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Abstract

   Context. Species translocations are used in conservation globally. Although harvest for translocation may have negative impacts on source populations, translocation programs rarely explore ways of minimising those impacts. In fluctuating source populations, harvest timing may affect its impact because population size and trajectory vary among years.

   Aims. We explored whether the timing and scale of harvest can be altered to reduce its impact on a fluctuating source population of Mallee Emu-wrens, *Stipiturus mallee*; an endangered passerine in south-eastern Australia. Mallee Emu-wren populations fluctuate with ~5–10-year drought–rain cycles.

   Methods. We used population viability analysis (PVA) to compare the impact of five harvest scales (no harvest, 100, 200, 300 or 500 individuals) under three population trajectories (increasing, stable or decreasing) and two initial population sizes (our model-based estimate of the population size and the lower 95% confidence interval of that estimate). To generate a model-based estimate of the population size, we surveyed 540 sites (9 ha), stratified according to environmental variables known to affect Mallee Emu-wren occurrence. We used an information-theoretic approach with N-mixture models to estimate Mallee Emu-wren density, and extrapolated results over all potential habitat.

   Key Results. We estimate that in spring 2019, the source population consisted of 6449 individuals, with a minimum of 1923 individuals (lower 95% confidence interval). Of 48 harvest scenarios, only seven showed no impact of harvest within 5 years (15%). Those seven all had increasing population trajectories and carrying capacity set to equal initial population size. Twenty-six populations showed no impact of harvest within 25 years (54%). These were either increasing populations that had reached carrying capacity or decreasing populations nearing extinction.

   Conclusions. Initial population size, carrying capacity, harvest scale and population trajectory were all determinants of harvest impact. Given the importance of carrying capacity, further research is required to determine its role in the Mallee Emu-wren source population.

   Implications. Harvesting Mallee Emu-wrens after high-rainfall years will have the least impact because source populations are likely to be large with increasing trajectories. For fluctuating source populations, flexibility in the timing of harvest can reduce its impact and should be considered during translocation planning.

Keywords: abundance, conservation management, conservation planning, endangered species, population modelling, population viability, population management, threatened species.

Introduction

Translocations are increasingly used in the management of threatened species (Seddon *et al.* 2014; Berger-Tal *et al.* 2020). Translocations aim to supplement small populations or establish new populations, most often within a species' current range or former range (Seddon *et al.* 2007; IUCN 2013). When assessing the net benefit conferred to a species by a translocation program, it is important to consider both the benefits of translocation for

the recipient population *and* the risk of harvest for the source population (Pérez *et al.* 2012). However, many translocation programs do not have capacity to assess the impact of harvest on the source population (Berger-Tal *et al.* 2020).

   Barriers to assessing impact on source populations include time and budgetary constraints, a lack of basic biological information regarding species' rates of reproduction and mortality and a lack of information regarding the size of source populations

(Clarke *et al.* 2003; Wolf *et al.* 2015; Garnett and Geyle 2018; Furlan *et al.* 2020). An estimate of population size is an important pre-requisite for assessing impact on source populations in a population viability analysis (PVA) framework (Lande *et al.* 2003). It is difficult and costly to precisely estimate population size, especially for widespread, low-density populations or species that are difficult to detect (Clarke *et al.* 2003; Wolf *et al.* 2015; Garnett and Geyle 2018). Likewise, the necessary data on species' demography, breeding system and vital rates are rarely available for input to PVA models (Wolf *et al.* 2015). Because these parameters influence dynamics of source populations post-harvest, poor data quality for these parameters leads to uncertainty when deciding among management strategies and may reduce the utility of PVA (Miller *et al.* 2019).

Despite potential uncertainty, many translocation programs use PVA to inform decisions regarding impacts of harvest and harvest strategy (Armstrong and Reynolds 2012). This is because information regarding species biology and population size may take decades to acquire, and species targeted in translocation programs often face a level of extinction risk that requires immediate intervention (Burgman and Possingham 2000; Martin *et al.* 2012; Wolf *et al.* 2015). In many cases, PVA is still best placed to compare the relative impacts of harvest scenarios, even if estimates of population change and extinction risk are prone to high levels of uncertainty (Burgman and Possingham 2000; Reed *et al.* 2002; Armstrong and Reynolds 2012).

Assessing the impact of harvest is even more complex for populations that frequently undergo large-scale fluctuations in population size (Southgate and Possingham 1995; Bode and Brennan 2011; Céré *et al.* 2015). For example, many arid-zone species undergo population 'boom-and-bust' cycles, i.e. substantial increase in population size during years of above-average rainfall, followed by population decline in the following years (Holmgren *et al.* 2006; Céré *et al.* 2015). Fluctuations in population size and population trajectory present challenges to assessing impacts of harvest on source populations because (a) any estimate of population size is relevant for only a short period and (b) the impact of harvest is likely to vary among years depending on subsequent conditions for recruitment.

Fluctuating source populations also present an opportunity for translocation programs; if the capacity of a source population to recover post-harvest depends on the prevailing population trajectory, then harvest can be timed to promote the recovery of the source population. To the best of our knowledge, the present study is the first to examine whether harvesting of a fluctuating source population can be timed to optimise the rate of post-harvest recovery in the context of threatened species translocations.

The present study focussed on the Mallee Emu-wren, *Stipiturus mallee*, an endangered passerine endemic to the Murray–Mallee region of south-eastern Australia (Fig. 1; Higgins *et al.* 2001). Despite being sedentary and occupying their territories throughout the year, Mallee Emu-wrens are difficult to detect because they are poor flyers and, when disturbed, often shelter in dense hummock-grass rather than flush (Higgins *et al.* 2001). In addition, Mallee Emu-wrens have a soft and high-pitched call, are very small (5 g) and are present at low densities in a large (~700 000 ha) reserve network (Higgins *et al.* 2001; Brown *et al.* 2009; Menkhorst *et al.* 2017).

