 3a,b).

The overall cost of sterilizing the koala population increases with annual sterilization rate (Fig. 3c,d). Regardless of the scenario, > 20% sterilized individuals year-1 leads to the yearly costs declining over time. Planning to sterilize 12% of adult females only annually to reach the conservation target would be cheaper over time (~ AU$28 million in total; Fig. 3a) than trying to reach the same conservation target in the adult females and female back young scenario (> AU$39 million in total; Fig. 3b). While the difference in proportion of sterilized individual between the two scenarios is only 4%, the difference in the total cost over the next 25 years would be > $11 million (Fig. 3a,b).

Sterilizing both adult females and female back young reduced the initial population faster than sterilizing adult females only (Fig. 2a,b), because this scenario increased the proportion of animals sterilized per year. For example, sterilizing 50% of adult females only (0. 5; Fig. 4a) would cause a reduction of approximately 80% of the initial population (declining from 1 to 0.2, Fig. 4a). In comparison, the same reduction could be achieved by only sterilizing 35% of adult females and female back young each year (0.35; Fig. 4b). In the context of reaching the conservation target, this would translate into a decrease of ~ 22% of the founding population by sterilizing 12% of adult females only (Fig. 4a), while sterilizing 8% of adult females and female back young would lead to a decrease of ~ 30% of the founding population (Fig. 4b).

Our simulations projected that the actual number of sterilized koalas (males and females) under a sterilized adult females only scenario plateaued around 7 × 104 (Fig. 4c), whereas the number of sterilized adult females and female back young declined from 15 × 105 to 8 × 105 at an annual sterilization rate between 40% and 70%, before reaching 9 × 105 beyond 70% (Fig. 4d). The confidence intervals around the estimates derived for the second scenario (maximum confidence interval width = 20 × 105; Fig. 4d) were wider than those for the first scenario (maximum confidence interval width = 4 × 105; Fig. 4c). However, at < 30% of sterilized individuals, targeting adult females only produced a slower increase in the number of sterilized individuals compared to targeting adult females and female back young (reaching a median of 8.5 × 104 versus 15.3 × 104 sterilized individuals, respectively; Fig. 4c,d). This difference between scenarios has a large effect on the total population sterilized when it comes to meeting the conservation target. The adult females only scenario would result in ~ 40,000 sterilized individuals (Fig. 4c), whereas it would reach > 100,000 individuals under the adult females and female back young scenario (Fig. 4d).

The cost-effectiveness of fertility control strategies varies depending on the conservation goals set for koalas, particularly the population density threshold, so that adjusting these goals affects model outcomes (Table S3). For example, relaxing the density goal to 1 ha-1 leads to a 75–95% decrease in the areas exceeding the targeted density, reducing the number of sterilized koalas by 65–70%, and associated costs by 72–82%. Conversely, a more stringent conservation goal of 0.5 ha-1 results in up to a 128% increase in high-density areas, requiring more control measures to sterilize an extra 75–82% of individual and raising costs by 65–90% (Table S3)

Discussion

Using spatially explicit, de-biasing approaches, we can now estimate koala population abundance across the Mount Lofty Ranges to identify areas of current and future overabundance, as well as project population trajectories and the relative cost-effectiveness of management actions. With an estimated size of 32,231 to 38,119, the population in the Mount Lofty Ranges represents about 10% of Australia’s estimated total koala population (Adams-Hosking *et al.* 2016). This range aligns with expert-elicited estimates (Adams-Hosking *et al.* 2016) and corrects previous estimates based on *Great Koala Counts* by about 29% (Sequeira *et al.* 2014). The conservation target of maintaining the koala population density below ~0.7 ha-1 (National Parks and Wildlife South Australia 2002; Ramsey, Tolsma & Brown 2016)already suggests that approximately 9% of the region is overabundant in the areas of highest habitat suitability (Fig. 1a,b). In contrast to the declining populations in New South Wales, Australian Capital Territory, and Queensland (McAlpine *et al.* 2015; Whisson & Ashman 2020), we predict that the population in the Mount Lofty Ranges could theoretically increase by a mean of around 10% (95% confidence interval: 2.6–41.5%) within 25 years if unmanaged, with sub-populations within 12% of the current range becoming overabundant (Fig. 1c). The latter estimate is higher than that proposed by expert elicitation (+3%) (Adams-Hosking *et al.* 2016). While koala populations in other regions of South Australia such as Kangaroo Island and the lower Murray River are expected to report most population losses, the Mount Lofty Ranges could become a hub of overabundance because of increasing areas with high habitat suitability (Fig. 1a–c).