More than half of the historic range of the Mallee Emu-wren was cleared for agriculture during the past century and almost all remaining habitat is on public reserves (Fig. 1; White 2006; Brown *et al.* 2009; Garnett *et al.* 2011). Over the past four decades, drought and large (>10 000-ha) wildfires have contributed to the Mallee Emu-wren's decline in these public reserves (Paton *et al.* 2009; Garnett *et al.* 2011). A wild-to-wild translocation program aims to re-establish a population of Mallee Emu-wrens in Ngarkat Conservation Park in South Australia through re-introduction of birds from a source population in Victoria (Fig. 1; Mitchell *et al.* 2021). However, the likely impact of harvest on the source population is unknown for two main reasons. First, the most recent estimate of the Mallee Emu-wren population size (16 821 individuals) used data from 1999–2006 (Brown *et al.* 2009). Because of ongoing declines in this species, obtaining a contemporary estimate of population size is a critical first step in comparing the impact of harvest scenarios on the source population (Brown *et al.* 2009; Garnett *et al.* 2011; Verdon *et al.* 2019). Second, the influence of the prevailing population trajectory on post-harvest recovery is poorly understood for this species (Mitchell *et al.* 2021).

A recent study found that rates of Mallee Emu-wren occurrence undergo significant changes over short periods as a result of fluctuations in annual rainfall (Connell 2019). Although Connell (2019) did not directly measure changes in abundance, increases in abundance after years of above-average rainfall ('Big-Wet' years) have been observed in many species in arid and semiarid environments (Holmgren *et al.* 2006), and it is likely that the observed increase in the rate of Mallee Emu-wren occurrence was associated with increased abundance. Connell (2019) was limited by a small number of Mallee Emu-wren records. As a result, formal analysis comparing years was not possible. However, when resurveying sites at 4-year intervals, Mallee Emu-wren occurrences increased by 40% between 'Drought' (2006–2008) and 'Big-Wet' (2011–2012) periods and decreased by 65% from 'Big-Wet' to 'post Big-Wet' (2015–2016) periods (Connell 2019).

Given that the Mallee Emu-wren source population is known to fluctuate among years, it is important to determine the degree to which the impact of harvest depends on the population trajectory and the population size at the time of harvest. We aimed to (a) estimate the Mallee Emu-wren population size and test whether initial population size influences capacity for population recovery and (b) identify the timing of harvest (i.e. when population is increasing, stable or decreasing) and scale of harvest (number of birds) with the least negative impacts.

Methods

Estimating population size

Study area

We surveyed the Mallee Emu-wren source population in north-western Victoria (Fig. 1). Birds were harvested from this population for 'Phase 1' translocations of Mallee Emu-wrens in 2018 and will be used to source birds for any future translocations (Mitchell *et al.* 2021).

We restricted analysis to 'Triodia Mallee' vegetation (henceforth, 'Potential Habitat'; Fig. 1; Haslem *et al.* 2010). Within this part of the species' range, Mallee Emu-wrens are
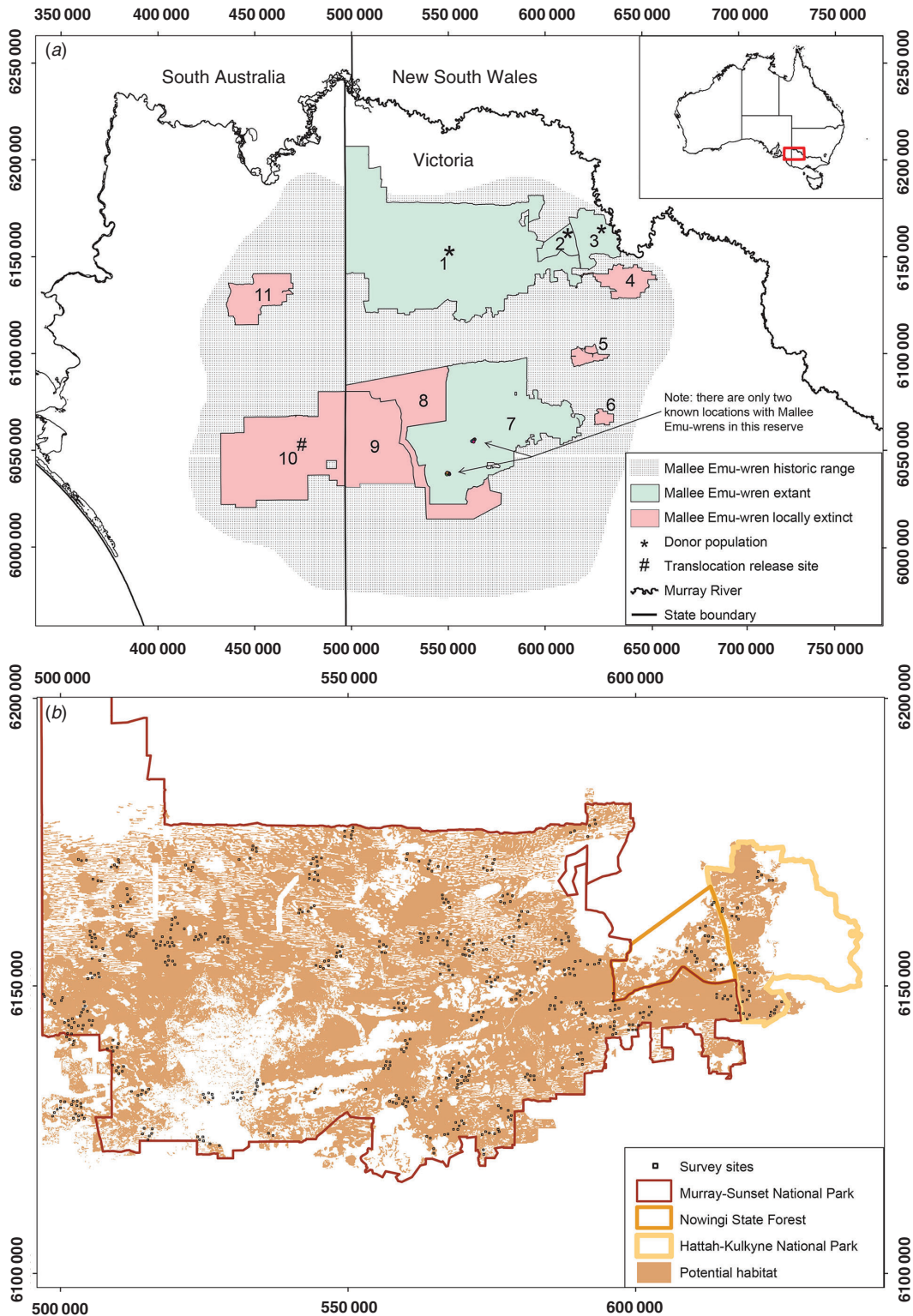
Fig. 1. (*a*) Map of the Mallee Emu-wren historic range overlaid with the protected area network and (*b*) the distribution of potential habitat and survey sites at the Mallee Emu-wren source site in Victoria. The historic range of the Mallee Emu-wren shown is intended as a guide only and was estimated using historic Mallee Emu-wren occurrence records and the extent of soil types known to support Mallee Emu-wren habitat (White 2006). The reserves shown in (*a*) are Murray-Sunset National Park (1), Nowingi State Forest (2), Hattah-Kulkyne National Park (3), Annuello Flora and Fauna Reserve (4), Bronzewing Flora and Fauna Reserve (5), Wathe Flora and Fauna Reserve (6), Wyperfeld National Park (7), Big Desert State Forest (8), Big Desert Wilderness Park (9), Ngarkat Conservation Park (10) and Billiatt Wilderness Protection Area (11). Eastings and northings are indicated at 50-km intervals.

found in this vegetation type only due to a close association with the hummock-grass, *Triodia scariosa* (often called spinifex), which they use for foraging, nesting and protection from predators (Higgins *et al.* 2001; Verdon *et al.* 2020). Wyperfeld National Park was not included in the present study because the population size in this reserve is likely to be less than 200 individuals (Chris Hedger, pers. comm.; Brown *et al.* 2009).

Study design

Selection of covariates. This study design is based on random sampling of sites, stratified according to important covariates of Mallee Emu-wren occurrence determined in earlier studies (Table 1). Covariate values were binned wherever previous studies indicated that such bins were appropriate and have an ecological basis (Table 1). In addition to the covariates selected for Mallee Emu-wren state models, covariates were required for

Mallee Emu-wren detection models (Table 1). We used four detection covariates in total (Table 1).

Survey site selection. We selected 540 survey sites (9 ha each). We distributed sites across the 120 unique covariate combinations according to the area of potential habitat covered by each combination. We increased the proportion of sites allocated to more common combinations of covariates, at the expense of rarer combinations because we judged that the combinations that cover the greatest area would have the greatest effect on the final population estimate. We used a $\log(x) + 1$ transformation to distribute the number of sites per combination. This transformation was necessary to ensure that rarer combinations still received adequate replication and that all combinations were surveyed (Supplementary material S1).

Survey method. Our survey protocol included an average of 2.8 (2–4) repeat surveys at 540 sites. Surveys ($n = 1508$)

Table 1. State and detection covariates used in the present study (including the evidence of their importance for Mallee Emu-wren occurrence)

Covariate name	Unit	Reference	Number of bins	Bin no.	Range
State covariates					
Time since fire (TSF)	Years	Brown *et al.* 2009; Verdon *et al.* 2019 Clarke et al. 2010[C] Callister et al. 2016[c]	5	1	05–15[A]
				2	16–30
				3	31–45
				4	46–60
				5	>60
Elevation[B] (ELEV)	m asl	Verdon *et al.* 2019	3	1	25–49
				2	50 – 56
				3	>56
Ecological Vegetation class[C] (EVC)	NA	Brown *et al.* 2009	2 (categorical)	1	Woorinen sands
				2	Loamy sands
Topographic wetness index (TWI)	NA	Hedger (unpubl. data)[D]	3	1	59–79
				2	80–90
				3	>90
Index of gypsum conc. (GYPSUM)	NA	Verdon et al. 2019[E]	Continuous (but 2 bins for stratification)	1	0.33–0.60
				2	>0.60
Triodia Mallee in surrounding 1 km^{2}[F] (PERC_TM)	%	Haslem et al. 2010[E] Watson *et al.* (unpubl. data)	Continuous (but 2 bins for stratification)	1	11–80
				2	>80
Detection covariates					
Observer skill[G]	NA		2 (categorical)	1	Beginner
				2	Experienced
Time since sunrise	Min		Continuous	NA	
Date	NA		2	1	10 Aug. – 15 Sep.
				2	21 Sep. – 27 Oct.
Wind[H]	NA		6	1	No wind
				2	Only leaves moving
				3	Small branches moving
				4	Large branches moving
				5	Trunk moving (gusts)
				6	Trunk moving (constantly)

[A]Areas with less than 5 years since fire were not considered potential habitat in the present study (Brown *et al.* 2009).
[B]Department of Environment, Land, Water and Planning. Vicmap Elevation DTM 20 m (https://www.data.vic.gov.au/).
[C]Department of Environment, Land, Water and Planning. NV2005_EVCBCS (https://www.data.vic.gov.au/).
[D]Evidence of TWI as an important factor is from another vegetation system: heathland vegetation in Ngarkat Conservation Park.
[E]Reference contains details of spatial layer used.
[F]Calculated in Arcmap 10.5.1. Percentage of 100×100-m raster cells surrounding site that are Triodia Mallee (Haslem *et al.* 2010).
[G]Observers were classified in the field by SJV.
[H]Wind was scored on a modified Beaufort scale that assessed the effect of the wind on the surrounding mallee eucalypts.

consisted of a single person conducting a 45-min 9-ha (300 × 300 m) area search, walking 1500 m per survey. All surveys were conducted in the austral spring of 2019 (10 August – 27 October). Each person surveyed three to six sites per day and surveys started at dawn (±1 h).

Surveys began by playing 1 min of the Mallee Emu-wren contact calls in the centre of the site, followed by 2 min of listening. All call playback was performed using the surveyor's smartphone at full volume. Playback of the contact call was repeated wherever appropriate habitat was encountered. At the end of the survey, the surveyor returned to the centre of the site and played a 1 min recording of the Mallee Emu-wren territorial song, followed by 2 min of listening. The territorial song was played only at the centre to reduce the likelihood of 'calling birds in' from outside of the site. Surveyors used georeferenced pdf maps on their smartphones for navigation (Avenza Maps 3.9.1). Surveyors recorded the location of each Mallee Emu-wren group, the number of birds present and their sexes.