Based on predicted habitat suitability, average November rainfall, minimum temperature, and the abundance of native vegetation drive the relative abundance of koala population across the Mount Lofty ranges (Fig. 2). While the relationship between predicted habitat suitability and species abundance varies regionally and by taxon (Murphy, VanDerWal & Lovett-Doust 2006; Rondinini *et al.* 2011; Dallas & Hastings 2018), Australian mammal abundance is generally positively correlated with the outputs of species distribution models (VanDerWal *et al.* 2009). Such a relationship is important for identifying climate and weather refugia for koalas today and in the future (Kearney et al., 2010; Krockenberger et al., 2012). In the Mount Lofty Ranges, increasing rainfall during the warmer summer months increases habitat suitability (> 70%, Fig. 2c) because it mitigates the effects of rising temperatures and drought, and potentially reducing fire risk. While extreme temperatures can increase mortality (Lunney & Hutchings 2012), low minimum temperatures (< 11°C, Fig. 2b) challenge koala thermoregulation (Adam *et al.* 2020). As such, koalas have adapted by selecting specific tree species (Fig. 2d) that offer better insulation and moisture (Degabriele & Dawson 1979), such as *Eucalyptus viminalis* and *E. ovata* (Menkhorst 2008), which are preferred in cooler climates for their high moisture and nutrient content (Moore & Foley 2005; Clifton *et al.* 2007). Although the likelihood of native vegetation being present in the grid cell is a weak predictor of koala habitat suitability (Fig. 2b–d), the species’ reliance on native vegetation as food makes it vulnerable to native forest loss. An unmanaged koala population that increases in density enough to cause overbrowsing can reduce food availability, thereby reducing survival and the probability of persistence (Todd, Forsyth & Choquenot 2008).

While expensive and controversial, artificial fertility reduction remains a relevant strategy to minimize the likelihood of overabundance leading to catastrophic mortality events (Fig. 3a,b). Regulating the koala population via fertility interventions in areas of high habitat suitability (Fig. 2) could achieve target densities of ~ 0.7 ha-1. Sterilizing both females and their dependent daughters would achieve these conservation goals slightly faster than targeting females only (Fig. 3a,b), but the cost difference over the next 25 years would be substantial (Fig. 3c,d; Fig. 4c,d). Our cost-benefit analysis therefore suggests that focusing on adult female-only sterilization is more economical for fertility control (Fig. 3c,d). Adult female-only sterilization would have the additional benefit of avoiding the ethical challenges of fertility interventions (i.e., surgical sterilization, hormonal implant, etc.) for young animals (Australian Government Department of Agriculture 2011; Hampton *et al.* 2015; RSPCA 2024). Regardless of the intervention scenario implemented, the total cost required to achieve acceptable density targets would be < $40 million over the next 25 years, averaging $1.6 million year-1 (Fig. 3c,d). That amount is < 20% of the Australian Government's investment in wildlife recovery following the 2019–2020 Black Summer bushfires (Quarterly Summary, August 2023). Additionally, fertility reduction is ~AU$10 million cheaper than the most cost-effective method to eradicate cats on Kangaroo Island (AU$46.5 million–AU$51.6 million, Venning et al., 2021) and is comparable to the annual cost of deer and pig control and eradication programs in South Australia ($1.1 million year-1; Government of South Australia 2023).

Conclusion

Managing the koala population in the Mount Lofty Ranges is a complex challenge due to overpopulation concerns, habitat suitability, and the species’ cultural significance. While koalas have adapted to local environmental conditions, unchecked population growth could lead to overbrowsing, eliciting mass die-offs, suffering, and negative implications for many other forest-dependent species. We show that despite logistical challenges, spatially targeted fertility control is cost-effective. In addition to cost, ethical considerations and long-term conservation goals (such as population density thresholds) also play an important role in deciding whether intervention is necessary and socially acceptable.