Analysis

Statistical approach. We used N-mixture modelling to estimate Mallee Emu-wren population size. N-mixture models incorporate a binomial model to estimate the detectability of a species (detection model) and a Poisson or negative binomial model to estimate the density of a species (state model; Kéry and Royle 2015). Pre-requisites for effective N-mixture modelling and our capacity to meet them are outlined in Table S1.

Broadly, this statistical approach involved conducting repeat surveys of sites that differed in their environmental conditions. By surveying sites on multiple occasions, we were able to model Mallee Emu-wren detectability and use this estimate of imperfect detection to estimate the density of Mallee Emu-wrens per 9-ha survey site.

For N-mixture modelling we used the 'unmarked' package in R version 3.6.1 (Fiske and Chandler 2011; R Core Team 2019). We undertook an information-theoretic approach, using Akaike's information criterion (AIC) to determine the most parsimonious model (Akaike 1974). We restricted candidate detection models to univariate because of issues with over-fitting. As a result, we had four candidate detection models, each with one covariate (Table 2). We included no state covariates when comparing candidate detection models.

For the state models, we had six covariates and candidate models fell into the following three categories: additive models; two-way interaction models; two-way interaction models with additive covariates. For additive models, candidate models were selected by beginning with the global model and by using stepwise removal of covariates until only one covariate remained. For interaction models, we compared all possible two-way interaction models. For two-way interaction models with additive covariates, we began with the most parsimonious two-way interaction model plus the remaining four covariates included as additive terms. We then used stepwise removal of additive terms until the two-way interaction and only one additive term remained. This model development process led to a total of 24 candidate state models, all of which included the most parsimonious detection covariate in the detection component of the N-mixture model. We selected the candidate N-mixture model with the lowest AIC as the most parsimonious model and used this model to develop the Mallee Emu-wren population estimate.

We used a zero-inflated Poisson distribution for all N-mixture models (Kéry and Royle 2015). We evaluated goodness of fit for

Table 2. Demographic parameters used in population viability analysis

Parameters related to reproduction were set year-by-year by sampling from a normal distribution with a mean (parameter value) and a standard deviation (s.d.). This variation in the parameter values represented environmental variation among years

Demographic parameter	Value	Population trajectory			Reference
		Increasing	Stable	Decreasing	
Breeding system	Monogamous				Rowe and Pruett-Jones 2008[A]
					Maguire and Mulder 2004[A]
Breeding age range	1–6 years				Maguire and Mulder 2004[A]
Life span (maximum)	6 years				Maguire 2005[A,B]
Sex ratio	50:50				Maguire and Mulder 2004[A]
Carrying capacity	12 013				NA[C]
	6449				
	1923				
Percentage adult females breeding (s.d.)		100 (10)	100 (10)	90 (10)	NA[D]
Clutch size (s.d.)[D]		3 (1)	3 (1)	2.7 (1)	Maguire and Mulder 2004[A]
					Maguire 2006[A]
% Mortality for first year[D]		76	78	86	Maguire 2006[A]
% Annual mortality after first year[D]		26	28	31	Maguire and Mulder 2004[A]

[A]Derived from data on the closely related species *S. malachurus*.
[B]Estimated from observations of birds that were 4 years old and still alive when surveys ceased.
[C]Set to either the population size estimate, upper 95% confidence interval or lower 95% confidence interval (this study).
[D]Adjusted to create population trajectory with realistic change in population size over 5 years (Connell 2019).

the final model using the parametric bootstrapping function 'parboot' in the 'unmarked' package in R. Goodness-of-fit testing compares the observed data with the quantity that we would expect to see under the model when we use simulated datasets generated with the model's distribution. We ran 100 bootstrap simulations using the most parsimonious model. We used the Freeman–Tukey test to test for a significant deviation between our dataset and the simulated datasets (Kéry and Royle 2015).

We also undertook an informal assessment of the capacity of the model to predict the occurrence of Mallee Emu-wrens in the study area. We used predicted Mallee Emu-wren density to divide potential habitat in the study area into two categories of equal area, namely, Predicted high-density or Predicted low-density (183 093 ha each). We used incidental occurrence records of Mallee Emu-wrens collected during fieldwork as an independent dataset (24 presence records >200 m from the nearest survey site). We compared the number of incidental records in each density category with the number of records that was predicted by the model to be in each density category. We report the expected and observed values for comparison.

We used the 'raster' package in R to predict Mallee Emu-wren density, estimate population size and calculate 95% confidence intervals across potential habitat in the study area (Hijmans *et al.* 2015).

Comparing the impact of harvest scenarios

Harvest scenarios

We compared the impact of harvest under three different prevailing population trajectories (increasing, stable and decreasing) and compared the impact of five different scales of harvest (no harvest, 100, 200, 300 or 500 birds harvested). We made these comparisons with the initial population size set to either the population estimate, or the lower 95% confidence interval, derived from the present study.

We compared the impact of harvest scenarios over two different 'prediction horizons'. First, we plotted post-harvest change in population size (mean ± standard deviation) over a 5-year period to assess short-term impact. The 5-year prediction horizon is important because (a) it is a realistic timeframe over which a population may maintain an increasing or decreasing population trajectory in this system due to the cyclical nature and duration of drought and non-drought periods (Letnic and Dickman 2006) and (b) it is a relevant timeframe for the planning and funding of translocation programs (IUCN 2013).

Second, we used a 25-year prediction horizon to compare the number of years over which the impact of harvest was observable. The 25-year prediction horizon adds uncertainty because the prevailing population trajectory is likely to change over this period. Despite this, the 25-year prediction horizon provides important information regarding the potential for long-term impacts of harvest on source populations. For this component, we present the number of years required under each harvest scenario for the source population size to intersect with the population size predicted under a 'no harvest' scenario.

PVA parameterisation

We used Vortex10 software to parameterise a non-spatial, individual-based PVA model that simulates changes in Mallee Emu-wren population size over time (Lacy and Pollak 2020). Using an annual time-step, models simulated individual birds as they are born, mature, breed and die. Models were structured by age and sex, so that mate limitation at low densities, could be incorporated (Lacy and Pollak 2020). Models were also stochastic, meaning they included variation in the simulated population trajectory due to chance differences in the survival and reproductive rates among individuals in the population (i.e. demographic stochasticity). We ran 1000 iterations of each harvest scenario simulation. We used a non-spatial PVA because studies of Mallee Emu-wren genetics found a lack of genetic structuring, indicating gene flow through dispersing birds moving across potential habitat (Brown *et al.* 2013).

All simulations except for 'no harvest' scenarios included a one-off harvest at Year 1. Given that demographic information for the Mallee Emu-wren is limited, we substituted vital-rate estimates from the Southern Emu-wren, *Stipiturus malachurus*, a closely related species that has been studied in greater detail (Table 2; IUCN 2013). Models also incorporated uncertainty around these parameters (Table 2). Where demographic data are limited for a species, using the vital rates of a closely related species is recommended by the IUCN (2013) Guidelines for Re-introductions and other Conservation Translocations. However, clearly, such a strategy is flawed because even closely related species may differ in terms of their vital rates. Ultimately, delaying the analysis required for this research until more data on Mallee Emu-wren vital rates is not a viable option because harvesting of this species for translocations is already underway. Nevertheless, future work that elucidates Mallee Emu-wren vital rates would improve population modelling for this species.

To simulate each of the prevailing population trajectories (increasing, stable, decreasing), we altered parameters relating to reproductive output, juvenile mortality and adult mortality to achieve rates of population change consistent with those observed in drought and Big-Wet periods (Table 2; Connell 2019).

Carrying capacity

We set the carrying capacity to the upper 95% confidence interval of the population size estimate (the present study). To test the influence of carrying capacity on our PVA model outputs, we repeated PVA simulations with carrying capacity set to the same value as initial population size. As a result, simulated populations with an otherwise increasing trajectory could not increase over years. However, these populations did have higher reproductive rates and lower mortality rates.

Results

Estimating population size

We detected Mallee Emu-wrens on 75 occasions in 42 of 540 survey sites (7.8%). This comprised 50 independent groups and 25 resightings of groups that were detected in a previous survey round(s). Multiple groups of Mallee Emu-wrens were detected at eight sites, indicating that the 9-ha site size was sufficiently large to incorporate two Mallee Emu-wren territories in some instances.

Model selection

The N-mixture model with the lowest AIC included wind as the sole detection covariate and all six candidate state covariates,

with an important interaction between time since fire and elevation i.e. Estimate ± 95% confidence interval did not overlap zero (Tables S2, S3).

Goodness of fit

The bootstrap *P*-value for the model based on the Freeman–Tukey's statistic was 0.38, indicating that our model provided an adequate fit to the data. Eighteen incidental Mallee Emuwren records (75%) were in the category 'predicted highdensity of Mallee Emu-wrens' with the remaining six records (25%) being in the 'predicted low-density of Mallee Emuwrens' category (Fig. 2). This result is very similar to the model predicted rates of 19 records (78%) occurring in the 'high-density Mallee Emu-wrens' category and five records (22%) occurring in the 'low-density Mallee Emu-wrens' category.

Population estimate

We estimate that in the austral spring of 2019, the Mallee Emu-wren source population consisted of 6449 individuals (lower95% CI: 1923, upper95% CI: 12013).

Comparing the impact of harvest scenarios

In all, 7 of the 48 harvest scenarios showed no impact of harvest within 5 years (Table 3, Figs 3, 4). These scenarios all had increasing population trajectories and carrying capacity set to equal the initial population size (Table 3, Fig. 4). For simulations with an initial population size of 6449, the impact of harvest lasted for only 1 year at all the scales of harvest we tested (Table 3, Fig. 4). Simulations with an initial population size 1923 showed an impact of harvest for a slightly longer period, but still showed no impact of harvest within 5 years for three of the four scales of harvest tested (Table 3, Fig. 4).

A further 19 harvest scenarios showed no impact of harvest within the 25-year prediction horizon used in the present study (Table 3). Four simulations that had an increasing population trajectory, initial population size of 6449 and carrying capacity set to the upper 95% confidence interval showed no impact of harvest after 15–20 years (Table 3). This timeframe was associated with the time required for populations to reach the greater level set for carrying capacity. Fourteen simulations that had a decreasing population trajectory showed no impact of harvest after 19–23 years. This timeframe was associated with those populations nearing extinction (<50 individuals remaining).
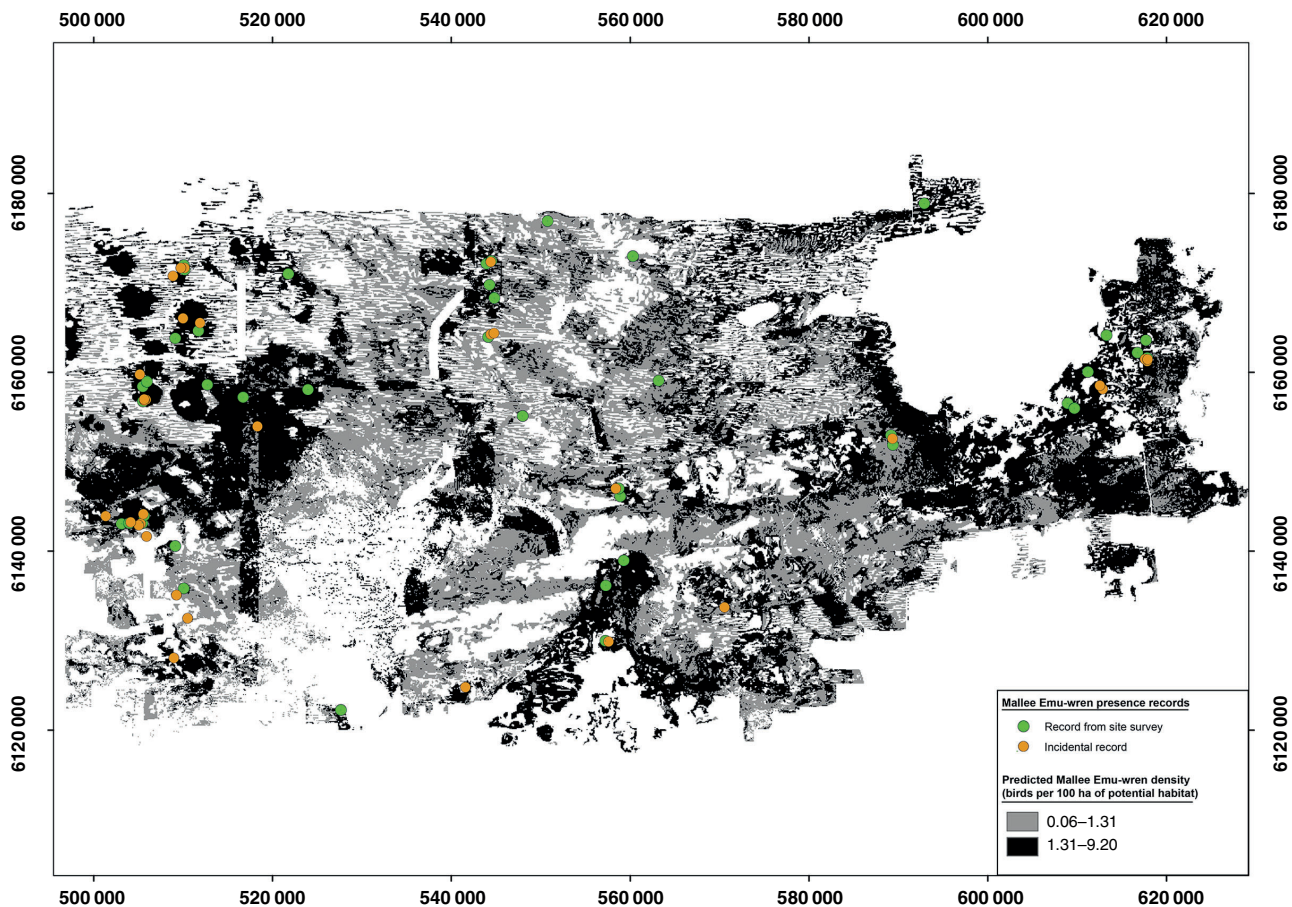