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Author contribution statement

F.S.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, resources, software, validation, visualization, writing—original draft, writing—review and editing; K.J.P.: formal analysis, investigation, visualization, writing—original draft, writing—review and editing; D.J.R.: resources, writing—original draft, writing—review and editing; J.C.: analysis, methodology, software, writing—original draft, writing—review and editing; V.W.: investigation, writing—original draft, writing—review and editing; C.J.A.B.: conceptualization, funding acquisition, investigation, formal analysis, methodology, resources, software, writing— original draft, writing—review and editing.

Conflict of interest statement

The authors declare no conflict of interest.

Data availability statement

Data and code that support the findings of this study are openly available on: https://github.com/FredSaltre/Koala\_MLR

Figure captions & table

**Table 1** – Variable importance (median and confidence interval) for present-day ensemble modelling of habitat suitability for koala (*Phascolarctos cinereus*) in the Mount Lofty ranges. Values were summarized across all 100 training datasets with the lower and upper limit of the confidence interval calculated as the 25th and 75th percentile respectively.

|  |  |  |
| --- | --- | --- |
| **variable** | **median** | **confidence**  **interval** |
| average rainfall for November (mm) | 0.79 | [0.78 – 0.80] |
| minimum temperature (°C) | 0.16 | [0.15 – 0.17] |
| likelihood of native vegetation being present in the grid cell (%) | 0.06 | [0.06 – 0.07] |
| distance to water bodies (m) | 0.02 | [0.02 – 0.02] |
| solar exposure (MJ m-2), | 0.02 | [0.02 – 0.02] |
| distance to roads (m), | 0.01 | [0.01 – 0.01] |
| total water index | 0.01 | [0.01 – 0.01] |
| water vapour pressure (hPa) | 0.01 | [0.01 – 0.01] |
| elevation (m) | 0 | [0 – 0] |

Figure 1 – Local koala densities in the Mount Lofty Ranges at a spatial resolution of 1 km × 1 km. (a) Present-day mean population densities, (b) current simulated mean koala density beyond the density target of 0.7 ha-1 (National Parks and Wildlife South Australia 2002; Ramsey, Tolsma & Brown 2016), and (c) projections of areas beyond the density target 25 years into the future. Gradients range from dark blue and dark red (low population density) to light green and orange (high population density).

**Figure 2 –** Koala habitat suitability and environmental drivers in the Mount Lofty Ranges. (a) Present day (2003–2018, 16-yr mean) ensemble averaged probability of koala presence across the Mount Lofty Ranges at a spatial resolution of 1 × 1 km. Gradient ranges from dark to light blue indicating low to high habitat suitability. Ensemble model outputs are based on 9 modelling algorithms (see Methods) for which we calculated a weighted average based on their relative performance. White/red-circle dots indicate koala presences based on the *Great Koala Counts* 1 and 2, grey areas show the urbanized area, and green gradient shows vegetation density from dark to light green). Also shown are the response curves for the three most important predictor variables for koala habitat suitability (Table 1): (b) average rainfall for November (mm, 20-years average), (c) monthly minimum temperature (°C, 20-years average) and (d) likelihood of native vegetation being present in the grid cell (%). Envelopes represent the confidence intervals calculated as the 25 and 75th percentile across 20 different training and evaluation datasets use to generate pseudo-absences (see Method). For each predictor tested, we varied values from the minimum to the maximum (100 increments) while holding the other variables constant (at mean value).

**Figure 3 –** Impact of fertility control on koala population size and its associated cost. **(a, b)** Projected total population size as a function of the proportion of females sterilized considering (a) only mature females sterilized, or (b) mature females and their female offspring sterilized. Blueline indicates median values from 10,000 iterations (see Method) and light blue-shaded areas represent 95% confidence intervals of the simulations calculated from the 95% confidence interval of initial population size (i.e., 32,231–38,119). Also shown are (*i*) the targeted population size at threshold of ≤ 0.7 ha-1 (horizontal green line and green area), (*ii*) present-day reconstructed population size based on an inhomogeneous Poisson point process model combined with a habitat suitability model (horizontal orange line), and (*iii*) projected unmanaged total population size (horizontal red line). Green area represents all possible population sizes that would meet the density target of 0.7 ha-1, while orange and red areas show how much the population size already exceeds this target, or will exceed in the future, if the population is unmanaged. Vertical dotted black line indicates the proportion of sterilized females that should be sterilized to meet the density target. **(c, d)** Projected estimated median yearly costs over time for two sterilization scenarios: (c) only mature females sterilized, or (d) mature females and their female offspring sterilized. Sterilization costs (in AU$) shown as a function of year and the proportion of sterilized individuals; costs are indicated by colour bar ranging from lowest (dark blue) to highest (yellow). Horizontal dotted red line indicates the proportion of females that should be sterilized to meet the density target. Contours and white values indicate cost isoclines in AU$.