Fig. 2. Predicted Mallee Emu-wren density across the study region divided into 'high density' and 'low density' categories of equal area. All incidental records made during the field season are shown (31). However, for our validation dataset, we excluded incidental records <200 m from another incidental record or a survey site before analysing the remaining records (24). Eastings and northings are indicated at 20-km intervals

Table 3.   Population viability analysis outputs indicating the number of years post-harvest required for population to reach a level expected under the 'no harvest' scenario

We tested four scales of harvest (100, 200, 300 or 500 individuals) for each population trajectory that was simulated (increasing, stable or decreasing). The top section of the table shows simulation results when carrying capacity is set well above the initial population size ($K = 12013$). The bottom section of the table shows simulation results when carrying capacity is set to equal the initial population size. We used a 25-year prediction horizon in simulations. Values in bold indicate that the population showed no impact of harvest within 25 years. K, carrying capacity. *At the year indicated, population was near extinction, with less than five individuals remaining. **At the year indicated, population was near extinction, with less than 50 individuals remaining

Scenario parameters	Increasing population				Stable population				Decreasing population			
	100	200	300	500	100	200	300	500	100	200	300	500
Initial population: 1923 individuals ($K = 12\,013$)	>25	>25	>25	>25	>25	>25	>25	>25	**19***	**21***	**22***	**23***
Initial population: 6449 individuals ($K = 12\,013$)	**15**	**15**	**15**	**20**	>25	>25	>25	>25	**20****	**21****	**23****	>25
Initial population: 1923 individuals ($K = 1923$)	**2**	**4**	**4**	**8**	>25	>25	>25	>25	**19***	**21***	**22***	**23***
Initial population: 6449 individuals ($K = 6449$)	**1**	**1**	**1**	**1**	>25	>25	>25	>25	**20****	**21****	**23****	>25

Despite variation in its impact between simulations, harvest did not change the prevailing population trajectory of any simulated population (Figs 3, 4).

Discussion

Initial population size, carrying capacity, scale of harvest and population trajectory all influenced the impact of harvest on simulated Mallee Emu-wren source populations. Although translocation planners have little capacity to alter initial population size or carrying capacity, they can decide the number of birds to take (scale of harvest) and they can time harvest to coincide with a favourable population trajectory. Our study indicated that these measures can reduce the impact of harvest on fluctuating source populations.

Comparing the impact of harvest scenarios

Of the scenarios tested, the impact of harvest on the source population was least when the population was increasing, near carrying capacity and large (6449 rather than 1923 individuals). The influence of harvest scale on the impact of harvest depended on other simulation parameters. Restricting harvest to 300 individuals reduced the impact of harvest for two of the four scenarios with an increasing population trajectory. For the remaining two scenarios, one showed little impact of harvest at all scales of harvest tested and the other did not recover under any of the scales of harvest tested.

To minimise the impact of harvest on source populations, we recommend that translocation planners use population modelling to define limits on harvests and to identify the timing of harvests that has the least negative impact on source populations. In the case of the Mallee Emu-wren, we recommend limiting harvests to less than 300 birds and aiming to undertake future harvests when the source population has an increasing trajectory. However, we acknowledge that translocation planning decisions must weigh potential for negative impacts on the source population against potential benefits of supplementing a population or establishing a new population (Pérez *et al.* 2012; IUCN 2013). Given that none of the harvest scenarios tested changed the trajectory of the Mallee Emu-wren source population, translocation planners may determine that the potential benefits of translocation outweigh the costs of harvest for this species (Pérez *et al.* 2012; Colomer *et al.* 2020). Such decisions

are complex and must be made on a case-by-case basis after considering the level of threat faced by the source population, the likelihood of successful translocation, the benefits of successful translocation and the impact of harvest on the source population.

Feasibility of flexible timing of harvest

In the case of the Mallee Emu-wren, timing harvest to coincide with an increasing population trajectory is logistically feasible because evidence suggests that Mallee Emu-wren populations fluctuate in a predictable way in response to years of above average rainfall or 'Big-Wet' years (Connell 2019). This provides translocation planners with a method by which they can easily monitor a proxy for the Mallee Emu-wren population trajectory, through national weather and climate monitoring infrastructure (http://www.bom.gov.au/climate/data/). By delaying harvest until during or directly after Big-Wet years, translocation programs may also benefit from improved condition at the release site, thereby increasing the likelihood of establishment success while also minimising the potential for negative impacts on the source population (Berger-Tal *et al.* 2020). However, access to funders that allow delayed implementation of translocation is still likely to be a limiting factor for many translocation programs (Berger-Tal *et al.* 2020).