**Figure 4 –** Impact of fertility control on the koala population in the Mount Lofty Ranges. **(a, b)** Projected proportion of the initial koala population (i.e., males and females) and **(c, d)** number of sterilized koalas as a function of the proportion of females sterilized considering: **(a, c)** only mature females sterilized, or **(b, d)** mature females and their female offspring sterilized. Orange **(a, b)** and brown **(c, d)** lines indicate median values from 10,000 iterations. Light green **(a, b)** and light brown (c, d) shaded areas represents 95% confidence intervals from the simulation based on a median initial population size of 32,851 koalas (see Methods). Dark green **(a, b)** and brown **(c, d)** envelopes represent 95% confidence intervals calculated from the 95% confidence interval of median initial population size (i.e., 32,231–38,119).

**References**

Adam, D., Johnston, S.D., Beard, L., Nicolson, V., Gaughan, J.B., Lisle, A.T., FitzGibbon, S., Barth, B.J., Gillett, A., Grigg, G. & Ellis, W. (2020) Body temperature of free-ranging koalas (Phascolarctos cinereus) in south-east Queensland. *International Journal of Biometeorology,* **64,** 1305-1318.

Adams-Hosking, C., Grantham, H.S., Rhodes, J.R., McAlpine, C. & Moss, P.T. (2011) Modelling climate-change-induced shifts in the distribution of the koala. *Wildlife Research,* **38,** 122-130.

Adams-Hosking, C., McBride, M.F., Baxter, G., Burgman, M., de Villiers, D., Kavanagh, R., Lawler, I., Lunney, D., Melzer, A., Menkhorst, P., Molsher, R., Moore, B.D., Phalen, D., Rhodes, J.R., Todd, C., Whisson, D. & McAlpine, C.A. (2016) Use of expert knowledge to elicit population trends for the koala (Phascolarctos cinereus). *Diversity and Distributions,* **22,** 249-262.

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology,* **43,** 1223-1232.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution,* **22,** 42-47.

Australian Government Department of Agriculture, F.a.F. (2011) Australian Animal Welfare Strategy and National Implementation Plan 2010–2014. Canberra.

Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution,* **3,** 327-338.

Black, K.H., Price, G.J., Archer, M. & Hand, S.J. (2014) Bearing up well? Understanding the past, present and future of Australia's koalas. *Gondwana Research,* **25,** 1186-1201.

Bookhout, T.A. (1994) *Research and management techniques for wildlife and habitats*.

Briscoe, N.J., Kearney, M.R., Taylor, C.A. & Wintle, B.A. (2016) Unpacking the mechanisms captured by a correlative species distribution model to improve predictions of climate refugia. *Global Change Biology,* **22,** 2425-2439.

Bryan, B.A. (2000) Strategic revegetation planning in an agricultural landscape: a spatial information technology approach.

Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates.

Clifton, I.D., Ellis, W.A.H., Melzer, A. & Tucker, G. (2007) Water turnover and the northern range of the koala (Phascolarctos cinereus). *Australian Mammalogy,* **29,** 85-88.

Crall, A.W., Newman, G.J., Jarnevich, C.S., Stohlgren, T.J., Waller, D.M. & Graham, J. (2010) Improving and integrating data on invasive species collected by citizen scientists. *Biological Invasions,* **12,** 3419-3428.

Cretois, B., Simmonds, E.G., Linnell, J.D.C., van Moorter, B., Rolandsen, C.M., Solberg, E.J., Strand, O., Gundersen, V., Roer, O. & Rød, J.K. (2021) Identifying and correcting spatial bias in opportunistic citizen science data for wild ungulates in Norway. *Ecology and Evolution,* **11,** 15191-15204.

Dallas, T.A. & Hastings, A. (2018) Habitat suitability estimated by niche models is largely unrelated to species abundance. *Global Ecology and Biogeography,* **27,** 1448-1456.