Whereas predicting the prevailing trajectory of the Mallee Emu-wren source population is relatively straightforward, significant time and effort are required to maintain an up-to-date estimate of the population size (Garnett and Geyle 2018; the present study). In addition, because Mallee Emu-wrens are distributed over a large area and are difficult to detect, estimates of their population size are prone to substantial uncertainty around the true number of individuals present (Knape and de Valpine 2012; Kéry and Royle 2015; this study). Any decisions regarding future translocations will have to be made in the context of uncertainty around the impact of harvest on the source population because of the uncertainty around the true population size (Dimond and Armstrong 2007).

The influence of carrying capacity

When carrying capacity was set to equal the initial population size, more simulated populations recovered to 'no harvest' levels. In addition, populations that recovered at both levels of
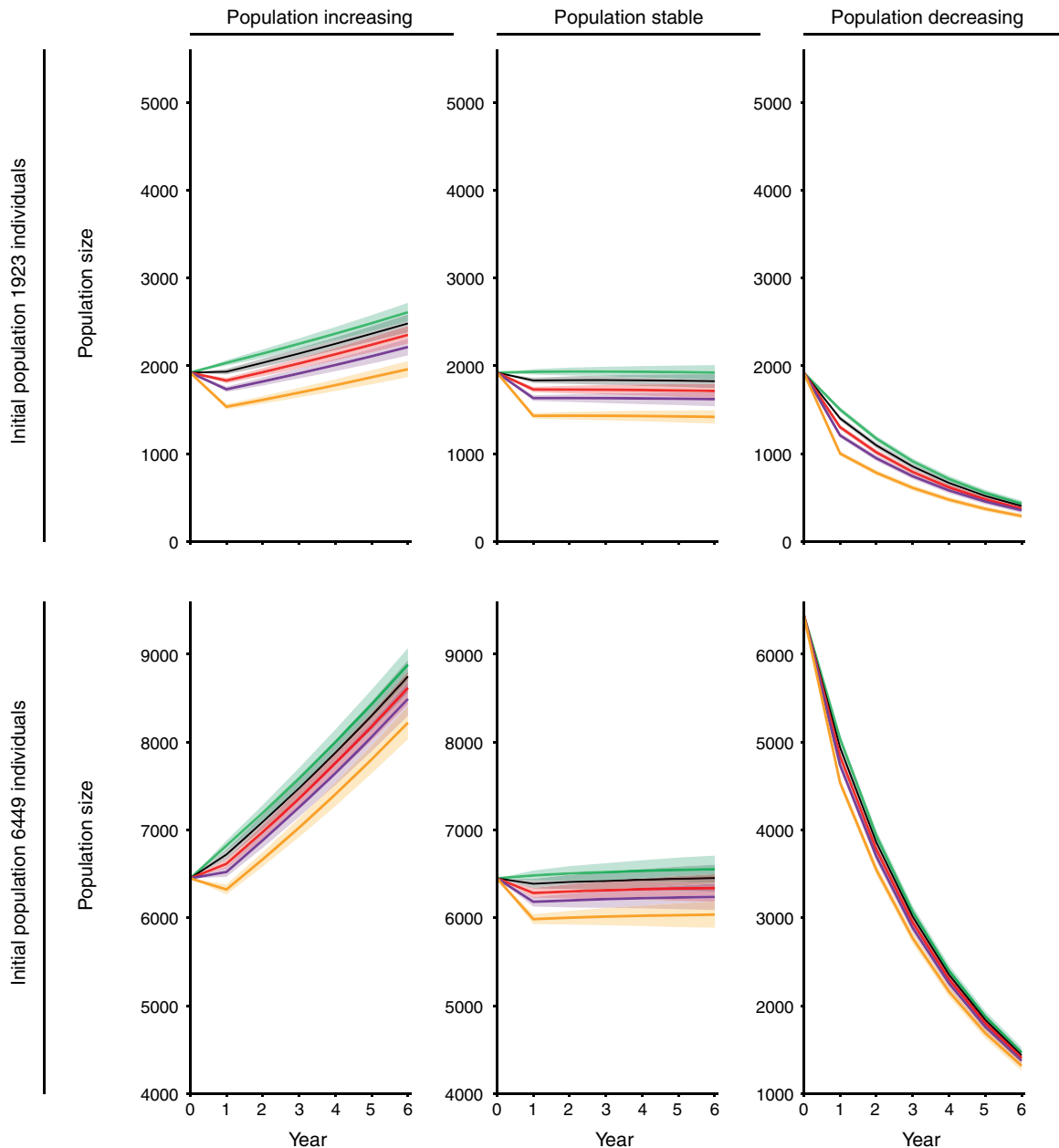
Fig. 3. Comparing the impact of harvest scenarios when carrying capacity is set to 12 013, which is the upper 95% confidence interval of the population size from the present study. We used population viability analysis with a 5-year prediction horizon to simulate population changes after harvest at Year 1. The five harvest rates tested were 'no harvest' (green), harvest 100 (black), harvest 200 (red), harvest 300 (purple) and harvest 500 (orange). We repeated harvest simulations at three different population trajectories and two different initial population sizes. Lines and shading indicate the mean ± standard deviation after 1000 iterations of each simulated harvest scenario.

carrying capacity required fewer years to do so when carrying capacity was set to equal initial population size. However, the scenario with the least impact of harvest remained the same regardless of whether carrying capacity was set at initial population size or at the upper 95% confidence level. Therefore, we conclude that the level used for carrying capacity strongly influenced results but PVA models nevertheless appear robust to changes in the level of carrying capacity used (Lande *et al.* 2003).