Degabriele, R. & Dawson, T.J. (1979) Metabolism and heat balance in an arboreal marsupial, the koala (Phascolarctos cinereus). *Journal of Comparative Physiology,* **134,** 293-301.

Delean, S., Prowse, T. & Cassey, P. (2013) Kangaroo Island Koala Management Model. *Report to Department of Environment, Water and Natural Resources, South Australia. University of Adelaide*.

Dique, D.S., Thompson, J., Preece, H.J., de Villiers, D.L. & Carrick, F.N. (2003) Dispersal patterns in a regional koala population in south-east Queensland. *Wildlife Research,* **30,** 281-290.

Duka, T. & Masters, P. (2005) Confronting a tough issue: fertility control and translocation for over‐abundant koalas on Kangaroo Island, South Australia. *Ecological Management & Restoration,* **6,** 172-181.

Elith, J., Phillips, S.J., Hastie, T., Dudik, M., Chee, Y.E. & Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions,* **17,** 43-57.

Ellis, W., Bercovitch, F., FitzGibbon, S., Melzer, A., De Villiers, D. & Dique, D. (2010) Koala birth seasonality and sex ratios across multiple sites in Queensland, Australia. *Journal of Mammalogy,* **91,** 177-182.

EPBC (2023) the Environment Protection and Biodiversity Conservation Act 1999.

Fabijan, J., Caraguel, C., Jelocnik, M., Polkinghorne, A., Boardman, W.S., Nishimoto, E., Johnsson, G., Molsher, R., Woolford, L. & Timms, P. (2019) Chlamydia pecorum prevalence in South Australian koala (Phascolarctos cinereus) populations: Identification and modelling of a population free from infection. *Scientific reports,* **9,** 6261.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation,* **24,** 38-49.

ForestrySA (2014) Mount Lofty Ranges Forest Reserves Management Plan.

Fourcade, Y., Engler, J.O., Rodder, D. & Secondi, J. (2014) Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias. *Plos One,* **9**.

Government of South Australia (2023) Strategic Plan for the South Australian Feral Deer Eradication Program 2022-2032.

Guisan, A., Theurillat, J.-P. & Kienast, F. (1998) Predicting the potential distribution of plant species in an alpine environment. *Journal of Vegetation Science,* **9,** 65-74.

Guisan, A., Thuiller, W. & Zimmermann, N.E. (2017) *Habitat Suitability and Distribution Models: with Applications in R*. Cambridge University Press.

Hampton, J.O., Hyndman, T.H., Barnes, A. & Collins, T. (2015) Is Wildlife Fertility Control Always Humane? *Animals (Basel),* **5,** 1047-1071.

Hauser, C.E., Pople, A.R. & Possingham, H.P. (2006) Should Managed Populations Be Monitored Every Year? *Ecological Applications,* **16,** 807-819.

Hollow, B., Roetman, P.E.J., Walter, M. & Daniels, C.B. (2015) Citizen science for policy development: The case of koala management in South Australia. *Environmental Science & Policy,* **47,** 126-136.

Hughes, A.C., Orr, M.C., Ma, K., Costello, M.J., Waller, J., Provoost, P., Yang, Q., Zhu, C. & Qiao, H. (2021) Sampling biases shape our view of the natural world. *Ecography,* **44,** 1259-1269.

Hynes, E.F., Shaw, G., Renfree, M.B. & Handasyde, K.A. (2019) Contraception of prepubertal young can increase cost effectiveness of management of overabundant koala populations. *Wildlife Research*.

Illian, J., Penttinen, A., Stoyan, H. & Stoyan, D. (2008) *Statistical analysis and modelling of spatial point patterns*. Wiley, West Sussex, England.

Isaac, N.J.B., van Strien, A.J., August, T.A., de Zeeuw, M.P. & Roy, D.B. (2014) Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution,* **5,** 1052-1060.

IUCN (2024) The IUCN Red List of Threatened Species. Version 2024-1.

Johnson, D.H. (1980) The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology,* **61,** 65-71.

Lee, A.K. & Martin, R.W. (1988) *The koala: a natural history*. UNSW Press.

Lunney, D., Gresser, S., O'neill, L.E., Matthews, A. & Rhodes, J. (2007) The impact of fire and dogs on koalas at Port Stephens, New South Wales, using population viability analysis. *Pacific Conservation Biology,* **13,** 189-201.