The increased rate of recovery observed when carrying capacity was set to initial population size is not surprising (Lande *et al.* 2003; Knape and de Valpine 2012). Carrying capacity limits population growth through density-dependent effects (Lande *et al.* 2003). After harvest, survival and reproductive capacity of the remaining individuals increases as density-dependent effects are temporarily reduced (Lande *et al.* 2003; Miller *et al.* 2019). Given the lack of information regarding Mallee Emu-wren carrying capacity at the source site,
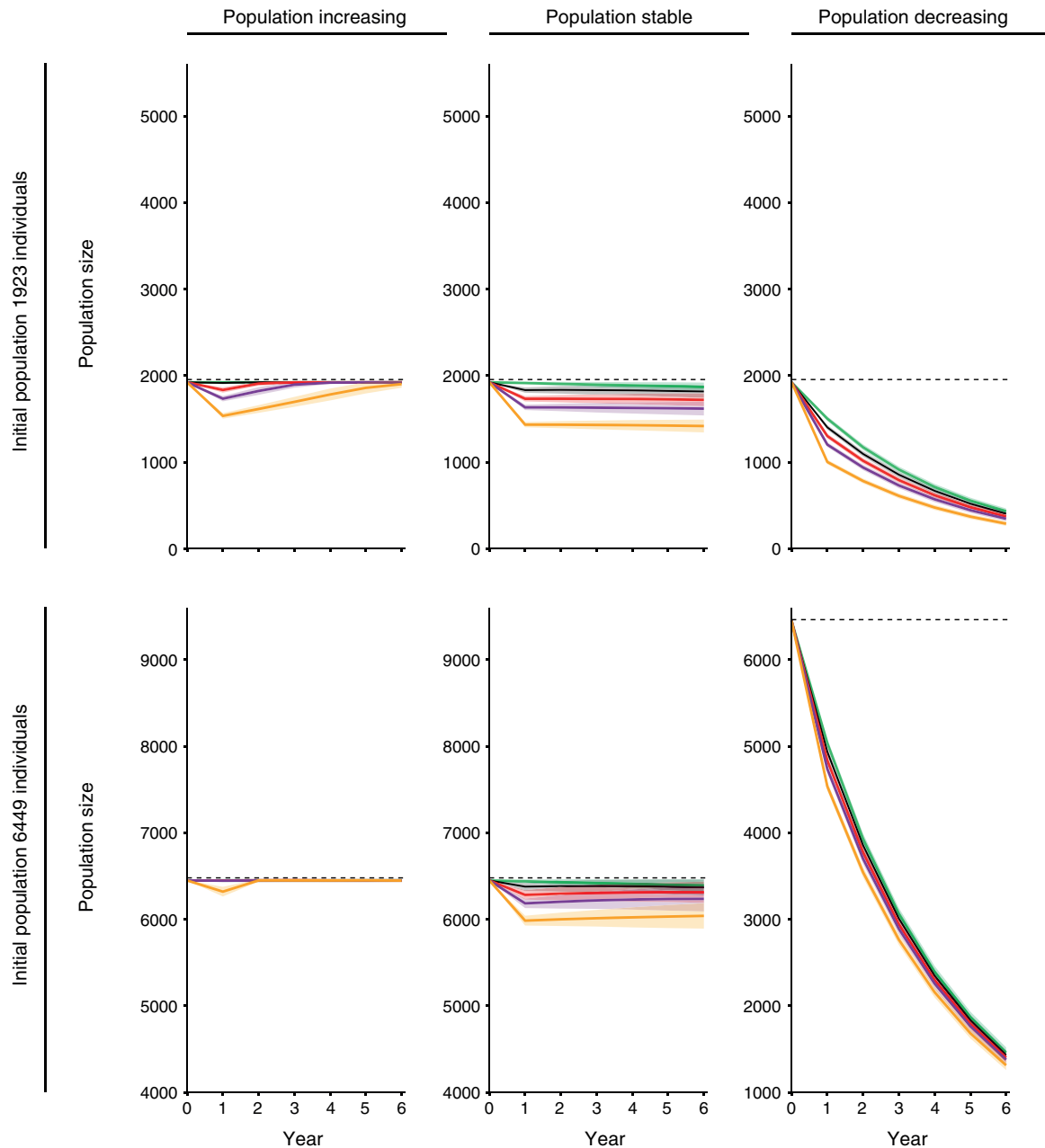
Fig. 4. Comparing the impact of harvest scenarios when the landscape is at carrying capacity at the beginning of simulations (dotted line). Note that because of the lower setting used for carrying capacity, 'increasing' populations did not actually have capacity to increase over years. We used population viability analysis with a 5-year prediction horizon to simulate population changes after harvest at Year 1. The five harvest rates tested were 'no harvest' (green), harvest 100 (black), harvest 200 (red), harvest 300 (purple) and harvest 500 (orange). We repeated harvest simulations at three different population trajectories and two different initial population sizes. Lines and shading indicate the mean ± standard deviation after 1000 iterations of each simulated harvest scenario.

we recommend invoking the precautionary principle for this parameter, i.e. setting a high carrying capacity at the source site to ensure that potential for recovery in the Mallee Emu-wren source population is underestimated, rather than overestimated (Miller *et al.* 2019). Further field-studies on this topic may shed light on the effect of Mallee Emu-wren carrying capacity on population dynamics. For example, Mallee Emu-wren source sites from 'Phase 1' translocations (harvested in 2018) are

currently being monitored to determine whether density dependence influences the rate of recovery post-harvest at a fine scale (25 ha; Brook and Bradshaw 2006; Mitchell *et al.* 2021).

Conclusions

We recommend that flexible timing of harvest be explored for any species with fluctuating source populations for which translocations are planned. However, incorporating flexible

timing of harvest in translocation planning is likely to be more feasible for species whose populations fluctuate in a somewhat predictable manner, for example, arid-zone species that increase after Big-Wet years. For the Mallee Emu-wren, timing harvest to coincide with an increasing source population (after Big-Wet years) is likely to reduce the impact of harvest on that population. The extent to which carrying capacity is limiting population growth in the Mallee Emu-wren source population remains unresolved (Brook and Bradshaw 2006). Research on the influence of carrying capacity on source populations generally, and the Mallee Emu-wren source population specifically, will help develop appropriate harvest rates for future translocations.

Conflicts of interest

The authors declare no conflicts of interest.

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