Lunney, D. & Hutchings, P. (2012) *Wildlife and Climate Change: Towards robust conservation strategies for Australian fauna*. Royal Zoological Society of New South Wales.

Manly, B.F.J. (2006) *Randomization, Bootstrap and Monte Carlo Methods in Biology, Third Edition*. Taylor & Francis.

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature,* **405,** 243-253.

Massei, G. & Dave, C. (2014) Fertility control to mitigate human–wildlife conflicts: a review. *Wildlife Research,* **41**.

Masters, P., Duka, T., Berris, S. & Moss, G. (2004) Koalas on Kangaroo Island: from introduction to pest status in less than a century. *Wildlife Research,* **31,** 267-272.

McAlpine, C., Lunney, D., Melzer, A., Menkhorst, P., Phillips, S., Phalen, D., Ellis, W., Foley, W., Baxter, G. & De Villiers, D. (2015) Conserving koalas: A review of the contrasting regional trends, outlooks and policy challenges. *Biological Conservation,* **192,** 226-236.

McLean, N. (2007) Ecology and management of overabundant koala (Phascolarctos cinereus) populations. PhD, The University of Melbourne.

Melzer, A., Carrick, F., Menkhorst, P., Lunney, D. & John, B.S. (2000) Overview, critical assessment, and conservation implications of koala distribution and abundance. *Conservation Biology,* **14,** 619-628.

Menkhorst, P. (2008) Hunted, marooned, re-introduced, contracepted: a history of koala management in Victoria. *Too Close for Comfort: Contentious Issues in Human–Wildlife Encounters’.(Eds D. Lunney, A. Munn and W. Meikle.) pp***,** 73-92.

Molsher, R. (2017) Kangaroo Island koala population survey 2015. *Natural Resources Kangaroo Island: SA, Australia*.

Moore, B.D. & Foley, W.J. (2005) Tree use by koalas in a chemically complex landscape. *Nature,* **435,** 488-490.

Murphy, H.T., VanDerWal, J. & Lovett-Doust, J. (2006) Distribution of Abundance across the Range in Eastern North American Trees. *Global Ecology and Biogeography,* **15,** 63-71.

National Parks and Wildlife South Australia (2002) A review of the Kangaroo Island Koala Management Program. 1996-2001.National Parks and Wildlife South Australia., Adelaide, South Australia

Nenzen, H.K. & Araújo, M.B. (2011) Choice of threshold alters projections of species range shifts under climate change. *Ecological Modelling,* **222,** 3346-3354.

Penn, A.M., Sherwin, W.B., Gordon, G., Lunney, D., Melzer, A. & Lacy, R.C. (2000) Demographic forecasting in koala conservation. *Conservation Biology,* **14,** 629-638.

Pepin, K.M., Davis, A.J. & VerCauteren, K.C. (2017) Efficiency of different spatial and temporal strategies for reducing vertebrate pest populations. *Ecological Modelling,* **365,** 106-118.

Phillips, S.S. (2000) Population trends and the koala conservation debate. *Conservation Biology,* **14,** 650-659.

Ramsey, D.S.L., Tolsma, A.D. & Brown, G.W. (2016) Towards a habitat condition assessment method for guiding the management of overabundant Koala populations. Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water and Planning.

Reed, D.H., O'Grady, J.J., Ballou, J.D. & Frankham, R. (2003) The frequency and severity of catastrophic die-offs in vertebrates. *Animal Conservation forum*, pp. 109-114.Cambridge University Press.

Rhodes, J.R., Ng, C.F., de Villiers, D.L., Preece, H.J., McAlpine, C.A. & Possingham, H.P. (2011) Using integrated population modelling to quantify the implications of multiple threatening processes for a rapidly declining population. *Biological Conservation,* **144,** 1081-1088.

Robbins, A., Hanger, J., Jelocnik, M., Quigley, B.L. & Timms, P. (2019) Longitudinal study of wild koalas (Phascolarctos cinereus) reveals chlamydial disease progression in two thirds of infected animals. *Scientific reports,* **9,** 13194.

Robinson, A. & Bergin, T. (1978) The koala in South Australia. *The Koala: Proceedings of the Taronga Symposium’.(Ed. TJ Bergin.) pp*, pp. 132-143.

Robinson, A., Spark, R. & Halstead, C. (1989) The distribution and management of the koala (*Phascolarctos* *cinereus*) in South Australia. *South Australian Naturalist,* **64,** 4-25.

Rondinini, C., Di Marco, M., Chiozza, F., Santulli, G., Baisero, D., Visconti, P., Hoffmann, M., Schipper, J., Stuart, S.N., Tognelli, M.F., Amori, G., Falcucci, A., Maiorano, L. & Boitani, L. (2011) Global habitat suitability models of terrestrial mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **366,** 2633-2641.

RSPCA (2024) RSPCA Australia Policies on Wildlife Management.

Sbrocchi, C., Pecl, G., Gillies, C. & Roetman, P. (2015) How to recruit 23 million scientists. *Australasian Science,* **36,** 33-35.

Sequeira, A.M., Roetman, P.E., Daniels, C.B., Baker, A.K. & Bradshaw, C.J. (2014) Distribution models for koalas in South Australia using citizen science‐collected data. *Ecology and Evolution,* **4,** 2103-2114.

Shabani, F., Ahmadi, M., Peters, K.J., Haberle, S., Champreux, A., Saltré, F. & Bradshaw, C.J. (2019) Climate‐driven shifts in the distribution of koala‐browse species from the Last Interglacial to the near future. *Ecography,* **42,** 1587-1599.

Sicacha-Parada, J., Steinsland, I., Cretois, B. & Borgelt, J. (2021) Accounting for spatial varying sampling effort due to accessibility in Citizen Science data: A case study of moose in Norway. *Spatial Statistics,* **42,** 100446.

Silvertown, J. (2009) A new dawn for citizen science. *Trends in Ecology & Evolution,* **24,** 467-471.

Smith, M. (1979) Notes on reproduction and growth in the koala, *Phascolarctos cinereus* (Goldfuss). *Wildlife Research,* **6,** 5-12.

Stenhouse, A., Roetman, P., Lewis, M. & Koh, L.P. (2020) Koala Counter: Recording Citizen Scientists’ search paths to Improve Data Quality. *Global Ecology and Conservation,* **24,** e01376.

Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science,* **240,** 1285-1293.

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD – A Platform for Ensemble Forecasting of Species Distributions. *Ecography,* **32,** 369-373.

Todd, C.R., Forsyth, D.M. & Choquenot, D. (2008) Modelling the effects of fertility control on koala–forest dynamics. *Journal of Applied Ecology,* **45,** 568-578.

VanDerWal, J., Shoo, L.P., Johnson, C.N. & Williams, S.E. (2009) Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Naturalist,* **174,** 282-291.

Venning, K.R.W., Saltré, F. & Bradshaw, C.J.A. (2021) Predicting targets and costs for feral‐cat reduction on large islands using stochastic population models. *Conservation science and practice,* **3,** n/a.

Wedrowicz, F., Wright, W., Schlagloth, R., Santamaria, F. & Cahir, F. (2017) Landscape, koalas and people: A historical account of koala populations and their environment in South Gippsland. *Australian Zoologist,* **38,** 518-536.

Westphal, M.I., Field, S., Tyre, A., Paton, D. & Possingham, H. (2003) Effects of landscape pattern on bird species distribution in the Mt. Lofty Ranges, South Australia. *Landscape Ecology,* **18,** 413-426.

Whisson, D.A. & Ashman, K.R. (2020) When an iconic native animal is overabundant: The koala in southern Australia. *Conservation Science and Practice,* **2,** e188.

Whisson, D.A., Dixon, V., Taylor, M.L. & Melzer, A. (2016) Failure to respond to food resource decline has catastrophic consequences for koalas in a high-density population in southern Australia. *Plos One,* **11,** e0144348.

Whisson, D.A., Orlowski, A. & Weston, M.A. (2018) Tree canopy defoliation impacts avifauna. *Forest Ecology and Management,* **428,** 81-86.

Woosnam-Merchez, O., Cristescu, R., Dique, D., Ellis, B., Beeton, R., Simmonds, J. & Carrick, F. (2012) What faecal pellet surveys can and can't reveal about the ecology of koalas Phascolarctos cinereus. *Australian Zoologist,* **36,** 192-200.